Research review

Below-ground process responses to elevated CO_2 and temperature: a discussion of observations, measurement methods, and models

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Summary

Rising atmospheric CO_2 and temperatures are probably altering ecosystem carbon cycling, causing both positive and negative feedbacks to climate. Below-ground processes play a key role in the global carbon (C) cycle because they regulate storage of large quantities of C, and are potentially very sensitive to direct and indirect effects of elevated CO_2 and temperature. Soil organic matter pools, roots and associated rhizosphere organisms all have distinct responses to environmental change drivers, although availability of C substrates will regulate all the responses. Elevated CO_2 increases C supply below-ground, whereas warming is likely to increase respiration and decomposition rates, leading to speculation that these effects will moderate one another. However, indirect effects on soil moisture availability and nutrient supply may alter processes in unexpected directions. Detailed, mechanistic understanding and modelling of below-ground flux components, pool sizes and turnover rates is needed to adequately predict long-term, net C storage in ecosystems. In this synthesis, we discuss the current status of below-ground responses to elevated CO_2 and

temperature and potential feedback effects, methodological challenges, and approaches to integrating models and measurements.

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Introduction

In the coming century, atmospheric CO_2 concentrations are expected to double, and global average temperature may increase by 1.8–5.8°C (IPCC, 2001). The terrestrial C cycle is already probably changing in response to these perturbations (e.g. Raich *et al.*, 2002; Lenton & Huntingford, 2003), but substantial uncertainties remain in the sensitivity of ecosystems to global change forcing factors, particularly regarding the role of feedback among key processes. The capacity of ecosystems to store C depends on net ecosystem production (NEP), which is the balance between net primary production (NPP) and heterotrophic respiration (Rh). Knowledge of the underlying

mechanisms driving changes in NEP is essential to predict terrestrial C cycle responses to rising temperature and CO_2. Current understanding suggests that the primary direct ecosystem response to increased CO_2 concentration is an increase of NPP (i.e. 'CO_2 fertilization'), which is potentially a negative feedback on atmospheric CO_2 concentrations. Rising temperatures could exert their strongest influence over microbial processes such as heterotrophic respiration, which would be a positive feedback on atmospheric CO_2 (Fig. 1a). Simulations suggest that these effects may nearly counteract one another (Kirschbaum, 2000). However, both elevated CO_2 and warming have other direct and indirect effects, which make it unlikely that the primary direct effects will simply
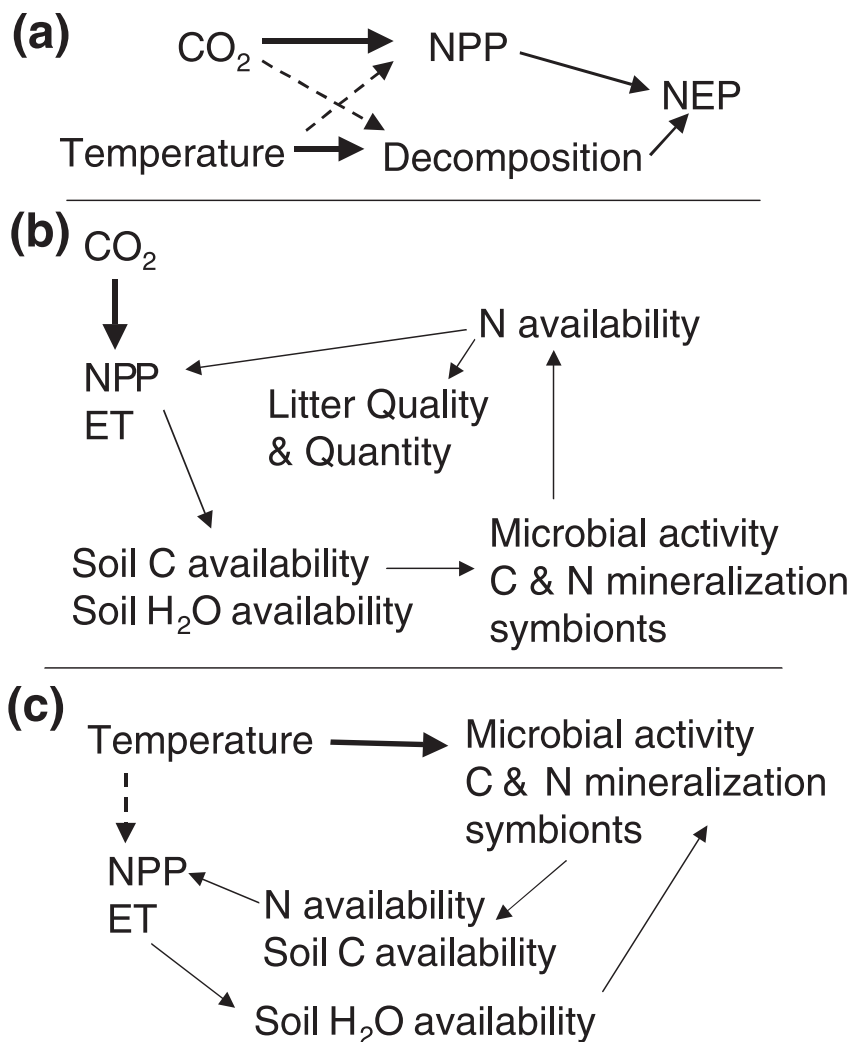

