

Chapter 11

Quantifying Soil Respiration at Landscape Scales

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Abstract Soil CO₂ efflux, or soil respiration, represents a substantial component of carbon cycling in terrestrial ecosystems. Consequently, quantifying soil respiration over large areas and long time periods is an increasingly important goal. However, soil respiration rates vary dramatically in space and time in response to both environmental conditions and biological activity. Our objective in this chapter is to characterize the challenges in capturing this variability and accurately estimating soil respiration. We first review approaches to collecting individual soil respiration measurements, with particular focus on their applicability to landscape-scale studies. We then identify the major sources of variability in respiration rates and discuss how individual measurements can be structured in space and time to capture that variability. Lastly, we present a set of recommendations for an integrated approach that combines spatially distributed measurements with temporally intensive measurements to develop annual, landscape-scale soil respiration estimates.

Keywords Net ecosystem carbon balance, soil carbon dioxide efflux, spatial and temporal scaling

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143

11.1 Introduction

Soil surface CO₂ efflux is the release of carbon dioxide from the soil surface to the atmosphere and is commonly called soil respiration. This flux comprises 50–80% of ecosystem respiration (Davidson et al. 2002a, Giardina and Ryan 2002) and consists of respiration from roots and associated mycorrhizae and from heterotrophic microbes using root exudates and recent and older organic material as an energy substrate (Wiant 1967a, Anderson 1973). Instantaneous CO₂ flux rates range from near zero during winter to >10 μmol m⁻² s⁻¹ for high productivity ecosystems during the growing season (Raich et al. 2002) and annual estimates range from less than 200 g C m⁻²year⁻¹ in xeric systems to nearly 2000 g C m⁻²year⁻¹ in wet temperate forests (Hibbard et al. 2005).

As with many ecological processes, interest in soil respiration has shifted from addressing site-specific or treatment-related questions to characterizing respiration rates for large areas over long time periods (Underwood et al. 2005). Large-area and long-term estimates of soil respiration are needed to: (1) reduce uncertainties in landscape, regional and global carbon budgets (Law et al. 2002), (2) characterize the spatial and temporal dynamics in plant physiological processes, including belowground carbon allocation (Giardina and Ryan 2002), (3) facilitate direct comparisons with eddy-covariance measurements (Pypker and Fredeen 2002, Kutsch et al. 2005, Tang and Baldocchi 2005, Tang et al. 2005a), and (4) provide parameterization and validation for ecological simulation models (Chen et al. 2000, Soegaard et al. 2000, Tate et al. 2000). There is also a need to improve understanding of mechanisms controlling soil CO₂ fluxes through experimentation to advance models that provide continuous estimates of fluxes and processes contributing to net ecosystem exchange of CO₂.

Large-area and long-term estimates of soil respiration are complicated by the high variability of soil respiration in both space and time and by the limited spatial and temporal extent of actual measurements. Soil respiration has been shown to vary dramatically in temporal scales ranging from hours (Ekblad et al. 2005) to years (Raich et al. 2002) and in spatial scales ranging from meters (Tang and Baldocchi 2005) to regions (Reichstein et al. 2003). In addition, individual soil respiration measurements typically cover less than 0.25 m² and represent only a snapshot of a few minutes (Lavigne et al. 1997, Murthy et al. 2003). These two realities complicate the process of generating accurate large-area and long-term soil respiration estimates because, unlike many ecological processes, soil respiration has not been clearly linked to aboveground structural or functional patterns (Fahey et al. 2005) that are easily mapped with remote sensing (although see Reichstein et al. 2003, Tang et al. 2005a). Studies are beginning to explicitly characterize the scales and drivers of this spatial and temporal variability and these results will undoubtedly contribute to the up-scaling of soil respiration.

Our objectives in this chapter are: (1) to briefly describe the methods for measuring soil respiration, focusing on the applicability of these methods to generating landscape-level annual estimates, (2) to identify the sources of variability in soil respiration and characterize approaches to scaling soil respiration over space and time

and (3) to recommend standard methods for quantifying annual, landscape-level soil respiration fluxes. Our overall goal is to address the question: how do we obtain large-scale long-term estimates of a flux that can only be measured for very small areas over very short intervals? Several detailed reviews have examined small-scale soil respiration methods and controls over soil respiration (Hanson et al. 2000, Rustad et al. 2000, Davidson et al. 2002b, Hibbard et al. 2005, Ryan and Law 2005).

