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CaRTE THEMATIC SET

Carbon respired by terrestrial ecosystems – recent progress and challenges

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Abstract

Net ecosystem production is the residual of two much larger fluxes: photosynthesis and respiration. While photosynthesis is a single process with a well-established theoretical underpinning, respiration integrates the variety of plant and microbial processes by which CO_2 returns from ecosystems to the atmosphere. Limits to current capacity for predicting ecosystem respiration fluxes across biomes or years result from the mismatch between what is usually measured – bulk CO_2 fluxes – and what process-based models can predict – fluxes of CO_2 from plant (autotrophic) or microbial (heterotrophic) respiration. Papers in this Thematic Issue and in the recent literature, document advances in methods for separating respiration into autotrophic and heterotrophic components using three approaches: (1) continuous measurements of CO_2 fluxes and assimilation of these data into process-based models; (2) application of isotope measurements, particularly radiocarbon; and (3) manipulation experiments. They highlight the role of allocation of C fixed by plants to respiration, storage, growth or transfer to other organisms as a control of seasonal and interannual variability in soil respiration and the oxidation state of C in the terrestrial biosphere. A second theme is the potential for comparing C isotope signatures in organic matter, CO_2 evolved in incubations and microbial biomarkers to elucidate the pathways (respiration, recycling, or transformation) of C during decomposition. Together, these factors determine the continuum of timescales over which C is returned to the atmosphere by respiration and enable testing of theories of plant and microbial respiration that go beyond empirical models and allow predictions of future respiration responses to future change in climate, pollution and land use.

Keywords: Soil respiration, carbon cycle, ecosystem respiration, root respiration, radio carbon, below ground, decomposition, carbon isotopes

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Introduction

Carbon enters terrestrial ecosystems through a single process, photosynthesis, but is returned through a variety of processes, collectively referred to as respiration (Fig. 1). Functionally, respiration is divided into CO_2 released by living plant leaves, stems and roots (autotrophic respiration), and CO_2 released during decomposition of nonliving organic matter (heterotrophic respiration). Episodic C loss mechanisms, most importantly, fire, can be as important as decomposition in returning C to the atmosphere, particularly in ecosystems where decomposition is limited by drought or cold (Schimel *et al*., 1997; Harden *et al*., 2000). Losses of C through leaching of dissolved organic or inorganic C, or by erosion, while important on century to millennial timescales, are too small to be major contributors to interannual C balance in ecosystem NEP. The net status of the land surface as a C source or sink on annual to decadal timescales therefore depends on the balance of photosynthesis and respiration plus episodic losses.

Globally, terrestrial photosynthesis and respiration (plus fire) represent enormous C fluxes that approximately balance (Schimel, 1995). Roughly, one-sixth of atmospheric CO_2 ($\sim$ 115 petagrams of C; Prentice *et al*., 2001) passes through ecosystems every year. As ecosystem respiration is one of the largest gross fluxes in the annual global C budget, $\sim$ 18 times the rate of fossil

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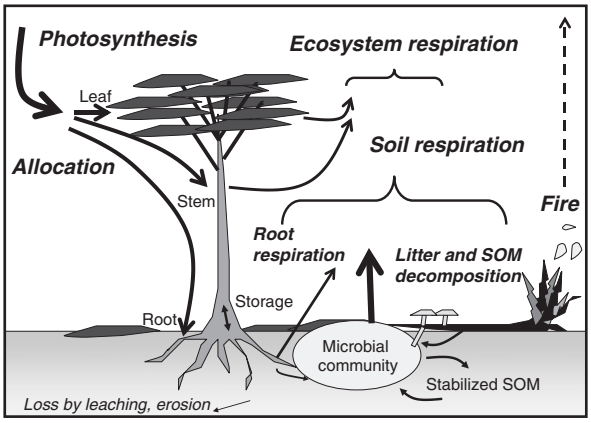

Fig. 1 Pathways of carbon flow through ecosystems.

fuel release in the 1990s (Prentice *et al*., 2001), small imbalances in photosynthesis and respiration can lead to significant interannual variation in atmospheric [CO_2]. Such changes have been linked to large-scale regional climate variations acting on terrestrial ecosystems – for example, changes in respiration following the Pinatubo eruption, or increased fires during ENSO events (Trumbore *et al*., 1996; Schimel *et al*., 2001; van der Werf *et al*., 2004). Isotopic imbalances between C taken up and released by ecosystems ('isodisequilibrium'; Fung *et al*., 1997; Ciais *et al*., 1999), or imbalances in the ratio of $CO_2 : O_2$ exchanged between atmosphere and biosphere (Randerson *et al*., 2005) complicate efforts to deconvolve the relative strengths of biosphere vs. ocean sources and sinks of C over the past decades.

While the overall factors that govern respiration are well known, critical details that allow quantitative prediction of how respiration fluxes will respond to changing environmental variables are lacking. For example, the rate of CO_2 production by decomposition clearly relates to factors controlling microbial activity such as temperature, moisture availability, and the quality and supply of decomposable substrate material. However, the specific details of how soil or total ecosystem respiration measured, at any given time, depends on these variables are still largely beyond our grasp. The problem is both with a lack of a 'theory' of respiration that explains how all the driving variables may interact, as well as in obtaining relevant data to test models based on theory.

A major problem is that what we can measure at the ecosystem level (CO_2 fluxes) integrates quite different processes of plant and microbial function. Spatially, ecosystem respiration is divided into aboveground (canopy respiration) and belowground (soil respiration) components (Fig. 1). Aboveground respiration may be assumed to be largely autotrophic, but soil respiration combines plant root respiration (autotrophic) with heterotrophic respiration of substrates ranging from fresh plant litter to C inherited from parent rocks, and integrates production from the surface to depths of many meters. The so-called 'rhizosphere' respiration, in which exudates from roots are used as energy sources by symbiotic (mycorrhizal) fungi and other organisms, although by definition 'heterotrophic' – is often combined conceptually with autotrophic respiration. CO_2 produced by soil macrofauna is similarly combined with heterotrophic respiration.

Measurements such as the overall flux of CO_2 emitted from soils or ecosystems, therefore, integrate a lot of complex biological activity, and it is not surprising that simple empirical relationships between CO_2 fluxes and driving variables do not scale well across space and time. Plants and microbes respond to environmental conditions that may not be simply related to a single standard measure such as air or soil temperature at a prescribed soil depth. Further, factors such as land cover history, soil mineralogy, nutrient availability, litter quality, or plant phenology differ from site to site, and these will influence the partitioning of respiration among autotrophic and heterotrophic components across landscapes.

Flux measurements alone cannot distinguish CO_2 produced by autotrophic vs. heterotrophic sources. Hence, most respiration studies to date have developed empirical equations that relate CO_2 fluxes to temperature and moisture variations within a site. For example, total ecosystem respiration in eddy covariance studies is estimated from a site-based relationship between night-time net ecosystem exchange and canopy or soil temperature; this model is then applied to estimate daytime respiration (Goulden *et al*., 1996). Similarly, annual soil respiration is estimated by applying relationships linking respiration to soil temperature and moisture (developed from a limited data set), to more continuous records of soil or weather conditions. Such empirical models can explain up to 90% of the seasonal and annual variation in soil respiration for the site where they are developed (Janssens *et al*., 2001; Savage & Davidson, 2001). However, bulk system responses of respiration to factors like temperature, while useful for filling data gaps, are ultimately likely to be misleading as they integrate temperature responses of a number of different processes, and because they may be confounded by other factors that covary with temperature (e.g. moisture, phenology/rates of photosynthesis; for more thorough discussion, see Davidson *et al*., 2005a).