Fig. 1 Direct and indirect effects of elevated CO_2, temperature, and their interactions on C cycling below-ground. (a) Elevated CO_2 directly stimulates net primary production (NPP) by enhancing the efficiency of Rubisco, which increases net ecosystem production (NEP). Increased temperature directly stimulates decomposition rates by enhancing enzyme activity and chemical reaction rates, thereby reducing NEP. Elevated CO_2 indirectly affects decomposition rate, either suppressing it via decreased litter quality or enhancing it via the priming effect (see text). Temperature has smaller direct effects on NPP than atmospheric CO_2 concentration; interactions and indirect effects make predicting C storage (NEP) challenging. (b) Feedbacks effected by elevated CO_2 include water and nutrient cycling. As NPP is stimulated, more C is available in soils, feeding substrate limited microbes. Enhanced microbial activity stimulates C and N mineralization and increases N availability to a limit. Activity of symbionts is likely to be affected by increased C availability below-ground. Litter quantity increases, and as N becomes immobilized in microbes, litter quality may decrease. Elevated CO_2 reduces evapotranspiration (ET) and increases available soil water in some systems, which may enhance NPP and mineralization rates. (c) Increased temperature most strongly stimulates microbial activity, increasing N availability and NPP. In some systems, enhanced ET dries soils, and microbial activity is not stimulated. Temperature may have strong effects on symbiotic interactions.

cancel out; for example, elevated CO_2 also affects microbial activities, and temperature influences NPP (Fig. 1a). This complex web of interactions and feedbacks is slowly being untangled by experiments and modelling to improve our understanding of the combined effects of elevated CO_2 and temperature on the global C cycle.

Direct effects of elevated CO_2 on below-ground C cycling include stimulation of root growth (below-ground net primary production, BNPP) and respiration, increased C inputs from canopy litter fall and root turnover, and changes in litter quality or decomposability (Norby, 1994; Norby *et al.*, 2001, Fig. 1b). Direct effects of increased temperature accelerate losses of CO_2 and CH_4 from the soil by increasing the activity of roots and soil heterotrophs (Hobbie, 1996; Van Cleve *et al.*, 1990; Joslin & Wolfe, 1993; Peterjohn *et al.*, 1994; Lükewille & Wright, 1997). Higher temperatures are also associated with increased NPP, potentially providing more substrate for heterotrophs in the long term if other resources are not limiting (Jenkinson *et al.*, 1991; Raich & Schlesinger, 1992; Lloyd & Taylor, 1994; Kirschbaum, 1995; Trumbore, 1997, Fig. 1c).

