Soil Carbon Measurement and Modeling in Forest and Savanna Ecosystems of the Sierra Nevada: Temporal and Spatial Patterns and Management Impact

by

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Abstract

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Professor Ye Qi, Chair

Soil respiration and its variation are influenced by soil temperature, moisture, and root density, and also affected by management activities. By conducting multivariate regression I analyzed the impact of a forest thinning in May 2000 on soil respiration in a young ponderosa pine plantation in the Sierra Nevada. The thinning decreased the spatial heterogeneity of soil respiration, but did not change the sensitivity to temperature and moisture. Although the thinning would theoretically decrease soil respiration, the actual change of soil respiration was not significant due to the varied temperature and moisture with the thinning. The impact of thinning on soil respiration was explained by the change of root density, soil temperature and moisture.

I partitioned soil respiration into autotrophic and heterotrophic respiration by conducting trenching experiments to exclude roots in the pine plantation, and separately modeled these three components between October 2001 and 2002. In addition to environmental variables, root respiration was affected by plant physiology and

phenology. The ratio of autotrophic respiration to total soil respiration was not a constant seasonally with an average of 0.33. The spatial variation of soil respiration was mainly explained by root density.

I compared the soil respiration in a young and mature plantation between October 2001 and 2002. The difference of soil respiration was not significant, but soil respiration in the mature plantation would be 1.2 times greater than that in the young plantation if the difference of soil temperature and moisture between two sites is removed. A model that I developed incorporated soil temperature, moisture, stand density, and tree size, and well explained the spatial variation of soil respiration and soil carbon dynamics.

I developed an automated flux measurement system by burying small CO_2 sensors and continuously measuring CO_2 concentration gradients in a savanna ecosystem in California in the summer, 2002. I calculated diffusion coefficient, and then estimated CO_2 efflux. The diurnal variation of CO_2 concentration and efflux was more significant than day-to-day variation. The temperature sensitivity (Q_{10}) was 1.27 in the dry season. The high correlation between CO_2 efflux and temperature explained the diurnal pattern of CO_2 efflux, but moisture may become another factor driving the seasonal pattern when moisture changes over seasons.

_____

Prof. Ye Qi, Committee Chair

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Chapter 1 Introduction: A Review of Soil Respiration Measurement and Modeling

Abstract

Soil respiration and its temporal and spatial variation are important in understanding global carbon cycles and climate change. This chapter reviews and evaluates methods of soil carbon measurement and modeling in the literature. *In situ* measurement methods of soil carbon include biomass survey, CO_2 gradient measurements, chamber measurements, and micrometeorological techniques (eddy covariance). Manipulative experimental methods include laboratory incubation, warming experiments, and CO_2 enrichment experiments. All these methods have advantages and disadvantages.

Our knowledge about the mechanism of soil carbon storage and fluxes is limited. Soil respiration has been modeled using different factors such as temperature, or temperature and water combined. Environmental variables are used to study temporal variation. Spatial variation is difficult to quantify. The impact from forest management on soil respiration is not well understood.

The objective of the dissertation aims to advance the method and knowledge of soil respiration, specifically including developing measurement and modeling methods of soil respiration, assessing soil respiration impacts from forest management, modeling inter-annual temporal variation of soil respiration, investigating spatial variation, and partitioning soil respiration into root respiration and microbial decomposition.

1. Soil carbon pool and flux

The global average surface temperature has increased $0.6 \pm 0.2°C$ over the 20^{th} century (Houghton et al. 2001). Contemporary global warming and climate change are mainly induced by accumulation of atmospheric greenhouse gases, most importantly CO_2, due to anthropogenic emissions and land-use change. This human-induced rapid change is imposing impacts on terrestrial ecosystems and receiving feedbacks from ecosystems as well. Soils, the substrate of terrestrial ecosystems, are large carbon pools and sensitive to climate change and elevated atmospheric CO_2 concentration.

The soil carbon pool has been estimated to be 1500 PgC, only second to the oceanic carbon pool (38000 PgC), three times the terrestrial vegetation carbon pool (500 PgC), and over twice the atmospheric carbon pool (730 PgC) (Houghton et al. 2001). Soils exchange carbon with the atmosphere by releasing CO_2 and collecting litterfall, dead roots, and other biomass. Soil surface CO_2 efflux, commonly called soil respiration, is composed of microbial heterotrophic respiration and rhizosphere respiration (including root autotrophic respiration and associated mycorrhizae respiration). Global soil respiration has been estimated to be about 68-80 PgC/year (Raich & Schlesinger 1992; Raich & Potter 1995; Raich *et al.* 2002), a figure more than 10 times the annual fossil fuel combustion (5.4 PgC/year), and 10% of the total atmospheric carbon pool (Houghton et al. 2001). Therefore, a small change in soil carbon storage and fluxes will significantly affect the atmospheric CO_2 concentration and hence climate variability.

Despite the importance of soil carbon in global carbon cycles, our understanding of the magnitude, temporal variation, spatial variation, and sensitivity of soil respiration to environmental variables is still limited. This limitation has affected the implication of

sustaining or increasing the terrestrial soil carbon pool to mitigate climate change. This scientific uncertainty, among others, is one of the reasons that caused the debate on ratifying and implementing the Kyoto Protocol, an international treaty that requires the industrialized countries to reduce their emissions of greenhouse gases (most importantly anthropogenic CO_2) by an average of 5.2% based on the 1990 levels between 2008-2012.

To advance our knowledge in soil carbon cycles, measuring soil carbon fluxes and modeling the temporal and spatial variations are critical. In the following sections I will review and evaluate soil carbon measurement and modeling methods in the literature, and then present the objectives of this dissertation, which target to address some important questions to which the answers have not been investigated or need to be improved.

2. *In situ* measurement methods in soil carbon

Since there are no general mechanistic-based soil respiration models to date that can be applied to various ecosystems, developing and parameterizing empirical soil carbon models becomes critical for studying soil respiration. *In situ* measurements of soil carbon are the first step toward soil carbon studies. Measurement methods in soil CO_2 efflux include biomass survey, CO_2 gradient measurements, chamber measurements, and micrometeorological techniques. In addition, remotely sensed data have provided useful information such as normalized difference vegetation index (NDVI) and environmental variables including temperature and moisture (for example, Potter *et al.* 1993; Sellers *et al.* 1996) for scaling up *in situ* measurements to a global level.

2.1 Biomass surveys

Biomass surveys and forest inventory studies are traditional methods in forestry and ecology. They provide aboveground biomass storage and variation on a multiyear to decadal scale. Belowground biomass and aboveground litterfalls are beyond traditional forest inventory studies. Belowground biomass can be estimated either by directly sampling soil and estimating root biomass (Eamus et al. 2002), or by building allometric relationships with aboveground components such as biomass, diameter at breast height (DBH) or crown size (Kurz et al. 1996; Li et al. 2003). Decomposition rate of litter is often measured by enclosing litter in litter bags and observing the decrease in biomass (Shanks & Olson 1961; Crossley & Hoglund 1962; Shaw & Harte 2001). Recently developed minirhizotron techniques allow us to directly observe root dynamics by placing transparent tubes in the soil and videotaping root morphology and turnover through small video cameras (Upchurch & Ritchie 1983; Ferguson & Smucker 1989; Cheng *et al.* 1990).

Soil respiration can be estimated by relationships with root biomass and/or microbial biomass. Heterotrophic respiration can also be estimated by mass balance methods, that is, carbon storage is equal to the difference between carbon input and output within a certain period of time. Carbon storage can be measured by organic carbon content in soil samples. Carbon input is mainly from litterfalls. Thus accumulative heterotrophic respiration can be estimated.

The biomass survey method is labor-intensive and often takes only a small amount of samples over a large area. Belowground biomass is often estimated based on allometric relationships, which are empirical and site specific.

2.2 CO_2 gradient measurement

The flux of CO_2 diffused from the soil can be calculated by Fick's first law of diffusion if we measure the CO_2 concentration gradient in the soil:

$$F = -D_s \frac{dC}{dz}, \quad (1)$$

where F is the CO_2 efflux ($\mu molm^{-2}s^{-1}$), D_s is the CO_2 diffusion coefficient in the soil (m^2s^{-1}), C is the CO_2 concentration at a certain soil depth ($\mu mol\ m^{-3}$), and z is the depth (m). The negative sign is to show that the efflux is in the direction of decreasing concentration. Here D_s is an important parameter, which is mainly controlled by the volumetric air content (air-filled porosity) and the volumetric water content in the soil. There are several empirical models in the literature for computing D_s (Sallam *et al.* 1984). D_s varies vertically and horizontally in the soil.

The CO_2 gradient method involves periodically extracting soil gas samples from different depths and measuring CO_2 concentration by a gas chromatograph or an infrared gas analyzer (IRGA). CO_2 samples in the field are extracted by syringes (De Jong & Schapper 1972), gas sampling tubes (Buyanovsky & Wagner 1983; Burton & Beauchamp 1994; Davidson & Trumbore 1995), or gas traps (Fang & Moncrieff 1998b). After measuring CO_2 profiles and gradients, and then computing diffusivity, we can estimate CO_2 efflux by applying Fick's Law.

CO_2 gradient measurements provide detailed information on soil CO_2 production at different depth of soils as well as overall fluxes. The potential errors for gradient methods include non-uniformly distributed CO_2 source in the soil and non-diffusive

transport involved (Livingston & Hutchinson 1995). Traditional gradient measurements based on gas extraction cannot provide *in situ* continuous data on CO_2 efflux, and they disturb the soil environment. An unavoidable bias may happen during the processes of gas extraction, storage, transportation, and measurements.

Other than gas extraction methods, continuous measurements of soil CO_2 gradients are in development. Chapter 5 of this dissertation describes a new CO_2 gradient method by burying small CO_2 sensors (IRGA) and directly measuring CO_2 concentration at different depth of soils.

2.3 Chamber-based measurement

Chamber-based measurements allow us to directly measure CO_2 efflux from soils on a small scale. Chambers are normally categorized as static chambers, closed dynamic chambers, and open dynamic chambers (Norman *et al.* 1997; Rochette *et al.* 1997). To avoid the confusion of terminology by noting that the closed chamber is often not a really closed system, Livingston and Hutchinson (1995) named the first two classes as non-steady-state chambers since the circulation inside the chamber is a closed loop, and named open dynamic chambers as steady state chambers because of the open path circulation. However, the first classification is still widely used although the term may not be scientifically meaningful.

Static chambers use an absorption agent like dry soda lime or alkali solution to absorb CO_2 fluxes over a certain time and thus measure the CO_2 evolution (Monteith *et al.* 1964; Witkamp 1966; Kucera & Kirkham 1971; Biscoe *et al.* 1975; Janssens & Ceulemans 1998), or extract air samples through tubes and measure CO_2 by a gas

chromatograph (Loftfield et al. 1992). Though static chambers are relatively cheap and easy to employ in the field, the temporal resolution of data is low and it is less accurate than IRGA (Edwards & Sollins 1973; Janssens & Ceulemans 1998). In addition, absorption agent is often sensitive to temperature. This causes errors due to temperature dependence.

Closed dynamic chambers measure CO_2 efflux based on the changing rate of concentration in a closed system measured by an infrared gas analyzer (IRGA). They are so called dynamic is because that flux measurements are based on the temporal change of CO_2 concentration measured by the IRGA. The principle of the close dynamic chamber method can be expressed as Eq.(2):

$$F = \frac{\Delta c}{\Delta t}\frac{V}{A} = \frac{\Delta c}{\Delta t}H \qquad (2)$$

where F is the CO_2 flux ($\mu molm^{-2}s^{-1}$), ?c is the CO_2 concentration difference ($\mu molm^{-3}$) inside the chamber within a certain time interval, ?t is the time interval (s), V is the volume of the chamber (m^3), A is the soil surface area covered by the chamber (m^2), and H is the effective height of the chamber (m).

Closed dynamic chambers are often vented to keep an equilibrium air pressure between inside the chamber and in the atmosphere (Norman et al. 1992). The closed dynamic chambers are commercially available (such as LiCor 6400, LiCor Inc, Lincoln, NB) and extensively used. However, the errors induced by closed chambers, so called the chamber effect (Mosier 1990), were widely discussed (Kanemasu *et al.* 1974; Nakayama 1990; Nay *et al.* 1994; Livingston & Hutchinson 1995; Healy *et al.* 1996; Norman *et al.* 1997; Rayment 2000; Davidson *et al.* 2002). The major reason for the chamber effect is

the disturbance of natural conditions by chambers including the air pressure, wind speed, and CO_2 concentration gradient. Norman at al. (1997) and Nay at al. (1994) found that a closed dynamic chamber system underestimated soil CO_2 efflux by 10-15%. Conen and Smith (1998) reported that vented chambers may cause systematical underestimation of efflux despite the advantage of venting allowing pressure fluctuation inside the chamber. Rayment (2000) contended that the underestimation of chamber measurements is partially due to the fact that the effective chamber volume including air-filled spaces in the soil is larger than the chamber volume alone.

Open dynamic chambers allow a continuous stream of air to pass through chambers and the flux to be computed from the difference of CO_2 concentration between entering and exiting the chamber. The equation for open dynamic chambers is as Eq. (3):

$$F = \frac{f \Delta c}{A} \qquad (3)$$

where F is the CO_2 flux ($\mu molm^{-2}s^{-1}$), ?c is the CO_2 concentration difference ($\mu molm^{-3}$) between inflowing and outflowing the chamber, f is the air flowing rate (m^3s^{-1}), and A is the soil surface area covered by the chamber (m^2).

Open dynamic chambers (Garcia *et al.* 1990; Rayment & Jarvis 1997; Fang & Moncrieff 1998a; Russell *et al.* 1998) have advantages of minimizing the disturbance of CO_2 gradient in soils and providing possibility of continuous measurements. However, the major problem of open chamber is the control of flow rate and the change of pressure inside and outside the chamber (Nakayama 1990; Norman *et al.* 1997; Longdoz *et al.* 2000). Fang and Moncrieff (1998a) pointed out that a pressure difference between the inside and outside of the chamber with a few tenths Pa will cause several-fold difference

in measured CO_2 efflux. Because of these reasons, there are no commercially available open dynamic chambers to date.

Portable chambers such as the commercial LiCor 6400 have the advantage over fixed chambers in that it covers more spatial variation of soil CO_2 efflux. To increase the temporal resolution of efflux, automated systems have been developed for continuous and semi-continuous measurements (Goulden & Crill 1997; McGinn *et al.* 1998; Russell *et al.* 1998; Scott *et al.* 1999; Drewitt *et al.* 2002; King & Harrison 2002). Automated systems help us monitor the long term CO_2 evolution from soils, but reasonable precaution has to be made to minimize the disturbance to natural conditions (temperature and pressure) and address the technical uncertainty that chambers involve.

Because of the easy deployment in the field, chamber measurements have become a complementary method to the eddy covariance technique (Law et al. 1999). Chambers can measure ecosystem components contributing to NEP while the eddy covariance technique lack this ability. Chamber measurements help to partition eddy covariance data into respiration and photosynthesis and to verify nighttime measurements of eddy fluxes.

2.4 Micrometeorological measurement

Unlike chambers, which can measure the soil CO_2 efflux at a special location but may disturb the natural environment, micrometeorological methods provide the integrated CO_2 flux information with the minimum disturbance on a continuous and long term basis (Baldocchi et al. 1988; Verma 1990). The most widely used micrometeorological method in the recent decade is the eddy covariance technique (Baldocchi *et al.* 1986; Wofsy *et al.* 1993; Baldocchi *et al.* 2001). The basic equation is as Eq. (4):

$$F = \overline{w'c'} \qquad (4)$$

where F ($\mu molm^{-2}s^{-1}$) is the averaged CO_2 flux in a certain period of time (normally 30 minutes), w is the vertical wind velocity (ms^{-1}), c is the instant CO_2 concentration ($\mu molm^{-3}$), $\overline{w'c'}$ is the covariance between w and c, the prime means the deviation from the mean value, and the overbar means time average.

Eddy covariance techniques and the global network, Fluxnet (Baldocchi et al. 2001), provide data calibration, inter-comparison, distribution and communication, and help us to understand carbon sinks/sources of a particular ecosystem and to parameterize global carbon models. The eddy covariance method, however, is unable to answer many questions that we may originally expect to be solved. First, it suffers from systematic problems when we continuously record flux data. Due to the weak turbulence and low wind velocity at nighttime, the nighttime data are often biased despite the importance of these data (Goulden et al. 1996; Moncrieff et al. 1997; Baldocchi et al. 2000). We use nighttime data to estimate respiration and thus decompose the net ecosystem exchange (what we measure) into photosynthesis and respiration two parts. Without the partitioning, it is impossible for us to study the mechanism of photosynthesis and respiration and to model these two processes. The storage of CO_2 during nighttime also induces errors. The storage during the calm night often results in a pulse flux during sunrise when vertical velocity increases. In addition, the eddy covariance method can only be used in a flat terrain with homogeneous vegetation. Using this method in a complex terrain causes significant horizontal advection, which violates the assumption of the eddy covariance method that the mean horizontal wind velocity should be zero. This

assumption makes the spatial upscale of this method difficult since the typical landscape is not level and homogeneous.

The second shortcoming of this method is the difficulties in partitioning net ecosystem productivity (NEP) into each component such as leaf photosynthesis and leaf, stem and soil respiration. These processes are driven by different factors. A mechanistic ecosystem model treats these processes separately. Without carbon flux data from each component, it is hard to build models only based on NEP data.

If nighttime data are unbiased, we can calculate gross primary productivity (GPP) by summing up NEP and ecosystem respiration, which are derived from nighttime fluxes (Goldstein *et al*. 2000). But problems occur when we attempt to extrapolate nighttime respiration to daytime respiration. Although temperature can be used to adjust the difference between daytime respiration and nighttime respiration, it will be biased to directly predict the daytime ecosystem respiration based on nighttime data without partitioning ecosystem respiration into leaf respiration, stem and branch respiration and soil respiration, because these components correspond differently to temperature.

Under-story eddy covariance methods can provide continuous information on soil respiration. However, similar to the over-story eddy covariance methods, under-story eddy covariance methods require strong turbulence of the air, horizontal homogeneity and a flat terrain. It may be biased for soil respiration measurement at night when turbulence is weak and drainage flows dominate the transfer of CO_2. The low height of under-story towers corresponds with small areas of footprint. Furthermore, under-story eddy covariance data cannot separate soil CO_2 efflux, bole respiration below sensors, and overlay herbaceous vegetation, when it is present. Therefore, though eddy covariance

techniques may provide high temporal resolution soil respiration data, it cannot provide spatial variation of respiration. Combing eddy covariance techniques and chamber measurements provide a solution to record both spatial and temporal variation of soil respiration (Lavigne *et al.* 1997; Law *et al.* 1999; Janssens *et al.* 2001a).

In addition to the tower-based eddy covariance method, aircraft-based eddy covariance measurements (Crawford *et al.* 1996; Desjardins *et al.* 1997) complement the small spatial coverage of eddy covariance towers. They can measure carbon and energy fluxes on landscape or regional scales. However, it is hard to spatially scale up data from temporally continuous flux data from towers. The temporally discontinuous aircraft-based eddy covariance data should cooperate with other information such as biomass surveys in order to incorporate into modeling.

3. Manipulative experimental methods in soil carbon

The above methods are all *in situ* methods without human manipulation. *In situ* methods have the advantage of reflecting the real ecosystem conditions, but their disadvantages also exist. *In situ* methods often need long time monitoring, which may cover a whole season or more. Because of the difficulty in excluding control variables in the field, *in situ* measurement data often confuse us from understanding ecosystem processes and thus predicting the future variability.

As widely used in physiological studies, manipulative experiments are also used in ecosystem studies. Manipulative experiments help us control key variables while holding other conditions constant. They are useful in calibrating carbon models and predicting future changes. They also decrease the time we need. Munipulatable variables

include temperature, moisture, CO_2, light, nutrients, and plant coverage. Laboratory incubation, warming experiments, and CO_2 enrichment experiments are often used manipulation methods.

3.1 Laboratory incubation

Laboratory incubation methods use growth chambers to manipulate environmental variables such as temperature, moisture, nutrient, and light. Growth chambers often contain intact or assembled soil samples from the field. This laboratory system is also referred to as microcosms or "bottled" experiments in ecology (Daehler & Strong 1996). Growth chambers allow us to precisely control environmental conditions and generate replicable and quick experimental results compared with the field observation. The advanced form of growth chambers is called mesocosms, or the Ecotron, which is comprised of a series of chamber units for simulating the soil community or ecosystems (Huhta & Setala 1990; Naeem *et al.* 1994; Lawton 1996; Verhoef 1996).

Despite the major advantages of growth chambers -- they speed up research and allow repeatability -- there are many limitations (Carpenter 1996; Lawton 1996). Growth chambers diverge from the real ecosystems due to small spatial scales; the species assembled are an unnatural assemblage with less shared evolutionary history; they lack fundamental energy and matter cycles. The discussion of the value of microcosms has been raised to philosophical thinking about the methodology of studying ecological systems (Lawton 1996).

3.2 Field warming experiments

Warming experiments aim to simulate global warming by increasing temperature or radiation density. Increased temperature will stimulate biochemical reactions produced by microbes or plant cells, which will increase soil respiration. Greenhouses, soil warming and overhead heater are generally used methods. Greenhouses are the simplest methods to warm the field (Chapin & Shaver 1985; Chapin *et al.* 1995; Kennedy 1995; Oechel *et al.* 1998; Robinson *et al.* 1998) and have been used for a long time. Despite the advantage of easy deployment, greenhouses have many limitations. Greenhouses, as a passive approach with no artificial power (Kennedy 1995), cannot actively control temperature. Greenhouses affect not only temperature but also other microclimate such as moisture, light intensity and quality, and wind velocity; it blocks precipitation and reduces turbulence (Shen & Harte 2000). Similar to greenhouses, Luxmoore (1998) proposed another passive warming approach – the nighttime warming experiment – by deploying at night infrared reflecting curtains around four sides of a forest canopy and across the top of the forest to mimic the top-down warming effect of crowd cover, and study soil respiration under the nighttime warming condition.

Unlike greenhouses, which provide many disturbances to natural conditions, soil direct warming methods can increase soil temperature while minimizing the influence on the atmosphere. Direct soil warming methods include burying electrical resistance wires in soils (Rykbost *et al.* 1975; Van Cleve *et al.* 1990; Peterjohn *et al.* 1993) and deploying fluid-filled pipes on aboveground (Hillier et al. 1994). Direct soil warming can well control the temperature elevated, but buried wires in soils may create unrealistic vertical temperature profile (Shen & Harte 2000). The ground surface pipe heating may overheat

the surface in the presence of an insulating layer of vegetation (Hillier et al. 1994). In addition, direct soil warming does not change the air temperature, which may cause the vegetation to react differently from the real warming (Wan et al. 2002).

Overhead heaters have the advantages over the above methods in that this technique more closely simulates the actual mechanism of global warming caused by elevated downward radiation and corresponding feedbacks (Harte & Shaw 1995; Harte *et al.* 1995). This method uses infrared radiators to heat the soil downward. It warms the ecosystem, including soils and vegetation, in the form of mimicking the real nature of global warming with the minimum disturbance of ecosystems. It was first reported by Harte and Show (1995) and then applied by a few workers (Nijs et al. 1996; Bridgham et al. 1999; Wan et al. 2002) to simulate the impact of warming on microclimate and vegetation. Saleska et al. (1999) reported the effect of experimental warming on soil respiration and found that the overall ecosystem carbon storage is reduced due to warming, but the mechanism behind this is not driven by increased temperature but by the influence of water limitation. Luo at al. (2001) reported a similar result that experimental warming causes no significant change in soil respiration due to the decreased or acclimatized temperature sensitivity of soil respiration.

Overhead heaters provide a practical method for warming experiments. However, currently it is only applied to tundra, meadow, and agricultural systems. Installing heaters in forests is impractical because the dense canopy will isolate the heat from reaching soils (Shen & Harte 2000) . In addition, heating changes the soil moisture availability and soil properties as well as temperature. Thus, results from heating should be carefully explained: they are caused by confounding factors, not by temperature alone.

3.3 CO_2 enrichment experiments

CO_2 concentration enrichment experiments mimic the elevated atmospheric CO_2 concentration while holding other environmental variables unchanged. They provide critical information on interaction of the atmosphere and biosphere and the impact of climate change on ecosystems. Enhanced atmospheric CO_2 concentration may stimulate the growth of plantations by acting as the "CO_2 fertilizer," which in turn may increase growth respiration of roots and thus affect soil respiration. Saxe at al. (1998) published a recent review on the response of trees and forests on the enriched CO_2 atmosphere.