Empirical relationships developed at a single site, where characteristics such as long-term climate, vegetation, soil type, etc., are constant; do not necessarily scale to other sites, or to the globe. Models optimized to predict diurnal or seasonal variation in respiration

may not perform well for predicting soil respiration over annual or longer timescales as factors like substrate supply clearly are important in controlling seasonal variation (e.g. Verburg *et al*., 2004; Scott-Denton *et al*., 2005). Compilations of soil respiration measurements show that annual rates of CO_2 emission correlate with factors like mean annual temperature at the global scale (e.g. Raich & Schlesinger, 1992; Raich & Potter, 1995). However, there is large variation within a given temperature range, indicating that factors other than temperature also play a role across larger spatial and longer time scales that include factors like succession or disturbance (Davidson *et al*., 2002).

Estimates of future change in atmospheric [CO_2] and [O_2] depend strongly on the feedbacks of terrestrial ecosystems to climate change, in particular the balance of C uptake and loss from ecosystems in a warmer world. In high latitude ecosystems, there is already debate as to whether increased heterotrophic respiration is changing local net ecosystem exchange (Goulden *et al*., 1998; Oechel *et al*., 2000). Controversy exists as to the relative importance of changes in autotrophic and heterotrophic respiration components with short-term and longer term variation in climate (e.g. Davidson *et al*., 2000; Giardina & Ryan, 2000). Other factors, like CO_2 enrichment, increased N deposition and O_3 exposure, and shifts in vegetation community, change patterns of C flow through ecosystems and will affect the amount and residence time of C on land, as well as the oxidation state of the terrestrial biosphere as a whole (Randerson *et al*., 2005). Improving our understanding of the processes by which ecosystems return C to the atmosphere, and the time required for C to transit ecosystems, is of fundamental importance to informing national and international action to stabilize atmospheric CO_2 levels; it is also crucial for explaining what role terrestrial ecosystems play in interannual and decadal changes in [CO_2].

Papers in this Thematic Issue focus on developing methods for separating ecosystem (particularly soil) respiration into autotrophic and heterotrophic components. These methods can be grouped into three approaches: (1) collection of continuous data on CO_2 fluxes and assimilation of data into process-based models (Sacks *et al*., 2005; Davidson *et al*., 2005b); (2) application of isotopic measurements, particularly radiocarbon (Borken *et al*., 2005; Cisneros Dozal *et al*., 2005; Schuur & Trumbore, 2005; Trumbore *et al*., 2005) and O_2/CO_2 (Randerson *et al*., 2005); and (3) manipulation experiments that remove autotrophic respiration (Scott-Denton *et al*., 2005). While not yet fully incorporated into efforts to constrain models of soil or ecosystem respiration, these advances highlight opportunities for designing experiments to test hypotheses about the most critical controls on ecosystem respiration. Two general themes emerge from these studies and those in the recent literature: (1) the importance of understanding plant C allocation, including the role of substrate supply as a control of the autotrophic component of soil respiration fluxes; and (2) evidence for linkages between short- and long-term processes that determine what carbon gets heterotrophically respired vs. stored in ecosystems.

Methodological Advances – Separation of Respired C into Component Sources

Hanson *et al*. (2000) reviewed the use of various techniques to separate CO_2 respired by soils into autotrophic and heterotrophic sources. They identified three basic approaches: component integration, isotopic methods, and removal of plant photosynthetic products by manipulations like girdling or trenching. They also point out that one of the difficulties in comparing results obtained using these different approaches arises from how each treats CO_2 respired from the metabolism of root exudates (commonly referred to as rhizosphere respiration).

Component integration

Component integration methods measure the respiration rates of spatially separable contributors to CO_2 fluxes to estimate the relative importance of each component to the total flux. In soils, for example, autotrophic respiration is estimated from the rate of CO_2 production by roots excised from soil, which are then scaled by the total root length or volume to estimate the volume- or area-based flux of CO_2 from root respiration for comparison with soil respiration measurements. Such measurements show regular variation of respiration rates with root type (diameter, position, species), temperature, and N content (e.g. Burton *et al*., 2002) that may allow for such scaling. However, successful extrapolation of length or mass-specific respiration rates on a soil area basis requires knowledge of how many roots are in the soil, as well as their size distribution (e.g. Ruess *et al*., in press) which is itself a difficult undertaking. Roots that are cleaned of soil before being incubated are separated from at least part of their associated microbial community; hence estimates based on incubations emphasize root but not necessarily rhizosphere respiration.

Similarly, the heterotrophic component of soil respiration may be estimated by incubating soil and litter layers under different temperature and moisture conditions. While such studies have been successful in determining the role of leaf litter as a cause of variability

in overall soil respiration fluxes (e.g. Hanson *et al*., 2003b), incubations of mineral soils are less likely to mimic field conditions and may not yield reasonable flux estimates. More critically, the rate of substrate supply to the microbial community in an incubation jar may differ substantially from that in a soil with living roots.

The recent proliferation of automated soil respiration chambers, soil and canopy gas profiling systems and eddy covariance measurements of total ecosystem respiration are providing continuous data sets that demonstrate how short-term variation in CO_2 fluxes correlates with factors like surface litter moisture content and air or soil temperature, and plant phenology. This in effect allows component integration on larger scales and elucidation of relationships between driving variables and component CO_2 fluxes without the need for separate incubations. For example, Davidson *et al*. (2005b) compare soil respiration from automated chambers with total ecosystem respiration using eddy covariance towers to estimate the relative importance of soil respiration to total ecosystem CO_2 emission. As more, continuous, data are collected over a variety of conditions of varying temperature, drought, and season, statistical methods can begin to test hypotheses about how these factors interact to determine soil and ecosystem respiration. For example, large data sets have enabled new developments in modeling techniques ('model-data fusion') that simulate process level controls of the component respiration fluxes and test whether a single parameter set is sufficient to describe respiration fluxes over seasonal and diurnal time scales (Hui & Luo, 2004; Braswell *et al*., 2005; Sacks *et al*., 2005). Such studies will help in deciding the minimum number of processes required for robust predictions of soil respiration.

Isotopic methods

Isotopic methods are being applied more frequently since the publication of Hanson *et al*. (2000), yielding encouraging results for separating heterotrophic and autotrophic contributions to soil CO_2 efflux. These approaches rely on distinguishable differences in the isotopic signatures of autotrophic and heterotrophic respiration sources. An isotope mass balance can then be used to determine the fractional contribution of each source to total soil or ecosystem respiration (Fig. 2). As with component integration methods, plant and heterotrophic respiration components are incubated separately to determine the isotopic signatures of endmember sources. Organic matter is not just carbon, and the ratio of O_2 consumed to CO_2 produced can provide an integrated measure of the stoichiometry of the substrates that are being oxidized. Randerson *et al*. (2005) summarize how changes in the kinds of plant tissue and soil organic matter may affect the $[O_2]:[CO_2]$ ratio globally.

