Biogeochemistry (2005) 73: 3–27
DOI 10.1007/s10533-004-5167-7
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Interpreting, measuring, and modeling soil respiration

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Key words: Belowground carbon allocation, Carbon cycling, Carbon dioxide, CO_2, Infrared gas analyzers, Methods, Soil carbon, Terrestrial ecosystems

Abstract. This paper reviews the role of soil respiration in determining ecosystem carbon balance, and the conceptual basis for measuring and modeling soil respiration. We developed it to provide background and context for this special issue on soil respiration and to synthesize the presentations and discussions at the workshop. Soil respiration is the largest component of ecosystem respiration. Because autotrophic and heterotrophic activity belowground is controlled by substrate availability, soil respiration is strongly linked to plant metabolism, photosynthesis and litterfall. This link dominates both base rates and short-term fluctuations in soil respiration and suggests many roles for soil respiration as an indicator of ecosystem metabolism. However, the strong links between above and belowground processes complicate using soil respiration to understand changes in ecosystem carbon storage. Root and associated mycorrhizal respiration produce roughly half of soil respiration, with much of the remainder derived from decomposition of recently produced root and leaf litter. Changes in the carbon stored in the soil generally contribute little to soil respiration, but these changes, together with shifts in plant carbon allocation, determine ecosystem carbon storage belowground and its exchange with the atmosphere. Identifying the small signal from changes in large, slow carbon pools in flux dominated by decomposition of recent material and autotrophic and mycorrhizal respiration is a significant challenge. A mechanistic understanding of the belowground carbon cycle and of the response of different components to the environment will aid in identifying this signal. Our workshop identified information needs to help build that understanding: (1) the mechanisms that control the coupling of canopy and belowground processes; (2) the responses of root and heterotrophic respiration to environment; (3) plant carbon allocation patterns, particularly in different forest developmental stages, and in response to treatments (warming, CO_2, nitrogen additions); and (4) coupling measurements of soil respiration with aboveground processes and changes in soil carbon. Multi-factor experiments need to be sufficiently long to allow the systems to adjust to the treatments. New technologies will be necessary to reduce uncertainty in estimates of carbon allocation, soil carbon pool sizes, and different responses of roots and microbes to environmental conditions.

Introduction

Belowground processes exert a large control on terrestrial carbon cycling. Plants send an estimated 35–80% of the carbon fixed in photosynthesis belowground for root production and respiration, mycorrhizae, and root exudates (Raich and Nadelhoffer 1989; Davidson et al. 2002a; Giardina et al.

2003; Ryan et al. 2004), and also transfer about 10% of annual photosynthesis to aboveground litter (Raich and Nadelhoffer 1989). The carbon stored in litter and labile and recalcitrant soil carbon pools is a large fraction of the carbon stored in the ecosystem in forests (30–90%, Dixon 1994; Sun et al. in press) and in grasslands (>90%). In forests, the carbon stored in roots (mostly woody support structures) is also a large pool – about 20% of aboveground biomass (Jackson and Chittenden 1981; Misra et al. 1998). Changes in the belowground carbon pools can have a major impact on carbon storage in terrestrial ecosystems and change carbon flux to the atmosphere.

CO_2 efflux from the litter surface originating as plant and microbial respiration reflects this large belowground activity. This 'soil respiration' is the main pathway for carbon moving from the ecosystem to the atmosphere and can strongly influence net carbon uptake from the atmosphere, or net ecosystem production (NEP) – the balance between photosynthesis (GPP) and ecosystem respiration. Eddy covariance studies have shown that on average, 80% of GPP is respired back to the atmosphere (Law et al. 2002) and that ~70% of ecosystem respiration in temperate forests is from soil (Goulden et al. 1996; Law et al. 1999; Janssens et al. 2001). Respiration may be more important than photosynthesis in controlling interannual variability in NEP (Valentini et al. 2000).

The CO_2 produced at the soil surface results from several respiratory processes, making modeling and interpretation of data complicated. About half the soil respiration is derived from metabolic activity to support and grow roots and associated mycorrhizae (Hanson et al. 2000; Högberg et al. 2001). Most of the remainder is associated with heterotrophic respiration from microbial communities using recently produced organic material as an energy substrate (Trumbore 2000; Giardina et al. 2004). Only a small fraction (~10%) of soil respiration is derived from decomposition of older, more recalcitrant carbon compounds (Gaudinski et al. 2000; Trumbore 2000; Giardina et al. 2004). The proportion of soil respiration from autotrophic and heterotrophic contributions may vary seasonally and among ecosystems (Hanson et al. 2000). Across a range of studies, the heterotrophic contribution varied from 10 to 95% and averaged 54% annually and 40% during the growing season (Hanson et al. 2000).

Because of its major role in carbon loss from ecosystems, soil respiration has received much recent attention, and the number of studies of soil respiration has increased rapidly. However, this flurry of studies has uncovered many new problems and opportunities. How can we untangle the components of this complex flux to understand the underlying processes that contribute to it? What are the short-term and long-term controls over the component fluxes and how do we model them so that we can predict changes in carbon stored in the ecosystem and atmosphere? How do we make unbiased measurements? Would standardizing measurements and accompanying information yield broader understanding?