A simple approach of CO_2 enrichment experiments is to use either open-top chambers (for example, Murray et al. 1996; Norby et al. 1997), or closed top chambers (for example, Beerling & Woodward 1996; Veteli *et al.* 2002), or branch bags (Barton et al. 1993). These approaches involve partial or full enclosure of vegetation and soils in order to increase CO_2 concentration. Thus, they change microclimate conditions as well as CO_2 concentration.

A newly developed approach is called the free-air CO_2 enrichment experiment (FACE). FACE increases atmospheric CO_2 concentration without disturbing other conditions. FACE was firstly used in short-stature vegetation ≤2m height (Hendrey & Kimball 1994; Hebeisen *et al.* 1997; Miglietta *et al.* 1997). Hendrey at al. (1999) described a prototype FACE system for tall forest vegetation in the Duke Forest, North Carolina with elevated CO_2 of 200 μ mol mol^{-1} above ambient CO_2. A number of studies have been published based on FACE (for example, DeLucia *et al.* 1999; Allen *et al.* 2000; Matamala & Schlesinger 2000; Andrews & Schlesinger 2001; Hamilton *et al.*

2002). Allen at al. (2000) found that elevated CO_2 caused significant increase in litterfall biomass and fine root increment due to the increase in photosynthetic rates, and marginally significant increase in soil CO_2 efflux. Andrews and Schlesinger (2001) reported a significant increase in soil CO_2 efflux and soil CO_2 concentration due to increased root and rhizosphere respiration as a result of CO_2 enrichment.

In addition to the above manipulation methods that control driven variables such as temperature and CO_2 concentration, soil water content and soil nutrition have also been controlled. For example, Chapin at al. (1995) studied responses of arctic tundra to experimental treatments including nutrients addition, increased temperature and light attenuation. Liu at al. (2002) studied the response of soil CO_2 efflux to water manipulation by simulating 8 levels of rainfall, and found CO_2 efflux dramatically increased immediately after the water addition.

In summary, measurement data provide information on parameterizing and validating soil carbon models for studying soil carbon cycles. *In situ* measurements retrieve data directly from natural ecosystems with less disturbances than manipulation experiments. They provide spatial variation, daily or seasonal variation to help us understand how soil carbon responds to environmental variables. Manipulative experiments simulate the natural environment while changing one or more variables. They stand between field observations and mathematical models, and provide quick and simplified results for supporting modeling. But manipulative experiments cannot mimic confounding factors that always occur in natural conditions. Combination of these two approaches may be preferable for building sound carbon models.

4. Soil carbon modeling

Soil respiration is controlled by many factors including microclimate, soil physical, chemical and biological properties, and aboveground vegetation. The dominant factors may vary with ecosystem types and seasons. Our knowledge in understanding the mechanism and variation of soil respiration is still limited. Thus, there are no widely-accepted soil respiration models that can be applied to different ecosystems or to the global scale. As a result, the contribution of soil respiration to global carbon cycles and climate change is widely debated. For example, soil respiration is considered to accelerate global warming by acting as a positive feedback in the global carbon cycle due to sensitivity to temperature (Jenkinson et al. 1991; Kirschbaum 1995; Trumbore et al. 1996; Cox et al. 2000). However, contrast to the above conclusion, some researchers argued that the response of soil respiration to temperature may be offset by other factors such as limitation of moisture or acclimation to temperature (Liski *et al.* 1999; Giardina & Ryan 2000; Luo *et al.* 2001; Xu & Qi 2001b). The focus of this uncertainty can be attributed to functional forms and driven factors of soil respiration models.

Soil respiration has been modeled using different factors such as temperature (Lloyd & Taylor 1994; Kirschbaum 1995; Katterer *et al.* 1998; Rayment & Jarvis 2000; Reichstein *et al.* 2000), temperature and water (Howard & Howard 1993; Raich & Potter 1995; Davidson *et al.* 1998; Epron *et al.* 1999; Xu & Qi 2001a; Raich *et al.* 2002; Treonis *et al.* 2002), net or gross primary productivity (Raich & Schlesinger 1992; Janssens *et al.* 2001b), or carbon content (Raich et al. 1991). The factors controlling soil respiration have been widely reviewed and discussed (Singh & Gupta 1977; Raich & Schlesinger 1992; Lloyd & Taylor 1994; Kirschbaum 1995; Kirschbaum 2000). Because it is

infeasible to incorporate all factors, which vary significantly with sites, at a large scale study, Q_{10} function is often used as a simple model to simulate soil respiration.

The Q_{10} (exponential) function was firstly developed by van't Hoff (1898) for describing the temperature dependency of chemical reactions (Eq. 5).

$$R = R_0 e^{b(T-T_0)} = R_0 Q_{10}^{\frac{T-T_0}{10}},$$

$$Q_{10} = e^{10b} \qquad (5)$$

where R is the respiration rate, R_0 the respiration at the reference temperature T_0, T is the temperature in degree Celsius, ß$_0$ is a constant coefficient. Q_{10} is the temperature sensitivity, which literally means the increasing ratio of respiration when temperature is increased by 10ºC.

Lundegårdh (1927) reported that soil respiration followed a Q_{10} of 2 when temperature is between 10ºC and 20ºC. Following that, the Q_{10} function was widely used to study soil respiration. Raich and Schlesinger (1992) surveyed literature and found Q_{10} varied between 1.3 and 3.3. It has been recognized by many studies (Lloyd & Taylor 1994; Kirschbaum 1995; Thierron & Laudelout 1996; Xu & Qi 2001b) that the Q_{10} value is temperature dependent: lower temperature has greater temperature sensitivity.

Another widely used soil respiration model is the Arrhenius function. Arrhenius (1889, in Lloyd & Taylor 1994) derived a theoretical equation based on the principle of chemical reactions to describe respiration (Eq. 6).

$$k = de^{\frac{-E}{\Re T}} \qquad (6)$$

where k is the chemical reaction rate, $\Re$ is the universal gas constant (8.314 $Jmol^{-1}K^{-1}$), T is the absolute temperature (K), d is a constant for a particular reaction, and E is the activation energy ($Jmol^{-1}$).

Lloyd and Taylor (1994) provided a modified Arrhenius equation, called the Lloyd-Taylor equation (Eq. 7), after finding out that both Q_{10} and Arrhenius equations underestimated respiration rates at low temperatures and overestimated respiration rates at high temperatures.

$$R = Ae^{\frac{-E_0}{T-T_0}} \qquad (7)$$

where A, T_0, and E_0 are fitted parameters.

Besides Q_{10} functions and Arrhenius-type functions, other functional forms such as linear functions (Fung et al. 1987) and power functions (Kucera & Kirkham 1971) have also been used to simulate soil respiration. Whatever the functional form is selected, the disadvantage of soil respiration modeling using temperature alone is the inapplicability to many places especially in dry areas when temperature sensitivity is significantly affected by summer drought (Reichstein et al. 2002; Rey et al. 2002). It has been reported that temperature sensitivity is moisture dependent (Carlyle & Ba Than 1988; Xu & Qi 2001b). Therefore, moisture is often employed as one of independent variables to simulate soil respiration.

Bi-variable equations have been used to simulate soil respiration. For example, Epron et al. (1999) reported a linear relationship for soil respiration with moisture while exponentially responding to temperature. Davidson at al. (1998) used an exponential function to express the response of soil respiration to soil matric potential estimated from volumetric water content. Xu and Qi (2001a) and Qi and Xu (2001) reported that soil

respiration responded to soil temperature with an exponential function while responding to soil moisture with a power function. More complex correlations between respiration and moisture have been described in global carbon models such as the Terrestrial Ecosystem Model (TEM) (Raich et al. 1991) and the Carnegie-Ames-Stanford Approach (CASA) (Potter et al. 1993).

Due to limited knowledge on processes of soil carbon production and transport, most of soil respiration models published in the literature to date are regression-based models with site-specific parameters. Fang and Moncrieff (1999) addressed this problem and developed a process-based model to simulate soil respiration by modeling biochemical and physical processes involved in two stages: the first stage is the production of CO_2 by plant roots and microbes; the second stage is the gas transport between the soil and atmosphere. Recently, Kuzyakov and Cheng (2001) and Hogberg at al. (2001) presented evidences indicating that root respiration (or total soil respiration) may also correlate with photosynthesis in addition to environmental variables, but the mechanism behind this is still not well explained.

5. Temporal and spatial variation of soil respiration

It is difficult to simulate temporal and spatial variation of soil respiration because soil is a complex system containing various biological, chemical, and physical reactions, and these reactions coupled with soil properties vary temporally and spatially. Soil respiration contains root components, which vary with trees' growth, senescence and other physiological activities. Temporal variation of soil respiration is often examined by changing driven variables such as temperature and moisture, both of which vary diurnally

and seasonally. Temperature and moisture not only are driven factors controlling soil respiration, but also act as temporal variables simulating soil respiration in time series. Compared with temporal variations, modeling spatial variation of soil respiration has proved to be more difficult (Rayment & Jarvis 2000). The reason for this difficulty is that most of soil respiration models are developed from a specific site with parameters only feasible to that site. The model results often address the spatial average of a particular site without considering the spatial homogeneity. Inter-site comparison of soil respiration is often conducted by plotting soil respiration in various sites against environmental conditions (e.g. Raich et al. 2002). Another reason for this difficulty is the lack of suitable major spatial variables to drive models. Spatial heterogeneity of soil respiration is often not quantified in the literature.

As a result for our limited understanding on spatial variability of soil respiration, there are fewer publications addressing spatial variation of soil respiration than temporal variations. Goulden at al. (1996) described considerable heterogeneity of soil respiration. Hanson at al. (2000) documented the spatial variability of forest floor respiration by investigating the reason from topographically distinct locations. Rayment & Jarvis (2000) studied spatial variation of soil respiration in a Canadian boreal forest and correlated spatial variation empirically with the thickness of the dead moss layer. Shibistova at al. (2002) reported the difference of soil CO_2 efflux measured by chambers and by eddy covariance techniques, and concluded that the spatial variability may be related to root density. Xu and Qi (2001a) reported the significant spatial variation of soil respiration and pointed out the inadequacy of their model in explaining spatial variation while

adequate in explaining temporal variation. All above studies did not quantify spatial patterns and nor applied their results into different forest stands or ecosystem types.

To advance our knowledge in temporal and spatial variation of soil respiration, partitioning soil respiration into root respiration (including associated mycorrhizae respiration) and microbial heterotrophic decomposition is necessary since these two components respond differently to abiotic and biotic drivers. Root respiration accounts for 10% to 90% of total soil respiration depending on vegetation types and seasons of the year (Hanson et al. 2000). Microbial decomposition may be mainly driven by soil temperature and moisture, but root respiration are driven not only by environmental variables, but also by plant physiology and phenology as a part of plant autotrophic respiration. Evidence has shown 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 was 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 additional to environmental parameters. Janssens et al. (2001b) 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. The reason behind the above results may be due to root respiration, which is coupled to photosynthesis and productivity.

Temporal variation of microbial decomposition can be simulated by temperature and moisture, but root respiration may be decoupled with environmental variables particular during the switching period between growing seasons and dominant seasons. Root growth respiration, a part of root respiration, may be determined on carbon availability, which is produced through photosynthesis. Light quantity and quality, one of driven factors determining photosynthesis, may affect root respiration other than temperature and moisture, as indicated by shading experiments conducted by Craine at al. (1999). Thus, separately modeling root respiration and microbial decomposition will help us better understand temporal variation of soil respiration.

Partitioning root respiration also helps us understand the spatial heterogeneity of soil respiration. Among many factors, the distribution of roots below ground accounts for the spatial variation of soil respiration. The root density and activity may partially explain the site difference of soil respiration with different stand densities and age classes. Thus, roots and root respiration could be one of quantitative variables explaining spatial variation of soil respiration.

6. Management impact on soil carbon

Besides the temporal and spatial variation of soil respiration caused by natural factors, human management will also affect soil respiration and soil carbon pools. Forest management practices such as thinning, pruning, harvesting, fertilization, and prescribed fire may affect soil carbon by changing ground surface energy balance, soil water content, nutrition availability, and aboveground vegetation production. Johnson and Curtis provided a recent review (2001) concluding that forest harvesting and fire had no

significant effects on soil carbon storage while fertilization and nitrogen-fixing vegetation will cause overall increase in soil carbon.

Compared with extensive studies in management impacts on soil carbon pools, the studies on the soil respiration affected by management actions are few. Nakane et al. (1986) found soil respiration decreased after harvesting due to the cessation of root respiration. Toland et al. (1994) reported that soil respiration in intact and clear-cut plots did not differ significantly between two plots because the increase in microbial respiration in clear-cut plots offset the decrease in root respiration after clear-cut. Striegl and Wickland (1998) concluded that clear-cutting in a mature jack pine woodland reduced soil respiration due to the disruption of soil surface and the death of tree roots. Ohashi et al. (1999) reported that soil respiration in a Japanese cedar forest 3-4 years after thinning in a thinned stand was higher than those of a intact stand, but there was no difference 5 years after the thinning.

The importance of studying management impacts on soil carbon is not only because it advances our knowledge on soil carbon and helps test soil carbon models, but also because it links to the Kyoto Protocol. This international treaty allows a country to earn credits for carbon sinks and to trade carbon. This economic mechanism provides an incentive for a country or region to increase carbon storage for mitigating climate change. Because of the huge carbon storage in soils, soils provide a potential to increase the carbon sink. It was estimated that the potential net carbon sequestration in U.S. forest soils ranges from 48.9 to 185.8 Mt C/year (Heath et al. 2003). Studying the impact of forest management on soil carbon will help to address such an open question, “can we and how can we sequester more carbon in soils by management activities?”

7. Objectives of this dissertation

The above review indicates that despite the importance of soil respiration in global carbon cycles, our knowledge in both theory and methodology in soil respiration is still limited. We need continuous measurement instruments for soil respiration with minimum disturbance to natural conditions, which can be used to decompose and validate eddy covariance measurements; we need sound soil respiration models to capture temporal variation both in dry seasons and non-dry seasons; we need to develop methods to partition soil respiration into root respiration and microbial decomposition since these two processes may be simulated by different functional forms and variables; we need to understand the main variables controlling spatial variation of soil respiration; we also need to understand how forest management activities will affect soil respiration.

The objectives of this dissertation are to address the above questions. In Chapter 2 I aim to study how forest thinning, an important forest management practice, affects soil respiration; I develop a bi-variable soil respiration model and conduct multivariate regression analysis to compare soil respiration before and after the thinning. In Chapter 3 I partition soil respiration into root respiration and microbial decomposition by conducting a trenching experiment; I separately model total soil respiration, root respiration and microbial decomposition, and examine the seasonal variation of the ratio of root respiration over total respiration. In Chapter 4 I compare soil respiration in a young plantation with a mature plantation; a general model is developed to explain the difference between two sites with independent variables including stand density, tree size, soil temperature, and moisture. To overcome the disadvantage of temporally

discontinuous measurement of soil respiration, in Chapter 5 I develop a novel method to measure soil CO_2 profiles by burying small CO_2 sensors in soils; soil CO_2 efflux is calculated by measured CO_2 gradient and a diffusivity model; automated continuous measurements are validated by portable flux measurements.

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Chapter 2 Effects of Forest Thinning on Soil Respiration in a Ponderosa Pine Plantation in the Sierra Nevada, California

Abstract

Soil respiration is controlled by soil temperature, soil moisture, fine root biomass, microbial biomass, and soil physical and chemical properties. Forest thinning changes soil temperature, soil moisture, and root activity, and thus soil respiration. We measured soil respiration using an LI-6400 photosynthesis system as well as soil temperature and moisture in a young ponderosa pine plantation in the Sierra Nevada Mountains in California from June 1998 to May 2000 before a pre-commercial thinning, and from May to November 2001 after the thinning.

Thinning did not change the temporal variation of soil respiration but it increased the spatial homogeneity of soil respiration. After conducting multivariate analysis, we used a model $F = b_0 e^{b_1 T} e^{b_2 M + b_3 M^2}$, which incorporates exponential and polynomial functions with two variables, soil temperature (T) and moisture (M), to simulate soil respiration before and after the thinning. The model indicated that the thinning did not change the relationship between soil CO_2 efflux, temperature and moisture, but it decreased the constant coefficient b_0 and thus the total soil respiration by 13%. After using daily mean values of soil temperature and moisture to drive the model, we estimated that in the year 1999, soil CO_2 emission was 78.41 mol $m^{-2}y^{-1}$; in the year 2000, soil CO_2 emission was 78.89 mol $m^{-2}y^{-1}$; between day 147, 1999 and day 146, 2000 (365 days before thinning), the accumulation of CO_2 emission was 75.71 mol $m^{-2}y^{-1}$; and between day 147, 2000 and day 145, 2001 (365 days after thinning), the accumulation of

CO_2 emission was 76.14 mol $m^{-2}y^{-1}$. Although the model indicated that the thinning will theoretically decrease CO_2 efflux holding temperature and moisture constant, because the independent variables, temperature and moisture, varied with the time before and after thinning, the actual change of CO_2 efflux was not significant. The effect of forest thinning on soil CO_2 efflux is the combined result from the decrease in root respiration, increase in soil organic matter, and the change of soil temperature and moisture.

1. Introduction

Studies on soil carbon have received much attention because a small change in soil carbon pool will significantly affect the global carbon cycle and climate system. There is a controversy that soil respiration may accelerate global warming by acting as a positive feedback in the global carbon cycle (Jenkinson *et al.* 1991; Kirschbaum 1995; Trumbore *et al.* 1996; Cox *et al.* 2000), or the positive feedback may be not so significant as to accelerate the global temperature (Liski *et al.* 1999; Giardina & Ryan 2000; Luo *et al.* 2001; Xu & Qi 2001b). The main focus of this uncertainty is what factors drive soil CO_2 efflux and how the driving mechanisms operate.

Soil surface CO_2 efflux, commonly referred to as soil respiration, is produced by roots and associated mycorrhizae (autotrophic respiration) and soil microorganism (heterotrophic respiration). Soil CO_2 efflux is controlled by many factors such as vegetation property, microbial activity, soil organic carbon content, soil temperature and moisture, and soil physical and chemical properties. It has been measured and modeled by different methods in various ecosystem types (Crill 1991; Raich & Schlesinger 1992;

Davidson *et al.* 1998; Russell *et al.* 1998; Epron *et al.* 1999a; Savage & Davidson 2001; Xu & Qi 2001a; Drewitt *et al.* 2002; Franzluebbers *et al.* 2002; Treonis *et al.* 2002). Although there has been much consensus on modeling soil respiration by soil temperature, particularly using exponential functions, there is less consensus on the functional form of moisture effect (Lloyd & Taylor 1994; Fang & Moncrieff 2001; Qi & Xu 2001). Moreover, there are fewer studies on how to model the response of soil CO_2 efflux to forest management practices and treatments.

Forest management practices such as thinning, selective harvest, and prescribed fire will affect soil respiration by changing ground surface energy balance, soil water content, nutrient availability, and aboveground production. Nakane et al.(1986) found soil respiration decreased after harvesting due to the cessation of root respiration. Toland et al.(1994) reported that soil respiration in intact and clear-cut plots did not differ significantly between two plots because the increase in microbial respiration in clear-cut plots offset the decrease in root respiration after clear-cut. Striegl and Wickland (1998) concluded that clear-cutting in a mature jack pine woodland reduced soil respiration due to the disruption of soil surface and cutoff of root respiration.

Thinning, partial removal of trees, is different from clear-cutting. Thinning changes soil temperature and moisture, and underground root systems and microbial community. Although forest thinning is a common silvicultural practice, there are limited careful studies on the impact of forest thinning on soil respiration. The exception is Ohashi et al.(1999), who reported that soil respiration in a thinned stand of a Japanese cedar forest 3-4 years after thinning was higher than those of an intact stand, but there was no difference 5 years after the thinning.

The purpose of this study is 1) to investigate and compare the spatial and inter-annual patterns of soil respiration before and after a pre-commercial thinning; 2) to model soil respiration incorporating two variables, temperature and moisture, and two stages, before and after the thinning, by conducting multivariate regression analysis; and 3) to analyze the effect of thinning on soil respiration by adjusting the impact from soil temperature and moisture.

2. Materials and Methods

2.1 Site description

The study site, a part of the Ameriflux network, is in a young ponderosa pine plantation ($38^{o}53'42.9''$N, $120^{o}37'57.9''$W, 1315 m), which is located adjacent to Blodgett Forest Research Station, a research forest of the University of California, Berkeley. The plantation was dominated by 7-8 year old ponderosa pine (*Pinus ponderosa*) in 1998. Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), giant sequoia (*Sequoiadendron giganteum*), and California black oak (*Quercus kelloggii*) are occasionally seen in the overstory canopy. The plantation had an average diameter at breast height (DBH) of 7.6 cm, an average height (DBH > 3 cm) of 3.4 m, and a density (DBH > 3 cm) of 1213 stems/ha in 1998. Overstory leaf area index (LAI) was about 4.5. The major shrubs are manzanita (*Arctostaphylos* spp.) and *Ceonothus* spp. In 1998 about 58% of the ground area was covered by trees, 24% by shrubs, and the remaining 18% by grass, stumps, and bare soils (Xu *et al.* 2001).

The site is characterized by a Mediterranean climate with a hot, dry summer, and a cool, wet winter. The majority of precipitation, averaged 1660mm since 1961, falls

between September and May with almost no rain in the summer. The winter has an average of 254 cm snow. The average (over 33 years) minimum daily temperature in January was 0.6°C and the average maximum daily temperature in July was 28.3°C. Trees generally break bud in May and set bud in late July to early August.

The study site is relatively flat with slopes less than 3 degrees in our sampling area. The site soil is a fine-loamy, mixed, mesic, ultic haploxeralf in the Cohasset series whose parent material was andesitic lahar. It is relatively uniform and dominated by loam and sandy-loam with sand of 60%, silt of 29%, and clay of 11%. Coarse woody debris is scattered on the forest floor from the residuals of previous harvesting (clear-cutting). The soil has an average pH value of 5.5, organic matter of 6.9%, and total nitrogen of 0.17% (Xu & Qi 2001a).

A pre-commercial thinning was conducted on May 25, 2000. About 60% of trees and most of shrubs were cut down and ground into detritus. The location where we measured soil respiration, temperature and moisture was protected to avoid disturbance during the thinning. Trees were more evenly spatially distributed after the thinning.

2.2 Field measurements

We established two 20×20 m^2 sampling plots with 40 m between the two plots. In each plot, soil CO_2 efflux and 10cm depth of soil temperatures were measured on a 3×3 matrix spacing 10 m apart. We also monitored 0-30cm depth average of volumetric soil moisture at the center of each plot. Soil CO_2 efflux was measured using an LI6400-09 soil chamber connected to an LI-6400 portable photosynthesis system (LI-COR, Inc. Lincoln, NE), for data collection and storage. A soil collar, with a height of 4.4 cm and a diameter of 11

cm, was permanently inserted into the soil at each sampling point. The collar was left out of the soil surface of 1cm, supporting the chamber and allowing the chamber to directly touch the soil. We used custom-built thermocouple sensors to monitor soil temperature, and time domain reflectometry (TDR, CS615 Campbell Scientific, Inc., Logan, UT) to monitor volumetric soil moisture. Thermocouple sensors and TDR were connected to dataloggers (CR10X and 23X, Campbell Scientific, Inc.). The dataloggers are programmed to store output data every 5 minutes.

The measurement of soil CO_2 efflux started in June 1998. The data collection covered the period from June 1998 to November 2001. Soil CO_2 efflux measurement was normally conducted once (1-2 days) every month except for the winters when snow covered the ground. We had 8-10 measurements for each sampling location within one day when we conducted soil CO_2 efflux measurement. We divided all data into two groups, that is, one before May 2000 (before thinning) and one after May 2000 (after thinning).

2.3 Data analysis and model building

Soil CO_2 efflux and its temporal variation were investigated before and after thinning. The spatial variation of 18 samples was compared before and after thinning. We built models with two variables, soil temperature and moisture, to simulate temporal variation of soil CO_2 efflux and investigate the difference before and after thinning.