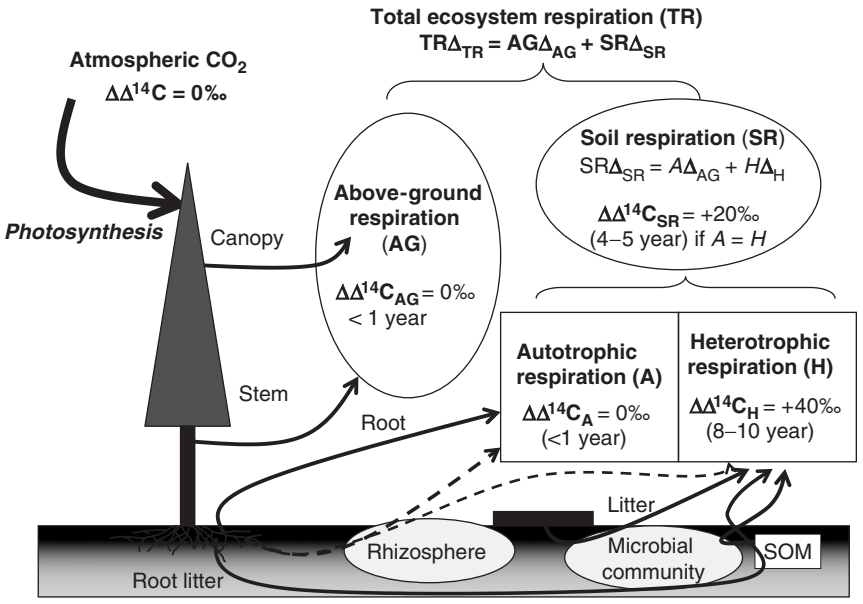

Fig. 2 Example of how an isotope mass balance is used to partition soil respiration into autotrophic and heterotrophic sources, using radiocarbon as the example (for stable isotopes, see Dawson *et al*., 2002). The radiocarbon values given are the difference (in parts per thousand, or ‰) between atmospheric CO_2 (assumed to be the same as fresh photosynthetic products, or $\Delta\Delta^{14}C = 0$) and respired C. As the rate of ^{14}C decline in the atmosphere over the past decade has been 5–7‰ yr^{-1}, an average 'age', or mean time as the original C was fixed from the atmosphere, can be derived from the ^{14}C signature of respired CO_2 – although it must be recognized that this average may integrate faster and more slowly cycling components.

Stable isotopes of CO_2 have yielded good results for differentiating sources of total respiration in some cases, reviewed in Dawson *et al*. (2002). The ^{13}C signature of plant structural material includes compounds like lignin that are significantly depleted in ^{13}C compared with photosynthetic products or the plant as a whole. Hence, the C respired by plants must be enriched in ^{13}C on average, although the differences may be small on any given day due to variations in the ^{13}C of fresh photosynthetic products with factors like the seasonal change in ^{13}C of atmospheric CO_2, and others that influence how fast CO_2 diffuses into the leaf and the fractionation factor associated with photosynthesis. An overall balance between the ^{13}C of C fixed by photosynthesis and respired at the ecosystem level is achieved because more ^{13}C enriched, autotrophically respired CO_2 is offset by ^{13}C-depleted, heterotrophically derived CO_2. At any given time, however, stable isotope signatures of both autotrophic and heterotrophic respiration integrate mass-dependent fractionation processes that are affected by environmental conditions like temperature and drought. The ^{13}C signature of whole ecosystem respired CO_2 can show large changes over periods of days (McDowell *et al*., 2004) that may be associated with shifts in the importance of autotrophic vs. heterotrophic sources, or changes in the discrimination of plants during photosynthesis or respiration.

Other studies using C isotopes rely on isotopic labeling associated with a change in ecosystem conditions. In Free Air CO_2 Enrichment studies, where photosynthetic products in enriched CO_2 conditions have very different ^{13}C signatures, stable isotopes have been useful for showing allocation patterns in CO_2-enriched treatments (reviewed in Pendall *et al*., 2004). The use of ^{13}C-labeled leaf or root litter can trace C through microbial pathways (e.g. Waldrop & Firestone, 2004b) and allow partitioning of components of heterotrophically respired CO_2 (e.g. Subke *et al*., 2004). On longer timescales, researchers have taken advantage of a past vegetation shift from C3 to C4 photosynthetic pathway to determine the importance of 'old' heterotrophically respired CO_2 to total soil respiration (reviewed in Hanson *et al*., 2000).

The tracing of 'bomb' ^{14}C through terrestrial ecosystems has emerged as a powerful tool for investigating the components contributing to soil respiration, and is used in a number of the papers in this Thematic Issue. Radiocarbon data are corrected for mass-dependent fractionation (using ^{13}C data), so that ^{14}C signatures of respired C reflect only differences in the combination of substrates that are producing CO_2. 'Bomb' radiocarbon was produced by atmospheric weapons testing in the 1960s, when the amount of radiocarbon in atmospheric CO_2 was nearly doubled. After the atmospheric testing moratorium in 1963, the amount of ^{14}C in atmospheric CO_2 has declined as bomb-^{14}C mixes into ocean and land C reservoirs, and as atmospheric [$^{14}CO_2$] is diluted by burning of radiocarbon-free fossil fuel. Over the past several decades the $\Delta^{14}C$

$$(\Delta^{14}C = \left[\frac{^{14}C/^{12}C)sample, -25}{0.95^{14}C/^{12}C)OXI, 1950} - 1\right] \times 1000,$$

where the ratio of $^{14}C/^{12}C$ in the sample is corrected to a common $\delta^{13}C$ value of $-25‰$, and the $^{14}C/^{12}C$ of the oxalic acid I standard has $\delta^{13}C$ of $-19‰$ and is decay corrected for radioactive decay since 1950) of atmospheric CO_2 has been declining at the rate of 5–10‰ yr^{-1} (Levin & Hesshaimer, 2000), at least twice the precision of the $\Delta^{14}C$ measurement. Recent photosynthetic products have $\Delta^{14}C$ values equal to contemporary atmospheric CO_2, while CO_2 produced from decomposing organic matter that was made from photosynthetic products fixes years to decades ago will have elevated ^{14}C signatures (Trumbore, 2000). As autotrophic respiration is known from labeling experiments to be derived from relatively recent photosynthetic products, the radiocarbon signature of respired CO_2 provides a way to quantitatively separate 'recent' from 'older' sources of decomposition (Gaudinski *et al*., 2000; Wang *et al*., 2000). Three papers in this Thematic Issue elaborate on the use of 'bomb' radiocarbon to quantify autotrophic and heterotrophic sources of soil respiration: Borken *et al*. (2005), Schuur & Trumbore (2005) and Trumbore *et al*. (2005). A fourth (Cisneros Dozal *et al*., 2005) takes advantage of a whole-ecosystem ^{14}C label to deconvolve soil respiration into components derived from root respiration and decomposition of leaf litter and mineral soil organic matter.

Isotopic methods only work if the isotope signatures of respired CO_2 sources differ significantly from one another. For example, the radiocarbon signatures of heterotrophic and autotrophic respiration are distinguishable in ecosystems where C can be stored for a long time in vegetation and/or decomposition is slow, but may not work as well when C is decomposed quickly and plants are predominantly annual. Isotopic methods make the critical assumption that the isotopic signature of CO_2 respired in incubations is not affected by artifacts associated with the incubation; in other words, the isotopic signature is more reliable and robust than the flux measurement. This assumption to date has not been well-tested (but see Cheng, 1999; Dioumaeva *et al*., 2002; Waldrop & Firestone, 2004a).