We convened a workshop in October, 2003 to address these conceptual, measurement, and modeling issues (Hibbard et al. 2004). The purpose of this introductory paper is to provide background and context for measuring and modeling soil respiration and belowground processes, and to synthesize and expand upon some of the ideas discussed at the workshop. Our objectives are to discuss: (1) the conceptual basis for using measurements of soil respiration to understand terrestrial ecosystem carbon cycling; (2) how observations can be used to assess ecosystem carbon fluxes; (3) how biological processes control CO_2 production (the timescales and magnitude of the fluxes from different components); (4) how wind and rain can decouple measured fluxes from biological production; (5) potential biases in measurement and sampling techniques; (6) experiments to define the controls over soil respiration; (7) modeling soil respiration; and (8) protocols for sampling, measurement, and reporting soil CO_2 fluxes (Appendix). Our paper is organized according to these objectives. It focuses on what we view as the background and critical issues for advancing understanding of soil respiration in ecosystem science, and is not intended to be an extensive review of the topic. For recent reviews and syntheses, see Raich and Potter (1995), Jackson et al. (1997), Gill and Jackson (2000), Hanson et al. (2000), Rustad et al. (2001), Davidson et al. (2002a), Pendall et al. (2004), and Hibbard et al. (this issue).

Conceptual basis for measurements of soil respiration to understand terrestrial ecosystem carbon cycling

Soil respiration is the major pathway for carbon exiting terrestrial ecosystems, and in many models and syntheses it has been treated as strictly a heterotrophic process, responding to temperature or moisture (for example, Kicklighter et al. 1994; Raich and Potter 1995). However, we now know that plant metabolism (Högberg et al. 2001) or the decomposition of recently produced organic material (Trumbore 2000; Giardina and Ryan 2002; Giardina et al. 2004) generates most of the 'soil' respiration and that soil respiration strongly reflects plant metabolism (Ekblad and Högberg 2001; Bowling et al. 2002). Changes in the recalcitrant soil carbon stocks – the largest C pools in soil and the soil pools most important to changes in ecosystem carbon storage and atmospheric CO_2 – contribute only a minor portion of soil CO_2 efflux at any point in time (Trumbore 2000; Giardina et al. 2004). These insights suggest that soil respiration is a good indicator of ecosystem metabolism but a poor indicator of changes in ecosystem carbon storage.

Measurements of soil respiration have great potential as an indicator of ecosystem metabolism and fine-scale process. Integrated measurements can be used to estimate belowground carbon allocation (Giardina and Ryan 2002), and can be coupled with estimates of canopy photosynthesis from eddy covariance measurements to rapidly increase our understanding of carbon allocation. High frequency measurements of soil respiration can help uncover

the environmental controls over decomposition (Irvine and Law 2002), and aid with understanding the links between above and belowground processes. High frequency measurements, coupled with measurements of carbon isotopes may also help reveal the source of the respired carbon (Goulden et al. 1998).

Soil respiration and aboveground processes are strongly linked, but the links can be complicated (Figure 1). Photosynthesis supplies carbon substrate for root metabolism and growth, and a decrease in substrate supply can decrease soil respiration within days (Högberg et al. 2001). In addition to this direct effect, the fraction of photosynthesis used belowground can vary with nutrition (Giardina et al. 2003), water availability (Stape 2002), and phenology. Many plants have a large carbohydrate storage capacity, which serves as a capacitor that can decouple photosynthesis and belowground processes (Bhupinderpal et al. 2003). Litter production and timing and allocation to roots, mycorrhizae, and exudates can also alter soil respiration and carbon storage belowground. These allocation changes are an important but poorly understood component of the terrestrial carbon cycle.

Soil respiration measurements by themselves are poorly linked to changes in belowground carbon pools or to the controls on such changes. Changes in carbon stored belowground take place when there are changes in three pools:

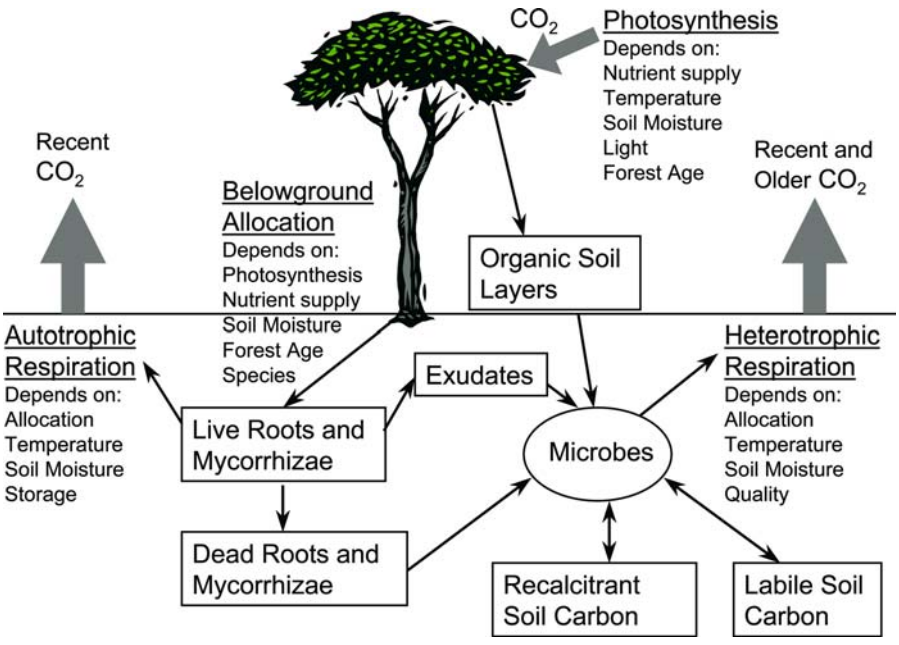

Figure 1. Conceptual model of the components and responses of CO_2 efflux from soil. Both the autotrophic and heterotrophic components of soil respiration are strongly controlled by substrate availability – phloem transport of carbohydrate supply for root and mycorrhizal respiration, and dead organic material for microbial respiration.

soil C stored in the mineral soil and the organic layers, generally modeled as a series of pools with different degrees of decomposability; live vegetation, because root biomass will vary with the amount of vegetation; and dead wood. Soil respiration is poorly linked with the size of these three components: coarse roots (>2 mm) contain most of the biomass and respiration from coarse roots is low (Ryan et al. 1996; Pregitzer et al. 1998; Vose and Ryan 2002), decomposition of the largest, recalcitrant soil C pools is slow (Giardina and Ryan 2000), as is decomposition of dead wood (Marra and Edmonds 1996; Bond-Lamberty et al. 2002). Root, mycorrhizal and rhizosphere respiration, together with decomposition of recently produced foliage and fine root litter, contributes the most to soil respiration (Bhupinderpal et al. 2003; Giardina et al. 2004). Changes in the three pools are likely influenced by these 'fast cycling' processes, but net changes in belowground carbon stocks contribute little to soil respiration.