Soil respiration has been recognized as a primary component of ecosystem carbon dynamics for several decades (e.g. Lundegardh 1927, Witkamp 1966, Schulze 1967, Wiant 1967b, c, Reiners 1968). Initial measurements of soil respiration provided insight into relative rates between locations and through time, but were not able to accurately quantify absolute rates. As interest in quantifying absolute rates of soil respiration grows, researchers are becoming increasingly critical of measurement techniques. Laboratory (Nay et al. 1994, Widen and Lindroth 2003, Butnor and Johnsen 2004) and field (Le Dantec et al. 1999, Janssens et al. 2000, Pumpanen et al. 2003) examinations have led to modifications of existing approaches and entirely new techniques to measure soil respiration. Three general methods for quantifying soil respiration are currently in use: chambers using a closed system (dynamic or static), chambers using an open system, and flux gradient sensors. In addition to these techniques, some approaches have arisen for quantifying soil respiration under snow.

11.2 Chambers Using a Closed System

11.2.1 Approach

Closed chamber systems for measuring soil respiration are currently the most common and represent the only commercially available systems. Closed systems estimate flux by measuring change in CO_2 concentration inside a closed chamber over the soil surface, usually fixed onto a plastic ring embedded into the soil. These systems are named 'closed' because no air is exchanged between the chamber and the outside environment during measurement. However, between measurements the system is open to the environment. Most closed systems utilize a dynamic approach that continually circulates air from the chamber to an infrared gas analyzer and back to the chamber (Norman et al. 1992). Other systems avoid circulating air and use a static approach that measures CO_2 in the chamber by extracting and analyzing gas in a syringe (Parkinson 1981), absorbing CO_2 in soda lime within the chamber (Edwards 1992), or, in the future, using laser spectroscopy (Gianfrani et al. 2004) or small infrared gas analyzers (for example, Vaisala CARBOCAP® Carbon Dioxide Probe GMP343, Vaisala Group, Vantaa, Finland) inside the chamber to continuously monitor CO_2 concentration. Static systems have been demonstrated to underestimate high fluxes and overestimate low fluxes (Nay et al. 1994, Pongracic et al. 1997, King and Harrison 2002), perhaps

because of problems with the rate of absorption of CO_2 onto the soda lime, or because of high CO_2 concentrations inside the chamber impeding diffusion.

Regardless of the approach, all closed systems quantify the rate of increase in CO_2 concentration ($\mu\text{molCO}_2 \text{ mol}^{-1} \text{ air s}^{-1}$) inside a chamber of known volume. This rate is divided by the volume (mol) of air in the chamber to yield flux in CO_2 per unit time ($\mu\text{molCO}_2 \text{ s}^{-1}$), and is divided by the surface area covered by the chamber to estimate temporal CO_2 flux per area ($\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

11.2.2 Challenges

Two challenges are inherent in closed systems. First is that the estimated soil respiration depends on the total volume of the chamber, tubing, IRGA and soil pore space (in moles of air). Soil pore space may influence the calculated efflux rate by serving as additional volume where CO_2 concentration will increase during measurement, effectively increasing the total system volume and therefore decreasing estimated flux rates. Consequently, soils with extremely high soil pore space will require more CO_2 efflux to yield the same change in CO_2 concentration, which is the measured indicator of efflux rate in closed systems. Although some studies use a nominal system volume calculated from the above-soil collar and chamber volume, plus tubing and IRGA gas path, effluxed CO_2 is also stored in the soil pore space. Rayment (2000) estimated soil pore space by combining CO_2 efflux rate and initial rate of change in CO_2 concentration in an open system. Results from this study indicate that the equivalent depth of air in the soil averaged 15.5 mm, which translates into underestimation of soil respiration of 9.1% if soil pore space were ignored in closed systems.

Another approach to quantifying the total system volume is to add CO_2 at a constant known rate to the closed system during measurement and compare the calculated flux from a paired measurement without this standard addition (M.G. Ryan personal communication). In this “standard addition” approach, the total system volume (mol air) is calculated by dividing the constant CO_2 addition ($\mu\text{molCO}_2 \text{ s}^{-1}$) by the amount that this addition increases the rate of change in CO_2 concentration ($\mu\text{molCO}_2 \text{ mol}^{-1} \text{ air s}^{-1}$). This increased rate of change is simply the rate of change with standard addition minus the rate of change without standard addition. Regardless of the approach, closed systems require accurate representation of total system volume. The magnitude of pore space depends on soil properties, including moisture, texture and bulk density, which can vary through time and between sites. Thus, the importance of quantifying total system volume will depend on the ecosystem; consistently wet areas with fine textured soils may not require quantifying pore space whereas locations with coarse textured soils and high seasonal variation in soil moisture likely require multiple measures of pore space in each year (Butnor and Johnsen 2004, Butnor et al. 2005). Measuring the volume of each measuring point will yield more precise flux estimates than assuming a standard volume across the site.