Manipulations

The third method for separating autotrophic and heterotrophic respiration sources removes the supply of

fresh photosynthetic products to roots by either cutting tree phloem (girdling; Högberg *et al*., 2001; Bhupinderpal-Singh *et al*., 2003), or by trenching an area to cut roots off from the tree (Boone *et al*., 1998; Bond-Lamberty *et al*., 2004a, b). Both manipulations offer the advantage of minimal ground disturbance, but the potential artifact of increases in heterotrophically derived CO_2 production rates due to the presence of newly dead roots (Scott-Denton *et al*., 2005), and uncertainty about how much of root and rhizosphere respiration is derived from fresh photosynthetic products vs. stored C pools (Bhupinderpal-Singh *et al*., 2003). As noted by Schuur & Trumbore (2005), care must be taken in comparing results from isotopic and girdling methods, especially when considering how autotrophic respiration from surface vegetation like mosses (as opposed to roots) is counted, and whether rhizosphere respiration is included as an 'autotrophic' or 'heterotrophic' source.

Autotrophic and heterotrophic respiration

The observations reported in this Thematic Issue have a few common features. First, the relative proportions of autotrophic and heterotrophic respiration had relatively wide ranges, and are not necessarily constant over the season, although trends are likely to be site dependent. For example, in a temperate deciduous forest autotrophic respiration accounted for the highest percentage of total respired C in spring when soils are cold (Cisneros Dozal *et al*., 2005). In contrast, a 'pulse' of rhizosphere respiration in spring thaw could be observed in a montane forest fueled by a pool of available substrate built up over the winter in frozen soils (Scott-Denton *et al*., 2005). Schuur & Trumbore (2005) observed no seasonal trend in the fraction of autotrophically respired CO_2 in mature black spruce stands in Alaska. As pointed out by Cisneros Dozal *et al*. (2005), it is important to calculate not only the fraction of total respiration that is autotrophic or heterotrophic, but the absolute flux due to each. When this is done, it is clear from all of the studies here that heterotrophic respiration is more variable than autotrophic respiration; in particular summer drought causes a drop in heterotrophic respiration in forests, mostly due to the reduction of decomposition in very dry litter layer. This drop could be observed in total ecosystem respiration (Davidson *et al*., 2005b), as well as soil respiration, and highlights the importance of the surface litter layer in causing large spatial and temporal variability in CO_2 fluxes. Borken *et al*. (2005) also observed a decline in autotrophically respired CO_2 in a simulated drought experiment. Papers by Sacks *et al*. (2005) and Scott-Denton *et al*. (2005) highlight the potential differences in substrate availability and microbial community in winter and thaw periods.

Common Themes Driving Future Research

Better measures of autotrophic and heterotrophic respiration sources reported in the papers in this Thematic Issue and in the recent literature highlight two areas where theoretical, measurement, and modeling advances are particularly needed. The first requires that we identify factors governing how C fixed by plants is allocated among respiration, storage, growth, and transfer to other (symbiotic) organisms. Differences among plant functional types or alterations in the way plants allocate C in response to environmental changes will affect whether C gets respired above- or belowground, and the ratio of what gets respired quickly (leaf, stem, root and rhizosphere respiration) vs. what is built into longer lived plant components. The second major issue involves the factors that govern the fate of nonliving plant material added to soils: whether it gets respired quickly or transformed into components that stay in the soil for decades or longer.

Plant allocation and the role of substrate supply in autotrophic respiration

Vascular plants, such as trees, are complex organisms with sophisticated strategies for resource management. Factors controlling how they allocate the products of photosynthesis are still very poorly understood. Amthor (2000) summarized the current modeling approaches to estimate three components of the plant respiration flux: metabolic respiration, respiration to fuel growth, and futile cycle, or 'wastage' respiration. Carbon not respired by these processes may be used for storage, tissue growth, or to provide fuel for symbiotic organisms and herbivores.

Many ecosystem level models assume that autotrophic respiration is implicitly or explicitly linked to photosynthesis rates (Gifford, 2003). This assumption is based on observations that in many ecosystems $\sim 50\%$ of the carbon fixed annually by photosynthesis (GPP or gross primary production) is used to fuel metabolism, and the other 50% is used to build plant tissues (NPP; net primary production). While this is true in many temperate forests (Ryan & Waring, 1992; Waring *et al*., 1998; Nabuurs *et al*., 2003), NPP is only ~ 25–30% of GPP in several boreal (Ryan *et al*., 1997) and tropical (Chambers *et al*., 2004) forests studied; in other words, a much higher fraction of C fixed in boreal and tropical forests is respired quickly, for reasons that are not yet totally understood. Davidson *et al*. (2005b) show that the ratio of soil to total respiration changes over time in

the growing season, which could mean that ratios of NPP : GPP calculated on an annual basis are averaging significant seasonal variation. Changes in [CO_2], climate, and N deposition are all likely to manifest themselves through altered C allocation patterns in plants. Simply assuming that 50% of GPP will be respired will overestimate the potential role of boreal and tropical forest ecosystems for sequestering C if their photosynthetic rates increase in the future.

One component of plant productivity not often accounted for in ecosystem-level C budgets is carbon stored in nonstructural carbohydrate pools, reviewed by Körner (2003). This pool is large compared with the amount of C stored in the leaf canopy and fine root biomass (Körner, 2003; Würth *et al*., 2005), but little is known about its rate of resupply or use (i.e. turnover time). Carbon allocated to storage can offer a buffer against uncertainty in growing conditions, and changes in this C pool can represent a significant source of interannual variability in the stand-level C budget (Hanson *et al*., 2003a).

The potential importance of storage pools as sources of autotrophic respiration is highlighted in two papers in this Thematic Issue (Cisneros Dozal *et al*., 2005; Schuur & Trumbore, 2005). While it is clear that storage pools must maintain plant tissues and fuel growth in seasons when photosynthesis is less than respiration (e.g. deciduous forests in winter), the residence time of C in storage pools, and their potential to support plant respiration in other seasons, are not well known. The continued presence of a whole-ecosystem ^{14}C label in root respiration, even several years after the labeling event, suggests that storage reservoirs persist for years and continue to contribute to root respiration (Cisneros Dozal *et al*., 2005). The $\Delta^{14}C$ of root-respired CO_2 in mature Alaskan black spruce roots indicates the C source being respired is on average $\sim$ 3 years old (Schuur & Trumbore, 2005); these data are corroborated by measurements in a second boreal forest in Canada (Czimczik & Trumbore, 2004). It is clear from the rapid reduction in soil respiration rates following tree girdling (e.g. Högberg *et al*., 2001) that at a portion of total root respiration is derived from recently fixed C; however, continued declines in respiration have been attributed to the slower exhaustion of storage pools in roots (Bhupinderpal-Singh *et al*., 2003). To date, few studies have investigated the role of storage pools and their residence times in the C budgets of higher plants. In addition to complicating the interpretation of isotope ratios in ecosystem and soil respiration, the use of storage pools in roots could provide a method to buffer soil respiration changes from substrate supply by fresh photosynthetic products and a link to explain variations in observed NPP/GPP ratios among individual plants or ecosystems.

The allocation of C to root respiration, growth, and transfer to rhizosphere symbionts is another area critical to understanding the supply of substrates for soil respired CO_2. While total annual belowground C accumulation in some ecosystems may be estimated from a steady-state assumption and the difference between total respiration and leaf litterfall (Raich & Nadelhoffer, 1989; Nadelhoffer & Raich, 1992; Davidson *et al*., 2002), the amount allocated to root respiration vs. exudation and root growth, and the seasonal variation in C transfer belowground are still only poorly known. Recent measurements of fine root lifetime using isotopic methods (Gaudinski *et al*., 2001; Tierney & Fahey, 2002; Matamala *et al*., 2003; Trumbore *et al*., 2005) indicate that the majority of living fine (<2 mm) root biomass in temperate and tropical forests can live on average for several years up to a decade, longer than previously assumed. Less C allocated to slow growing, longlived, roots implies that a greater fraction of the C allocated belowground is respired quickly, allocated to very short-lived and rapidly decomposing roots, or transferred to the rhizosphere. Trumbore *et al*. (2005) attempt to reconcile this evolving picture of root dynamics with the radiocarbon signature observed in CO_2 respired in Amazonian soils, and conclude that decomposing root litter must reside in microbial or aggregate pools for some additional time to explain all observations.