If a change in stocks is the largest belowground contributor to terrestrial and atmospheric carbon levels, why do not we simply measure stock changes and abandon soil respiration measurements? As noted above, aboveground processes, including allocation, can also greatly affect belowground carbon storage and exchange with the atmosphere. Measuring changes in stocks can be difficult and involves an intensive sampling effort (Yanai et al. 2003). Additionally, the method works best when changes are assessed over long periods (typically several years, Conen et al. 2003). Because any time span of that length has enormous environmental variability, linking stock changes with environmental change through a particular and generalizable mechanism is unlikely. Information on stock changes does constrain process understanding, and advances in our ability to quantify these changes are urgently needed.

So, we have a dilemma – we can measure soil respiration fluxes at very fine time scales, but most of this flux reflects recent plant activity and this activity only indirectly affects carbon storage belowground. Or, we can measure long-term changes in pools, but, because the period is so long, it is difficult to link any changes in the pools to climate, atmospheric CO_2 or N deposition. How do we move forward?

We can think of no easy solution to this dilemma, but we can make some recommendations. First, we need to abandon the firmly entrenched idea that soil respiration largely reflects heterotrophic activity, and structure our measurements and models differently. Current plant metabolism and decomposition of recently produced organic material supplies the bulk of soil respiration. Short-term fluctuations in soil respiration reflect changes in plant metabolism (Ekblad and Högberg 2001; Bowling et al. 2002) and carbon allocation (Giardina et al. 2003; Ryan et al. 2004), as well as changes in heterotrophic activity (Borken et al. 2003). Second, we will gain more insight if we link measurements of soil respiration with measurements of plant activity (photosynthesis or canopy conductance for the short-term measurements and aboveground productivity for longer measurements). An understanding of the small changes in respiration associated with stock changes will not be possible

until we separate them from the large contribution from plant metabolism and recent production. Phenomenological measurements of soil respiration without a context of pool changes or information on aboveground inputs will not contribute as much insight as measurements placed in the context of other fluxes. Third, further insight will come from linking soil respiration measurements with measures of carbon allocation belowground because shifts in allocation moderate the transfer of carbon from photosynthesis to belowground. Fourth, if we couple soil respiration measurements with periodic measurements of pool changes, we can place what we learn about the short-term controls in the context of the longer-term changes in carbon storage. Finally, we encourage more manipulative experiments and the use of carbon isotopes to identify the contribution from the large soil carbon pools with slow turnover.

How observations can be used to assess ecosystem carbon fluxes

Measurements of soil respiration are increasingly useful for a variety of studies on terrestrial carbon cycling. We summarize these aims below.

Comparison with night measurements of NEE by eddy covariance

Assumptions for valid flux estimates by eddy covariance (EC) are rarely met at night when low wind conditions are common, and subcanopy advection can remove carbon without it being detected at the measurement height above the canopy (Lee 1998; Staebler and Fitzjarrald 2004). Soil respiration, coupled with measurements of dark respiration from aboveground parts can assess the performance of measurements of net ecosystem carbon exchange with eddy covariance. Some studies showed chamber measurements gave 20–30% greater respiration estimates than even well selected EC measurements at sites where low wind conditions or advection occur at night (Goulden et al. 1996; Lavigne et al. 1997).

Partitioning sources of ecosystem fluxes

Eddy covariance measures *net* exchange of CO_2 (NEE) between the ecosystem and the atmosphere, and, during the day, respiration from soil and aboveground plant parts offsets photosynthesis. To estimate GPP from NEE requires *adding* estimated respiration fluxes to the NEE measurements. Typically, ecosystem respiration is derived from nighttime eddy covariance measurements using empirical equations to adjust for temperature and compute respiration during daytime. Soil respiration measurements can be used to discern processes responsible for seasonal and interannual changes in

NEE, and may help identify whether photosynthesis or respiration alter NEE more.

Respiration may be more variable than photosynthesis from year to year (Valentini et al. 2000), or not (Barford et al. 2001), but several studies have linked changes in carbon stored in ecosystems to differences in respiration. For example, soil water availability and timing of rainfall in semi-arid systems appear to cause a large interannual variability in soil respiration (Irvine and Law 2002). Thawing of permafrost and the subsequent aerobic conditions in boreal systems increased soil respiration and ecosystem carbon loss (Goulden et al. 1998). When partitioning eddy flux data into component fluxes, the most effective means of characterizing soil respiration over time and space is a combination of automated chambers that measure hourly soil CO_2 effluxes, and periodic measurements with portable chambers that provide good spatial coverage of the apparent flux footprint (Savage and Davidson 2003).

Phenomenological studies linked to the environment or treatments

Many studies aim to quantify soil respiration and examine its response to the environment or to various treatments or conditions. The explicit or implicit assumption for many of these studies is that we can use soil respiration to understand changes in ecosystem carbon storage or changes in net fluxes to the atmosphere. Some of these studies recognize the important link between soil respiration and aboveground processes and photosynthesis, but most do not, and treat soil respiration as a single process. Soil respiration, temperature and moisture are strongly correlated, particularly in temperate ecosystems where root phenology and aboveground productivity are also linked with temperature and moisture. Models of soil respiration using temperature and moisture often work well within a site for a given year, but do not predict well across sites (Hibbard et al. this issue). The site-specific correlations with environmental variables are useful for producing annual estimates of soil respiration when only periodic measurements are available or there are gaps in automated soil respiration data.