Using one variable, temperature, soil efflux is commonly estimated through an exponential function (Q_{10}) function:

$$F = b_0 e^{b_1 T}, \qquad (1)$$

or $F = b_0 Q_{10}^{T/10}$, where $Q_{10} = e^{10 b_1}$, (2)

where F is the soil CO_2 efflux, T is the soil temperature, Q_{10} is the temperature sensitivity, and β_0 and β_1 are coefficients.

Soil moisture is also an important variable controlling soil efflux, particularly when soil moisture becomes a critical stress limiting respiration. We found a bivariate model will be more accurate to simulate soil respiration than a univariate model. The moisture function can take the form of a linear, power or exponential function:

$$F = b_0 e^{b_1 T} f(\text{moisture}) \qquad (3)$$

We conducted multivariate analyses to explore the relation between efflux, temperature and moisture. Moisture has two opposite effects on CO_2 efflux: when soil volumetric moisture is below some threshold values (about 15-20%), soil CO_2 efflux increases with moisture; efflux decreases with soil moisture when the moisture is greater than the threshold value. After comparing different functional forms and checking residue plots, we found the following model fitted our data best:

$$F = b_0 e^{b_1 T} e^{b_2 M + b_3 M^2},$$

or $$\ln(F) = \ln(b_0) + b_1 T + b_2 M + b_3 M^2, \qquad (4)$$

where F ($\mu molm^{-2}s^{-1}$) is the soil CO_2 efflux, T (°C) is the soil temperature at 10cm depth, M (%) is the soil volumetric moisture at 0-30cm average, and β_0, β_1, β_2, and β_3 are model coefficients. The model can be log-transformed to a linear model.

To explore the effect of thinning on CO_2 efflux, we added "thinning" as a binary variable to Eq. (4) so as to investigate the thinning effect while considering the influence

from soil temperature and moisture. This model was composed of two continuous independent variables and one categorical variable. The categorical variable "thinning" meant "after thinning", when thinning = 1, and "before thinning" when thinning = 0. Adding the categorical term allows us to evaluate the effects of temperature and moisture on soil CO_2 efflux while considering the difference of these effects caused by thinning. Categorical terms are accompanied by interaction terms with continuous variables. Interaction terms allow us to analyze the differences among dependent variables associated with categorical variables while accounting for the influence of continuous independent variables (Selvin 1995). Thus, this technique can help us to evaluate the effect of thinning on soil CO_2 efflux while adjusting for temperature and moisture.

After adding the categorical term and interaction terms, our original Eq.(4) had 3 continuous independent variables T, M and M^2, one binary variable "thinning", and three interaction terms $T_{thinning}$ (T× thinning), $M_{thinning}$ (M× thinning), and $M^2{}_{thinning}$ (M^2× thinning):

$$\ln(F) = b_0 + b_1 T + b_2 M + b_3 M^2 + b_4 \cdot thinning + b_5 \cdot T_{thinning} + b_6 \cdot M_{thinning} + b_7 \cdot M^2{}_{thinning} \quad (5)$$

We used the "backward" elimination approach, that is, we first deployed all possible variables in our model and then eliminated some variables that failed to pass the statistical T test and F test. By adding the categorical variable we can pool the data both before and after the thinning together to do multivariate analysis. After processing the original data using "Excel" (Microsoft Corporation), we used the statistic software "Stata" (Stata Corporation, Texas) to do multivariate linear regression analysis. The regression results and associated T-test and F-test allow us to finalize our model and estimate coefficients with each variable.

3. Results

3.1 Seasonal variation

Figure 2.1 shows the seasonal variation of CO_2 efflux with soil temperature and volumetric moisture over three and half years from June 1998 to November 2001. Each datapoint of CO_2 efflux represents the daytime (7:00-19:00) average of soil CO_2 efflux.

Soil CO_2 efflux had strong correlations with soil temperature and moisture. Under the Mediterranean climate in California, soil temperature reached the highest in July and August while soil moisture was at the lowest level of the year. From January to March moisture reached the peak value while soil temperature was the lowest during the winter time. CO_2 efflux varied differently with soil temperature and moisture, positively correlated with soil temperature but negatively correlated with soil moisture. As a result, CO_2 efflux reached the peak value in May, June and July when the temperature and moisture lines almost intersect. In the early summertime, soil temperature increased while soil moisture is moderate. During this period environmental conditions were optimal for both microbes and trees. Thus, both root respiration and microbial decomposition have a high value, resulting in the high value of soil respiration.

3.2 Spatial variation of CO_2 efflux

We examined variations of 18 spatial sampling locations before and after thinning, and found the spatial variation decreased after thinning. We calculated the mean efflux of

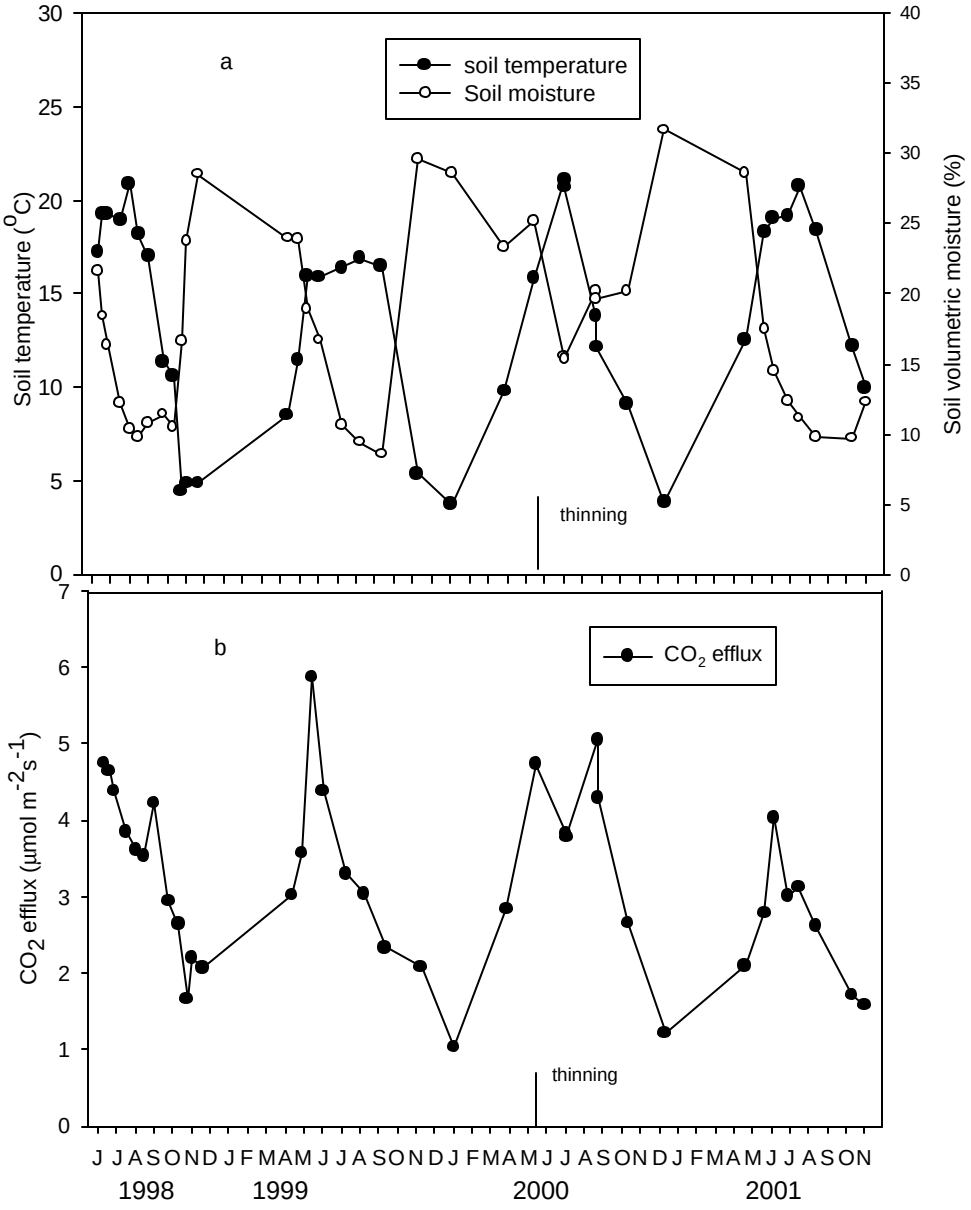

Fig. 2.1 Seasonal variation of soil temperature and moisture (a) and soil CO_2 efflux (b) before and after the thinning, which was conducted on day 146 (May 25) in 2000.

each sample over a year before thinning and a year after thinning, and then examined the difference between these samples (Table 2.1, and Fig. 2.2).

Table 2.1 Spatial variation of CO_2 efflux before and after the thinning

	CO_2 efflux ($\mu molm^{-2}s^{-1}$)		Temperature (°C)	
	Before thinning	After thinning	Before thinning	After thinning
Mean (n=18)	3.26	3.78	12.63	14.67
Standard deviation	1.04	0.89	1.50	1.48
Coefficient of variation	31.9%	23.4%	11.9%	10.1%

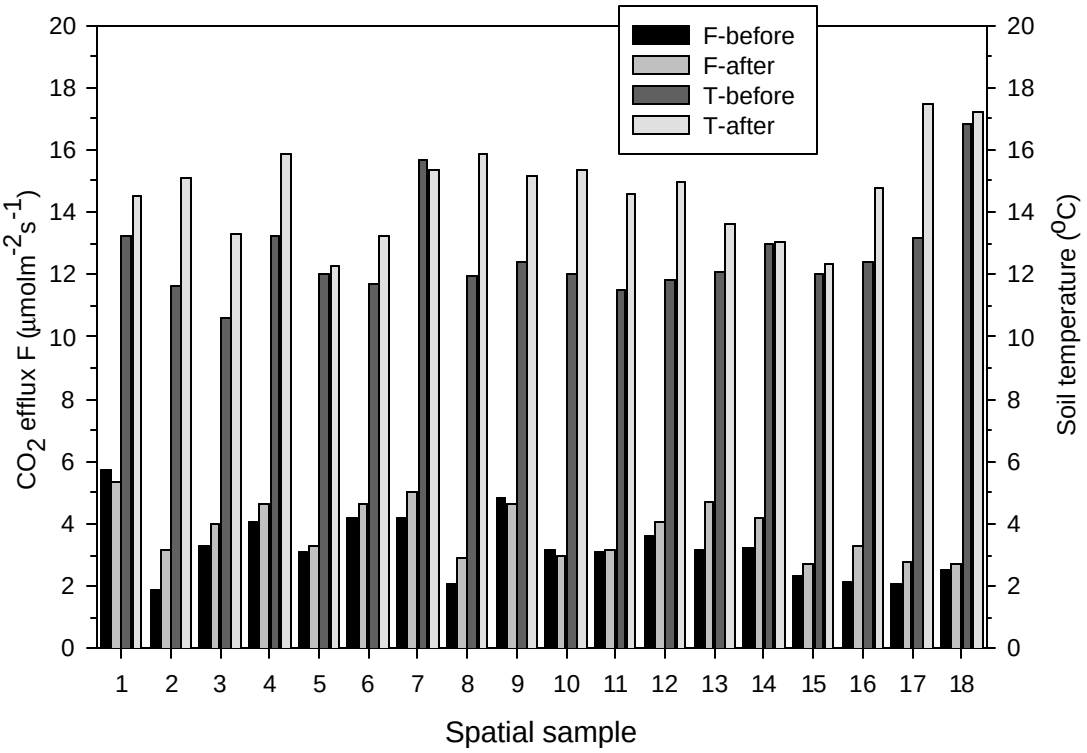

Fig. 2.2 Spatial variation of CO_2 efflux before and after the thinning. The horizontal axis is the number of spatial samples. F-before and F-after represent CO_2 efflux before and after thinning; T-before and T-after represent soil temperature before and after thinning.

Table 2.1 and Fig. 2.2 show that after thinning, the spatial variation of soil temperature did not change much, but the spatial variation of soil CO_2 efflux decreased significantly. This indicates that the thinning increases the spatial homogeneity of soil respiration. The 60% cutting of trees and 100% cutting of shrubs make the site more evenly covered with trees after the thinning. Indeed, this is one of the purposes of thinning as a forest management practice. Our earlier study found that root respiration covers 47% of the total soil surface CO_2 efflux at the site (Xu *et al.* 2001). The varied root distribution and activity may explain the reduction of spatial variation of soil respiration after the thinning.

3.3 Correlation of CO_2 *efflux vs. temperature and moisture*

In order to study the correlation between soil CO_2 efflux and soil temperature and moisture, we spatially averaged the 18 sampling locations to represent the CO_2 efflux of our site at a certain time, and used the time-series efflux data to conduct regression analysis. We plotted soil CO_2 efflux data versus soil temperature and moisture over 3 and half years covering the time before and after the thinning. We used a statistical software package, Stata (Stata Corporation, Texas), to optimize coefficients in Eq. (5) by conducting multivariate linear regression analysis. The thinning effect was treated as a categorical variable in the analysis.

After conducting regression and testing for Eq. (5), we found the coefficients β_5, β_6, and β_7 did not pass the T test at 95% confidence level with P values of 0.309, 0.065 and 0.365, respectively. We further conducted 3 pairs of two-variable F tests ($T_{thinning}$ &

$M_{thinning}$, $T_{thinning}$ & $M^2_{thinning}$, and $M_{thinning}$ & $M^2_{thinning}$) and found that the coefficients β_5, β_6, and β_7 were not significantly different from zero and thus the null hypothesis ($\beta_5 = \beta_6 = \beta_7 = 0$) was accepted. Therefore, we dropped the variables corresponding to the coefficients β_5, β_6, and β_7 from Eq. (5), and kept the first four variables with coefficients β_o, β_1, β_2, β_3, and β_4. The refined model has 4 variables, namely T, M, M^2, and "thinning," with n =169, R^2=0.69 and P values of each coefficient < 0.001 (Eq. 6).

$$\ln(F) = b_0 + b_1 T + b_2 M + b_3 M^2 + b_4 \cdot thinning \qquad (6)$$

The regression analysis gave us the best fitted coefficients with β_0 =-1.148, β_1=0.0439, β_2=0.200, β_3= -0.00506, and β_4= -0.137. In another word, the model has the form of Eq. (7). Fig. 2.3 demonstrates three-dimensionally the shape of this model.

$$F = 0.317\, e^{0.0439T} e^{(0.2M - 0.00506M^2)}, \quad \text{before thinning}$$
$$F = 0.277\, e^{0.0439T} e^{(0.2M - 0.00506M^2)}, \quad \text{after thinning.} \qquad (7)$$
$$(R^2 = 0.69,\ n = 169,\ p < 0.0001)$$

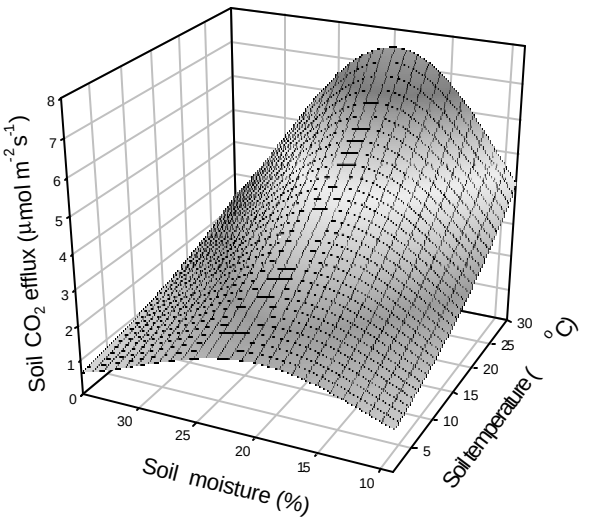

Fig. 2.3 3D demonstration of the soil respiration model

Dropping of the coefficients β_5, β_6, and β_7 indicated that thinning had no interaction with temperature and moisture; in another word, thinning did not change the relationship between CO_2 efflux, temperature, and moisture. Keeping of coefficients β_4 indicated that the thinning changed the magnitude of CO_2 efflux by changing the constant coefficient β_0. After separating models from Eq. (6) to Eq. (7), we found that the thinning decreases the constant coefficient β_0 by about 13%.

The constant coefficient β_0 represents the effects of soil microbial biomass, soil organic carbon content, root biomass, and root activity, other than soil temperature and moisture. Soil microbial biomass and soil organic carbon content contribute to microbial decomposition, and root biomass, and root activity contribute to root respiration. Thus the change of β_0 may result from the change of soil microbial biomass, soil organic carbon content, root biomass, and/or root activity.

Similarly, we also explored each spatial sample's correlation between CO_2 efflux, soil temperature and moisture. We found no statistical difference of correlation among samples except for the difference of the constant β_0.

Q_{10} is defined as the increasing ratio of CO_2 efflux when temperature is increased by 10°C. Holding moisture constant, we derived from the Eq. (7) that $Q_{10} = 1.55$. This means that if soil moisture does not change while temperature is increased by 10°C, soil CO_2 efflux will increase by 55% of the original value. This situation may explain the daily variation of efflux at our site, but it cannot explain the seasonal variation since the seasonal change of soil temperature is always accompanied by the change of soil moisture. The effect of the increased temperature on soil respiration may be either offset or enlarged by the corresponding change of soil moisture.

Eq. (7) tells us that soil moisture has two opposing effects on soil CO_2 efflux. The quadratic term indicated that there is a maximum value when M=19.8%. Holding soil temperature constant, when volumetric moisture is increased but no more than 19.8%, soil CO_2 efflux will increase; when volumetric moisture is increasing and greater than 19.8%, soil CO_2 efflux will decrease. The latter situation may be due to the decrease in soil porosity and oxygen availability to microbes.

3.4 Modeled inter-annual CO_2 *efflux*

We used Eq. (7) to estimate the annual soil CO_2 efflux based on continuous soil temperature and moisture data (Fig. 2.4). Fig. 2.4a shows daytime (7:00-19:00) mean soil temperature and moisture from day 175, 1998 to day 314, 2001. Fig. 2.4b is the modeled CO_2 efflux vs. measured data. Since we have only daytime measurement of soil CO_2 efflux, we used daytime mean values of temperature and moisture to drive the model for comparing the measured efflux data.

On day 147, 1999 there is an outlier much greater than the modeled result. This happened during the period when soil CO_2 efflux has the peak value. In the late May early June, when trees begin to grow fast, soil CO_2 efflux often shows some "pulse" with extreme high value. This is probably caused by root phenology as is also observed by Law at al. (1999) and Xu & Qi (2001a).

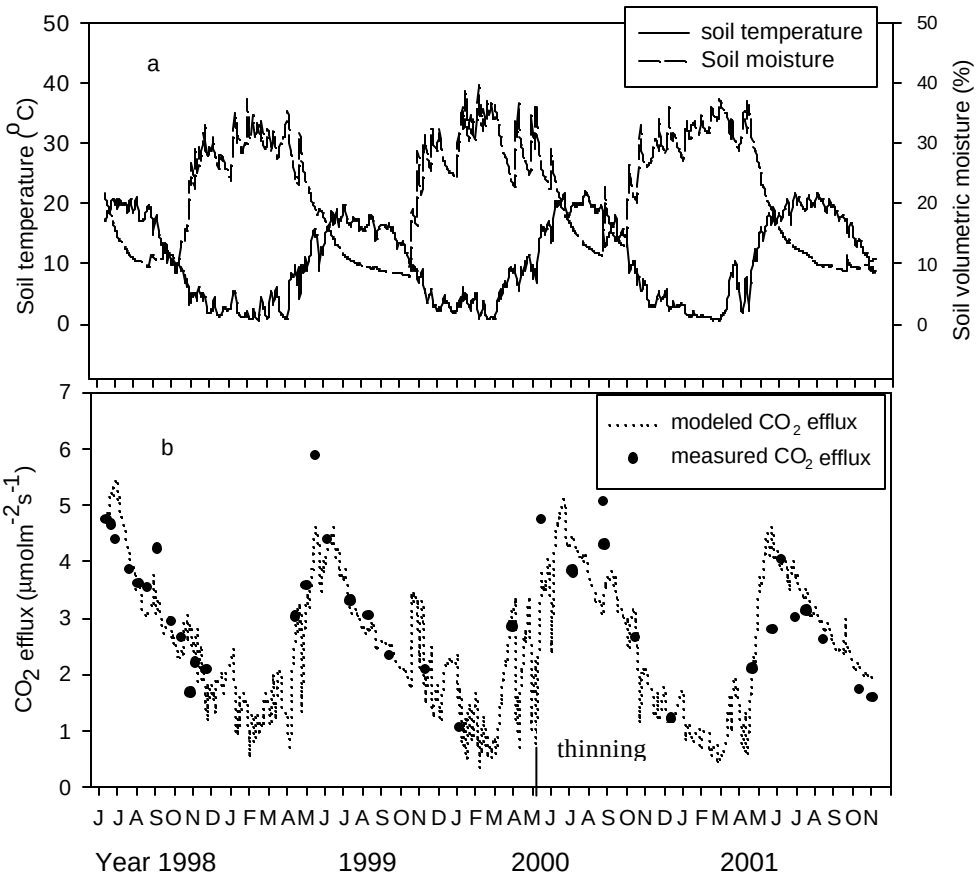

Fig. 2.4 Temporal patterns of soil temperature and moisture (a), and modeled CO_2 efflux based on soil temperature and moisture, compared with measured CO_2 efflux (b).

During the days after thinning in 2000, several measured data do not fit well with the modeled curve. This suggests that soil CO_2 efflux change abnormally soon after the thinning. Several months after the thinning, the model works well again for simulating the efflux. We speculate that the thinning might stimulate root respiration, similarly to the so-called "wound respiration" caused by traumatic stimulus (Muller 1924), shortly after the thinning. In addition, the dead roots, especially the fine roots, from the thinning may add considerable amount of easy-composed carbon in the soil, thus leading to the short-term abrupt increase of soil surface CO_2 efflux.

The inter-annual variation of soil CO_2 emission is small. To calculate yearly accumulation of CO_2 efflux, we used daily mean values of soil temperature and moisture to drive our model. Between July 1 and December 31, 1998, soil CO_2 emission was 48.05 mol m^{-2}; in the year 1999, soil CO_2 emission was 78.41 mol m^{-2}; in the year 2000, soil CO_2 emission was 78.89 mol m^{-2}; Between January 1 and June 30, 2001, soil CO_2 emission was 30.59 mol m^{-2}.

Between day 147, 1999 and day 146, 2000 (365 days before thinning), the accumulation of CO_2 emission was 75.71 $molm^{-2}$; while between day 147, 2000 and day 145, 2001 (365 days after thinning), the accumulation of CO_2 emission was 76.14 $molm^{-2}$. Although our model indicates the thinning will decrease CO_2 efflux holding temperature and moisture constant, because soil temperature and moisture varied inter-annually, the accumulation of CO_2 emission increased only by 0.57 $molm^{-2}$ compared to the year prior to the thinning. This may be caused by the increase in soil temperature: the daily mean soil temperature within a year before thinning increases from 9.73 °C to 9.88 °C after thinning.

4. Discussion

4.1 Determinants of soil CO_2 efflux

Soil respiration can be partitioned into microbial respiration and root respiration; root respiration can be further partitioned into root maintenance respiration and growth respiration. The effects of forest thinning on soil respiration are determined by many interacting factors, among which are soil temperature, soil moisture, microbial respiration rate, root respiration rate, and decomposition of dead root due to thinning. Using temperature alone to simulate CO_2 efflux may not be applicable in our site since in the summer moisture is an extreme constraint to CO_2 efflux. This chapter treats soil temperature and moisture as driven variables for soil CO_2 efflux, while incorporating other factors as a constant coefficient β_0, which varies with thinning. Because of opposite effects of moisture on soil CO_2 efflux, the moisture variable has a quadratic form that is placed as an exponent of an exponential function (Eq. 7).

More generally, the binary variable "thinning" in Eq. (6) can be replaced by other forest management treatments or continuous variables. Although two variables, temperature and moisture, represent the temporal variation of CO_2 efflux, they cannot fully represent the controlling variables of soil respiration if we want to compare different stages due to forest management treatments or different spatial locations. The other factors, such as fine root biomass, microbial carbon, soil nutrient, soil chemical and physical compositions, also play important roles influencing carbon efflux. If these factors vary, we need to add another variable, either binary or continuous, to simulate the different stages and locations.