Short- and long-term controls on heterotrophic respiration

A consequence of the assumption that $\sim$ 50% of GPP is allocated to plant growth, is that eventually this C will return to the atmosphere through decomposition (i.e. at steady state, $\sim$ 50% of ecosystem respiration will be derived from heterotrophic activity). The total time elapsed between C fixation and its return to the atmosphere by microbially mediated pathways is predicted to vary among ecosystems (e.g. Fung *et al*., 1997; Thompson & Randerson, 1999), although there have been few measurements that can be directly compared with model estimates. Soil organic matter, and the plant tissues that are its precursors, are a heterogeneous mixture of materials of different ages (Fig. 3a, b). In a living forest, most of the biomass resides in tree stems that can be hundreds of years old, while most of the litter production is derived from short-lived leaf and fine root pools. Similarly, most of the carbon in soils resides in forms with slower turnover times, while the small portion of the overall mass that is made up of more active components is responsible for most of the decomposition flux (Trumbore, 2000; Fig. 3b). Some carbon can reside in soils for millennia, stabilized through association with mineral surfaces, or because it is forms that are not readily decomposed, or have

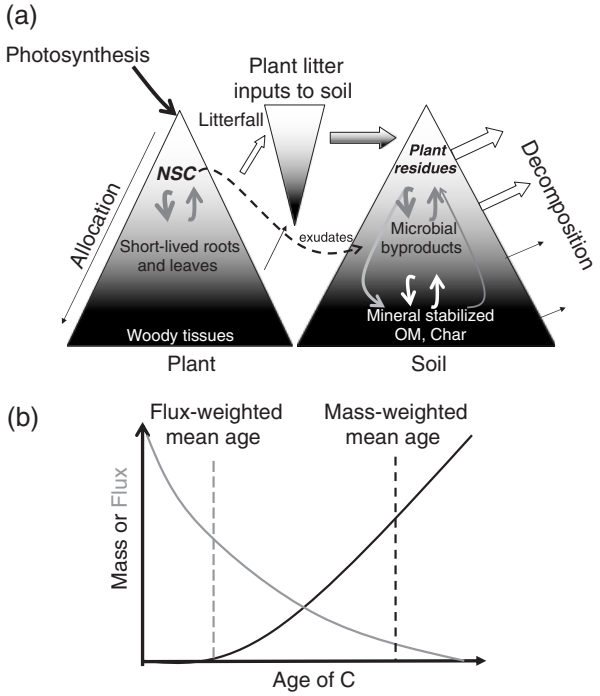

Fig. 3 (a) Carbon flows through plant and soil organic matter with differing residence times; darker shading indicates older C. Fresh photosynthetic products not respired in the plant may transferred directly to the soil microbial community (NSC, nonstructural carbohydrates), or allocated to growth of structural tissues that will live for years (fine roots, leaves) to centuries (stems in forests). Short-lived (lighter-colored) components will dominate the litterfall flux (small triangle), but the fresh plant material being added to soils has a spectrum of ages. Fresh plant material may be metabolized, or transformed into different forms that may reside in soils because of chemical or physical stabilization. The majority of C is in these more recalcitrant forms, while the flux of C lost from soils will reflect the more rapidly cycling compounds (although there are contributions from older pools; see text). (b) The graph schematically depicts the consequence of the fact that most of the C residing in plant or soil standing stocks reflects the slower cycling pools, while the mean age of C lost from these reservoirs reflects the faster cycling pools.

been physically protected in long-lived aggregates. These pools do not significantly contribute to soil respiration fluxes (e.g. Schuur & Trumbore, 2005; Trumbore *et al*., 2005) but may make up the majority of soil carbon stocks. Hence, the age of C leaving ecosystems is younger than the age of C residing in ecosystems or soils.

Controls on the balance between photosynthesis and respiration vary with timescale. On seasonal to interannual timescales, the phenology of plants, the supply of decomposable litter or exudates, and weather conditions like drought, create temporary C storage or loss (Borken *et al*., 2005; Sacks *et al*., 2005; Scott-Denton *et al*., 2005; Davidson *et al*., 2005a). It is on decadal and longer timescales, where changes in vegetation composition, age or structure, or associated changes in soil physical or chemical conditions may be important, that we lack robust explanations for why C accumulates or is lost from soils. On these longer timescales, controls on the photosynthesis–respiration balance have to do with factors not often considered in studies emphasizing instantaneous flux measurements: the frequency and type of land disturbance such as fire, the surface area and reactivity of mineral surfaces in soil, the tendency to form soil aggregates; interactions between soil fauna and soil structure; the availability of substrates and electron donors; and the history of land cover at the site (e.g. Czimczik *et al*., 2004).

Once again, our understanding of the key factors controlling what fraction of C in plant residues gets decomposed as opposed to stored in soil organic matter is limited by our ability to make measurements that can provide stringent tests of theories of organic matter stabilization. Incubation of soils emphasizes the more rapidly cycling organic matter pools that contribute the most to decomposition fluxes (Fig. 3). However, calculating an overall turnover time for soil organic matter by dividing the evolved CO_2 by the amount of C in the bulk soil obscures the fact that different factors may control decomposition of these 'active' vs. 'slow' or 'passive' pools that make up the bulk of soil organic matter. While many studies now acknowledge the need to progress beyond modeling soil organic matter as a homogeneous pool with a single turnover time when predicting response on timescales shorter than millennia, we still lack a theoretical underpinning that can successfully explain the observed range of residence times of soil C.

Even a good definition of the so-called 'slow' pool, the C that cycles on decadal timescales and represents the most important factor in determining response of soils over the next century, is lacking. Definitions of this C pool are operational – based on chemical, physical, and biological characteristics, or on the age of the material itself. An example of a chemical definition is the hydrolysable portion of C associated with mineral surfaces, while a physical definition would use the amount of C protected in aggregate structures that can last for decades. A biological definition could be the C that supports respiration which is not exhausted after 1 year of incubation. The most seemingly logical definition might be to use the age of the C, as determined using ^{14}C. However, the radiocarbon signature gives the overall time as the C was fixed from the atmosphere and may be a poor measure of the lability of organic C in a soil on short timescales. For example, a leaf that has lived on a tropical forest tree for a decade will decom-

pose in less than a year when it falls to the forest floor, but the C derived from its decomposition will be 10 years 'old.'

Comparisons of incubation- and radiocarbon-based approaches demonstrate links between long- and short-term C cycling. Isotope measurements comparing the ^{14}C or ^{13}C signature of potential C substrates in soil with the CO_2 evolved in incubations can be used to demonstrate the overall importance of C that is decades old as a source of heterotrophically produced CO_2 (Dioumaeva *et al*., 2002; Waldrop & Firestone, 2004a, b). Along a soil chronosequence in Hawaii, the abundance of noncrystalline silicate minerals with large amounts of surface area controls C storage on millennial timescales, as well as the overall C storage by soils across the landscape (Torn *et al*., 1997). However, turnover of C in surface organic horizons also varies along the chronosequence because of indirect factors associated with soil development, including plant productivity litter quality, and potentially other confounding factors like microbial community composition (Torn *et al*., 2005).