Manipulations to separate autotrophic and heterotrophic contributions

Separating autotrophic and heterotrophic contributions to soil respiration is an important first step for interpreting measurements and for modeling, because only organic material consumed by heterotrophs can be stored as soil carbon and autotrophic respiration is rapidly released from the soil. In addition, autotrophic and heterotrophic respiration may respond differently to environmental factors. Methods to separate autotrophic and heterotrophic contributions can be grouped into four categories: (1) comparing soil respiration from soils with roots excluded (usually by trenching) to intact soils (Edwards

and Norby 1998); (2) summing individual components of root respiration and litter decomposition, with decomposition in mineral soil usually determined by difference (Ryan et al. 1997; Law et al. 2001); (3) the use of stable or radioactive isotope methods (Pendall et al. 2004); and (4) girdling of tree cambium, which cuts off the supply of photosynthates to roots (Högberg et al. 2001). Seasonal and spatial differences may also help separate autotrophic and heterotrophic contributions to soil respiration (Tang and Baldocchi this issue).

Hanson et al. (2000) reviewed the advantages and disadvantages of approaches 1–3 for determining autotrophic and heterotrophic contributions to soil respiration. Trenching methods may underestimate root respiration because they initially increase the substrate supply for microbial respiration (Bhupinderpal et al. 2003). Summing components requires accurate, unbiased measurements of each component and an assumption that the rates measured after separating components represent *in situ* rates. Stable carbon isotopes allow non-destructive partitioning of respiration components if there is a large isotopic difference between soil carbon and live plants – for example, where isotopically distinct CO_2 is added (Pataki et al. 2003), or where vegetation changed between plants with a C_3 or a C_4 photosynthetic pathway (Rochette et al. 1999). This approach requires a difference in $\delta^{13}C$ of 4–5‰ between plants and soil carbon, a difference that is not often found in C_3 ecosystems. Girdling, an approach not used before the Hanson et al. (2000) review, is permanent and apparently roots can continue to use stored carbohydrates for some time (Bhupinderpal et al. 2003). We see a strong need for technological advances to develop an approach to separate the autotrophic and heterotrophic components of soil respiration that will be widely applicable.

Manipulations may help us understand how autotrophic and heterotrophic respiration varies with climate or resource availability. For example, daily soil respiration strongly varied with transpiration and eddy flux estimates of daily GPP (Irvine et al. 2002), suggesting that changes in plant metabolism (autotrophic respiration) promoted much of the day-to-day differences in soil respiration. Irvine and Law (this issue) found that soil respiration increased on the dry side of trees watered on one side, where hydraulic redistribution provided water to roots on the dry side. They estimated that autotrophic (or root + rhizosphere) respiration doubled in response to the watering, because photosynthesis increased for the whole tree. This study suggests a strong influence of recently fixed carbon on root respiration during the growing season.

Soil respiration used to estimate total belowground carbon allocation (TBCA)

Quantifying the plant belowground carbon flux and the fraction of photosynthesis used belowground remain important challenges for ecosystem science and for modeling. A carbon balance approach (TBCA = soil respiration – aboveground litter inputs + changes in root, soil and litter carbon

stores) can quantify this flux (Raich and Nadelhoffer 1989; Davidson et al. 2002a; Giardina and Ryan 2002). Soil respiration is the largest component in this equation and roughly equal to 75% of TBCA on an annual basis (estimated using the data presented in Davidson et al. 2002a). TBCA can also be used together with aboveground production and respiration measurements to provide an independent estimate of GPP (Möller et al. 1954; Law et al. 2002; Ryan et al. 2004). The TBCA estimate does not provide information to separate root and mycorrhizal respiration from heterotrophic respiration generated from decomposition. Thus, TBCA estimates may be most useful as a constraint on belowground process estimates, as a component of the plant carbon budget, and for understanding carbon allocation by plants.

How biological processes control CO_2 production

Overview

Substrate supply strongly controls soil respiration (Figure 1), but other environmental factors, such as soil moisture, oxygen supply, and the belowground community are also important. For autotrophic respiration (root, rhizosphere and mycorrhizal respiration), photosynthesis and carbon allocation largely control substrate supply, but changes in plant carbohydrate storage and phenology can decouple root substrate supply from photosynthesis. Activity of the decomposer microbes (heterotrophic respiration) is largely limited by the supply of labile substrate found in new detritus, such as foliage and fine root litter, and its chemical composition. The amount of above and belowground litter production is related to photosynthesis over a year or several years, but the timing of litter production may not be. Limits to substrate availability for older, more recalcitrant soil carbon include its chemical composition (Sollins et al. 1996), physical protection in soil aggregates (Swanston et al. 2002), and other sources of labile carbon available in the system (the 'priming' effect, Pendall et al. 2004; Sulzman et al. this issue). The interactions among the autotrophic and heterotrophic components are poorly understood, particularly those of mycorrhizae (Pendall et al. 2004).