4.2 Spatial and seasonal variation of soil CO_2 efflux

By measuring 18 spatial samples of soil CO_2 efflux over 3.5 years, we found the forest thinning changes soil CO_2 patterns by many aspects. The spatial variation of soil CO_2 efflux decreased after thinning. Intentional cutting of trees makes root distribution belowground more homogenous at this site. Clustered trees were removed. As a result, the spatial variation of soil temperature decreased due to the lack of shaded areas. Decreased variations of root distribution and soil temperature may explain the decreased spatial variation of soil CO_2 efflux.

Unlike the investigation of spatial variation, which is measured within one hour without changing soil temperature and moisture, it will be biased to directly compare the magnitude of soil CO_2 efflux before and after thinning. The reason is that we are unable to differentiate quantitatively that the difference of CO_2 efflux due to thinning is influenced by thinning or by other environmental variables such as soil temperature and moisture. Multivariate regression analysis incorporating continuous variables and categorical variables provides a tool to solve this problem.

4.3 Modeling

Eq. (6) has two continuous independent variables, soil temperature and moisture, and a categorical variable, thinning. By conducting multivariate regression after pooling data before and after thinning together we can examine the effect of thinning on soil CO_2 efflux while removing the influence from temperature and moisture. The reason why we do not conduct two separate regressions (before and after thinning) is that it is hard to statistically evaluate the difference of two regressions if coefficients are different

between two equations. This technique of multivariate analysis can be applied to evaluate other forest management practices such as the effects of clear-cutting or fertilizer treatments on soil CO_2 efflux.

The model form indicates that soil respiration will decrease after thinning in a short term if the effects of soil temperature and moisture are excluded. The model results, however, show that soil respiration slightly rises within a year after thinning. This may because that the effect of increase in soil temperature may offset or greater than that of decrease in the root respiration due to cutting. The inter-annual variation of soil temperature can be either because of thinning or just because of random fluctuation of air temperature.

4.4 Root respiration

Root or rhizosphere respiration is an important part of soil respiration. It may account for 10-90% of total soil respiration over various vegetation types and seasons of the year, with a mean value of 45.8% for forest vegetation (Hanson *et al.* 2000). The reason that thinning will decrease soil respiration in a short term is partially because of the decrease in root respiration. Our model indicates the soil respiration decreased by 13% after thinning. If the root respiration accounts for 47% of total respiration, and if 60% cutting of trees kills 60% of root respiration, the soil respiration should have been decreased by 28%. The difference between 13% and 28% may be come from the increase of microbial decomposition after thinning due to the increase in organic carbon, and also from the increase of the living root respiration rate and quantity due to the thinning.

The root respiration from un-thinned trees after thinning may increase due to the increased photosynthetic rate and growth of new roots. It has been suggested that root respiration and soil respiration may depend more on photosynthesis and vegetation productivity than on temperature (Hogberg *et al.* 2001; Janssens *et al.* 2001; Kuzyakov & Cheng 2001). Forest thinning will increase the un-thinned trees' nutrient, water, and light availability, and thus may increase photosynthesis and productivity of un-thinned trees. The increased part of carbon efflux will partially offset the loss of root respiration due to cutting.

Dead roots from cutting will also contribute more carbon efflux from soil. Chen (2000) suggested that the effect of temperature on decomposing woody roots follow exponential functions. Both by cutting roots using trenches, Bowden *et al.* (1993) suggested that root decomposition will not have influence on soil respiration 9 months after trenching, while Epron et al. (1999b) estimated that root decomposition will influence CO_2 efflux within 2 years after trenching. In our site within 1.5 years after thinning, the decomposition of dead roots may influence the total soil respiration.

4.5 Traumatic respiration

Our model does not have consistent results with measurement data during first several months after thinning. This may be because of traumatic or wound respiration. Muller (1924) originally described this phenomenon when measuring branch respiration after cutting branches from live trees. Traumatic respiration is one of the reasons that bringing cut sections of stems or branches to the laboratory and then measuring respiration is not accepted (Sprugel 1990). After thinning, the cutting of aboveground parts of plants may

stimulate belowground respiration by consuming stored carbon in large roots. The increased dead fine roots and debris due to thinning may also contribute to the abnormality of soil CO_2 efflux in a short time after thinning.

4.6 Q_{10} value

Based on Eq. (4), we can theoretically analyze Q_{10}. Q_{10}, a temperature sensitivity to soil CO_2 efflux, is defined as the increase factor when temperature is increased by 10°C (van't Hoff 1898). By definition, only using an exponential function to model CO_2 fluxes is Q_{10} a constant:

$$Q_{10} = \frac{F(T+10)}{F(T)} = \frac{b_0 e^{b_1(T+10)}}{b_0 e^{b_1 T}} = e^{10 b_1} \qquad (8)$$

Q_{10} can be a function of temperature if other functional forms, such as linear, quadratic or Arrhenius functions, are used to model flux since the temperature term cannot be cancelled when we compute Q_{10}. It has been recognized by many studies (Lloyd & Taylor 1994; Kirschbaum 1995; Thierron & Laudelout 1996) that Q_{10} value is temperature dependent. By adding another variable moisture to simulate CO_2 efflux, as we did in this study, Q_{10} becomes more complex. Holding moisture constant, Q_{10} can still be a constant if an exponential function is used to express the effect of temperature. If moisture varies when temperature is increased by 10°C, Q_{10} can be a function of moisture since the moisture term may not be removed. This has been empirically observed by Xu & Qi (2001b). In addition, Q_{10} may also vary with different ecosystem types. As we discussed before, we should add another variable to represent site effect or treatment effects. In this situation, Q_{10} may vary with this extra valuable. This is consistent with many reports that Q_{10} varies widely with ecosystem types (for example, Raich &

Schlesinger 1992; Kirschbaum 1995; Davidson *et al.* 1998). Therefore, under the consideration of multiple variables controlling soil CO_2 efflux, the value of Q_{10} varies and depends on how one treats variables other than temperature: Q_{10} may be a constant if temperature is increased while other variables are held constant; Q_{10} may vary if other variables vary correspondingly with temperature.

At our site before and after thinning, we found Q_{10} does not vary because the thinning treatment does not change the relationship of CO_2 efflux with soil temperature and moisture. If Q_{10} is computed within a day, it is a constant since there is almost no moisture variation. However, Q_{10} seasonally varies with moisture because moisture is a significant contributor to soil CO_2 efflux as well as soil temperature.

4.7 Pulse efflux

Our model does not predict some pulse values of soil CO_2 efflux in the early summer caused by tree phenology and in the fall after the first rain. Similar to the extra respiration by branches during the period of rapid shoot elongation in early growing seasons (Sprugel 1990), the pulse soil CO_2 efflux in the early summer may be contributed by high root growth respiration and photosynthate mobilization. Our current model does not consider this phenological effect on soil CO_2 efflux. To simulate more precisely phenological effect other than environmental driven factors, separating soil respiration into microbial heterotrophic respiration, root growth respiration, and root maintenance respiration is a necessity. In addition to the above pulse effect, after the first rain in the fall, CO_2 efflux may also have a pulse value due to the activation of microbes within a

short period of time (several hours), as studied firstly by Birch (1958). More studies are needed to explain this event.

5. Conclusions

Soil temperature alone cannot explain well the temporal variation of soil. Combining soil temperature and moisture explain most of the temporal variations in soil CO_2 efflux. However, soil temperature and moisture explain only part of the spatial variation of soil CO_2 efflux. The other part is determined by the constant coefficient β_0 in Eq. (4), which may be decided by soil organic matter, and root biomass and other soil properties. A thinning intensity of 60% of the trees significantly changed the microclimate in the forest and decreased the spatial variation of efflux (coefficient of variation from 31.5% to 23.9%).

By conducting multivariate regression analysis with two continuous variables and one categorical variable, we conclude that thinning does not significantly change the relationship between CO_2 efflux, soil temperature and moisture. But forest thinning statistically significantly decreases CO_2 efflux during the first 1.5 years after thinning by decreasing the constant coefficient assuming temperature and moisture do not change. In year 1999 and 2000, soil CO_2 emission was 78.41 mol m^{-2} and 78.89 mol m^{-2}, respectively. The inter-annual variation of soil efflux is small.

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Chapter 3 Separating Root Respiration from Soil Respiration in a Ponderosa Pine Plantation in the Sierra Nevada, California

Abstract

Partitioning soil respiration into autotrophic and heterotrophic respiration is of critical importance for building process-based soil carbon models since these components respond differently to abiotic and biotic drivers and have different spatial and temporal variations. To remove the influence of root autotrophic respiration from total soil respiration, we trenched a 3m × 3m plot in a ponderosa pine plantation in the Sierra Nevada. We measured soil CO_2 efflux in the trenched plot as well as in two non-trenched plots between August 2001 and October 2002. We used two bi-variable models with independent variables of soil temperature and moisture to simulate total soil respiration and heterotrophic respiration. Root respiration was computed as the difference between total soil respiration and heterotrophic respiration. We found root respiration is not only affected by environmental variables, but also by plant physiology, phenology, and photosynthesis.

The annual accumulations of total soil respiration, heterotrophic respiration, and autotrophic respiration between October 1, 2001 and September 30, 2002 were 78.2 mol m^{-2} $year^{-1}$, 52.2 mol m^{-2} $year^{-1}$, and 26.0 mol m^{-2} $year^{-1}$, respectively. Total soil respiration, heterotrophic respiration, and autotrophic respiration peaked in June. The ratio of autotrophic respiration to total soil respiration (F_a/F) is not a constant seasonally, ranging from 0.44 to 0.04 with an annual average of 0.33. In the growing seasons

between May and October F_a/F averaged 0.37 while in non-growing seasons F_a/F averaged 0.28. The spatial variation of soil respiration was mainly explained by root density per ground area. It was also influenced by soil nitrogen content and soil carbon content.

1. Introduction

Soil surface CO_2 efflux, or soil respiration, is composed of microbial heterotrophic respiration and rhizosphere respiration (including root autotrophic respiration and associated mycorrhizae respiration). The role of soil respiration as a positive or negative feedback to global warming and climate change has been widely debated (for example, Trumbore *et al.* 1996; Liski *et al.* 1999; Cox *et al.* 2000; Giardina & Ryan 2000; Kirschbaum 2000; Luo *et al.* 2001). Soil respiration is generally modeled as a function of soil temperature or a combination of soil temperature and moisture (e.g., Crill 1991; Raich & Schlesinger 1992; Davidson *et al.* 1998; Epron *et al.* 1999a; Xu & Qi 2001; Treonis *et al.* 2002). However, few reports separately model root autotrophic respiration and microbial heterotrophic respiration due to difficulty in partitioning these two components.

Partitioning soil respiration into autotrophic and heterotrophic respiration is important for building process-based models since these two components respond differently to abiotic and biotic drivers and thus demonstrate different seasonal patterns. While heterotrophic respiration may be mainly driven by soil temperature and moisture, root respiration may be closely affected by plant physiology as a part of plant autotrophic

respiration. Recently, 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 was 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. To verify these speculations and results, separately modeling root respiration and microbial decomposition and carefully examine the determinants of root respiration is a key approach.

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 published partitioning methods and results, and concluded that F_a/F varies from 10% to 90% depending on vegetation type and season of the year. They summarized partitioning methods into three categories: integration of components' biomass measurements, root exclusion methods, and isotope methods. Each method has its advantages and disadvantages.

The trenching experiment, which is one of the root exclusion methods and involves digging a plot boundary and severs existing roots, is an *in situ* experimental method to partition soil respiration. By conducting trenching experiments, Ewel et al. (1987) found the F_a/F ratio of 51% in a 9-year-old slash pine plantation and 62% in a 29-

year-old slash pine plantation. Bowden at al. (1993) compared a series of treated plots including control, no-litter, twice litter, and no root (trenched), and concluded that F_a/F is a constant proportion of 33% in a temperate mixed hardwood forest. Boone et al. (1998) compared Q_{10} values in a trenched plot with other manipulated plots in a mixed temperate forest. Epron et al. (1999b) reported F_a/F value of 60% in a beech forest by trenching experiments. By comparing four treatment plots including two trenched ones, Rey et al.(2002) reported Fa/F value of 45% in a coppice oak forest. Most of these projects did not explore the seasonal variation of root respiration and F_a/F, and none of them studied carefully how root respiration influences the spatial variation of total soil respiration.

Ponderosa pine (*Pinus ponderosa*) is the most common conifer in North America, but the contribution of roots to soil respiration is rarely studies. The exception is Xu et al. (2001), who estimated an F_a/F ratio of 47% at the same site as this chapter did based on measurements of root biomass but did not give seasonal variation of the ratio. In addition, Johnson et al. (1994) studied the effects of elevated CO_2 and N on soil CO_2 efflux and root biomass in open-top chambers planted with ponderosa pine seedlings.

This chapter aims to 1) separate heterotrophic respiration and autotrophic respiration from soil respiration using the trenching approach in a ponderosa pine plantation in the Sierra Nevada, California; 2) model the seasonal variation of heterotrophic respiration, autotrophic respiration, and F_a/F ratio; and 3) analyze the spatial variation of soil respiration with the influencing factors of root distribution, soil organic carbon content, and soil nitrogen content.

2. Materials and Methods

2.1 Site description and field measurement

The study site is in a young ponderosa pine plantation which is located adjacent to Blodgett Forest Research Station, a research forest of the University of California, Berkeley. The site is described in detail in Chapter 2.

We established two 20×20 m^2 sampling plots with 40 m between the two plots. In each plot, soil CO_2 efflux and 10cm depth of soil temperatures were measured on a 3×3 matrix spacing 10 m apart. We also monitored 0-30cm depth average of volumetric soil moisture at the center of each plot. Soil CO_2 efflux was measured using an LI6400-09 soil chamber connected to an LI-6400 portable photosynthesis system (LI-COR, Inc. Lincoln, NE) for data collection and storage. A soil collar, with a height of 4.4 cm and a diameter of 11 cm, was permanently inserted into the soil at each sampling point. We used custom-built thermocouple sensors to monitor soil temperature, and time domain reflectometry (TDR, CS615 Campbell Scientific, Inc., Logan, UT) to monitor volumetric soil moisture. Thermocouple sensors and TDR are connected to dataloggers (CR10X and 23X, Campbell Scientific, Inc.). The dataloggers are programmed to store output data every 5 minutes.

To analyze spatial information of the study site, a set of 1:8000 aerial photos was taken in May 2000. After the aerial photos were developed, they were scanned with 1000 dpi resulting in an actual spatial resolution of 20.32 cm on the ground. Fig. 3.1 is a cutting from the aerial photos illustrating the plantation and two sampling plots. The white circles in Fig. 3.1 indicate CO_2 efflux sampling locations. The image and location feature were produced by the GIS package Arcview 3.2 (ESRI, Inc., CA).

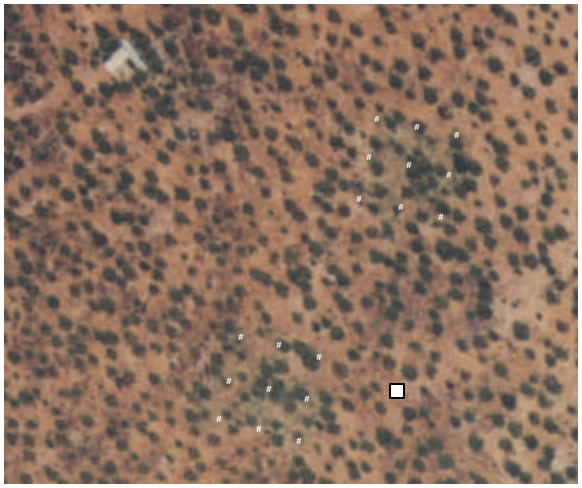

Fig. 3.1 Aerial photo of the study site with a resolution of 20.32 cm and scale of 1: 2000. 18 white circles indicate sampling locations of soil CO_2 efflux (two 20 m by 20m plots); the white square indicates the trenching plot (3m by 3 m). All dark gray areas are trees. The original image is in color.

The measurement of soil CO_2 efflux started in June 1998. This chapter covers data from May 2000 to October 2002. Soil CO_2 efflux measurement was normally conducted once (1-2 days) every month except for the winters when snow covered the ground. We had 3-5 measurements for each sampling location within one day when we conducted soil CO_2 efflux measurement.

2.2 Trenching

We selected a relatively open space and established a new small plot of 3 m × 3 m about 20 m from one of the 20m × 20m plots on July 2, 2001. A white square in Fig. 3.1 indicates the trenched plot. There was no tree inside the plot. We dug a trench 0.2 m wide and 1.2 m deep around the plot. After lining the trench with polyethylene sheets we refilled the soil back to the trench according to its original soil profiles as undisturbed as possible. The trenching cut down most of live roots that extended into the plot. The plot was further kept free of seedlings and herbaceous vegetation. Thus we assumed there were no root influences within this plot when we measured soil respiration. We installed two soil collars, two soil thermocouple sensors and a moisture sensor (TDR) for measuring soil respiration, soil temperature and moisture. The spatial average of two soil respiration readings was used to represent the soil respiration in the trenched plot at a certain time, which is only composed of heterotrophic respiration from microorganisms.

2.3 Data analysis and model building

Soil CO_2 efflux and its temporal variation were investigated in each plot. The spatial variation of 18 samples from non-trenched plots was analyzed. We selected a bi-variable

model with variables, soil temperature and moisture, to simulate temporal variation of soil CO_2 efflux. The coefficients of the model were estimated by conducting multivariate regression analysis. The model has a form as Eq. (1).

$$F = b_1 e^{b_2 T} e^{b_3 M + b_4 M^2},$$
$$\text{or} \qquad \ln(F) = \ln(b_1) + b_2 T + b_3 M + b_4 M^2, \qquad (1)$$

where F ($\mu molm^{-2}s^{-1}$) is the soil CO_2 efflux, T (°C) is the soil temperature at 10cm depth, M (%) is the soil volumetric moisture at 0-30cm average, and β_0, β_1, β_2, and β_3 are coefficients. The model can be log-transformed to a linear model. Regression was conducted using the spreadsheet software Excel 2000 (Microsoft Corporation).

Eq. (1) was used to model both total soil respiration and heterotrophic respiration after we estimated the constant coefficients. The measurement data from two 20m × 20m plots was used to estimate the coefficients for the total soil respiration model; the data from the 3m × 3m trenched plot was used to fit the coefficients for heterotrophic respiration.

We did not directly measure autotrophic respiration. We estimated autotrophic respiration by subtracting soil respiration from heterotrophic respiration shown in Eq. (2):

$$F_a = F - F_h = b_1 e^{b_2 T} e^{b_3 M + b_4 M^2} - b_5 e^{b_6 T} e^{b_7 M + b_8 M^2}, \qquad (2)$$

where F ($\mu molm^{-2}s^{-1}$) is the soil CO_2 efflux, F_a ($\mu molm^{-2}s^{-1}$) is the autotrophic respiration, F_h ($\mu molm^{-2}s^{-1}$) is the heterotrophic respiration, T (°C) is the soil temperature at 10cm depth, M (%) is the soil volumetric moisture at 0-30cm average, β_1, β_2, β_3, and β_4 are

model coefficients estimated from the non-trenched data, and β_5, β_6, β_7, and β_8 are model coefficients estimated from the trenched data.

Soil respiration has a significant spatial variation. We used Eq. (1) to simulate the mean soil respiration and temporal variation but not spatial difference. To analyze the spatial variation of soil respiration, we compared the modeled mean soil respiration with each spatial sample (measurement). The ratio of the spatial measurement value to the modeled mean value is called the spatial index of soil respiration. At a certain time, the spatial index at each spatial location is calculated as

$$\text{Spatial index} = \text{measured respiration} / \text{modeled mean respiration} \quad (3)$$

When calculating the above ratio, we removed the temperature and moisture factors since the temperature and moisture data for the measured respiration data are the same as we used to drive the respiration model. Thus, any difference between the measured respiration and modeled mean respiration is due to root distribution or other factors rather than temperature and moisture. Therefore, Eq. (3) allows us to analyze the spatial variation of soil respiration. The spatial index, or indicator of spatial heterogeneity of soil respiration is mainly produced by root distribution, the random error from sampling, soil organic carbon, and soil nitrogen content.

To explore the influence of roots on spatial variation of soil respiration, we analyzed relationship between sample locations and their distances from trees. We assumed the root distribution is a circle radiating from the center where the tree bole is located. The influence of trees is inversely related to closeness to the circle center. For

each sample location (of the collar), the total influence from trees is the accumulation of influence from each tree, or called accumulation of root density per area, D. D is computed by

$$D = \sum_{i}^{n} \frac{1}{p r_i^2}, \qquad (4)$$

where D is the accumulated root density (m^{-2}) at a particular location, r_i is the distance of the ith tree from the collar (m), n is the total number of trees which are fewer than 5m away from the collar. Here we assumed that a tree more than 5m away from the sample location has no influence on soil respiration from this location. The distance r_i was measured by Arcview software (ESRI, Inc., CA) after measurement collars were located in the image file. The results from image analysis were verified by field measurements.

We explored the correlation between spatial index of soil respiration at each location and root density D. We also analyzed the correlation between spatial index and soil organic carbon content, and between spatial index and soil nitrogen content.

3. Results

3.1 Measurements of soil respiration and heterotrophic respiration

Based on the field measurement of all samples in non-trenched plots and a trenched plot, we averaged spatial samples of both the non-trenched plots and trenched plot, and calculated the daily mean values. CO_2 efflux in the non-trenched plots is from total soil respiration; CO_2 efflux in the trenched plot is from heterotrophic respiration; and the difference from above is autotrophic respiration. Fig. 3.2 shows measurements of the variation of total soil respiration (F), heterotrophic respiration (F_h), autotrophic

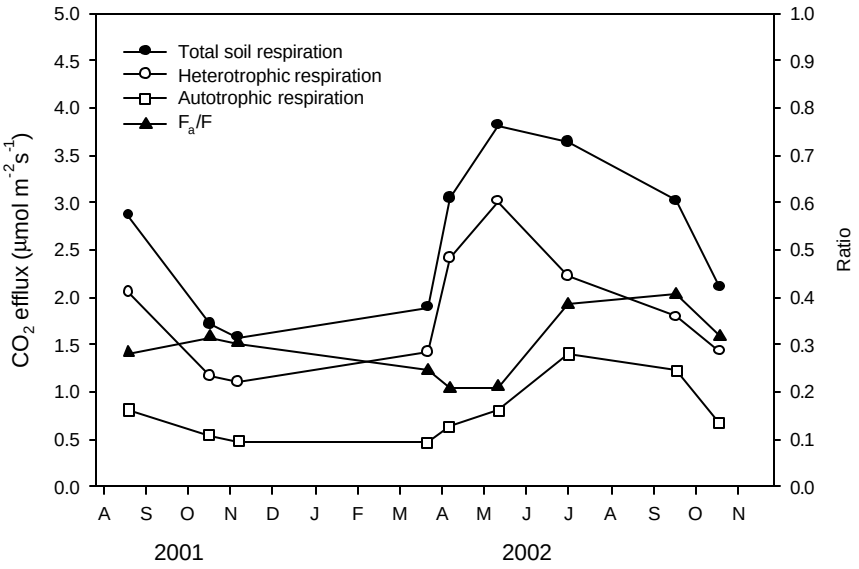

Fig. 3.2 Measurements of total soil respiration (F), heterotrophic respiration (F_h), autotrophic respiration (F_a), and ratio of autotrophic respiration to total respiration (F_a/F) between August 24 (day 236), 2001 and October 23 (day 296), 2002.

respiration (F_a), and ratio of F_a/F between August 24 (day 236), 2001 and October 23 (day 296), 2002.

Daily mean soil respiration peaked in May-June at about 3.8 $\mu molm^{-2}s^{-1}$, and then decreased to 1.6 $\mu molm^{-2}s^{-1}$ in the winter. Soil heterotrophic respiration had a similar seasonal variation, peaking in the early summer at about 3.0 $\mu molm^{-2}s^{-1}$ and going down to 1.1 $\mu molm^{-2}s^{-1}$ in the winter. The difference between soil respiration and heterotrophic respiration is estimated autotrophic respiration. Autotrophic respiration peaked in June-July, later than total soil respiration and heterotrophic respiration, at 1.4 $\mu molm^{-2}s^{-1}$ and decreased to the winter at 0.67 $\mu molm^{-2}s^{-1}$. The ratio of autotrophic respiration to total respiration varied, ranging from 0.21 to 0.41. In April and May, the ratio decreased compared with other months. This may be due to the significant increase in heterotrophic respiration and thus relatively low root respiration during this period.