The second challenge for closed systems is the possibility of pressure differences between inside and outside the chamber influencing perceived CO₂ flux rates. Soil pore space has very high CO₂ concentrations, which represent a large reservoir of CO₂. High pressures outside the chamber, caused by variable wind speeds, can force CO₂-rich air from the soil pore space into the chamber, increasing CO₂ concentration and artificially elevating estimates of soil respiration (Davidson et al. 2002b, Bain et al. 2005). As a consequence, most closed systems have been equipped with vents to equalize pressure; however, some vented systems have been shown to underestimate soil respiration, possibly as a result of leaking CO₂ through the vent (Conen and Smith 1998).

11.3 Chambers Using an Open System

11.3.1 Approach

Chambers using the open system estimate flux by precisely measuring the rate of airflow through the chamber and the inlet and outlet CO₂ concentrations at equilibrium (Fang and Moncrieff 1996, Liang et al. 2004, Butnor et al. 2005). These are called 'open' systems because air is exchanged between the outside and the chamber. Open systems that are operated for continuous measurements (for example, Palmroth et al. 2005) typically have the chamber closed during the entire measurement period. Problems with changing the environment during long-term measurements are managed by alternating the chamber between two adjacent collars every two days.

When open chambers are initially placed over the soil surface, this difference is zero and as CO₂ builds up in the chamber, the difference increases until it reaches a steady state at which CO₂ leaving the chamber is in equilibrium with CO₂ efflux from the soil. At this point, the difference in CO₂ concentration ($\mu\text{molCO}_2 \text{ mol}^{-1}\text{air}$) between air in and out of the chamber can be multiplied by the flow rate (mol air s^{-1}) and divided by the soil surface area covered by the chamber to calculate the soil respiration rate ($\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Open chambers require a reservoir of input gas of consistent CO₂ concentration in order to avoid fluctuations in the reference CO₂ concentration that will increase measurement variability.

11.3.2 Challenges

One potential challenge associated with the open chamber approach is the possibility of the elevated CO₂ concentrations in the chamber inhibiting CO₂ efflux from the soil. While this inhibition could also occur in closed systems, the potential for bias in open systems is greater because the CO₂ concentration inside the chamber is elevated for the duration of the measurement, whereas it is only elevated

at the end of the measurement in the closed system. Observational evidence for elevated CO₂ concentration negatively impacting efflux is limited (Amthor 2000), but theoretically, elevated chamber CO₂ concentrations could decrease microbial and root metabolic activity and/or slow CO₂ diffusion from the soil by decreasing the gradient between CO₂ concentrations in soil pore space versus chamber air space. The actual consequence may be a combination of these two effects, decreasing CO₂ diffusion from lower layers. The primary obstacle to the open chamber approach is the practical difficulty of using it to acquire enough measurements to characterize a landscape. The instruments and air reservoir utilized by the open chamber method are more difficult to transport than the closed chamber apparatus. In addition, the open chamber approach requires several minutes to obtain a measurement, which represents substantial time investment. The combination of these two practical limitations makes open chambers difficult to apply to landscape-scale studies. However, the open chamber approach does have the advantage that it maintains relatively constant and ambient CO₂ concentration inside the chamber, which makes it well suited to collecting continuous measurements (discussed further below).

11.4 Soil CO₂ Gradient

11.4.1 Approach

An alternative to chamber methods for measuring soil respiration is to measure CO₂ concentration at multiple depths in the soil profile and use this gradient along with the CO₂ diffusivity to model soil CO₂ efflux (de Jong and Schapper 1972, Wagner and Buyanovsky 1983, Burton and Beauchamp 1994, Tang et al. 2003, Jassal et al. 2005). Quantifying the vertical gradient in soil CO₂ concentration is accomplished by burying small infrared detectors in the soil with openings to the soil pore space at specified depths. CO₂ diffusivity is calculated from soil properties and CO₂ diffusion coefficient in air (measured empirically for reference conditions and corrected for on-site conditions) (Tang et al. 2003).