Autotrophic respiration

Autotrophic respiration is associated with the metabolic energy expended in the synthesis of new plant tissue and in the maintenance of living tissue. We also consider respiration by mycorrhizae to be 'autotrophic', if they receive carbohydrate directly from the roots. When environmental conditions are favorable for growth, root respiration is controlled by canopy processes through metabolism of recently fixed carbohydrates. For example, stable isotope studies indicated that during the growing season, recently fixed

carbohydrates were used for root respiration within a few days of carbon uptake (Ekblad and Högberg 2001; Bowling et al. 2002). During periods of stress, such as freezing temperatures or summer drought, photosynthesis declines and stored non-structural carbohydrates are used to maintain living tissue so that root respiration is decoupled in time from canopy photosynthesis (Högberg et al. 2001). Another example of decoupling is the root growth in spring fueled by carbohydrate reserves. Drought can alter root respiration because of reduced photosynthesis, which leads to reduced root growth and growth respiration, increased root resistance and possibly root mortality, and then decreased maintenance respiration (Domec and Gartner 2003). More research on the linkage between canopy processes and root biology, including carbon allocation to roots and the role of storage will allow more detailed predictions of the response of soil respiration to changes in climate and atmospheric CO_2.

Root respiration rates are also directly related to temperature and tissue nitrogen concentrations (Ryan et al. 1996), because proteins and amino acids are needed for metabolism, and the response is similar across root size (Pregitzer et al. 1998) and species (Burton et al. 2002). Nitrogen also has the potential to alter whole-plant source-sink relationships and root and mycorrhizal biomass because of reduced allocation of carbon to roots (Oren et al. 2001; Rustad et al. 2001; Giardina et al. 2003; Ryan et al. 2004). Many basic phenological processes in forests are also genetically controlled, and these seasonal rhythms of growth likely constrain plant response to a changing climate (Oleksyn et al. 2000). We do not understand if root phenology is linked to the same environmental cues as canopy growth and senescence (Pregitzer et al. 2000), but genetic limitations are likely to constrain the response of root growth and respiration to environmental change (Oleksyn et al. 2000).

Acclimation generally limits the response of autotrophic respiration to temperature and reduces carbon loss at sustained higher temperatures (Tjoelker et al. 1999; Atkin and Tjoelker 2003; Bolstad et al. 2003), perhaps because respiration becomes limited by substrate supply (Dewar et al. 1999). Our knowledge of acclimation of root respiration to temperature is poor. Acclimation may occur for root respiration as it does for aboveground tissues (Tjoelker et al. 1999), or it may not (Pregitzer et al. 2000). Understanding the acclimation of belowground processes to temperature will be important in predicting their response to environmental change.

Heterotrophic respiration

Microbial respiration depends on substrate quality and quantity, maximum activity of respiratory enzymes, demand for respiratory products, and temperature and moisture. The functional behavior of different microbial communities may influence decomposition and carbon storage (Myrold et al. 1989), yet this link is poorly understood. Temperature and drought interact to control

enzyme activity and substrate pool size and hence microbial respiration (Pendall et al. 2004). Soil respiration can increase quickly following rain events in dry climates, and incubation experiments have indicated that the increase was primarily due to rapid microbial responses to water availability (Kelliher et al. 2004). Such events characterize some ecosystems and may have a strong influence on annual carbon fluxes. To determine the importance of these pulse events, investigations of responses need to be coupled with estimates of net ecosystem production and changes in carbon pools.

Inputs of labile biomass change seasonally, which is likely to have a larger effect on seasonal microbial respiration in biomes with more easily decomposable litter. Soil respiration in oak forests was higher in the autumn after leaf drop when more fresh material was available than at the same temperature during spring (Yuste et al. this issue), but this pattern was not observed in the pine forest where litter is more resistant to decomposition. Annual soil respiration across a wide range of sites was related to the supply of above- and belowground inputs and temperature (Hibbard et al. this issue; Campbell et al. 2004). Acclimation of heterotrophic respiration to temperature likely occurs in experimental treatments (Luo et al. 2001; Melillo et al. 2002), but was not seen in a natural temperature gradient (Kane et al. 2003).

How wind and rain can decouple measured fluxes from biological production

We assume that CO_2 flux from the soil surface represents biological production by roots and microbes. However, because the pore space in soil, litter, and snow can store CO_2 roughly equal to a day's production, and because this reservoir is easily disturbed, the flux measured may not reflect biological production. Instead, emptying or filling the pore space may enhance or diminish the measured flux relative to biological production. Three mechanisms can alter the CO_2 stored in the soil, litter, or snow pore space: pressure pumping (Massman et al. 1997), displacement of pore space gases by water after rain or snow melt, and the creation of a diffusion barrier by rain (Hirano et al. 2003).

Pressure pumping can act by three mechanisms: atmospheric turbulence, longer-period barometric changes when fronts move across, and quasi-static pressure fields induced by wind blowing across irregular topography. Atmospheric turbulence can alter CO_2 fluxes through snow, but the effect is likely to be minor in the long term – at most 2–5% (W. Massman personal communication). Additionally, soil respiration chambers do not interfere with pressure gradients between the atmosphere and soil pore space, so that any effect of turbulence on flux will be measured by the chamber (Takle et al. 2003). The effect of frontal barometric changes is likely negligible (W. Massman personal communication). Pressure fields induced by wind may have a larger effect for fluxes in snow – up to 10% or more depending on the wind speed and the relative spacing of the topographical features (W. Massman personal

communication). Wind from a consistent direction also will bias point flux measurements because high pressure on the upwind side and low pressure on the downwind side of hill or snowdrift will move CO_2. These effects vary with permeability of the medium and often soils have lower permeability than snow. For turbulent pressure pumping, flux measurements using eddy covariance or continuous point measurements will yield correct fluxes when integrated over sufficiently long periods.

Water from precipitation can lower diffusion, increase CO_2 concentration within the soil pore space, and decrease flux (Hirano et al. 2003). These effects can persist for several days (Hirano et al. 2003). Precipitation could displace CO_2 from soil pore space, but this effect has not been examined.