3.2 Modeling total soil respiration, heterotrophic respiration and autotrophic respiration

In order to see the continuous seasonal patterns of soil respiration, we used Eq. (1) to simulate (interpolate) total soil respiration and heterotrophic respiration based on measurement data and regression analysis. We averaged 18 spatial samples to represent soil respiration within a certain time (less than an hour) and conducted multivariate regression against temperature and moisture over the course of time. Eq. (5) is the regression result for modeling total soil respiration between August 2001 and October 2002.

$$F = 0.261\, e^{0.0334T} e^{0.215M - 0.00515M^2}$$

$$R^2=0.67,\ p<0.001,\ n=82, \qquad (5)$$

where F is the total soil respiration ($\mu molm^{-2}s^{-1}$), T is the soil temperature (°C), and M is the soil volumetric moisture (%)

Eq. (5) indicates that soil respiration exponentially increases with soil temperature. Holding soil moisture constant, the temperature sensitivity of soil respiration (Q_{10}) is 1.40. Soil respiration varies with moisture in two directions. From the quadratic form of the moisture term we can compute the maximum value of soil respiration. The results show that when moisture is less than 20.8%, soil respiration increases with moisture; when moisture is greater than 20.8%, soil respiration decrease with further increase in moisture.

Because there is no root influence on CO_2 measurement in the trenched plot, we assumed the heterotrophic respiration is spatially homogeneous. By conducting multivariate regression, we estimated the parameters for Eq. (1) in the trenched plot.

$$F_h = 0.206\, e^{0.0427T} e^{0.156M - 0.00320M^2},$$

$$R^2 = 0.68,\ p<0.001,\ n = 24, \qquad (6)$$

where F_h is the heterotrophic respiration ($\mu molm^{-2}s^{-1}$), T is the soil temperature (°C), and M is the soil volumetric moisture (%).

Eq. (6) indicates that soil heterotrophic respiration exponentially increases with soil temperature. Holding soil moisture constant, the temperature sensitivity of heterotrophic respiration (Q_{10}) is 1.53. Heterotrophic respiration varied with moisture in two directions. When moisture is less than 24.3%, soil respiration increases with moisture; when moisture is greater than 24.3%, soil respiration decrease with further increase in moisture.

Autotrophic respiration is the difference between total soil respiration and heterotrophic respiration:

$$F_a = 0.261\, e^{0.0334T} e^{0.215M - 0.00515M^2} - 0.206\, e^{0.0427T} e^{0.156M - 0.00320M^2} \qquad (7)$$

where F_a is the autotrophic respiration ($\mu molm^{-2}s^{-1}$), T is the soil temperature (°C), and M is the soil volumetric moisture (%).

3.3 Seasonal variation of soil respiration

We estimated soil respiration, heterotrophic respiration, and autotrophic respiration between October 1, 2001 and September 30, 2002 (Fig. 3.3). Fig. 3.3a indicates the variations of daily mean soil temperature and moisture; Fig. 3.3b is the temporal patterns of total soil respiration, heterotrophic respiration, and autotrophic respiration; and Fig. 3.3c is the variation of the ratio of autotrophic respiration to total respiration (F_a/F). Daily mean soil temperature at 10cm depth ranged between 0.69°C and 21.3°C with an annual average 9.80°C. Soil temperature was lowest in December to March, and peaked in July. In April through June 2002, soil temperature changed significantly. Soil moisture (at 0-30cm average) ranged between 9.27% and 33.3% with an average of 21.1%. Soil moisture increased rapidly in November from about 10% to 25% after the first rain in the winter, and varied between December to May due to raining, snow cover and snow melting, and peaked at 33.3%. After June, soil moisture decreased stably from about 30% to 10% in the summer until the first rain.

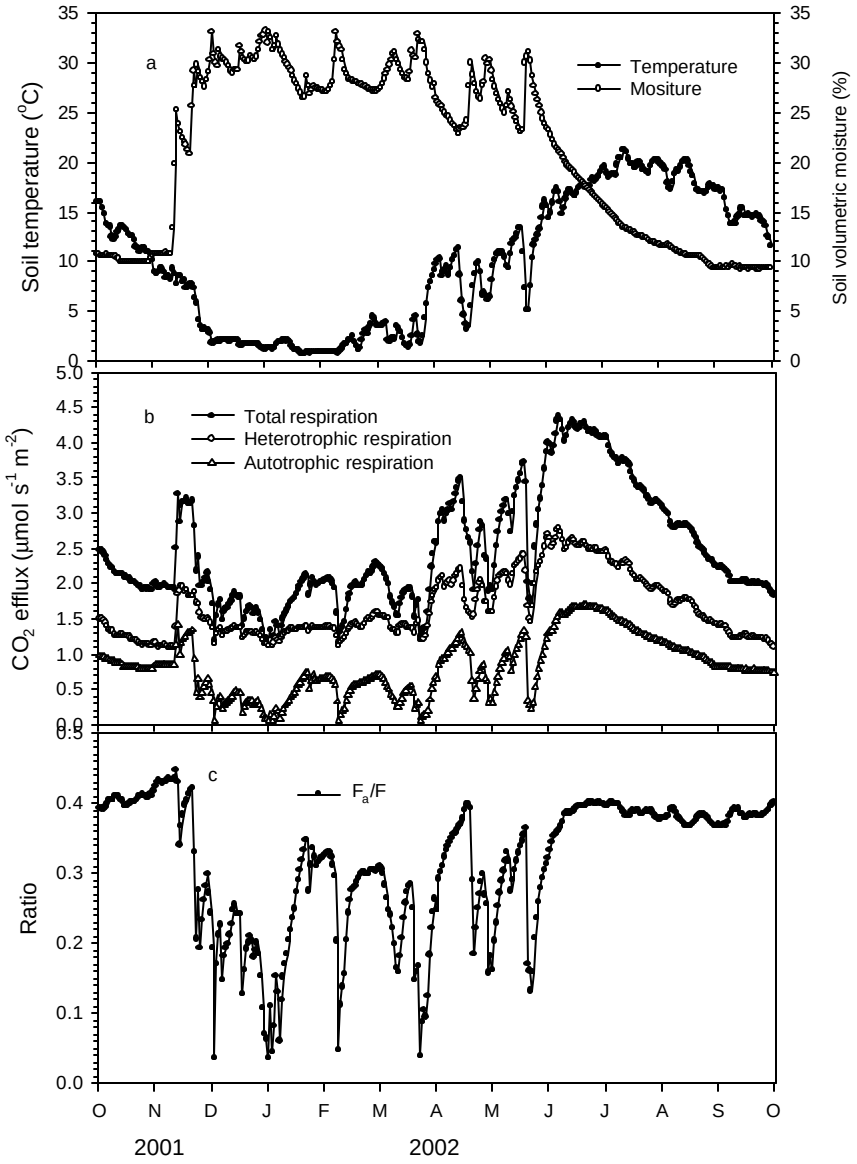

Fig. 3.3 Seasonal patterns of soil temperature (T), moisture (M), soil respiration (F), heterotrophic respiration (F_h), autotrophic respiration (F_a), and ratio F_a/F between October 1, 2001 and September 30, 2002. a. Daily mean T and M; b. modeled F, F_h and F_a; c. F_a/F ratio.

Soil respiration varied correspondingly with the variation of soil temperature and moisture. Total soil respiration, heterotrophic respiration, and autotrophic respiration peaked in June when moisture was decreasing while temperature was increasing. In the early summer, both of these two variables are not constraints to soil respiration. Thus soil respiration has the maximum. In the late summer, moisture is the stress to soil respiration while in the winter temperature is the constraint. Three respiration curves varied significantly between December and May and stably declined between July and November. Total soil respiration ranged between 1.15 $\mu molm^{-2}s^{-1}$ and 4.36 $\mu molm^{-2}s^{-1}$; heterotrophic respiration ranged between 1.09 $\mu molm^{-2}s^{-1}$ and 2.79 $\mu molm^{-2}s^{-1}$; autotrophic respiration maximized at 1.69 $\mu molm^{-2}s^{-1}$ and minimized to close to 0. The annual accumulations of total soil respiration, heterotrophic respiration, and autotrophic respiration were 78.2 $molm^{-2}$ $year^{-1}$, 52.2 $molm^{-2}$ $year^{-1}$, and 26.0 $molm^{-2}$ $year^{-1}$, respectively.

The ratio of autotrophic respiration to total soil respiration (F_a/F) is not a constant seasonally. It ranged from 0.44 to 0.04. The mean ratio based on accumulation of autotrophic respiration divided by total soil respiration within a year is 0.33. F_a/F varied significantly between November and June but was relatively a constant at about 0.39 between July and November when both total soil respiration and autotrophic respiration declined stably. The extreme low values of F_a/F happened when there were some anomalous events such as sudden increase in soil moisture due to the rain after a long dry or sudden decrease in soil temperature due to rapidly decreasing air temperature. In the growing seasons between May and October F_a/F averaged 0.37 while in non-growing seasons F_a/F averaged 0.28.

3.4 Influencing factors of spatial variation of soil respiration

To analyze the spatial variation of soil respiration, we compared the modeled mean soil respiration with each spatial sample, and calculated spatial index of soil respiration (Eq.3). We explored the correlation between the index and its influencing factors such as root density per ground area (Eq. 4), soil organic carbon content, and soil nitrogen content of each sample location. Table 3.1 shows the above factors from 18 sample locations and R^2 with the spatial index (I). Each location's index is the mean value over the period between May 2000 and October 2002.

Table 3.1 indicates that R^2 between the spatial index and root density was 0.49, greater than that between the index and nitrogen content (0.37), and between the index and carbon content (0.25). We further plotted the index values against D (Fig. 3.4). A linear line is fitted to the plot. This means that the spatial index has a linear relationship with D. In another word, spatially soil respiration linearly increases with root density; closer to trees, more respiration from the soil surface.

Table 3.1 18 samples of spatial index of soil respiration (I), accumulated root density per area (D), organic carbon (C), total nitrogen content (N), and correlation between I and D, I and C, and I and N.

Sample #	I	D (m^{-2})	C (%)	N (%)
1	1.299	0.390	4.12	0.32
2	0.794	0.071	3.28	0.20
3	0.995	0.063	3.56	0.22
4	1.333	0.932	4.31	0.27
5	0.959	0.238	4.69	0.27
6	1.202	0.444	2.75	0.19
7	1.287	0.441	5.00	0.47
8	0.753	0.134	2.46	0.18
9	1.108	0.199	4.29	0.25
10	0.929	0.096	1.31	0.07
11	0.997	0.500	1.66	0.09
12	1.145	0.442	6.00	0.34
13	0.906	0.245	4.05	0.20
14	1.258	0.187	4.76	0.27
15	1.284	0.400	3.21	0.22
16	0.923	0.154	2.80	0.17
17	0.762	0.180	1.40	0.10
18	0.731	0.058	3.74	0.20
R^2 with I	--	0.49	0.25	0.37

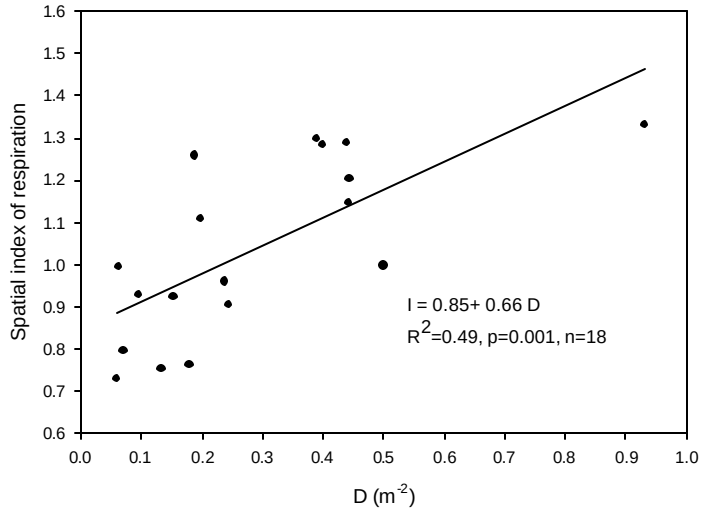

Fig. 3.4 Relationship between spatial index of soil respiration (I) and root density per ground area (D).

4. Discussion

4.1 Modeling autotrophic respiration

We used the equation form as Eq. (1) to estimate total soil respiration and heterotrophic respiration, but not autotrophic respiration. Autotrophic respiration was indirectly estimated by the difference between total soil respiration and heterotrophic respiration. Directly fitting an autotrophic respiration model using our measurement data is not feasible. This may be because root respiration, sourced from plant's production, is controlled by physiological and phenological factors in addition to soil temperature and moisture. The reason that we are still able to calculate root respiration (Eq. 2) may be because these biotic factors are correlated to some extent with environmental variables. For example, the response of root respiration to high soil temperature may be not only due to high respiratory rate per unit of root under high temperature, but also due to coincidence of high temperature with high density or total biomass of root (Rey *et al.* 2002). The ecophysiological factors on root respiration have been studied by several workers (Craine *et al.* 1999; Hogberg *et al.* 2001; Janssens *et al.* 2001; Kuzyakov & Cheng 2001), who concluded that photosynthesis and other ecophysiological factors are determinants to root respiration and soil respiration. It is possible for us to quantify the physiological factors using environmental variables if they are correlated.

Fig. 3.3b shows large variability of total soil respiration, heterotrophic respiration, and autotrophic respiration between November and June; total respiration and autotrophic respiration varied more significantly than heterotrophic respiration during this period. The variability of respiration in the wet season could be explained by the Mediterranean climate characteristics. Rapid change of temperature and moisture drive the variation of

respiration. Especially, the pulse increase in soil respiration in November was caused by the first rain after the long summer dry, as was observed initially by Birch (1958) and Griffiths and Birch (1961). The reason for more variability of autotrophic respiration than heterotrophic respiration may be due to physiology and phenology combined with temperature and moisture. In April to June, proliferation of shoots and fine roots in the early growing season may cause the large variation of root respiration, which peaked in June. This result is consistent with some previous work (e.g. Dickmann *et al.* 1996; Zogg *et al.* 1996).

4.2 Variation of F_a/F

Our results show that the ratio of autotrophic to total respiration is not a constant over the season. F_a/F varies greatly between November and June and keeps approximately constant after June (Fig. 3.3c). The significant variation between November and June may be due to the sudden changes of soil temperature and moisture (Fig. 3.3a) during this period. It may be also from effect of snowpack, which change the soil porosity and water and air contents. In winter time the depth of snow does not stably increase at this site; the snowpack will melt and reduce the depth in a warm day, and accumulate again when new snow fall. Between June and November, F_a/F is stable mainly due to the stable soil moisture. The average of F_a/F in growing seasons is calculated as 0.37, greater than that in non-growing seasons (0.28). Our result supports the review conclusion by Hanson at al. (2000). Because of seasonality of physiological, phonological, and environmental factors, it is important to characterize the seasonal variation of F_a/F, as is emphasized by

Hanson at al. (2000). It will be biased if using a constant F_a/F to partition soil respiration over seasons.

Spatial variation of F_a/F should also be addressed since root distribution is often not spatially homogeneous. F_a/F will also be influenced by ecosystem type, tree species, age, and density if we want to compare different stages or different ecosystems. We have pointed out a spatial correlation between soil respiration and root density. This may indicate that F_a/F is also correlated with root density. A previous study (Xu *et al.* 2001) estimated a constant F_a/F ratio of 0.47 at this site in the growing season of 1998. Our result does not contradict that study because although the mean DBH increased from 7.6cm in 1998 to 16.0cm in 2002, the density was decreased from 1213 stems/hectare to 378 stems/hectare due to a thinning in 2000. More than 2/3 loss of trees caused corresponding decrease in root density and F_a/F. With growth of trees and expanding of roots, F_a/F may increase again in this young plantation after the thinning until reaching a steady state. Further studies in F_a/F dynamics and spatial influencing factors such as stem density and vegetation type are suggested.

4.3 Spatial variation of soil respiration

Table 3.1 tells us that root density is the major determinant to the spatial variation of soil respiration and root respiration, more important than organic carbon content and nitrogen content. Woody debris and litter are scattered on the floor of this site due to the previous harvesting (clear-cutting) and a pre-commercial thinning. Thus carbon and nitrogen may not be constraints for soil respiration, and environmental variables and plant physiology are major determinants. When we analyze the spatial index of soil respiration, which is

mainly from the variation of root respiration, temperature and moisture factors are removed. Thus root density becomes the major dependent variable.

We used Eq. (4) to compute indirectly the root density assuming a horizontal radiation shape of root distribution. We did not consider the vertical variation of root distribution since the plantation is even-aged and assumed a vertically homogeneous root pattern. For uneven-aged forests with different vertical patterns of roots, we need to consider the vertical root distribution if we are to study the root contribution from a tree to total soil respiration. Gale and Grigal (1987) provided a model for computing vertical root distribution:

$$Y = 1 - b^{d} \qquad (8)$$

where Y is the cumulative root fraction (a proportion between 0 and 1) from the soil surface to depth d (cm), and β is the fitted parameter for a specific biome. Jackson et al. (1996) synthesized literature and gave a β of 0.976 for temperate coniferous forests.

The linear equation (Eq. 9) fitted from the spatial index of soil respiration against root density could be extended to model soil respiration with different root distribution:

$$I = \frac{F}{F_{model}} = 0.847 + 0.661D \qquad (9)$$

where I is the spatial index of soil respiration, F is soil respiration, F_{model} is the modeled soil respiration by Eq. (5), and D is root density computed by Eq. (4).

Eq. (9) quantified the root influence on soil respiration. When D=0, or when roots do not exist, soil respiration (heterotrophic respiration) is 85% of standard total soil respiration. This result is different from our measurement results, which indicates an average ratio of 0.67 for F_h/F, and 0.33 for F_a/F. This difference may be explained by the rhizosphere effect. Eq. (9) has included the effect from both root autotrophic respiration and associated mycorrhizae respiration. It may not be applied to sole heterotrophic respiration when D=0. The intercept, 0.85, may include mycorrhizae respiration. Thus the intercept is greater than the sole heterotrophic respiration when D=0.

4.4 Residue of roots in the trenched plot

It has been concerned that the residue of fine roots in the trenched plot may influence the measurement since we assumed the trenched plot only includes microbial decomposition (Epron *et al.* 1999b). Ewel et al. (1987) started to collect data 4 months after trenching. Bowden et al. (1993) allowed 9 months after trenching to pass before measurements, but they estimated that fine root influence would be small 4 months after trenching. We started measurements about 2 months after trenching and assumed the residue influence is negligible. There are two reasons for this. First, our trenched plot is in an open area (gap) of the site, which is a relatively sparse and unclosed young plantation. Thus the appearance of fine roots in the trenched plot is very little. This was supported by Brumme (1995), who estimated root respiration as the difference between soil respiration from a rooted mature stand and from a forest gap. Second, soil organic carbon content and humus quantity are high in this site; the small amount of dead fine roots that may increase the carbon content in the trenched plot could be negligible.

5. Conclusions

We compared soil respiration from non-trenched plots and a trenched plot in a young plantation. The difference was explained by root respiration. A bi-variable model (Eq. 1) with independent variables of soil temperature and moisture well fitted measurement data of soil respiration and heterotrophic respiration, and then we are also able to estimate root respiration as the difference between total soil respiration and heterotrophic respiration. Root respiration is affected by plant physiology, phenology, and photosynthesis, as well as environmental variables.

The annual accumulations of total soil respiration, heterotrophic respiration, and autotrophic respiration between October 1, 2001 and September 30, 2002 were 78.2 mol m^{-2} $year^{-1}$, 52.2 $molm^{-2}$ $year^{-1}$, and 26.0 $molm^{-2}$ $year^{-1}$, respectively. Total soil respiration, heterotrophic respiration, and autotrophic respiration peaked around min-June at the intersection of the temperature and moisture curves. Total soil respiration ranged between 1.15 $\mu molm^{-2}s^{-1}$ and 4.36 $\mu molm^{-2}s^{-1}$; heterotrophic respiration ranged between 1.09 $\mu molm^{-2}s^{-1}$ and 2.79 $\mu molm^{-2}s^{-1}$; autotrophic respiration reached a maximum at 1.69 $\mu molm^{-2}s^{-1}$ and a minimum close to 0.

The ratio of autotrophic respiration to total soil respiration (F_a/F) is not a constant seasonally. It ranged from 0.44 to 0.04. The mean ratio based on accumulation of autotrophic respiration divided by total soil respiration within a year is 0.33. In the growing seasons between May and October F_a/F averaged 0.37 while in non-growing seasons F_a/F averaged 0.28.

Aerial photos, image analysis, and GIS provide a useful tool to study the spatial variation of soil respiration. The spatial variation of soil respiration was mainly explained by root density per ground area, which is measured by the inverse of squared distance between sample locations and tree locations (Eq. 4). The variance explained (R^2) between the variation of soil respiration, measured by spatial index of soil respiration (Eq. 3), and root density was 0.49, greater than that between the index and nitrogen content (0.37), and between the index and carbon content (0.25). The spatial index value linearly responds to the change of root density.

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Chapter 4 Comparing Soil Respiration in a Young and a Mature Coniferous Plantation in the Sierra Nevada, California

Abstract

The study of site differences in soil respiration is important for extrapolating from small scales to large scales. We used bi-variable models including variables of soil temperature and moisture to compare the soil respiration between a young and a mature forest plantation. Driven by two datasets of soil temperature and moisture from two sites, the model results indicated that the annual accumulations of soil respiration between October 1, 2001 and September 30, 2002 in the young plantation and mature plantation were 78.2 mol $m^{-2}year^{-1}$ and 77.0 mol $m^{-2}year^{-1}$, respectively. The averages of daily mean soil temperature over the year were 9.8°C in the young plantation and 8.8°C in the mature one. When we used the averaged temperature and moisture over two sites to drive the day-to-day variation of soil respiration, we found the annual accumulations of soil respiration in the young plantation and mature plantation were 69.8 mol $m^{-2}year^{-1}$ and 84.9 mol $m^{-2}year^{-1}$, respectively. In the mature plantation soil respiration was 1.22 times greater than that in the young plantation, mainly due to more root density in the mature plantation.

We developed a general model incorporating soil temperature, moisture, stand density, and tree size to investigate the spatial variation of soil respiration at different sites. The model well explained the difference of soil respiration between the young and mature plantation. It also explained the difference of soil respiration due to the impact of

forest management such as thinning. Thus, we expect to use this model to simulate soil respiration from different forest stands and to analyze soil carbon dynamics as well as spatial variation.

1. Introduction

Soil carbon has been extensively studied because of the huge soil carbon pool in terrestrial ecosystems (Houghton *et al.* 2001), the large quantity of soil carbon fluxes (Raich & Schlesinger 1992; Raich & Potter 1995; Raich *et al.* 2002), and its sensitivity to environmental conditions. It is still uncertain whether or not soil carbon will exert a positive feedback to global warming (for example, Jenkinson *et al.* 1991; Kirschbaum 1995; Trumbore *et al.* 1996; Liski *et al.* 1999; Cox *et al.* 2000; Giardina & Ryan 2000; Kirschbaum 2000; Luo *et al.* 2001). To advance the understanding of this uncertainty, sound soil carbon models that are able to explain the temporal and spatial variability are critical.

Workers on soil carbon have been modeling temporal variation of soil respiration by using temperature, moisture and other variables. Extensively-used chamber-based measurements (for example, Meyer *et al.* 1987; Nakayama & Kimball 1988; Naganawa *et al.* 1989; Norman *et al.* 1992) and under-story eddy covariance techniques (Baldocchi & Meyers 1991; Law *et al.* 1999) provide parameterization necessary for soil carbon models. However, due to limitations of instrumentation and methods there are relatively few adequate studies on spatial variation of soil respiration compared to those on temporal variation. Hanson at al. (2000) documented the spatial variability of forest floor

respiration by investigating the cause from topographically distinct locations. Goulden at al. (1996) described considerable heterogeneity of soil respiration. Rayment & Jarvis (2000) studied spatial variation of soil respiration in a Canadian boreal forest and correlated spatial variation empirically with the thickness of the dead moss layer. Recently, Shibistova at al. (2002) reported the difference of soil CO_2 efflux measured by chambers and by eddy covariance techniques, and concluded that the spatial variability may be related to root density. However, most of these studies on spatial patterns are descriptive, without quantitative analysis.