11.4.2 Challenges

Although the CO₂ gradient approach avoids many of the challenges inherent in chamber measurements, it is limited by the fine spatial extent of its measurements, the difficulty of collecting multiple measurements across a landscape, and the potentially high variability of CO₂ diffusivity (Tang et al. 2003). The set of sensors in the CO₂ gradient method sample only a very small area of soil surface, requiring many more measurements to accurately characterize a landscape, especially in

ecosystems with high spatial variability at small scales. In addition, the sensors for the CO₂ gradient approach must be buried prior to measurement (to avoid disturbing the soil CO₂ concentrations and to allow CO₂ concentrations inside the sensors to reach equilibrium with the soil.) Consequently, individual sets of sensors are required for each sampled location, making large sample sizes financially unfeasible. Lastly, the estimates for soil respiration from the CO₂ gradient approach utilize CO₂ diffusivity, which depends on soil and air conditions that can both vary in space and time. Accurately characterizing CO₂ diffusivity at multiple locations over several time periods could dramatically increase the difficulty of using the CO₂ gradient approach to estimate landscape-scale soil respiration.

11.5 Under-Snow Measurements

11.5.1 Approach

Many ecosystems are characterized by long, cold winters and sufficient snowfall to create snowpack that persists for many months (Sommerfeld et al. 1993). Soil conditions under snow are highly variable, but can frequently include temperatures above freezing and/or high moisture availability, creating an environment suitable for respiration (Brooks et al. 1996, Brooks et al. 1997). Consequently, quantifying annual soil respiration in snowy locations requires measurement of soil CO₂ efflux under the snow. One technique for quantifying under-snow soil respiration is to use the difference between the CO₂ concentration above and below the snow and properties of the snowpack to model CO₂ efflux through the snow (Hubbard et al. 2005). Soil surface CO₂ concentrations are measured by inserting a probe through the snowpack to the soil surface. The probe is open to the air at the bottom, and contains tubing that is connected to a backpack gas analyzer and pump. Using Fick's first law, flux can be calculated from snowpack depth, porosity, and temperature and CO₂ molecular density and diffusion in air and tortuosity (Massman et al. 1995).

11.5.2 Challenges

Individual measurements with this under-snow method are relatively rapid, requiring less than a minute each, which facilitates the collection of numerous points across large areas. However, this technique requires enough snowpack to create a substantial gradient in CO₂ concentration between the soil surface and the snow surface, meaning that it is only feasible for locations with substantial snowfall that creates consistent snowpack across the landscape and throughout the winter. In addition, this approach could be sensitive to snowpack compaction caused by the person conducting the measurements, which could either increase perceived respiration

by increasing the barrier to CO₂ diffusion, or decrease the perceived respiration rate by decreasing the barrier. Some studies have found that under-snow respiration rates are highly susceptible to pressure pumping from varying wind speeds (Massman et al. 1997, Takagi et al. 2005). This suggests the need for many measurements, which is especially true in this method where each measurement represents only a very small point of soil surface. Lastly, this method is relatively new, and at least one study has suggested that it may underestimate soil CO₂ efflux (Takagi et al. 2005).

11.6 Generating Landscape and Annual Estimates

11.6.1 Sources of Variability in Soil Respiration

Variability in soil respiration can be conceptualized as temporal variation, which represents differences through time at individual locations, and spatial variation, which represents differences between locations (Fig11.1). Spatial variation in soil respiration occurs at scales as small as a meter (Murthy et al. 2003), where topography and vegetation patch structure influence microclimate, to intermediate scales where soil properties and ecosystem type impact carbon substrate and root density/activity (King et al. 2001, Sulzman et al. 2005), to large scales where climatic conditions dictate overall conditions (Campbell and Law 2005). Likewise, temporal variation in soil respiration ranges from high frequency, short-term variations in wind speed that impact pressure pumping (Massman et al. 1997) through intermediate scales of hours to days where pulse precipitation events and diurnal temperature