Potential biases in measurement and sampling techniques

Technique

Measurements of soil respiration are often made by placing a chamber over a PVC or metal collar inserted into the soil surface and measuring flux by measuring: (1) the change in CO_2 concentration over time (closed system or non-steady state); (2) the difference in CO_2 concentration between the chamber inlet and outlet that results from flow of a measured quantity of air through the system (open system or steady state); and (3) using chemicals inside the chamber to absorb CO_2 (static chambers). Most closed systems circulate air between the chamber and an infrared gas analyzer to measure CO_2 concentrations (also called 'dynamic' systems).

Measurement techniques can easily bias chamber measurements, because of the large reservoir of CO_2 inside the soil, litter, and snow pore space and the high diffusivity of these media. Davidson et al. (2002b) reviewed potential artifacts and biases in chamber measurements, focusing on closed systems that had air circulated by pumping and CO_2 measured with infrared gas analyzers. They conclude that:

- These chambers tend to systematically underestimate CO_2 efflux because the effective chamber volume includes some of the soil and litter pore space. However, the effective chamber volume can be calculated by introducing a known flux of CO_2 into the chamber (Goulden and Crill 1997).
- Chambers should be open to the atmosphere through a long, small diameter tube to minimize pressure gradients, particularly those caused by closing the chamber or wind.
- Chambers with fans may bias flux measurements by changing pressure inside the chamber (Janssens et al. 2000).
- Inlet and outlet pressure should be the same when circulating air with a pump, or pressure differences within the chamber may bias flux measurements.

- Scrubbing CO_2 in the chamber and assessing flux by measuring the rate of CO_2 increase centered around ambient CO_2 concentration, the method developed by LICOR (LI-COR, Inc., Lincoln, NE, USA), may reduce the influence of headspace CO_2 concentration on flux in closed systems. However, this method may also induce bias if the CO_2 concentration near the surface is higher than that in the bulk air (Davidson et al. 2002b).

The chemical absorbent in static chambers can alter the headspace CO_2 concentration and bias flux measurements (Nay et al. 1994), with the bias depending on the flux rate, chamber volume/area ratio, and the absorbent type and its surface area. Generally, biases are greater with high flux rates and soils with a high porosity. Despite these problems, soil respiration measurements taken with static chambers yielded a similar relationship to litterfall at the global scale (Davidson et al. 2002a), suggesting that the biases are not large in many ecosystems.

Butnor et al. (this issue) compare measurements made with open and closed systems using a laboratory system with known CO_2 flux and soil porosity. They found that flux measured with closed, dynamic systems varied with soil properties, and biases were important in soils with high air-filled porosity. In contrast, the open system underestimated CO_2 efflux because the headspace CO_2 concentration at steady state was always greater than ambient CO_2 concentration. This bias was consistent for different soil porosities and easily corrected.

Sampling

Sampling choices can bias chamber-based estimates of soil respiration and change their precision.

- Restricting sampling to certain conditions (for example, daytime or dry days) may bias flux estimates. Because the supply of carbohydrates to roots may vary diurnally and affect respiration (Rochette et al. 1992), measurements restricted to certain times will not reflect the diurnal pattern. Additionally, sampling only during dry conditions will miss the pulse of microbial or root activity immediately following precipitation (Sotta et al. 2004). Automated chambers that measure fluxes continuously can help determine the importance of these issues for a particular ecosystem.
- Microbial and root activity under snow can generate CO_2 fluxes that are a significant portion of the annual flux (Sommerfeld et al. 1993), particularly for boreal, subalpine, alpine, and cold-temperate ecosystems. Because of measurement and access difficulties, these fluxes are often ignored or assumed negligible. Hubbard et al. (this issue) examine measurement issues for a flux gradient method for estimating CO_2 efflux through continuous snowpack. They show that this method can resolve flux differences between

forests of different ages, and that flux under snow varies substantially through time.

- Most chamber measurements avoid rocks, dead wood, and plant stems, potentially biasing areal estimates of soil respiration. Rocks are virtually impermeable to CO_2 efflux, so that any CO_2 produced under a rock will diffuse out elsewhere. Dead wood has low permeability to CO_2 and may similarly block CO_2 efflux. Decomposition of dead wood also generates CO_2 (Marra and Edmonds 1996; Bond-Lamberty et al. 2002), particularly when wood moisture is relatively high, but is not commonly measured. Soil respiration is highest in the rhizosphere, often located directly under plant stems. If rock, dead wood, or plant stems cover a significant portion of a site, flux estimates for the area should be corrected for the area of the non-permeable components.
- Chambers covering a large area will lower the variability among subsamples, and this lower variability will decrease sample effort and increase precision for plot-level estimates. The standard LI-COR soil respiration chamber (6400-09, LI-COR, Inc., Lincoln, NE, USA) was designed to fit between closely spaced plant stems and has a surface area of $\sim$81 cm^2. Subsamples taken with this chamber typically have a coefficient of variation of 60–100%, compared lower CV for larger chambers ($\sim$30% for a chamber area of 300 cm^2 (Davidson et al. 2002b), $\sim$25% for a chamber area of 490 cm^2 (M.G. Ryan unpublished data)).
- Permanent chamber locations (generally accomplished by inserting permanent PVC collars) allow separation of environmental effects from location differences.
- A low sampling frequency can increase the variance of aggregated estimates, and using a regression model with soil temperature and moisture to extrapolate (rather than simple averaging) will reduce the variance of aggregated estimates (M. Reichstein personal communication).

Experiments to define the controls over soil respiration

A recent synthesis (Schimel and Manning 2003) of our current understanding of processes that affect terrestrial carbon stocks stated that our understanding of soil processes and nutrient cycling, fire cycles, frozen soils and atmospheric feedbacks are not yet sufficiently comprehensive to produce robust predictions of carbon fluxes at regional to continental scales. The report suggested that to understand mechanisms, particularly indirect effects, carefully planned multi-factor experiments of responses of processes to factors such as CO_2, temperature, and nitrogen deposition are needed. Both long-term and short-term processes need to be considered in these studies. These must be integrated with existing types of observation networks (inventories, remote sensing, and flux networks), and coordinated with modeling activities on sensitivities of biological processes. The current Free Air CO_2 Enrichment (FACE) studies are a

good example of multi-factor experiments, but syntheses have been limited by the differences in scope and measurements made at the individual sites (for example, Rustad et al. 2001), and model development would ideally be an integral part of the program.