Currently there is no applicable method to directly measure spatial variation of soil respiration. Eddy covariance techniques record continuous but integrative carbon fluxes representing the average from the ground. Though chamber-based measurements allow us to characterize the spatial variation of soil CO_2 efflux (Law *et al.* 1999), these measurements only provide point data without spatial continuums. As a result, soil carbon models rarely simulate the site difference, which makes spatial extrapolation from small scale to large scale difficult. Thus, ecosystem modelers often simulate global soil carbon efflux based on a simple Q_{10} function (for example, Raich *et al.* 1991; Potter *et al.* 1993) together with soil moisture/precipitation without distinguishing site differences.

An alternative to study the spatial variation of soil respiration is to review the literature from various sites. Raich at al. (2002) synthesized published reports and estimated inter-annual variability in global soil respiration with parameters of air temperature and precipitation following a regression-based model; they incorporated inter-site variability into environmental variables. Raich & Tufekcioglu (2000) reviewed the literature and examined the correlation between vegetation type and soil respiration,

but they did not explore in depth the relationship between soil respiration and site characters such as the density and age.

This study explores temporal and spatial variation of soil respiration by comparing a young plantation and mature plantation. A general model incorporating soil temperature, moisture, stand density, and tree size is developed to investigate the spatial variation of soil respiration at different sites. The model is validated by other independently estimated results.

2. Materials and methods

2.1 Site description

We established two adjacent study sites of a young ponderosa pine plantation and a mature mixed conifer forest with about 100m of distance between each other. The young plantation (located 38°53'43"N, 120°37'58"W, 1315m) is a part of the Ameriflux networks, adjacent to Blodgett Forest Research Station, a research forest of the University of California, Berkeley. The plantation, planted after a clearcut of the mature forest in 1990, was dominated by 11-12 year old ponderosa pine (*Pinus ponderosa*) in 2002. Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), giant sequoia (*Sequoiadendron giganteum*), and California black oak (*Quercus kelloggii*) are occasionally seen in the overstory canopy. In 2002 the plantation had an average diameter at breast height (DBH) of 16.0 cm, an average height (DBH > 3 cm) of 6.5 m, and a density (DBH > 3 cm) of 378 stems/hectare. The major shrubs are manzanita (*Arctostaphylos* spp.) and *Ceonothus* spp.

The mature mixed conifer plantation with a closed canopy was adjacent to the young plantation. The majority of trees were planted in 1913-1915. Some succeeding conifers grew naturally in the gap. The site had an average tree height of 22 m, an average DBH of 37.0 cm, and a similar density (382 stems/hectare) to the young plantation in 2002. Dominant species were Douglas fir (*Psedotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), and incense cedar (*Calocedrus decurrens*). Understory shrubs are scare.

Both sites are characterized by a Mediterranean climate with a hot and dry summer, and a cool and wet winter. The majority of precipitation, averaged 1660mm since 1961, falls between September and May with almost no rain in the summer. The winter has an average of 254 cm snow. The average minimum daily temperature in January over the recent 30 years was 0.6°C and the average maximum daily temperature in July was 28.3°C.

Both sites are relatively flat with slopes less than 3 degrees in our sampling areas. The soil is a fine-loamy, mixed, mesic, ultic haploxeralf in the Cohasset series whose parent material was andesitic lahar. It is relatively uniform and dominated by loam and sandy-loam with sand of 60%, silt of 29%, and clay of 11% at both sites measured in 2002. Coarse woody debris is scattered on the forest floor from the residuals of previous harvesting and thinning. Stubs from last harvest still exist at both sites. Both sites have the similar soil chemical properties with an average pH value of 5.5, organic matter of 6.1%, organic carbon 3.5%, and total nitrogen of 0.22% in 2002.

2.2 Field measurements

In the young plantation we established two 20×20 m^2 sampling plots with 40 m between the two plots. In each plot, soil CO_2 efflux and 10cm depth of soil temperatures were measured on a 3×3 matrix spacing 10 m apart. Totally we had 18 spatial samples. We also monitored 0-30cm depth average of volumetric soil moisture at the center of each plot. In the mature plantation we randomly set 7 sampling locations for measurements of soil CO_2 efflux and 10cm depth of soil temperature. Each location had different distance from the stub of trees. We selected one location for measuring 0-30cm depth of volumetric soil moisture.

Soil CO_2 efflux was measured using an LI6400-09 soil chamber connected to an LI-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE) for data collection and storage. A soil collar, with a height of 4.4 cm and a diameter of 11 cm, was permanently inserted into the soil at each sampling point. We used custom-built thermocouple sensors to monitor soil temperature, and time domain reflectometry (TDR, CS615 Campbell Scientific, Inc., Logan, UT) to monitor volumetric soil moisture. Thermocouple sensors and TDR are connected to dataloggers (CR10X and 23X, Campbell Scientific, Inc.). The dataloggers are programmed to store output data every 5 minutes.

The measurement of soil CO_2 efflux started in June 1998. This chapter covers data from July 2001 to October 2002. Soil CO_2 efflux measurement was normally conducted once (1-2 days) every month except for the winters when snow covered the ground. We had 3-5 measurements for each sampling location within one day when we conducted soil CO_2 efflux measurement.

2.3 Modeling temporal patterns of soil respiration

Soil CO_2 efflux and its temporal variation were investigated and compared between two sites. We built models with two variables, soil temperature and moisture, to simulate temporal variation of soil CO_2 efflux (Eq. 1).

$$F = b_1 e^{b_2 T} e^{b_3 M + b_4 M^2},$$

$$\text{or} \qquad \ln(F) = \ln(b_1) + b_2 T + b_3 M + b_4 M^2, \qquad (1)$$

where F ($\mu molm^{-2}s^{-1}$) is the soil CO_2 efflux, T (°C) is the soil temperature at 10cm depth, M (%) is the soil volumetric moisture at 0-30cm average, and β_0, β_1, β_2, and β_3 are model coefficients. The model can be log-transformed to a linear model. Regression was conducted using the spreadsheet software Excel 2000 (Microsoft Corporation). The spatial averages of measurement data during a round of measurement (no more than an hour) from both the young plantation and mature plantation were used to estimate the parameters for the soil respiration model from the young and mature sites, respectively.

To compare the difference of soil respiration between the young plantation and mature plantation over the course of a year, we calculated soil respiration at both sites by applying Eq. (1). The averages of daily mean temperature and daily mean soil moisture at two sites were used to drive two models from two sites with the same form but different parameters. Thus we were able to analyze the difference between two sites by normalizing the temperature and moisture factors.

2.4 Modeling spatial difference at two sites

By analyzing the spatial variation of soil respiration, Chapter 3 presented an equation for quantifying the influence of roots on soil respiration (Eq. 2)

$$\frac{F}{F_r} = 0.847 + 0.661D \qquad (2)$$

where F is soil respiration with a certain root density, F_r is the reference (modeled) soil respiration at the young plantation with a form of Eq. (3), and D is the root density at any spatial point computed by Eq. (4).

$$F_r = 0.261\, e^{0.0334T} e^{0.215M - 0.00515M^2}, \qquad (3)$$

$$D = \sum_i^n \frac{1}{p\, r_i^2}, \qquad (4)$$

where D is the accumulated root density (m^{-2}), r_i (m) is the distance between the measurement location and the ith tree, and n is the total tree number which is less than 5m away from the measurement location. Here we assumed that a tree more than 5m away from the sample location have no influence on soil respiration from this location.

Eq (4) is used to compute the root density at a specific location. To extend the model for computing the average root factor in the whole site, we mathematically integrated Eq. (4). Set a site with an area of A (m^{-2}), tree number of N and a stand density of ρ (ρ=N/A). Notice that for an even-aged homogeneous stand, the contribution of roots

from each tree to the whole site is approximately equal. Thus we only need to compute root density from one tree and then multiply the total number of trees at this site to get the overall D in this site. Suppose the distance with a threshold influence from a tree is d_l (m), which has zero root contribution to soil respiration from this tree; the minimum distance with the maximum root contribution from this tree is d_s (m). Given any spatial random point i, the probability of this point with the distance of r (r^2<A, and $d_s \le r \le d_l$) from the tree j is $2\pi r\, dr/A$. The root density D of this point i with the distance of r from the tree j is

$$D_{ij} = \frac{1}{p r^2}\frac{2p r\mathrm{d}r}{A} = \frac{2\mathrm{d}r}{rA} \qquad (5)$$

The average D of all spatial points at this site receiving the influence from the tree j is

$$\overline{D_j} = \int_{d_s}^{d_l}\frac{2}{rA}\mathrm{d}r = \frac{2}{A}\int_{d_s}^{d_l}\frac{1}{r}\mathrm{d}r = \frac{2}{A}\ln(\frac{d_l}{d_s}). \qquad (6)$$

Notice here, any D with r greater than d_l or less than d_s has been set to 0.

The accumulated D with N trees in this site is

$$\overline{D} = \frac{2N}{A}\ln(\frac{d_l}{d_s}) = 2\ r\ \ln(\frac{d_l}{d_s}). \qquad (7)$$

Since the size of trees will also influence D, we added the average DBH as a linear factor into Eq. (7) and thus we had Eq. (8).

$$D = 2\frac{DBH}{DBH_r} r \ln(\frac{d_l}{d_s}) , \qquad (8)$$

where D is the root density in a stand, DBH is the average tree diameter at breast height, DBH_r is the reference DBH (here we set the young plantation as the reference), ρ is the stand density, d_l is the maximum radius of a circle that a tree would influence soil respiration in the stand, and d_s is the minimum radium of a circle that a tree would influence soil respiration in the stand.

Combining Eq. (2) and Eq. (8) we have

$$\frac{F}{F_r} = a + br \frac{DBH}{DBH_r} \ln(\frac{d_l}{d_s}) , \qquad (9)$$

where α=0.847, β=1.322. Eq. (9) indicates that spatially soil respiration is proportional to stand density and DBH. We can apply Eq. (9) to modeling soil respiration at different sites after setting a reference site.

3. Results

3.1 Measurements of soil respiration in the young and mature plantations

Fig. 4.1 shows the daytime mean measurement values of soil respiration in the young and mature plantations between July 2001 (day 208) and October 2002 (day 265). Soil respiration ranged between 1.6 $\mu molm^{-2}s^{-1}$ and 4.4 $\mu molm^{-2}s^{-1}$ in the mature plantation, and between 1.7 $\mu molm^{-2}s^{-1}$ and 3.8 $\mu molm^{-2}s^{-1}$ in the young plantation. Soil respiration in both the young and mature plantation peaked in May. Generally soil respiration in the mature plantation is greater than that in the young plantation.

Soil temperature in the young and mature plantations is similar except in the summer between May and August, when daytime mean soil temperature in the young plantation is greater than that in the mature one. In the summer, because of less canopy shading in the young plantation, soil temperature is higher than that in the mature one. Soil moisture in the depth of 0-30cm has no big difference in the young and mature plantations.

3.2 Modeling soil respiration in the young and mature plantations

In order to see the continuous seasonal patterns of soil respiration, we conducted multivariate regression analysis to fit the respiration data. We used the Eq. (1) as the functional form to estimate coefficients from measurement data. In the young plantation, we averaged 18 spatial samples to represent soil respiration. In the mature plantation, 7 spatial samples were averaged to conduct multivariate regression. Eq. (10) and Eq. (11)

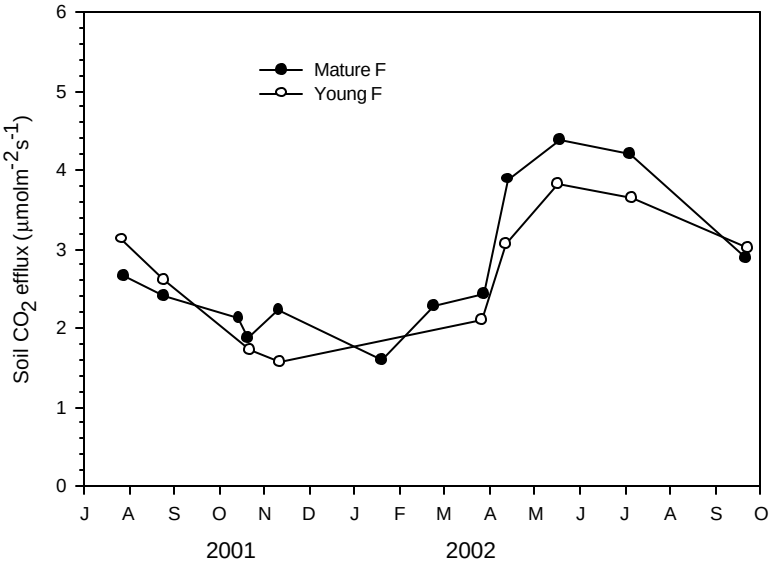

Fig. 4.1 Measurements of soil respiration in the young and mature plantations between July 2001 and October 2002.

are the regression results best fitting the data for young and mature plantations, respectively:

$$F = 0.261\, e^{0.0334T} e^{0.215M - 0.00515M^2}$$

R^2=0.67, p<0.001, n=82, (10)

$$F = 0.326\, e^{0.04T} e^{0.178M - 0.00386M^2}$$

R^2=0.81, P<0.001, n=30, (11)

where F is the soil respiration ($\mu molm^{-2}s^{-1}$), T is the soil temperature (°C), and M is the soil volumetric moisture (%).

Eq. (10) and Eq. (11) indicate that soil respiration exponentially increases with soil temperature. Holding soil moisture constant, the temperature sensitivities of soil respiration (Q_{10}) are 1.40 in the young plantation, and 1.50 in the mature plantation. Soil respiration varies with moisture in two directions. From Eq. (10) and Eq. (11) we can calculated that in the young plantation, when moisture is less than 20.8%, soil respiration increases with moisture; when moisture is greater than 20.8%, soil respiration decreases with further increase in moisture. In the mature plantation, when soil moisture is less than 23.0%, soil respiration increases with moisture; when moisture is greater than 23.0%, soil respiration decreases with further increase in moisture.

3.3 Seasonal variation of soil respiration

We used Eq. (10) and Eq. (11) to compute soil respiration in the young and mature plantations over seasons. Driven by two datasets of soil temperature and moisture from two sites, the model results indicated that the annual accumulations of soil respiration between October 1, 2001 and September 30, 2002 in the young plantation and mature plantation are 78.2 mol $m^{-2}year^{-1}$ and 77.0 mol $m^{-2}year^{-1}$ of carbon, respectively. The daily mean soil respiration ranged between 1.15 $\mu molm^{-2}s^{-1}$ and 4.36 $\mu molm^{-2}s^{-1}$ in the young plantation, and between 0.90 $\mu molm^{-2}s^{-1}$ and 4.67 $\mu molm^{-2}s^{-1}$ in the mature one. The averages of daily mean soil temperature over the year are 9.8°C in the young plantation and 8.8°C in the mature one.

In order to make comparison between the two sites and analyze the factors other than soil temperature and moisture influencing the difference of soil respiration between two sites, we removed the influences from soil temperature and moisture by using the averaged temperature and moisture over two sites to drive the day-to-day variation of soil respiration. Fig. 4.2a is the averaged soil temperature and moisture based on daily mean values between October 1, 2001 and September 30, 2002. Fig. 4.2b shows two patterns of soil respiration, one in the young plantation and the other in the mature plantation,

Fig. 4.2 indicates that daily mean soil temperature at the depth of 10cm ranged between 0.73°C and 20.11°C with a minimum on January 21 and a maximum on July 12. Daily mean soil volumetric moisture at the depth of 0-30cm ranged between 8.95% and 36.52% with a minimum on September 14 and a maximum on December 31.

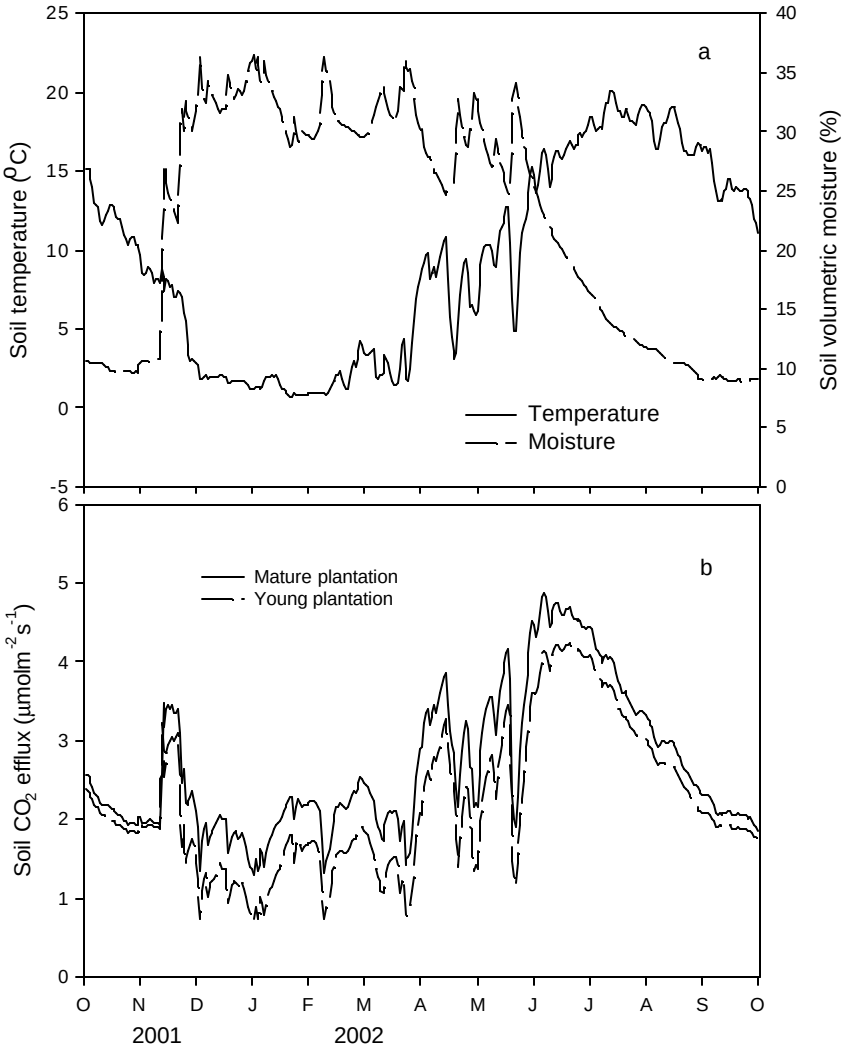

Fig. 4.2 Daily mean soil temperature and moisture averaged over two sites (a), and daily mean soil respiration in the young plantation and mature plantation between October 1, 2001 and September 30, 2002 (b).

In the young plantation daily mean soil respiration ranged between 0.72 $\mu molm^{-2}s^{-1}$ and 4.24 $\mu molm^{-2}s^{-1}$ with a minimum on December 31 and a maximum on June 20. In the mature plantation daily mean soil respiration ranged between 1.31 $\mu molm^{-2}s^{-1}$ and 4.88 $\mu molm^{-2}s^{-1}$ with a minimum on December 31 and a maximum on June 6. At both sites, soil respiration peaked almost when the soil temperature curve had an intersection with the moisture curve in June as indicated in Fig. 4.2a. The annual accumulations of soil respiration in the young plantation and mature plantation are 69.8 mol $m^{-2}year^{-1}$ and 84.9 mol $m^{-2}year^{-1}$, respectively. In the mature plantation soil respiration is 15.1 mol $m^{-2}year^{-1}$ or 1.22 times greater than that in the young plantation.

3.4 Relationship between soil respiration in the young and mature plantations

We explored the reason for the difference in soil respiration between the two sites. There is no significant difference in soil carbon content and nitrogen content between the two sites. We used the same dataset of soil temperature and moisture to drive the soil respiration models. Thus we reasoned that the root distribution would be the major factor explaining the difference in soil respiration between the young plantation and mature plantations.

We computed D (Eq.8) for the young (D_y) and mature (D_m) plantations. For the young plantation with a stand density of 0.0378 m^{-2} we used d_l=5m as the threshold influence from roots on soil respiration and d_s=0.15m as the maximum influence. Applying to Eq. (9) we have D_y = 0.260 and F/F_r=1.019. This result approximates to the derived one from Eq. (2): given F/F_r =1, D=0.227 for the young plantation.

For the mature plantation with a stand density of 0.0382 m^{-2} we used d_l=10m as the threshold influence from roots on soil respiration and d_s=0.37m as the maximum influence. Applying to Eq. (9) we have D = 0.582 and F/F_r=1.23. Thus we computed that F_{mature} = 1.21 F_{young}. This result approximates our previous result that in the mature plantation soil respiration is 1.22 times greater than that in the young plantation. Table 4.1 summarizes the results.

Table 4.1 Predict the difference of soil respiration between young and mature plantations

Site	Stand density (m^{-2})	DBH (m)	d_l (m)	d_s (m)	D (m^{-2})	F/F_r
Young	0.0378	0.16	5	0.16	0.260	1.02
Mature	0.0382	0.37	10	0.37	0.582	1.23

3.5 Assessment of forest management

Eq. (9) can be used to assess the impact of forest management such as thinning on soil respiration. Chapter 2 concluded that theoretically soil respiration will be decreased by 12.6% after thinning due to the decrease in root density. The result is based on the exclusion of soil moisture and temperature effects. We used this empirical result to verify Eq. (9).

After thinning in 2000, the stand density decreased from 0.121 m^{-2} to 0.0378 m^{-2}. We used tree size in 1999 to calculate soil respiration before thinning and the data in 2001 to calculate soil respiration after thinning. Inputting data in 1999 (before thinning) of DBH, ρ, d_l, and d_s into Eq. (9), we have F_{1999}/F_r=1.140. Inputting data in 2001 (after

thinning), we have F_{2001}/F_r=0.998. Therefore, F_{2001}/F_{1999}=87.5. Table 4.2 shows the prediction of the difference of soil respiration before and after thinning.

Table 4.2 Predict the difference of soil respiration before and after thinning

	Stand density (m^{-2})	DBH (m)	d_l (m)	d_s (m)	D (m^{-2})	F/F_r
Before	0.1213	0.087	2.5	0.087	0.443	1.140
After	0.0378	0.133	5	0.133	0.228	0.998

The above results suggest that after thinning soil respiration will be decreased by 12.5% according to our model. This result approximates to our empirical studies in Chapter 2. The result indicates that although the thinning cut down about 2/3 of the tree, soil respiration within 2 years only decreased about 13% because of the increased root biomass and activity of the remaining trees.

4. Discussion

4.1 Modeling soil respiration in the young and mature plantations

By running two regression models Eq. (10) and Eq. (11) we found soil respiration in the mature plantation is 1.216 times greater than that in the young plantation. This result is obtained by using averaged soil temperature and moisture over the two sites to drive the models. Thus we are able to compare the root influence by removing the temperature and moisture factors. If we use the separate dataset of temperature and moisture in the two

sites to drive our models, we find that the annual CO_2 efflux in the young plantation (78.2 mol $m^{-2}year^{-1}$) is 1.2 mol $m^{-2}year^{-1}$ greater than that in the mature plantation (77.0 mol $m^{-2}year^{-1}$). The reason for this result may be because the influence of roots on soil respiration is offset by the influence from relatively high soil temperature in the young plantation. The average of daily mean soil temperature over a year in the young plantation (9.8°C) is 1°C greater than that in the mature plantation (8.8°C). The difference of temperature could be explained by less crown areas, less LAI, less evapotranspiration in the young plantation, and thus more solar radiation received by the soil than that in the mature plantation.

4.2 Scaling up soil respiration

Eq. (9) allows us to derive soil respiration from various forest stands based on a reference stand. We verified this general model by driving two other independent regression models (Eq. 10 and Eq. 11) and found this general model explains the difference of soil respiration at two sites. We used the same temperature and moisture in two sites to test the general model, but in practice we need to use soil temperature and moisture in each site to simulate soil respiration. We may derive soil temperature from air temperature and soil moisture from precipitation and evapotranspiration. Thus we provide a method to spatially scale up soil respiration from one site to various sites.

Combining Eq. (3) and Eq. (9) we may be able to simulate soil respiration from different forest stands. Eq. (3) (computing F_r) may have different parameters if we apply this model to different ecosystem types. Two empirical constant coefficients, α and β, in Eq. (9) may also vary with different ecosystems. Variables d_l and d_s could be derived

from allometric relationship with DBH, tree height, or crown size. Thus, we are able to temporally and spatially model soil respiration with the variables of temperature, moisture, stand density, and tree size.