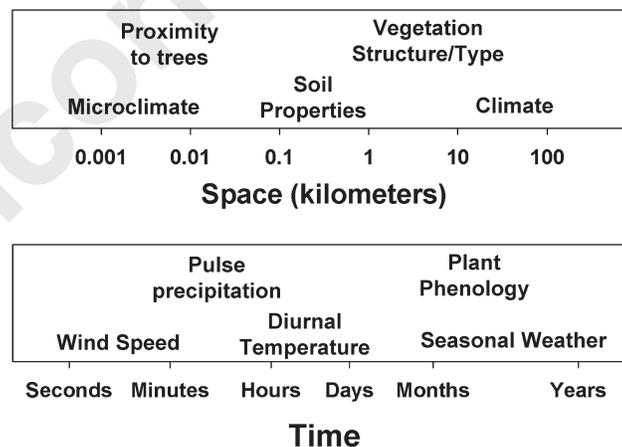


Fig. 11.1 Sources of variability in soil respiration across space and time

fluctuations influence decomposition rates and plant activity (Kabwe et al. 2005, Tang et al. 2005b) to seasonal weather and plant phenological variations that occur across months to years (Chambers et al. 2004, Hubbard et al. 2005, Sulzman et al. 2005).

11.6.2 Approaches to Extrapolating Soil Respiration

Soil respiration varies through time and space in response to soil temperature, soil moisture and vegetation composition. In many forest systems where soils rarely become extremely dry, soil temperature alone is a relatively good predictor of soil respiration rates and has been frequently used to estimate soil respiration (Rodeghiero and Cescatti 2005). In arid and semi-arid ecosystems, where soil moisture can decrease to levels that limit microbial and plant activity, variation in soil moisture must be considered to accurately estimate annual soil respiration (Chambers et al. 2004, Xu et al. 2004). Plant activity also influences soil respiration by dictating diurnal and seasonal trends in root respiration (Wang et al. 2005) and by influencing spatial and temporal patterns of microclimatic soil temperature and moisture status (Palmroth et al. 2005). Generating landscape-level annual or multi-year estimates of soil respiration requires knowing what influences soil respiration and at what scales those drivers fluctuate.

11.6.2.1 Temporal Scaling

Previous studies have identified three general temporal scales at which variation in soil respiration occurs: seasonal fluctuations due to climate and plant phenology (Rayment and Jarvis 2000), diurnal patterns controlled by temperature and plant activity (Tang et al. 2005a), and episodic peaks lasting for hours to days that are driven by pulse weather events (Reth et al. 2005). These results suggest that soil respiration measurements should include at least some measurements at each of these scales.

Some studies have generated annual estimates of soil respiration by using a combination of individual monthly soil respiration measurements (one measure per month) along with a few isolated diurnal measurements of soil respiration (at least two measures per day) (Tang and Baldocchi 2005). The monthly measurements provide insight into the seasonal variation and the diurnal measurements quantify fluctuations within individual days. These measures are typically incorporated into a simple statistical model for estimating soil respiration based on soil temperature (Rayment and Jarvis 2000, Zheng et al. 2005a) and occasionally soil moisture (Chambers et al. 2004, Martin and Bolstad 2005), possibly with separate functions for diurnal vs. seasonal fluctuations in these drivers (Litton et al. 2004). This approach has the advantage of being relatively easy to implement in the field, but relies on the assumption that the monthly measures are frequent enough to capture

seasonal trends, and on the assumption that diurnal patterns do not dramatically change throughout the year. In addition, this approach ignores the potentially important effects of pulse weather events, which have been shown to influence soil respiration in many ecosystems (Xu et al. 2004).

Other studies have utilized near-continuous measurements for all or part of the year to characterize temporal patterns of soil respiration (Liang et al. 2003, Butnor et al. 2005). This technique requires an automated system for measuring soil respiration, which can be applied to the chamber approach or the CO₂ concentration gradient approach. For the chamber approach, an automated system can maintain multiple chambers and requires hardware for closing and opening the chambers before and after the measurements, as well as a pump, gas analyzer and control system for dictating gas flow and data storage. This automated system cycles through the chambers collecting measurements for each chamber approximately every 1–1.5 hours. Automated systems utilizing closed systems can estimate total chamber volume (and thus overcome the primary challenge of closed chambers discussed above) by adding a standard addition of CO₂ once daily. Continuous measurements from the CO₂ concentration gradient approach are simpler, requiring only multiple buried detectors and a control system for data storage (Tang et al. 2003), but they incorporate the challenge of limited spatial extent, as mentioned above. Regardless of the approach, continuous or near-continuous measurements provide detailed insight into the temporal dynamics of soil respiration and the relationship between respiration rates and driving variables at all scales, including unpredictable pulse events. The only disadvantage of continuous measurements is the expense and operational time required to establish and maintain the automated system. A commercial automated soil respiration is now available to simplify capturing information on temporal variability (LICOR 8100, LICOR, Inc, Lincoln, NE, USA).