It is particularly critical for predicting how terrestrial ecosystems can influence atmospheric [CO_2] that we improve our ability to predict the response of decadally cycling organic matter pools to future changes in temperature, moisture and substrate supply. The possibility that decomposition of these pools might not be as sensitive to temperature as more labile pools (Giardina & Ryan, 2000) is difficult to test directly (Davidson *et al*., 2000). In an experiment where peat from a boreal forest was incubated at a temperatures ranging from -10 to $+8\,^{\circ}C$, Dioumaeva *et al*. (2002) compared the radiocarbon measured in respired CO_2 with organic matter components in the peat to test whether the contribution from different substrates changed with temperature. Although the total amount of evolved CO_2 increased more than 10-fold over the temperature range they studied, Dioumaeva *et al*. (2002) found no change in the radiocarbon signature of respired CO_2, implying that all component sources increased in proportion (i.e. all had the same temperature sensitivity). In contrast, Waldrop & Firestone (2004a) found a shift in the ^{13}C signature of CO_2 respired in incubations indicating that higher temperatures increased the fraction of 'old' C3 carbon contributing to the microbially respired CO_2 in a mineral soil that was converted from C3 to CAM vegetation more than a decade previously. Both studies showed the overall importance of microbial utilization of older substrates (which can make up 10–20% of all heterotrophically respired C).

Recent measurements of radiocarbon in specific phospholipid fatty acids (PLFAs) extracted from soils (Rethemeyer *et al*., 2004a, b) show that some of these very labile organic compounds (which are expected to decompose very rapidly in soils) can contain carbon that was fixed decades to centuries or more previously. As microbes 'are what they eat' isotopically, these results corroborate measures of isotopes in CO_2 evolved in incubations in demonstrating that the microbial community consumes substrates with a variety of ages, in some cases including fossil carbon normally thought to be inert. More such studies, especially ones comparing the ^{14}C age of C substrates for different types of microbes (e.g. derived from PLFAs specific to fungi and bacteria) with those in soil organic matter sources and total heterotrophic respiration, are required to gain much-needed insights into exactly C substrates contribute to decomposition fluxes, which facets of the microbial community are most important in processing those substrates, and what factors might control the contribution of decadal cycling C pools to total ecosystem respiration.

It is important to emphasize that the microbial recycling of older substrates can be the response that dominates the overall C storage change in soils in response to disturbance. An example can be found in the apparent acclimation of soil respiration in warming experiments (Jarvis & Linder, 2000; Melillo *et al*., 2002). In plots that are subjected to warming, soil respiration initially increases, but after several years it declines again to levels close to those in control plots. Using a multi-pool model in which decomposition rates are increased (Fig. 4; see also Kirschbaum, 2004), the initial loss of soil C can be attributed to response of the faster-cycling C pools that contribute most of the decomposition flux; however, in the longer term, decadally cycling pools continue to lose C at rates that are significant in terms of ecosystem level C storage, although these fluxes are not detectible as they represent a $<5\%$ increase in soil respiration rates after the first several years.

Several factors are critical to continued progress in understanding carbon storage in soils. First and foremost, is the recognition that organic matter cycles on a variety of different timescales. Just as we must separate total respiration into its autotrophic and heterotrophic components to understand how various factors combine to control the overall flux, we must come up with better definitions of soil C pools – more specifically, how to map our operationally defined fractions onto the 'active, slow and passive' pools in C cycle models. Second, is the need to understand the role played by microbial recycling of older compounds in determining the overall residence time of C in soils (Gleixner *et al*., 2002), including the potential role of labile C in facilitating decomposition of more recalcitrant substrates by 'priming' (Subke *et al*., 2004; Scott-Denton *et al*., 2005).

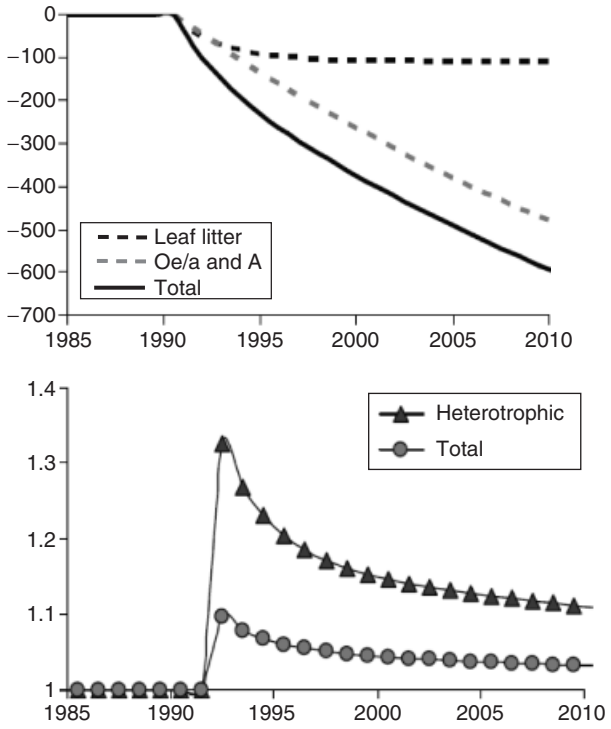

Fig. 4 Predicted response of a well-drained soil at Harvard forest to a sustained warming, beginning in 1992. Soil C pool turnover times were derived from Gaudinski *et al*. (2000), and assume a 10% increase in decomposition rates (i.e. 10% decreases in mean residence times) of each pool coincident with the start of the warming. The top panel shows the response of the soil organic matter pools, given as the cumulative change in inventory (in $gC\,m^{-2}$). While the rapidly cycling leaf litter approaches a new steady state within a few years, the decadally cycling pools of humified organic matter in the Oe/Oa and A horizons continue to lose C throughout the experiment. The lower panel shows the predicted change in soil respiration as a fraction of the mean value, and assuming (a) initially a 50–50 split in heterotrophic and autotrophic contributions to soil respiration (Gaudinski *et al*., 2000) and no effect of warming on autotrophic respiration fluxes. The continuing erosion of decadally cycling pools contributes <5% to a respiration increase after 5 years, which is not likely to be resolved in field measurements of soil respiration.

A final issue is how to determine the best model structure to represent the various timescales and processes controlling the storage and decomposition of soil carbon. Current approaches use either box models that assume there are distinct classes of organic matter that are naturally grouped because they have similar dynamics (e.g. Century; Parton *et al*., 1987), or continuum models that track degradation in quality as substrates decompose (e.g. Ågren & Bosatta, 1996). These models assume first-order decomposition kinetics, with decomposition rates proportional to the supply of substrate. Recycling of C from older pools through microbial biomass is allowed in both types of models. However, Schimel & Weintraub (2003) argue that models must also incorporate enzyme supply into kinetic models if they are to explain why some organic C remains undecomposed in soils over long periods; this idea and its consequences are reviewed in Ekschmitt *et al*. (2005). In particular, experiments are needed to determine to what degree the longer term turnover of C in soils determined using measurements of chemically or physically fractionated organic matter reflect issues of substrate and enzyme supply in different soil environments.

Conclusions

In order to create a 'theory' of respiration that allows us to predict how it may change in the next century, we need to be able to confidently differentiate between autotrophic and heterotrophic components and determine what controls their variations seasonally, interannually, over decades and across landscapes. Achieving this level of understanding requires: (1) robust methods to separate plant and microbial respiration and (2) ways to identify and separate the effects of different 'control points' such as substrate supply, enzyme kinetics, physical controls, and the composition of the decomposer community on measured fluxes. As many of these factors covary *in situ*, we need to be clever in designing manipulations or gradient studies to address factors singly or in simplified combinations, and to make measurements in parallel with modeling efforts.