4.3 Dynamics of soil respiration

Eq. (9) could be used to analyze soil carbon dynamics as well as spatial variation. It shows that soil respiration increases with the average DBH of a stand. In another word, old growth stand has more soil respiration than young stand. However, when we compare the absolute values of soil respiration at two sites, soil temperature and moisture are still two important variables. As indicated in our studies, soils in the mature plantation have lower soil temperature than those in the young plantation. Thus, the increased soil respiration due to roots in a mature plantation may be partially offset by the low soil temperature. The mature plantation may not necessarily have more soil respiration than young one. If we know the dynamics of soil temperature and moisture (or the dynamical correlation with air temperature) with the succession of a forest, we may derive the soil carbon dynamics based on Eq. (9).

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Chapter 5 Assessing Soil CO_2 Efflux Using Continuous Measurements of CO_2 Profiles in Soils with Small Solid-state Sensors

Abstract

This chapter describes a new method to monitor continuously soil CO_2 profiles by burying small CO_2 sensors at different depths in the soil. Based on the measurement of soil CO_2 profile and a diffusivity model, we estimated soil CO_2 efflux, which is mainly from heterotrophic respiration, and its temporal variation in a dry season in a Mediterranean savanna ecosystem in California. The daily mean values of CO_2 concentrations in soils had small variation, but the diurnal variation of soil CO_2 profile was significant and correlated well with soil temperature. Between day 200 and 235 in 2002, the daily mean CO_2 concentration averaged 396 μmol mol^{-1} of air at the depth of 2cm; the daily mean CO_2 concentration decreased from 721 μmol mol^{-1} to 611 μmolmol^{-1} at 8cm depth, and from 1044 μmol mol^{-1} to 871 μmol mol^{-1}at 16cm depth.

The vertical CO_2 gradient at a certain time was approximately a constant when the depth is less than 16cm, but the gradient varies over time. By running the Millington-Quick model, we found soil CO_2 diffusion coefficient ranged from 2.293 mm^{2}s^{-1} to 2.544 mm^{2}s^{-1} with a mean of 2.425 mm^{2}s^{-1}. The daily mean values of CO_2 efflux slightly decrease from 0.43 μmol m^{-2}s^{-1} to 0.33 μmol m^{-2}s^{-1} with a mean of 0.37 μmol m^{-2}s^{-1} or 0.0318 mol m^{-2}day^{-1}. The diurnal variation of CO_2 efflux is more significant than day-to-

day variation. The diurnal variation of soil CO_2 efflux ranged from 0.32 μmol $m^{-2}s^{-1}$ to 0.45 μmol $m^{-2}s^{-1}$ with the peak value reached at about 14:30-16:30 hrs. This pattern corresponded well with the increase in soil temperatures during this time.

By plotting CO_2 efflux vs. soil temperature, we found that CO_2 efflux correlates exponentially with soil temperature at the depth of 8cm with R^2 of 0.86 and Q_{10} of 1.27 in the summer dry season. The Q_{10} value increases with soil depth of temperature measurements. The diurnal pattern of CO_2 efflux shows a high correlation with soil temperature but the seasonal pattern does not show this because soil moisture is another control factor for seasonal pattern. By comparing estimated CO_2 efflux with measured CO_2 efflux data, we conclude that the described CO_2 sensors and diffusion method yielded satisfactory results.

1. Introduction

Soil surface CO_2 efflux, or soil respiration, is a major component of the biosphere's carbon cycle because it constitutes about three-quarters of total ecosystem respiration (Law *et al.* 2001). In recent years, soil CO_2 efflux has been the subject of intense studies because of its potential and controversial role in amplifying global warming (for example, Trumbore *et al.* 1996; Liski *et al.* 1999; Cox *et al.* 2000; Giardina & Ryan 2000; Kirschbaum 2000; Luo *et al.* 2001). Soil carbon modelers generally view soil CO_2 efflux as a function of soil temperature or a combination of soil temperature and moisture (for example, Crill 1991; Raich & Schlesinger 1992; Davidson *et al.* 1998; Epron *et al.*

1999; Xu & Qi 2001a; Treonis *et al.* 2002). However, there is no consensus in functional forms and parameterization in these models. The uncertainty is partly due to the instrumentation and methods used to measure soil CO_2 production and efflux (Livingston & Hutchinson 1995; Davidson *et al.* 2002).

Information on soil respiration is also needed to interpret eddy covariance measurements, which are now being acquired on a quasi-continuous basis across the global FLUXNET network (Baldocchi *et al.* 2001). The eddy covariance method measures ecosystem productivity (NEP), a net result of photosynthesis and respiration, but it does not provide individual information such as photosynthesis, autotrophic respiration, and heterotrophic respiration (though nighttime eddy covariance is a proxy of ecosystem respiration). Since these processes have different mechanisms and environmental drivers, partitioning of eddy covariance data is receiving much attention and criticism (Piovesan & Adams 2000). Continuous eddy covariance measurements need continuous soil CO_2 measurements at a similar frequency in order to decompose NEP, understand temporal variation, and explain some unusual episodic events that are observed.

Measurement methods of soil CO_2 efflux are still in development. An early method periodically extracts soil gas samples from different depths to study CO_2 profile and diffusion (De Jong & Schapper 1972; Wagner & Buyanovsky 1983; Burton & Beauchamp 1994; Davidson & Trumbore 1995). Gas extraction methods can provide information on soil CO_2 production profiles, but they cannot provide *in situ,* continuous and convenient data on CO_2 efflux. Furthermore, gas extraction methods will disturb the

soil environment. An unavoidable bias may happen during the processes of gas extraction, storage, transportation, and measurement.

Chamber-based measurements allow us to directly measure CO_2 efflux from soil on a small scale (for example, Meyer *et al.* 1987; Nakayama & Kimball 1988; Naganawa *et al.* 1989; Norman *et al.* 1992). Fixed chambers and portable chambers have evolved into automated systems for continuous and semi-continuous measurements (Goulden & Crill 1997; Russell *et al.* 1998; Scott *et al.* 1999; Drewitt *et al.* 2002; King & Harrison 2002). Shortages with chamber measurement methods, however, still exist. Efflux readings may be biased by disturbing air pressure and altering CO_2 concentration under the soil (Livingston & Hutchinson 1995; Healy *et al.* 1996; Davidson *et al.* 2002). By measuring accumulation of soil CO_2 productivity, chambers are unable to provide information about soil profiles and individual contributions at certain soil depths, which is important for understanding soil carbon mechanisms. Currently, no commercially available automated chambers can be employed conveniently in the field.

Under-story eddy covariance towers provide an alternative to study continuously soil CO_2 efflux without disturbing the soil (Baldocchi & Meyers 1991; Law *et al.* 1999). As with over-story eddy covariance techniques, under-story eddy covariance measurement may face difficulty in measuring respiration at night when turbulence is weak and drainage flows dominate the transfer of CO_2 (Goulden *et al.* 1996; Moncrieff *et al.* 1997; Baldocchi *et al.* 2000). The low height of under-story towers corresponds with small areas of footprint. Furthermore, under-story eddy covariance data cannot separate soil CO_2 efflux, bole respiration below sensors, and overlay herbaceous vegetation, when it is present.

Partitioning NEP into GPP (gross primary productivity) and NPP (net primary productivity), and partitioning soil respiration into autotrophic and heterotrophic respiration are of critical importance for building process-based models since these components respond differently to abiotic and biotic drivers. Despite the development of methods such as trenching and isotopic approaches for partitioning the source of soil CO_2 (Hanson *et al.* 2000), few studies have been reported that directly measure and model heterotrophic respiration *in situ* without any disturbance. As a result, studies on temperature sensitivity (Q_{10}) of soil CO_2 efflux often combine heterotrophic respiration with autotrophic respiration (for example, Raich & Schlesinger 1992; Lloyd & Taylor 1994; Xu & Qi 2001b), which may vary with plant physiological and phenological factors other than temperature. Thus, correlation coefficients between soil CO_2 efflux and temperature are often low, and results are often less explainable.

Due to the limitation of instrumentation, particularly due to the large size of commonly-used infrared gas analyzers, there are very few publications on continuous measurements of CO_2 profile in the soil. Recently, an innovative CO_2 sensor was developed by Vaisala Inc. (Finland) for air quality monitoring and control. This instrument has the potential to be buried in the soil and measure CO_2 in the soil atmosphere. Hirano et al. (2000) first used these small CO_2 sensors buried in the soil under a deciduous broad-leaved forest in Japan to deduce soil respiration, and therefore have demonstrated the feasibility of the instrument.

In order to address the lack of measurement methods in soil CO_2 efflux, this paper describes in detail the use of the new small solid-state CO_2 sensors, Vaisala GMT220, to continuously monitor soil CO_2 profiles and soil CO_2 efflux by burying these CO_2 sensors

at different soil depths. Based on the measurement of the CO_2 profile and a diffusivity model, we estimated rates of soil CO_2 efflux, which is mainly from heterotrophic respiration, in a dry season in a Mediterranean savanna ecosystem in California. The relationship between CO_2 efflux and soil temperature is explored. Soil CO_2 efflux measurements are used to validate estimated data.

2. Materials and Methods

2.1 Site description

The field study was conducted at an oak savanna forest, a member of the Ameriflux network, located on the lower foothills of the Sierra Nevada Mountains near Ione, California. The latitude, longitude and altitude at the site are 38.4311^o N, 120.966^o W and 177 m, respectively. Annual temperature at a nearby weather station with similar altitude and vegetation (Pardee, CA) is 16.3^{o}C. The mean annual precipitation is about 559 mm per year (from weather station in Ione, CA that operated between 1959 and 1977). Due to the Mediterranean climate of the region, essentially no rain falls during the summer months.

The overstory of the oak savanna consists of scattered blue oak trees (*Quercus douglasii*). 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*.

A demographic survey on stand structure was conducted on a 100 by 100 m patch of forest and along a 200 m transect (Kiang 2002). The mean height of the forest stand is 7.1 m, its mode is 8.6 m, and the maximum height is 13.0 m. The landscape supported 194 stems per hectare, whose mean diameter at breast height (DBH) was 0.199 m and basal area was $18 m^2\ ha^{-1}$. Also registered in the site survey were occasional grey pine trees (*Pinus sabiniana)* (3 per ha). The leaf area index of the savanna woodland was about 0.6. The grassland attains a leaf area index of about 1.0 during its peak growth period. But the herbaceous vegetation was dead while this study was conducted.

2.2 Soils

The soil of the oak-grass savanna is an auburn rocky silt loam (Lithic haploxerepts; soil survey of Amador Area, California, 1965, USDA, Soil Conservation Service). Physical properties (bulk density and texture) and chemical composition of the soils are presented in Table 5.1. Soil texture and chemical composition were analyzed at DANR Analytical Laboratory, University of California, Davis.

Table 5.1 Soil physical properties and chemical composition

	Bulk density ($g\ cm^{-3}$)	Soil Texture			Carbon and nitrogen content	
		sand %	silt %	clay %	Carbon (%)	Nitrogen (%)
Under canopy	1.58 +/- 0.136	37.5	45	17.5	1.09	0.11
Open Space	1.64 +/- 0.107	48	42	10	0.92	0.10

2.3 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). Static pressure was measured with a capacitance analog barometer (model PTB101B, Vaisala, Helsinki, Finland). Soil temperatures were measured with multi-level thermocouple probes. Volumetric soil moisture content was measured continuously in the field at several depths in the soil with frequency domain reflectometry sensors (Theta Probe model ML2-X, Delta-T Devices, Cambridge, 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) were made periodically and manually using an enhanced, time-domain, reflectometer (Moisture Point, model 917, E.S.I Environmental Sensors, Inc, Victoria, British Columbia).

Ancillary meteorological and soil physics data were acquired and logged on CR-23x and CR-10x 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.

2.4 Soil CO_2 efflux measurements by closed chambers

CO_2 efflux from the soil surface was manually measured across a 42.5m long transect between two oak trees in the savanna. Eleven soil collars, each with a height of 4.4 cm and a diameter of 11 cm, were inserted into the soil at each sampling point. The distances between No. 1 and 2, No. 2 and 3, and No. 10 and 11 are 2.5m; the other points are 5m apart. The collars are used to measure CO_2 efflux. Soil CO_2 efflux was measured using an

LI6400-09 soil chamber connected to an LI-6400 portable photosynthesis system for data collection and storage. CO_2 efflux was measured about one day every two weeks. The mean value of the soil CO_2 efflux in the open space is used to represent heterotrophic respiration in the dry season.

2.5 Soil CO_2 profile measurements

Soil CO_2 concentration was measured near the midpoint of the transect. We installed CO_2 sensors in the soil at a bare area between locations No. 6 and No. 7 of the transect. The two nearest oak trees were both about 20m away, so the impact of root respiration was minimal. Because the annual grasses are dead during the summer, it is assumed that the majority of CO_2 emanating from the soil is due to heterotrophic respiration.

We used Vaisala GMT 222 CO_2 sensors, one kind of the GMT220 series sensors, to measure CO_2 profiles in the soil. The GMT 220 CO_2 sensor consists of three parts, a remote probe, a transmitter body, and a cable. The probe is a new silicon-based, non-dispersive infra-red (NDIR) sensor for the measurement of CO_2 based on the patented CARBOCAP® technique. Using the same working principle as other high performance large NDIR analyzers, it assesses CO_2 concentration by detecting the attenuate of single-beam dual-wavelength infra-red light across a fixed distance. The sensor is small because the CARBOCAP® sensor possesses a tiny electrically controlled fabry-perot interferometer (FPI) made of silicon, replacing the traditional rotating filter wheel in larger scale NDIRs. Therefore, a true dual-wavelength measurement can be made by a simple and small sensor (http://www.vaisala.com).

The feature of the probe provides us with a new and novel means of measuring soil CO_2 concentration profiles and deducing estimation of CO_2 efflux by burying the probe (sensor) in the soil. The probe is a cylinder with 15.5cm in length and 1.85cm in diameter. Tiny holes on the surface of the probe allow CO_2 to diffuse three-dimensionally through membranes into the sensor. In order to measure CO_2 concentration at some specific depth of soil, we encased the probe with an aluminum pipe with the same length but 5mm larger in diameter. The casing was sealed with the probe on the upper end using a rubber gasket. The opening on the lower end allowed CO_2 molecule to diffuse to the sensor at the buried depth for CO_2 concentration measurement. We buried 3 sensors at depths of 2cm (with a range of 0-5000 μmol mol^{-1}), 8cm (with a range of 0-10000 μmol mol^{-1}), and 16cm (with a range of 0-10000 μmol mol^{-1}), respectively; they were separated horizontally by about 2cm. A schematic of the system is shown in Fig. 5.1.

The cable connected the probe in the soil with the transmitter body placed on the ground. After receiving the signal from the probe, the transmitter sends the output signal both to a datalogger (CR-23X, Campbell Scientific Inc., Utah, USA) and to an optional LCD display on the transmitter for the CO_2 concentration reading. We used custom-built thermocouple sensors to monitor soil temperature at the same depth where the CO_2 sensors were buried. Thermocouple sensors were also connected to the datalogger. The datalogger was programmed to take samples every 30 seconds but compute and store 5-minute averages.

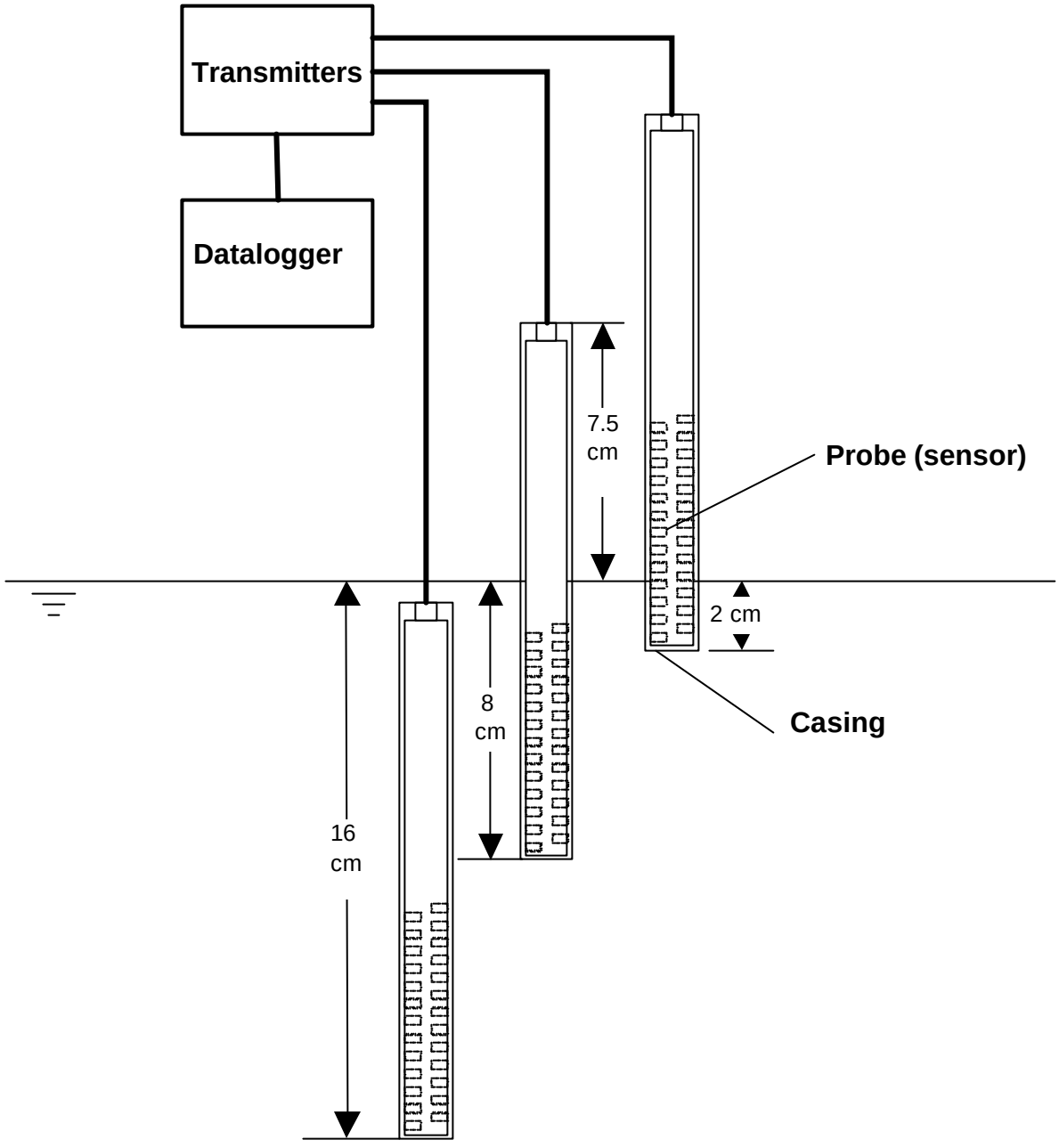

Fig. 5.1 A schematic of the system for measuring soil CO_2 profile.

The system was powered by 24V DC provided by two 12V batteries connected in series. Each sensor has the power consumption of 4W. The system was installed and tested in March 2002 and started to collect data on June 20, 2002. Continuous applicable data collection started on July 19, 2002. To provide continuous power, we installed a 24 V photovoltaic system on August 23, 2002 to continuously charge the batteries.

Vaisala GMT 220 series sensors have measurement range options from 0-2000$\mu molmol^{-1}$ to 0-20%. The technical specifications indicate an operating temperature ranging from -20°C to 60 °C, and the accuracy of GMT222, which we used, is ±20 $\mu mol\ mol^{-1}$ CO_2 plus 2% of reading. We calibrated the sensors using lab standards that are traceable to the NOAA/CMDL standards. We found the errors are within the accuracy range.

2.6 Data analysis

In order to decrease the systematic error, the concentration readings from the CO_2 sensor need to be corrected for variations in temperature and pressure. The reference temperature and pressure for the sensor are 25°C and 101.3 kPa, respectively. Based on the ideal gas law and instrument specifications, the manufacturer of the sensor (personal communication with Dick Gronholm, Vaisala Inc. in California) provided the following empirical formulas for correcting for temperature and pressure applicable to GMT222 sensors:

$$C_c = C_m - C_T - C_P \qquad (1)$$

where C is the CO_2 concentration in μmol mol^{-1}, and the subscripts c, m, T, and P stand for corrected, measured, temperature correction, and pressure correction.

The temperature correction was computed by

$$C_T = 14000 \times (K_T - K_T^2) \times [(25 - T_c)/25], \qquad (2)$$

where T_c is the temperature in degree Celsius, and

$K_T = A_0 + A_1 \times C_m + A_2 \times C_m^2 + A_3 \times C_m^3$,

$A_0 = 3 \times 10^{-3}$, $A_1 = 1.2 \times 10^{-5}$, $A_2 = -1.25 \times 10^{-9}$, $A_3 = 6 \times 10^{-14}$.

The pressure correction was computed by

$$C_P = K_P \times [(P - 101.3)/101.3], \qquad (3)$$

where P is the pressure (kPa), and $K_P = A \times C_m$, A = 1.38.

The data collected from CO_2 sensors are in volume fraction (μmol mol^{-1}), which can be changed to mole concentration (μmol m^{-3}). The flux of CO_2 diffused from the soil can be calculated by Fick's first law of diffusion:

$$F = -D_s \frac{dC}{dz}, \qquad (4)$$

where F is the CO_2 efflux (μmol$m^{-2}s^{-1}$), D_s is the CO_2 diffusion coefficient in the soil (m^2s^{-1}), C is the CO_2 concentration (μmol m^{-3}), and dC/dz is the vertical soil CO_2 gradient.

D_s can be estimated as:

$$D_s = x D_a \qquad (5)$$

where x is the gas tortuosity factor, and D_a is the CO_2 diffusion coefficient in the free air.

The effect of temperature and pressure on D_a is given by

$$D_a = D_{a0}(T/293.15)^{1.75}(P/101.3), \qquad (6)$$

where T is the temperature (K), P is the air pressure (kPa), D_{a0} is a reference value of D_a at 20°C (293.15K) and 101.3 kPa, and is given as 14.7mm^{2}s^{-1} (Jones, 1992).

There are several empirical models in the literature for computing x (Sallam et al., 1984). We used the Millington-Quirk model (Millington and Quirk, 1961):

$$x = \frac{a^{10/3}}{f^2} \qquad (7)$$

where a is the volumetric air content (air-filled porosity), f is the porosity, sum of a and the volumetric water content (q). Note,

$$f = a + q = 1 - \frac{r_b}{r_m}, \qquad (8)$$

where r_b is the bulk density, and r_m is the particle density for the mineral soil.

Eqs. (5)-(8) are used to compute the soil CO_2 diffusion coefficient D_s. ρ_b at the site was measured as 1.64 g cm^{-3}, and typical ρ_m of 2.65 g cm^{-3} was used. Thus f =1-1.64/2.65 = 0.38. A continuous q measured at the 5cm depth was used to represent the

average between 0-16cm to compute a and thus x by applying the Millington-Quirk model. Free air D_a is adjusted by soil temperature at 8cm depth and air pressure.

We measured manually soil CO_2 efflux periodically. The simultaneous measurements of soil CO_2 efflux and CO_2 concentration gradients were used to validate the model results by applying Fick's First Law and computing the diffusion coefficient.

3. Results and Discussion

3.1 CO_2 profile in measurements

Fig. 5.2 shows seasonal patterns with daily mean values between day 200 and 235 in 2002 of (a) CO_2 concentrations at three depth, (b) soil CO_2 efflux, (c) soil temperature, (d) soil moisture, and (e) diffusion coefficient. In Fig. 5.2a we plotted half-hour average of CO_2 concentration at depths of 2cm, 8cm and 16cm and their daily mean values. During the study period, the daily mean values of CO_2 did not vary significantly at the depth of 2cm, but decreased slightly at the depth of 8cm and 16cm. At the depth of 2cm, the daily mean CO_2 concentration varied between 386 μmol mol^{-1} and 403 μmol mol^{-1} with an average over 36 days of 396 μmol mol^{-1}. The daily mean CO_2 concentration decreased from 721 μmol mol^{-1} to 611 μmol mol^{-1} at the depth of 8cm; it decreased from 1044 μmol mol^{-1} to 871 μmol mol^{-1} at the depth of 16cm. Daily mean soil temperature measured at the depth of 8cm ranged from 32.6°C to 38.3°C during this period but the variation had no significant correlation with the daily mean CO_2 concentration (Fig. 5.2c).