11.6.2.2 Spatial Scaling

Previous studies have examined the effect of spatial patterns of soil temperature, soil moisture and vegetation composition on soil respiration and used these relationships to estimate soil respiration for areas ranging from plots to the globe. At the smallest scale, proximity to trees has been shown to influence soil respiration rates through root respiration and by intercepting precipitation (Tang and Baldocchi 2005). Other studies have chosen to account for this variability by examining overall variation within individual plots and quantifying the number of soil respiration measurements necessary to accurately characterize the plot. Estimates range from 25–30 points/ha in forest plantations to 40–50 points/ha in natural forests (Davidson et al. 2002b, Yim et al. 2003, Adachi et al. 2005) to generate an estimate with a standard error that is within 10% of the mean. The number of samples required may be lower under snowpack (Hubbard et al. 2005) when plant activity is minimal and temperature/moisture conditions are more spatially homogeneous. The sample size required to characterize a given area could likely be decreased by identifying controls

over variability at smaller scales and quantifying the distribution of those controls within individual plots, and by using larger collars (such as the 200 mm collar for the LICOR 8100, or even 250 mm collars).

At slightly larger spatial scales soil respiration is influenced by tree density, live biomass, species composition and vegetation type (Litton et al. 2003, Bolstad and Vose 2005, Campbell and Law 2005, Zheng et al. 2005b) and soil properties (Dilustro et al. 2005). Although many studies have observed these controls, few studies have attempted to directly scale ground measurements to estimate soil respiration for areas as large as entire watersheds. One exception is Fahey et al. (2005) who estimated soil respiration for the Hubbard Brook Experimental Forest using spatially dispersed periodic measurements across the watershed and found strong relationships between temperature and respiration rate but no clear relationships between forest composition and respiration. Thus, Fahey et al. (2005) quantified the relationship between respiration and soil temperature and estimated annual flux from continuous measurements of soil temperature. Large-scale estimates of soil respiration have been modeled from relationships with air temperature, precipitation and vegetative productivity (Aikio et al. 2000, Raich et al. 2002, Reichstein et al. 2003). However, there is some evidence that relationships with temperatures from the air or soil surface alone may not adequately capture the temperature dynamics that influence soil respiration (Reichstein et al. 2005).

11.7 Recommendations

Our recommendations include both a suggested protocol for collecting individual soil respiration measurements and a strategy for structuring these measurements in space and time to generate landscape-level annual soil respiration budgets.

11.7.1 Protocol for Individual Measurements

We propose using permanent soil collars and a closed system gas exchange measurement, with a measurement protocol similar to that used by the current LiCOR LI-6400 measurement system and soil chamber. The advantages of this approach are (1) the large chambers sample 6x the area of the standard LiCOR chamber and reduce within-plot variability (from a CV of ~100% to ~25% in a recent study (Ryan et al. unpublished data); (2) fixed chamber locations allow separation of environmental variability from spatial heterogeneity; (3) simple, quick measurements enable rapid sampling for spatial heterogeneity and allow the detection of flux differences among treatments or different vegetation conditions; (4) the closed system measurement is reliable for many soils (Butnor et al. 2006), although it tends to underestimate fluxes that are especially porous; and (5) scrubbing the CO₂ to below ambient levels prior to measurement and measuring CO₂ through ambient

levels has been shown to reduce bias from the accumulation of CO₂ in the chamber headspace. Disadvantages of the method are that measurements and models need to be developed to extrapolate between the point measurements in time, installation of collars may damage roots and time is needed for recovery, and the closed system approach can underestimate fluxes for some conditions.

11.7.1.1 Materials

Chamber collars are made from 10" (25 cm) inside diameter PVC sewer pipe with a bevel on the end to be inserted into the litter. Collar height is designed so that the lower part of the collar contacts a dense portion of the soil surface to minimize advective air flows and the upper portion is 5 cm above the litter surface. Typically, the collar is inserted through the litter and organic layer until the bottom contacts the mineral soil. We use cheap serrated knives to cut the litter around the collar and then insert the collar through the cut slot. We use a rubber mallet and a short piece of 2 x 4 on top of the collar to seat it into the mineral soil. Measurements are made using a homemade gas analysis system, with control provided by a Campbell data logger (23x or 10x) and the LiCOR 820 gas analyzer. The end cap is designed to fit the chamber collar. While we have not yet tested it, we believe that the LICOR 8100 with 200 mm diameter collars would be suitable for these measurements and the large collar should reduce measurement effort.