Controlled, large-scale experiments can help deduce key mechanisms of the response of soil respiration and belowground carbon stocks to the environment, and larger environmental manipulations could help understand scaling fluxes and stocks in space and time (Osmond et al. 2004). However, these large-scale manipulations face several challenges. First, multi-factor experiments become increasingly complex with confounding effects and fewer degrees of freedom as more treatments are added to the mix (for example, nitrogen, water, warming, CO_2 treatments). Second, important responses take many years to resolve, particularly in long-lived forests. Finally, large-scale experiments are very expensive, with estimated costs exceeding current ecosystem research funding levels (National Research Council 2001). Large-scale experiments also face the challenge of interpreting how the step changes imposed will provide information for natural, chronic change.

Despite the need for large, long-term manipulative studies, simple manipulations and interannual variability in climate can help understand the short-term and long-term processes that control soil respiration. Sulzman et al. (this issue) describe a simple set of long-term manipulations of root inputs (removed through trenching) and aboveground litter that provide an estimate of the contribution of root respiration to soil respiration and the influence of fresh litter inputs on soil carbon decomposition. Simple manipulations of rain and snow show dramatic short-term effects on soil respiration and will be easy to maintain for a long-term study (Chimner and Welker this issue). Differences in soil respiration between years with contrasting climate show how sensitive soil respiration is to soil moisture (Martin and Bolstad this issue; Yuste et al. this issue). Finally, chronosequences (Smith and Resh 1999; Campbell and Law this issue; Gough et al. this issue), repeated measurements on developing forests through time (Ryan et al. 2004), and different management regimes (Concilio et al. this issue) can help identify broad controls over ecosystem carbon exchange with the atmosphere. Replicated plots are essential, and, for chronosequences, finding sites that have similar environment and soils, but different disturbance and management history is challenging.

Modeling soil respiration and information needs

In modeling ecosystem carbon uptake and release in response to environment, we have a better understanding of how to quantify the controls on photosynthesis (Farquhar and von Caemmerer 1982) than carbon allocation and respiration. Simplifications in global models that describe biosphere–atmosphere interactions also lead to large uncertainty in estimates of respiration feedbacks (Cox et al. 2000). First, we will describe common features of

some process models, and then suggest model development and information needs.

In ecosystem process models such as CENTURY and Biome-BGC, carbon is fixed in photosynthesis, and fractions of this photosynthetic pool are partitioned to plant components (roots, leaves, wood) for growth, maintenance, and storage (Parton et al. 1993; Running and Hunt 1993). The size of these partitioning coefficients varies with resource availability within limits set by the model or by the user. In Biome-BGC, root growth respiration is calculated as a proportion of new carbon allocated to total growth, and root maintenance respiration is calculated as a function of the mass, nitrogen concentration, and temperature of root tissue (Thornton et al. 2002). To quantify heterotrophic respiration, plant litter is assigned to pools that undergo chemical degradation at different assigned rates, producing a connected series of progressively more recalcitrant soil organic matter pools with turnover times that range from days to millennia (Parton et al. 1987; Running and Hunt 1993). In these models, maximum decay rates for each pool are usually modified using temperature and moisture functions.

Models make many simplifying assumptions and these assumptions can have a large impact on model predictions. For example, in Biome-BGC, root phenology is not modeled, and root growth, respiration, and nutrient uptake do not respond to soil moisture. Acclimation of respiration to temperature is rarely included in models, nor are the complex effects of different populations of belowground microorganisms.

The patterns and controls of carbon allocation are poorly understood, particularly those for annual or seasonal partitioning of photosynthesis belowground. The simulation of soil respiration by process models is sensitive to the values used for partitioning photosynthesis – less allocation belowground results in less autotrophic and heterotrophic respiration and greater simulated annual NEP (Thornton et al. 2002). When simulating forests, it is often assumed that carbon allocation patterns remain the same with forest development following disturbance, but recent observations suggest this is not necessarily the case (Ryan et al. 2004; Law et al. in press). To improve modeled carbon allocation, more studies and improved techniques are needed to reduce the uncertainty in seasonal and annual carbon allocation estimates for different biomes, environmental conditions, and forest age classes.

An understanding of the controls on root phenology, and of the direct effects of environment on root respiration and heterotrophic respiration are needed to improve models. Temperature effects on soil carbon dynamics may be overestimated in the models (Giardina and Ryan 2000), which usually assume a fixed exponential effect of temperature on soil turnover times (e.g. Q_{10} of 2). Additionally, estimates of Q_{10} values for soil temperature >20 °C are uncertain, because information on soil respiration at high temperatures is rare. Although the amount of above- and belowground inputs of easily decomposable plant material varies through the year (Kirschbaum 1995), models usually assume inputs are evenly distributed through the year or they occur

once during the year. This assumed timing of substrate availability can affect the simulated heterotrophic responses to temperature and moisture (Gu et al. 2004). Del Grosso et al. (this issue) found improved CENTURY model predictions of soil respiration when they accounted for seasonal and site variation in factors such as litter quality, NPP, water and substrate availability.