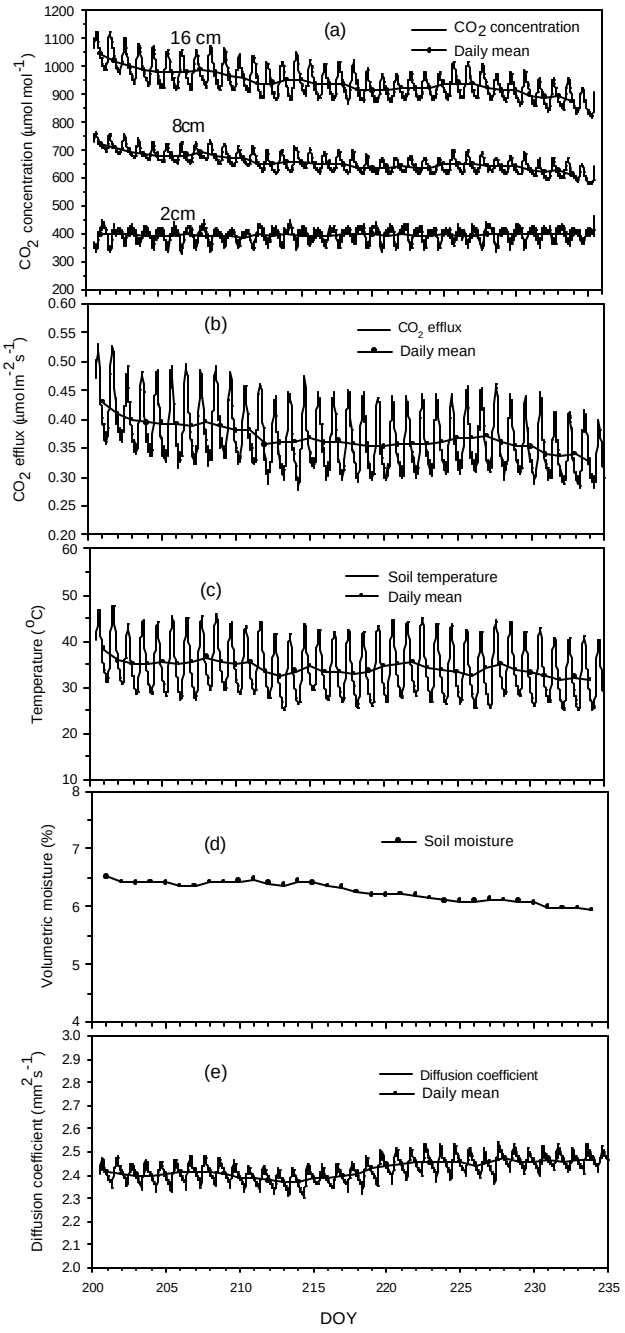

Fig. 5.2 Seasonal patterns with daily mean values between day 200 and 235 in 2002. (a) CO_2 concentrations in the soil at depths of 2cm, 8cm, and 16cm; (b) soil CO_2 efflux; (c) soil temperature at the depth of 8cm; (d) soil volumetric moisture at the depth of 5cm; (e) diffusion coefficient.

Soil volumetric moisture had no significant diurnal variation (Fig. 5.2d). Daily mean soil volumetric moisture at the depth of 5cm decreased slightly with an average of 6.3%.

The decrease in soil CO_2 concentration at the depth of 8cm and 16cm may be explained by the continuous decrease in soil moisture and carbon content at these two levels. At the depth of 2cm, soil moisture did not change since moisture was already at the threshold value of about 5%. Thus the daily mean CO_2 concentration indicated no decrease at the depth of 2cm.

Unlike the seasonal patterns of the soil CO_2 profile, the diurnal variation of the soil CO_2 profile was significant and correlated well with soil temperature. We computed mean diurnal patterns of soil CO_2 concentration and temperature at three depths, and their standard deviations over 34 days between day 201 and 234 (Fig. 5.3a, Fig. 5.3c). The 8cm and 16cm CO_2 concentration curves indicate a similar trend while the 2cm curve shows an opposition. During the time 14:30-16:30 when soil temperature is the highest within a day, the 8cm curve and 16cm curve reach the peak values, while the 2cm curve has a lowest value during this time.

The value of CO_2 concentration is determined by CO_2 production in a certain depth of the soil and by diffusion of CO_2 from deeper soil if we neglect the horizontal transportation. The 8cm and 16cm curves correlate positively with soil temperature but not the 2cm curve. This may be explained by the CO_2 production, which is sensitive to soil temperature. However, temperature sensitivity and CO_2 production may decrease with the increase in temperature (Singh & Gupta 1977; Xu & Qi 2001b; Nakadai *et al.* 2002). At the top soil layer, the temperature can reach as high as 50°C in the early afternoon. Thus the 2cm CO_2 concentration curve did not peak in the early afternoon.

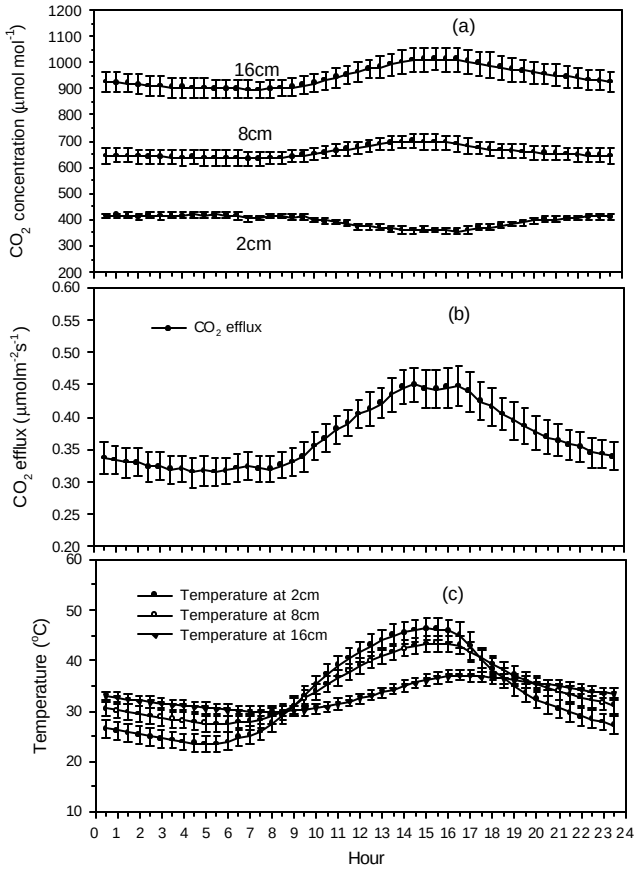

Fig. 5.3 Mean diurnal patterns and their standard deviations (n=34) between day 201 and 234 in 2002. (a) CO_2 concentrations in the soil at depths of 2cm, 8cm, and 16cm; (b) soil CO_2 efflux; (c) soil temperature at depths of 2cm, 8cm, and 16cm.

Another reason for the decreased CO_2 concentration under high temperature is the transportation of CO_2. The high transportation rate of CO_2 may prevent the CO_2 from building-up at the top layer during early afternoon because CO_2 diffusivity increases with temperature. In addition to soil biological and physical factors, the low ambient CO_2 concentration in the afternoon (data not shown) due to tree's photosynthesis may also affect soil CO_2 concentration at the top layer through the pressure pumping effect (Massman et al. 1997).

3.2 Soil CO_2 gradients

The vertical CO_2 gradient (dC/dz) was approximately a constant at different depths of soil in our site for the field conditions experienced during this study. By plotting CO_2 concentrations vs. depth, we found the CO_2 concentration linearly increases with depth when the depth is less than 16cm. Thus, through linear regression for CO_2 concentration over depth we computed the slope, which is used to represent CO_2 concentration gradient. The gradient changes over time. We conducted linear regressions for computing the gradient in each 5-minute. The average R^2 over 10090 regressions during the day 200 and 235 was 0.997.

The linearity of CO_2 gradient makes its calculation simple, with a finite difference ($dC/dz = \Delta C/\Delta z$); this approximation may not be valid at deeper soil depths and during other seasons. Soil CO_2 concentration will increase with depth until reaching a certain level where CO_2 concentration may either keep a constant if a barrier is present, or decrease if there is no barrier (Jury *et al.* 1991). The gradient will vary with soil temperature, moisture and carbon content.

3.3 Estimation of soil CO_2 diffusivity

The average of the soil CO_2 diffusion coefficient over the depth of 0-16cm was computed by the Millington-Quick model (Eq. 7) after it was corrected for changes in soil temperature and air pressure. Due to a small variation of soil moisture, soil CO_2 diffusion coefficient (Fig. 5.2e) did not vary significantly in the summer, although diurnal patterns are affected by soil temperature. Between day 200 and day 235, D_s ranges from 2.293 mm^2s^{-1} to 2.544 mm^2s^{-1} with a mean of 2.425 mm^2s^{-1}.

3.4 Soil CO_2 efflux and its correlation with soil temperature

After we measured soil CO_2 concentrations in the soil and estimated soil CO_2 diffusivity, we computed soil surface CO_2 efflux by Fick's Law. Fig. 5.2b shows the seasonal variation of soil CO_2 efflux between day 200 and day 235. Fig. 5.3b indicated the diurnal pattern of soil CO_2 efflux.

Between day 200 and day 235, the daily mean values of CO_2 efflux slightly decreased from 0.43 $\mu mol\ m^{-2}s^{-1}$ to 0.33 $\mu mol\ m^{-2}s^{-1}$ with a mean of 0.37 $\mu molm^{-2}s^{-1}$ or 0.0318 $molm^{-2}day^{-1}$. It corresponded with the small variation of daily mean soil temperature and moisture curves. Compared with the day-to-day variation, the diurnal variation of CO_2 efflux is more significant (Fig. 5.3b), and correlated well with the diurnal variation of soil temperature (Fig. 5.3c).

The mean diurnal pattern of soil CO_2 efflux and its error bars (standard deviation) over 34 days indicated a stable diurnal variation during this period. The diurnal variation of soil CO_2 efflux ranged from $0.32 \pm 0.023\ \mu mol\ m^{-2}s^{-1}$ to $0.45 \pm 0.026\ \mu mol\ m^{-2}s^{-1}$. Soil

CO_2 efflux increased after 9:00 and reached the peak values at about 14:30-16:30. This pattern corresponded well with the increase in soil temperatures, particularly with the ones at depths of 8cm and 16cm. The mean diurnal soil temperature over 34 days ranged from 23.4 ± 1.69°C to 46.3 ± 2.26°C at the depth of 2cm, 27.4 ± 1.63°C to 43.4 ± 1.65°C at the depth of 8cm, and 29.9 ± 1.05°C to 37.1 ± 1.10°C at the depth of 16cm. The 2cm temperature curve has the highest range while the 16cm curve has the lowest range within a day.

Unlike the diurnal temperature curve, which is smooth and has one maximum value, the diurnal curve of soil CO_2 efflux has a plateau without a sharp peak between 14:30 and 16:30. This may be caused by the decreased temperature sensitivity under very high temperature in the early afternoon. Microbial decomposition may be constrained by extremely high temperature and low moisture, too.

To investigate the temperature sensitivity (Q_{10} value) of soil CO_2 efflux at our site, we further plotted CO_2 efflux vs. soil temperature at the depth of 8cm (Fig. 5.4). An exponential curve is fitted to the plot:

$$F = 0.1623e^{0.0237T}, \ R^2 = 0.86, \ n = 10090, \qquad (9)$$

where F is the soil CO_2 efflux and T is the soil temperature; $Q_{10} = 1.27$.

Eq. (9) indicates that CO_2 efflux has a strong correlation with soil temperature. The reason may be from the fact that CO_2 efflux is mainly from heterotrophic respiration without the influence from root activity. Eq. (9) also indicates that the temperature sensitivity is relatively low in the dry season. The Q_{10} value is commonly considered ranging from 1.3 to 3.3 (Raich & Schlesinger 1992). Q_{10} itself is also temperature

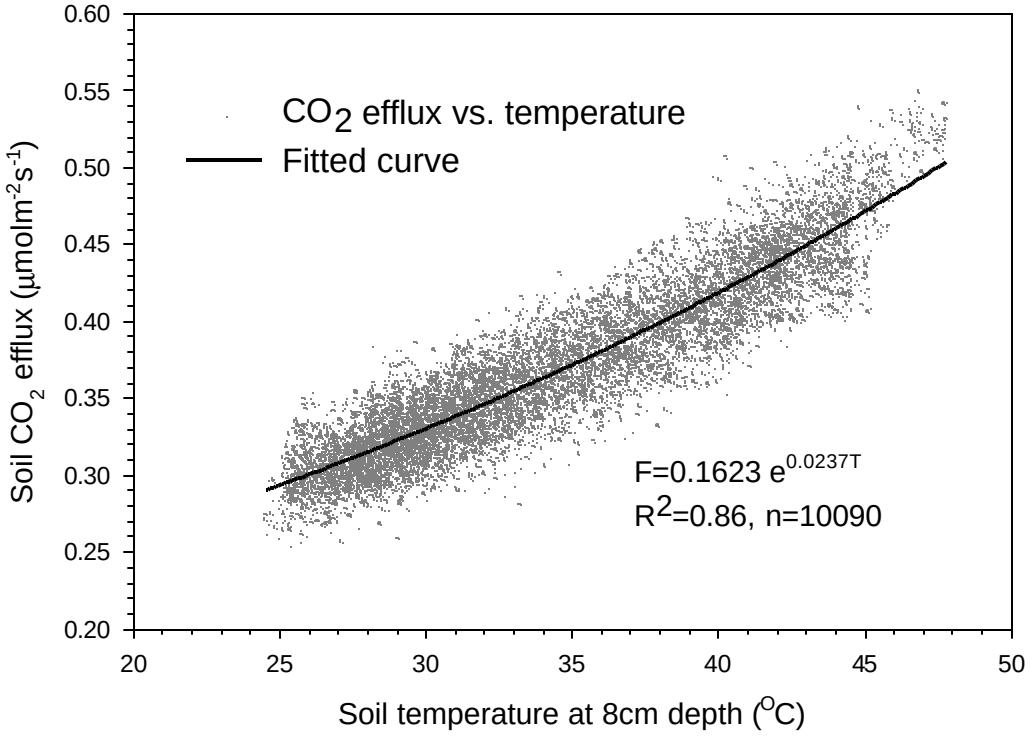

Fig. 5.4 Relationship between soil CO_2 efflux and temperature.

dependent (Lloyd & Taylor 1994) and may positively correlate with moisture (Xu & Qi 2001b). The extremely low moisture content in the summer at our site may explain the low Q_{10} value. This may be partially verified by the factor that the slightly decreased daily mean CO_2 efflux (Fig. 5.2b) correlates better with the slightly decreased daily mean moisture (Fig. 5.2d) than with the daily mean temperature (Fig. 5.2c). The high correlation between CO_2 efflux and soil temperature may explain well the diurnal patterns of CO_2 efflux driven by soil temperature, but not seasonal patterns, when moisture may be an important driven factor and change with seasons.

By plotting soil CO_2 efflux against soil temperature at different depths, we found the correlation to be highest at the depth of 8cm. The exponential curves of soil CO_2 efflux vs. soil temperature yielded R^2 of 0.78 and Q_{10} of 1.17 at the depth of 2cm, and R^2 of 0.64 and Q_{10} of 1.54 at the depth of 16cm. This indicated that the Q_{10} value increased with soil depth. The less constraint in moisture and more heat capacity at the deep soil may explain the higher temperature sensitivity of CO_2 efflux than that at the top soil.

To validate the estimated CO_2 efflux results, we used simultaneous and manually-measured data to compare with estimated ones. We measured the CO_2 efflux of two locations close to the automated CO_2 sensors but did not disturb them on the day 200, 214, and 235. Each day we had three measurements. The average of two locations was used to represent the CO_2 flux diffused from the soil where we buried CO_2 sensors. A linear relationship was found between measured efflux and estimated efflux (using the Millington-Quick model) with a slope = 0.907, intercept = -0.0348, and R^2= 0.84 (Fig. 5.5).

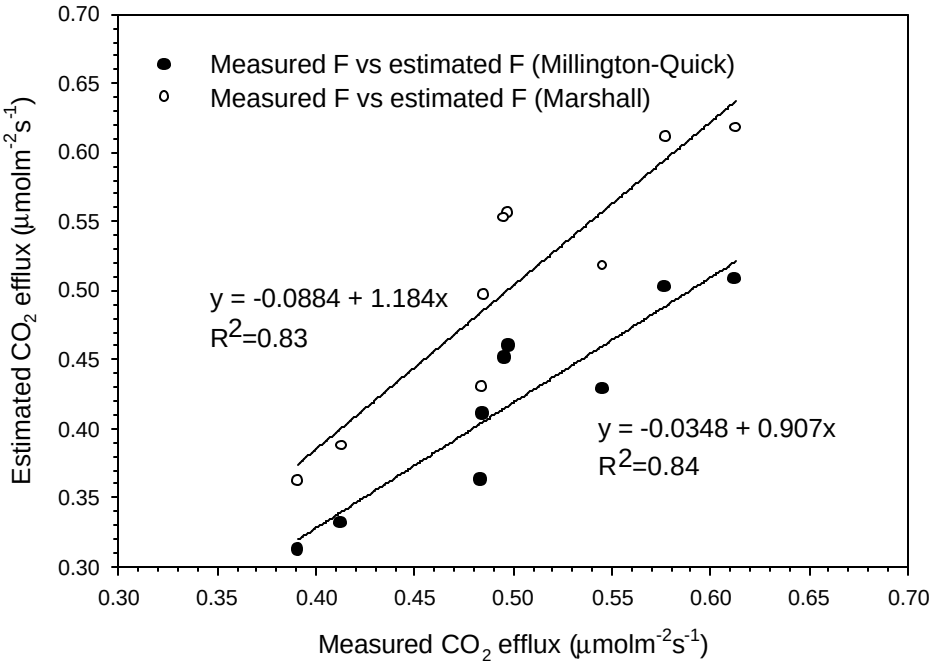

Fig. 5.5 Directly measured CO_2 efflux vs. estimated CO_2 efflux by the Millington-Quick model and by the Marshall model. The two straight lines are fitted regression lines.

The estimated CO_2 efflux is correlated well with measured data, but it is about 9% less than the measured ones. The method by which we computed diffusivity may explain this systematic difference. We selected the Millington-Quick model to calculate the tortuosity factor x, or the ratio of gas diffusion coefficient D_s/D_a. Sallam et al. (1984) plotted five models and compared the theoretical ratios including the Penman model, the Burger model, the Currie model, the Marshall model, and the Millington-Quick model, in the order from the highest value of x to the lowest value. They found that when the volumetric air content is less than 30%, the results of the Millington-Quick model is the lowest compared with other models. In addition to application of the Millington-Quick model, we used the Marshall model, the nearest model to the Millington-Quick model, to compute diffusivity and then CO_2 efflux in comparison with the result from the Millington-Quick model. As indicated in Fig. 5.5, the results from the Marshall model are systematically greater than measured ones by about 18%. The measured result falls between the Marshall model and Millington-Quick model. This may suggest that the difference between our estimated efflux and measured efflux comes from the diffusivity calculation, not from the CO_2 gradient measurement and computing. Further studies are suggested to modify the parameters of diffusivity models at our site so that we may improve CO_2 efflux results.

4. Conclusions

We describe a simple technique to measure continuously soil CO_2 profile by burying small CO_2 sensors at different soil depths. After calculating soil CO_2 diffusivity, we estimated CO_2 efflux, which is mainly from heterotrophic respiration, in a dry season in a Mediterranean savanna ecosystem in California. Between day 200 and 235 in 2002, the daily mean CO_2 concentration averaged 396 $\mu mol\ mol^{-1}$ at the depth of 2cm; the daily mean CO_2 concentration decreased from 721 $\mu mol\ mol^{-1}$ to 611 $\mu mol\ mol^{-1}$ at 8cm depth, and from 1044 $\mu mol\ mol^{-1}$ to 871 $\mu mol\ mol^{-1}$ at 16cm depth. Unlike the seasonal patterns of the soil CO_2 profile with small variation, the diurnal variation of soil CO_2 profile was significant and correlated well with soil temperature. During the time 14:30-16:30 when soil temperature is the highest within a day, the 8cm curve and 16cm curve reach the peak values, while the 2cm curve has the lowest value during this time.

The vertical CO_2 gradient at a certain time was approximately a constant when the depth is less than 16cm, but the gradient varies over time. By running the Millington-Quick model, we found soil CO_2 diffusion coefficient ranged from 2.293 mm^2s^{-1} to 2.544 mm^2s^{-1} with a mean of 2.425 mm^2s^{-1}. The daily mean values of CO_2 efflux slightly decreased from 0.43 $\mu mol\ m^{-2}s^{-1}$ to 0.33 $\mu mol\ m^{-2}s^{-1}$ with a mean of 0.37 $\mu mol\ m^{-2}s^{-1}$ or 0.0318 $mol\ m^{-2}day^{-1}$. The diurnal variation of CO_2 efflux was more significant than day-to-day variation. The diurnal variation of soil CO_2 efflux ranged from 0.32 ± 0.023 $\mu mol\ m^{-2}s^{-1}$ to 0.45 ± 0.026 $\mu mol\ m^{-2}s^{-1}$. Soil CO_2 efflux increased after 9:00 and reached the

peak value at about 14:30-16:30. This pattern corresponded well with the increase in soil temperatures during this time.

By plotting CO_2 efflux vs. soil temperature, we found CO_2 efflux exponentially correlates with soil temperature at the depth of 8cm with R^2 of 0.86 and Q_{10} of 1.27 in the summer dry season. The Q_{10} value increases with soil depth of temperature measurements. The extremely low moisture content in the summer at our site may explain the low Q_{10} value. The high correlation between soil CO_2 efflux and temperature may be due to the undisturbed and continuous measurements of heterotrophic respiration from soil. The diurnal pattern of CO_2 efflux shows a high correlation with soil temperature but the seasonal pattern does not show this because soil moisture is another control factor for seasonal pattern.

By comparing estimated CO_2 efflux with measured CO_2 efflux data, we concluded that the described CO_2 sensors and diffusion method yielded satisfactory results. This simple and commercially available technique provides continuous soil CO_2 profiles and thus help us estimate soil CO_2 production and efflux. It also helps to decompose NEP data, which is measured from the eddy covariance method. It may be also useful for calibrating and correcting eddy covariance data by providing CO_2 concentration at various depths of soil as well as at the surface layer.

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Conclusions

Soil respiration is controlled by both temperature and moisture in ecosystems under the Mediterranean climate. The temperature sensitivity (Q_{10}) of soil respiration is relatively low in the dry season. Diurnal patterns of soil respiration can be explained by the Q_{10} function with less moisture variability, but soil moisture is very important in explaining the seasonal patterns of soil respiration. A bi-variable model including driven factors of soil temperature and moisture explains the temporal variation of soil respiration.

Partitioning soil respiration into root respiration and microbial decomposition is important because these two processes may be driven by different functional forms and variables. Microbial decomposition is driven by soil temperature and moisture, but root respiration may be controlled by plant physiology and phenology in addition to environmental conditions. The ratio of root respiration to total soil respiration is not a constant over seasons.

Understanding spatial variation of soil respiration is important for extrapolating soil respiration. The spatial variation of soil respiration within a young plantation and between a young plantation and a mature one could be explained by stand density, tree size, soil temperature, and moisture. Modeling spatial variation between young and mature plantations make it feasible to understand soil carbon dynamics and impacts of soil respiration from management practices, which change the spatial patterns.

Forest thinning, an important forest management practice, will affect soil respiration. Forest thinning changes stand density, energy balance, and root distribution,

and thus changes the magnitude of soil respiration. But the sensitivity of soil respiration to temperature and moisture may not vary with the thinning. The difference of soil respiration before and after the thinning can be explained by the change of root density, soil temperature and moisture.

Portable chamber measurements of CO_2 fluxes are useful to quantify the spatial variation of soil respiration. But chamber measurements are not able to provide high-resolution temporal patterns. A newly developed flux measurement system which involves burying small CO_2 sensors in soils and measuring soil CO_2 gradients can generate high temporal resolution CO_2 efflux data, which can be used to understand mechanisms of soil CO_2 production and transport, and help to decompose and validate eddy covariance measurement data.