11.7.1.2 Measurement Protocol

The closed system estimates flux by measuring the rate of increase in CO₂ concentration ($\mu\text{mol mol}^{-1} \text{s}^{-1}$). Flux is calculated by using the standard addition protocol (outlined above) and should be completed often enough to capture temporal dynamics in soil water status, which can influence soil pore space. In the absence of standard addition volume estimates, system volume can be roughly estimated by summing the volume of component parts and adding an estimate of soil pore space. Temperature, pressure and collar dimensions must be known to calculate the molar volume of air in the chamber. Nominal volume is calculated using the volume of the chamber plus tubing plus LiCOR gas path (a constant) plus the volume of the collar above the litter (varies from collar to collar).

Face the chamber in the direction of the prevailing wind and measure ambient (air) CO₂ concentration. CO₂ concentrations in the chamber should center around this value, but in practice, this is difficult to exactly achieve given variability in flux rates. Choose values for the lower bound for CO₂ concentration during the scrub and the delay time to account for scrub overshoot that result in the measurement being taken while the internal CO₂ concentration crosses ambient. Higher fluxes require lower scrub values and shorter delay times. While LiCOR recommends averaging 2–3 readings per collar, we have found this variability trivial compared to the variability among collars (M.G. Ryan unpublished data); so we take one measurement per collar per sampling trip. Soil

(and perhaps litter) moisture and soil temperature are also measured for each chamber at depth(s) representative of soil carbon and rooting depth intensities.

11.7.2 Spatial and Temporal Sampling Strategy

Scaling soil CO₂ efflux measurements from instantaneous (or very short-term) measurements of small areas to landscape-scale annual soil respiration budgets requires addressing all of the sources of spatial and temporal variability. Partitioning variability into spatial and temporal components provides a starting point for understanding and managing this variation. Controls over spatial variability, like micro-environmental conditions, soil properties, ecosystem type and climate (not weather), must be spatially mapped across the landscape but need not be examined at multiple times throughout the year because these spatial controls may change over several years, but will be unlikely to change within individual years. However, controls over spatial variability can influence the temporal pattern of soil respiration (e.g. seasonal root respiration may differ between forests and meadows). Therefore, temporal variability must be characterized within each general category of spatial driver at a resolution that captures important seasonal, daily and possibly hourly fluctuations. Once this temporal variability is quantified, annual budgets can be generated for each spatial category and summed to yield landscape-scale estimates. To characterize both the spatial and temporal variability in soil respiration, we propose a protocol that includes spatially-distributed but infrequent sampling combined with a limited number of temporal intensive measurements.

11.7.2.1 Spatially Distributed Measurements

Within an individual plot, collars should be positioned using an unbiased method. We generally select a direction and distance from the plot center. Large logs and rocks should be avoided, as they make getting a seal difficult. If large logs and rocks are a substantial fraction of the surface (>10%), their area should be determined and the area represented by the collar samples adjusted during extrapolation because CO₂ will not diffuse through rocks or logs and will surface elsewhere. The number of collars that are necessary per subplot or plot will depend on the average variability within the subplots or plots. At our subalpine rocky mountain sites, we have observed within subplot coefficient of variability (CV) of approximately 26.7%. This suggests that, on average, seven collars would be required to get standard errors down to 10% (a somewhat arbitrary precision threshold chosen that can be varied as desired) of the mean within individual subplots (Fig.11.2). When we grouped all four subplots together our results indicate a CV of 34%, indicating that 11 collars per plot would achieve standard errors at 10% of the mean (Fig.11.2). We measure 12 collars per plot (3 per subplot) and as a result of the above variability results, we consider plots to be the experimental unit for soil respiration.

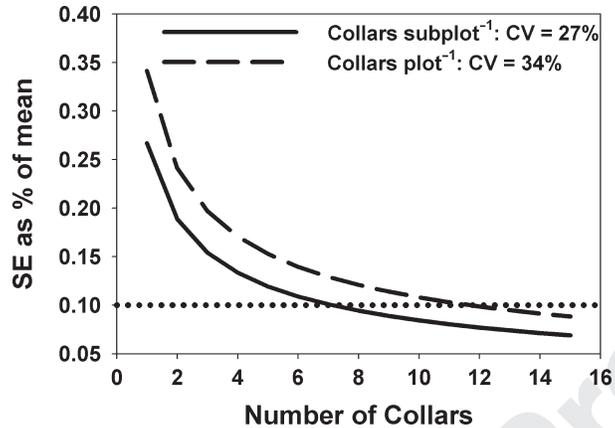


Fig. 11.2 Relationship between the number of collars within subplots or plots and soil respiration estimation accuracy, expressed as the standard error of individual collar measurements within either subplots (dotted line) or plots (solid line). Dotted line denotes SE = 10% of the mean