Papers in this Thematic Issue document the application of new measurement and modeling methods to successfully separate soil and ecosystem respiration into components by source (autotrophic vs. heterotrophic) and C residence time. Future work requires wider application of these methods to test model structure and specific predictions, using experimental approaches that will provide critical tests of mechanisms controlling plant and microbial allocation strategies. They highlight two areas especially lacking in a coherent theoretical or modeling framework are limiting our abilities to model or predict future C storage in ecosystems. The first need is to identify the factors that control how plants allocate C among respiration, storage, growth or transfer to other organisms, both at the scale of individual plants and ecosystems. The second, involves the factors that determine whether carbon in detrital plant material added to soils gets respired or stored, and the continuum of timescales over which C gets returned to the atmosphere. Presently, we gloss over these deficiencies in understanding using either constant factors (NPP is half of GPP; autotrophic respiration is half of soil respiration), or empirically defined relationships (Q_{10}; passive pool soil carbon

storage is proportional to clay content) that relate respiration or C storage to climatic or edaphic factors. When examined carefully, these empirical relations tend to average over confounding factors such that they obscure, rather than elucidate, true climatic, phenological and substrate control effects.

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References

Ågren GI, Bosatta E (1996) Quality: a bridge between theory and experiment in soil organic matter studies. *Oikos*, **76**, 522–528.

Amthor JS (2000) The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30 years later. *Annals of Botany*, **86**, 1–20.

Bhupinderpal-Singh, Nordgren A, Lofvenius MO *et al*. (2003) Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant Cell and Environment*, **26**, 1287–1296.

Bond-Lamberty B, Wang CK, Gower ST (2004a) Contribution of root respiration to soil surface CO_2 flux in a boreal black spruce chronosequence. *Tree Physiology*, **24**, 1387–1395.

Bond-Lamberty B, Wang CK, Gower ST (2004b) A global relationship between the heterotrophic and autotrophic components of soil respiration? *Global Change Biology*, **10**, 1756–1766.

Boone RD, Nadelhoffer KJ, Canary JD *et al*. (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature*, **396**, 570–572.

Borken W, Savage K, Davidson EA *et al*. (2005) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. *Global Change Biology*, doi: 10.1111/j.1365-2486.2005.01058.x

Braswell BH, Sacks WJ, Linder E *et al*. (2005) Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biology*, **11**, 335–355.

Burton AJ, Pregitzer KS, Ruess RW *et al*. (2002) Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes. *Oecologia*, **131**, 559–568.

Chambers JQ, Tribuzy ES, Toledo LC *et al*. (2004) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological Applications*, **14**, S72–S88.

Cheng W (1999) Measurement of rhizosphere respiration and organic matter decomposition using natural ^{13}C. *Plant and Soil*, **183**, 263–268.

Ciais P, Friedlingstein P, Schimel DS *et al*. (1999) A global calculation of the delta C-13 of soil respired carbon: implications for the biospheric uptake of anthropogenic CO_2. *Global Biogeochemical Cycles*, **13**, 519–530.

Cisneros Dozal LM, rumbore E, Hanson PJ (2005) Partitioning sources of soil-respired CO_2 and their seasonal variation using a unique radiocarbon tracer. *Global Change Biology*, doi: 10.1111/j.1365-2486.2005.01061.x

Czimczik CI, Mund M, Schulze E-D *et al*. (2004) Effects of reforestation, deforestation, and afforestation on carbon storage in soils. Chapter 15, In: *The Carbon Balance of Forest Biomes* (eds Griffiths H, Jarvis PJ), Garland Science/BIOS Scientific Publishers pp. 317–328.

Czimczik CI, Trumbore SE (2004) Seasonal changes of soil respiration sources in a boreal forest. *EOS, Transactions of AGU, Fall Meeting*, **84** (Suppl.), abstract #B23A-0943.

Davidson EA, Jassens IA, Luo Y (2005a) On the variability of respiration in terrestrial ecosystems: moving beyond Q10. *Global Change Biology*, doi: 10.1111/j.1365-2486.2005.01065.x

Davidson EA, Richardson AD, Savage KE *et al*. (2005b) A distinct seasonal patter of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest. *Global Change Biology*, doi: 10.1111/j.1365-2486.2005.01062.x

Davidson EA, Savage K, Bolstad P *et al*. (2002) Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. *Agricultural and Forest Meteorology*, **113**, 39–51.

Davidson EA, Trumbore SE, Amundson R (2000) Biogeochemistry – Soil warming and organic carbon content. *Nature*, **408**, 789–790.

Dawson TE, Mambelli S, Plamboeck AH *et al*. (2002) Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics*, **33**, 507–559.

Dioumaeva I, Trumbore S, Schuur EAG *et al*. (2002) Decomposition of peat from upland boreal forest: temperature dependence and sources of respired carbon. *Journal of Geophysical Research – Atmospheres*, **108**, 8222.

Ekschmitt K, Liu MQ, Vetter S *et al*. (2005) Strategies used by soil biota to overcome soil organic matter stability – why is dead organic matter left over in the soil? *Geoderma*, **128**, 167–176.

Fung I, Field CB, Berry JA *et al*. (1997) Carbon 13 exchanges between the atmosphere and biosphere. *Global Biogeochemical Cycles*, **11**, 507–533.

Gaudinski JB, Trumbore SE, Davidson EA *et al*. (2001) The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. *Oecologia*, **129**, 420–429.

Gaudinski JB, Trumbore SE, Davidson EA *et al*. (2000) Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. *Biogeochemistry*, **51**, 33–69.

Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858–861.

Gifford RM (2003) Plant respiration in productivity models: conceptualization, representation, and issues for terrestrial carbon-cycle research. *Functional Plant Biology*, **30**, 171–186.

Gleixner G, Poirier N, Bol R *et al*. (2002) Molecular dynamics of organic matter in a cultivated soil. *Organic Geochemistry*, **33**, 357–366.

Goulden ML, Munger JW, Fan SM (1996) Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation. *Global Change Biology*, **2**, 169–182.

Goulden ML, Wofsy SC, Harden JW *et al*. (1998) Sensitivity of boreal forest carbon balance to soil thaw. *Science*, **279**, 214–217.

Hanson PJ, Edwards NT, Garten CT *et al*. (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry*, **48**, 115–146.

Hanson PJ, Edwards NT, Tschaplinski TJ *et al*. (2003a) Estimating net primary and net ecosystem production of a southeastern upland Quercus forest from an 8-year biometric record. In: *North American Temperate Deciduous Forest Responses to Changing Precipitation* (eds Hanson PJ, Wullschelger SD), pp. 378–394. Springer-Verlag, New York.

Hanson PJ, O'Neill EG, Chambers MLS *et al*. (2003b) Soil respiration and litter decomposition. In: *North American Temperate Deciduous Forest Responses to Changing Precipitation* (eds Hanson PJ, Wullschelger SD), pp. 163–189. Springer-Verlag, New York.

Harden JW, Trumbore SE, Stocks BJ *et al*. (2000) The role of fire in the boreal carbon budget. *Global Change Biology*, **6**, 174–184.

Högberg P, Nordgren A, Buchmann N *et al*. (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, **411**, 789–792.

Hui DF, Luo YQ (2004) Evaluation of soil CO_2 production and transport in Duke Forest using a process-based modeling approach. *Global Biogechemical Cycles*, **18**, Art. No. GB4029.