The timing of catastrophic disturbances and the changes in dead plant material and soil carbon pools after disturbance are often prescribed in models. Additionally, heterotrophs may recover slowly after a disturbance (from loss of organic soil layer and microbial community in wildfire, or changes in microbial activity after logging) and this recovery is difficult to model. Intermittent or small-scale disturbances such as gap-formation or defoliation are often ignored. For regeneration of forests after disturbance, it is also often assumed that tree growth begins immediately after stand-replacing disturbance when studies show there can be a lag of several years before trees become established (Law et al. 2001). Carbon balance is eventually achieved for each modeled unit of ground over time since disturbance. Some of these issues may vary by model and the necessity for simplification, but in general, there is large uncertainty about the assignment of carbon to pools following disturbance, and this can influence heterotrophic respiration estimates.

In order to improve models of the terrestrial carbon cycle, our knowledge of the patterns of carbon stocks and the processes that control them must be improved. Our most critical information needs from observations and experiments in a range of biomes and ecoregions are given below:

- Carbon allocation patterns to different components, especially fine roots and belowground. Knowledge of the standing stocks (biomass), the annual fluxes, and the fraction of photosynthesis used by components are different facets of carbon allocation and all-important to modeling.
- Experiments to determine how fluxes and the fraction of photosynthesis used by a component vary with forest age, resource availability, functional groups, and competition.
- Improved estimates of the size and turnover times of the different soil carbon pools.
- Autotrophic and heterotrophic responses to environment and substrate.
- Experiments on changes in carbon and nitrogen linkages.
- Effects of disturbance history on carbon pools and fluxes.

A suggested suite of measurements for interpreting soil respiration responses is provided in the Appendix. It is by no means exhaustive, but it represents some of the key measurements that are needed in both experimental and observational studies. Studies of belowground processes often ignore aboveground processes; the suite of measurements is intended to form a basis of more comprehensive understanding of the connections between above- and belowground processes.

Conclusions

Soil respiration is strongly linked to plant metabolism and to the recent production of plant litter. Using measurements of soil respiration to assess the belowground carbon storage in ecosystems is difficult because of the strong link between soil respiration and aboveground processes, and because of the small contribution to soil respiration from changes in belowground pools. To advance our understanding of the contribution of soil processes to atmospheric carbon dioxide will require (1) knowledge of the key mechanisms controlling the coupling of canopy and belowground processes; (2) coupling soil respiration measurements with measurements of pool changes and aboveground processes; and (3) information on plant carbon allocation and how allocation varies with forest development, environment, and resource availability. New technologies are needed to reduce the uncertainty in estimates of carbon allocation, soil carbon pools, and different responses of roots and microbes to environmental conditions.

Acknowledgements

We thank the workshop participants for many their helpful suggestions and insights. This research was supported by the Office of Science, Biological and Environmental Research Program (BER), US Department of Energy, through the Great Plains Regional Center of the National Institute for Global Environmental Change (NIGEC) under Cooperative Agreement No. DE-FC03-90ER61010, and by the US Department of Energy Terrestrial Carbon Program (Award # DE-FG03-01ER63278) and NASA (NAG5-11223). M.G. Ryan acknowledges the support of the US Forest Service Global Change Program.

Appendix

Protocols for sampling, measurement, and reporting soil CO_2 fluxes (including associated variables)

Coupling between canopy and soil processes should be assessed in experiments and observational studies. The links between soil respiration and aboveground processes can be assessed with measurements of photosynthesis and root contribution to soil respiration, and with annual estimates of NPP, total belowground carbon allocation and soil respiration. Processes that affect soil organic matter pools over decades and longer need to be better quantified as part of long-term intensive studies and experiments. This will require a full complement of measurements that are made at multiple scales: for example, carbon turnover using ^{14}C dating, changes in stable carbon isotope signals and

Table 1. Protocols for sampling, measurements, and reporting soil CO_2 fluxes (including associated variables)

Variable	Method	Frequency, depth	Units
Soil CO_2 efflux and instantaneous soil temperature next to collar (10 cm below surface)	Closed or open dynamic system (Davidson et al. 2002b)	Monthly or automated	μmol m^{-2} s^{-1}
Litterfall	Litter traps. Divide into foliage and other as a minimum, include <1 cm diameter twigs (Clark et al. 2001)	Monthly	g C m^{-2} $year^{-1}$
Aboveground production	Foliage, wood, understory (Clark et al. 2001)	Annual	g C m^{-2} $year^{-1}$
Phenology	Date of bud swell, bud break, full leaf expansion, leaf senescence, leaf off	Annual	
Total soil C and N profile	Robertson et al. (1999)	0–10, 10–20, 20–50, 50–100 cm	g C or N m^{-2}
Light and heavy fractions of soil C and N in profile samples	Sollins et al. (1984)	0–10, 10–20, 20–50, 50–100 cm	
Fine root mass	From cores	Seasonal; 0–10, 10–20, 20–50, 50–100 cm	g C m^{-2}
Litter mass C and N		Min and max over year	g C or N m^{-2}
Litter decomposition rate	Litter bags (LIDET guidelines[a])	Pick up subset of bags monthly or annually depending on decomposition rate, continue for minimum 5 pickup dates to obtain decay constant	
Coarse woody debris, fine woody debris	Harmon and Sexton (1996) for forests	Once and after major disturbance	
Species composition	Include understory, identify nitrogen-fixers		
Site history	Disturbance type, timing and intensity	As far back in time as possible	
Soil temperature profile		Half-hourly, automated; 5, 10, 20, 50 cm or deepest possible	
Soil moisture profile	Soil moisture based on the difference between the soil wet and dry weight, measured once per time period in % by volume (Rundel and Jarrell 1991) overview of measurement of soil water content and soil water potential) (cm for depth)		

[a]http://www.fsl.orst.edu/lter/research/intersite/lidet/lidet_meth/lidet.htm

soil respiration with management and disturbance, soil C concentration and bulk density profiles, and above- and belowground inputs. Table 1 lists a suite of observations that we recommend for advancing understanding of belowground processes, and for further model development.

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