When attempting to estimate soil respiration for a large area, the purpose of plot locations is to characterize the spatial variation in soil respiration rates. These measurements should ideally span all the gradients in drivers of spatial variability. For example, we ensure that our plots include all the major plant communities and forest age categories and cover the elevation and aspect differences in the landscape. The number of plots required to characterize the entire landscape depends on the variability between plots. When treated independently, our subplots displayed a CV of 25%, suggesting that, if subplots were sufficiently sampled, only six subplots would be necessary to achieve a SE of 10% of the mean across the entire landscape (Fig. 11.3). We observed a CV of 18% between plots, indicating that three plots (or the equivalent of 12 subplots) would be required to achieve a SE of 10% of the mean (Fig. 11.3). At these spatially distributed locations, measurements should be collected at least several times throughout the year to get a reasonable measure of the relative respiration rate between points. We measure soil respiration once per month during the snow-free season and only 2–3 times during the winter when relatively consistent under-snow conditions create stable respiration rates.

11.7.2.2 Temporally Intensive Measurements

The purpose of these measurements is to characterize the temporal variability in soil respiration. They should be frequent enough to capture at least the diurnal fluctuations in soil respiration, and may need to be sampled at even higher frequency. In systems where pulse weather events are important, occasional diurnal

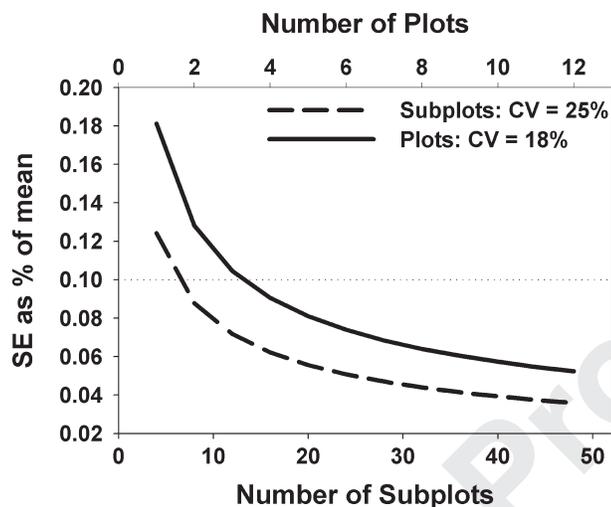


Fig. 11.3 Relationship between the number of plots or subplots and landscape-level soil respiration estimation accuracy, expressed as the standard error of subplots (dotted line) or plots (solid line). Dotted line denotes SE = 10% of mean

measurements are likely to miss the important consequences of these pulses. Even in ecosystems with relatively consistent weather conditions, the magnitude of diurnal variability in soil respiration may fluctuate throughout the year. Consequently, we suggest at least two diurnal collections per year (or an automated system), each consisting of soil respiration measurements every 2–4 hours for 24 hours. Placement of the diurnal collections within the landscape will depend on the sources of spatial variability, and should be located to span the major sources of spatial variability. For example, in a system where spatial variation is driven primarily by forest versus meadow, diurnal collections should sample from both forest and meadow. If elevation is the primary spatial driver, diurnal collections should be located at the top and bottom of the landscape. We utilize an automated system that samples from eight chambers divided between either forest and meadow or young and old stands, depending on the landscape.

11.8 Conclusions

Quantifying soil respiration at landscape scales is complicated by both the difficulties of accurately measuring soil respiration at a specific time and place and by the spatial and temporal variability inherent in soil respiration. Although multiple protocols for individual measurements have been developed, we recommend utilizing

closed chambers with volume estimation by standard addition. This protocol is cost effective, highly portable and generates consistent results. Variability in soil respiration rates is attributable to environmental conditions, vegetation composition and abundance, and soil substrate quality. We maintain that accurate estimates of annual soil respiration at large scales will require a sampling strategy that captures both the spatial and temporal components of variation. We recommend a landscape-level sampling protocol that is a practical approach to capture important variability of soil respiration. The temporally continuous measurements at a few locations can be converted into annual soil respiration estimates, which, when combined with the infrequent, spatially distributed measurements can be scaled to the entire landscape.

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