Janssens IA, Lankreijer H, Matteucci G *et al*. (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, **7**, 269–278.

Jarvis P, Linder S (2000) Botany – Constraints to growth of boreal forests. *Nature*, **405**, 904–905.

Kirschbaum MUF (2004) Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? *Global Change Biology*, **10**, 1870–1877.

Körner C (2003) Carbon limitation in trees. *Journal of Ecology*, **91**, 4–17.

Levin I, Hesshaimer V (2000) Radiocarbon – A unique tracer of global carbon cycle dynamics. *Radiocarbon*, **42**, 69–80.

Matamala R, Gonzalez-Meler MA, Jastrow JD *et al*. (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science*, **302**, 1385–1387.

McDowell NG, Bowling DR, Bond BJ *et al*. (2004) Response of the carbon isotopic content of ecosystem, leaf, and soil respiration to meteorological and physiological driving factors in a Pinus ponderosa ecosystem. *Global Biogeochemical Cycles*, **18**, GB1013.

Melillo JM, Steudler PA, Aber JD *et al*. (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science*, **298**, 2173–2176.

Nabuurs G-J, Schelhaas M-J, Godefridus F *et al*. (2003) Temporal evolution of the European forest sector carbon sink from 1950–1999. *Global Change Biology*, **9**, 152–160.

Nadelhoffer KJ, Raich JW (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology*, **73**, 1139–1147.

Oechel WC, Vourlitis GL, Hastings SJ *et al*. (2000) Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978–981.

Parton WJ, Schimel DS, Cole CV *et al*. (1987) Analysis of Factors controlling soil organic-matter levels in great-plains grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.

Pendall E, Bridgham S, Hanson PJ *et al*. (2004) Below-ground process responses to elevated CO_2 and temperature: a discussion of observations, measurement methods, and models. *New Phytologist*, **162**, 311–322.

Prentice IC *et al*. (2001) The carbon cycle atmospheric carbon dioxide, chapter 3. In: *Climate Change 2001: The Scientific Basis* (eds Houghton JT *et al*.), Cambridge University Press, Cambridge, UK.

Raich JW, Nadelhoffer KJ (1989) Belowground carbon allocation in forest ecosystems – global trends. *Ecology*, **70**, 1346–1354.

Raich JW, Potter CS (1995) Global patterns of carbon-dioxide emissions from soils. *Global Biogeochemical Cycles*, **9**, 23–36.

Raich JW, Schlesinger WH (1992) The Global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Series B – Chemical and Physical Meteorology*, **44**, 81–99.

Randerson JT, Masiello CA, Still CJ *et al*. (2005) Is carbon within the global terrestrial biosphere becoming more oxidized? Implications for trends in atmospheric O_2. *Global Change Biology*, in press.

Rethemeyer J, Grootes PM, Bruhn F *et al*. (2004a) Age heterogeneity of soil organic matter. *Nuclear Instruments & Methods in Physics Research Section B – Beam Interactions with Materials and Atoms*, **223–24**, 521–527.

Rethemeyer J, Kramer C, Gleixner G *et al*. (2004b) Complexity of soil organic matter: AMS C-14 analysis of soil lipid fractions and individual compounds. *Radiocarbon*, **46**, 465–473.

Ruess RW, Hendrick RL, Vogel JG *et al*. (in press) The role of fine roots in the functioning of boreal forests. In: *Alaska's Changing Boreal Forest* (eds Chapin III FS III, Oswood MS, Van Cleve K, Viereck L, Verbyla D), Oxford University Press, New York, NY.

Ryan MG, Lavigne MB, Gower ST (1997) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal of Geophysical Research – Atmospheres*, **102**, 28871–28883.

Ryan MG, Waring RH (1992) Maintenance respiration and stand development in a sub-alpine lodgepole pine forest. *Ecology*, **73**, 2100–2108.

Sacks WJ, Schimel DS, Monson RK *et al*. (2005) Assimilation modeling of diurnal and seasonal respiration fluxes at Niwot Ridge, Colorado. *Global Change Biology*, doi: 10.1111/j.1365-2486.2005.01059.x

Savage KE, Davidson EA (2001) Interannual variation of soil respiration in two New England forests. *Global Biogeochemical Cycles*, **15**, 337–350.

Schimel DS (1995) Terrestrial ecosystems and the carbon-cycle. *Global Change Biology*, **1**, 77–91.

Schimel DS, Emanuel W, Rizzo B *et al*. (1997) Continental scale variability in ecosystem processes: models, data, and the role of disturbance. *Ecological Monographs*, **67**, 251–271.

Schimel DS, House JI, Hibbard KA *et al*. (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature*, **414**, 169–172.

Schimel JP, Weintraub MN (2003) THe implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biology and Biochemistry*, **35**, 549–563.

Schuur EA, Trumbore S (2005) Partitioning sources of soil respiration in boreal black spruce forest using radiocarbon. *Global Change Biology*, doi: 10.1111/j.1365-2486.2005.01066.x

Scott-Denton LE, Rosenstiel TN, Monson RK (2005) Differential controls by climate and substrate over the heterotrophic and rhizospheric components of soil respiration. *Global Change Biology*, doi: 10.1111/j.1365-2486.2005.01064.x

Subke JA, Hahn V, Battipaglia G *et al*. (2004) Feedback interactions between needle litter decomposition and rhizosphere activity. *Oecologia*, **139**, 551–559.

Thompson MV, Randerson JT (1999) Impulse response functions of terrestrial carbon cycle models: method and application. *Global Change Biology*, **5**, 1365–2486.

Tierney GL, Fahey TJ (2002) Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **32**, 1692–1697.

Torn MS, Trumbore SE, Chadwick OA *et al*. (1997) Mineral control of soil organic carbon storage and turnover. *Nature*, **389**, 170–173.

Torn MS, Vitousek PM, Trumbore SE (2005) The influence of nutrient availability on soil organic matter turnover estimated by incubations and radiocarbon modeling. *Ecosystems* (in press).

Trumbore S (2000) Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications*, **10**, 399–411.

Trumbore SE, Chadwick OA, Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science*, **272**, 393–396.

Trumbore S, Salazar da Costa E, Nepstad DC *et al*. (2005) Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. *Global Change Biology*, doi: 10.1111/j.1365-2486.2005.01063.x

van der Werf GR, Randerson JT, Collatz GJ *et al*. (2004) Continental-scale partitioning of fire emissions during the 1997 to 2001 El Nino/La Nina period. *Science*, **303**, 73–76.

Verburg PSJ, Arnone JA, Obrist D *et al*. (2004) Net ecosystem carbon exchange in two experimental grassland ecosystems. *Global Change Biology*, **10**, 498–508.

Waldrop MP, Firestone MK (2004a) Altered utilization patterns of young and old soil C by microorganisms caused by temperature shifts and N additions. *Biogeochemistry*, **67**, 235–248.

Waldrop MP, Firestone MK (2004b) Microbial community utilization of recalcitrant and simple carbon compounds: impact of oak-woodland plant communities. *Oecologia*, **138**, 275–284.

Wang Y, Amundson R, Niu XF (2000) Seasonal and altitudinal variation in decomposition of soil organic matter inferred from radiocarbon measurements of soil CO_2 flux. *Global Biogeochemical Cycles*, **14**, 199–211.

Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology*, **18**, 129–134.

Würth MKR, Pelaez-Riedl S, Wright SJ *et al*. (2005) Non-structural carbohydrate pools in a tropical forest. *Oecologia*, **143**, 11–24.