Indirect effects of both elevated CO_2 and temperature on the below-ground C cycle are mediated through nutrient and water cycles. Nitrogen (N) mineralization may be stimulated by warming and act as a positive feedback to plant productivity (Strömgren & Linder, 2002). Increased temperature may dry upland soils, which could result in immobilization of essential elements and reduced decomposition; in wetland soils drying may increase aerobic respiration and decomposition by lowering water tables. However, drying may be alleviated if elevated CO_2 reduces transpiration rates (Megonigal & Schlesinger, 1997; Jackson *et al.*, 1998). Plant community shifts will mediate some of these feedbacks: in a montane meadow warming experiment, soil drying induced a shift from productive forbs to less productive shrubs. Warming thus decreased net C uptake, not because decomposition was stimulated, but because NPP was reduced (Saleska *et al.*, 1999). Finally, the net effect of warming and elevated CO_2 on radiative forcing is determined by indirect effects on the production and release of other trace gases such as N_2O and CH_4 (Dacey *et al.*, 1994; Smart *et al.*, 1997; McLain *et al.*, 2002). Separation of temperature, CO_2, moisture and nutrient effects on below-ground processes is a prerequisite for predictive understanding of ecosystem C cycling. The complexity of the interacting processes and their spatial and temporal variability requires greater integration of experimental manipulations and modelling.

The goals of this synthesis are: (i) summarize the current status of the combined effects of experimentally elevated CO_2 and temperature on below-ground processes; (ii) highlight the role of feedbacks mediated through the N and water cycles; (iii) discuss methodological challenges; and (iv) suggest approaches for integrating models and measurements. Below-ground processes include C allocation below-ground via roots; microbial and mycorrhizal processes; SOM pool sizes and turnover rates; and soil, microbial and rhizosphere respiration rates.

Although our ability to predict responses of below-ground processes to altered climate is still limited by a lack of long-term, multifactor experiments, understanding of basic mechanisms has greatly improved over the last 10 years. Here we focus on what we believe are the most important recent developments and future directions for below-ground ecosystem research.

Response of Below-ground C Pools and Processes to Elevated CO_2, Warming and their Interactions

Root production and turnover rates

Fine roots are a key link for plant water and nutrient uptake, soil C input, and soil microbial activity (Fig. 2; Norby, 1994). Turnover of fine roots (< 2.0 mm in diameter) plays a critical role in regulating ecosystem C balance, and accurate estimates of below-ground NPP are required for estimating NEP (Pendall *et al.*, 2004a). It is estimated that as much as 33% of global annual NPP is used for the production of fine roots (Jackson *et al.*, 1997). With their high turnover rate, fine roots will be sensitive to elevated atmospheric CO_2, temperature and their interactions (Hendrick & Pregitzer, 1992; Raich & Schlesinger, 1992; Fitter *et al.*, 1997; Eissenstat *et al.*, 2000; Gill & Jackson, 2000), and may influence sequestration of atmospheric CO_2 on annual to decadal timescales.

Increased photosynthesis under elevated CO_2 can stimulate below-ground C input and fine-root growth (Curtis, 1996; Curtis & Wang, 1998; Pendall *et al.*, 2004b), and root turnover rates and biomass (Berntson & Bazzaz, 1997; Fitter *et al.*, 1999; Allen *et al.*, 2000; Pregitzer *et al.*, 2000; Wan *et al.*, 2004). Higher temperatures are associated with increased fine-root production and mortality (Gill & Jackson, 2000), and therefore turnover rates (Hendrick & Pregitzer, 1993, 1997; Forbes *et al.*, 1997; Fitter *et al.*, 1999; King *et al.*, 1999; Wan *et al.*, 2004). A few experiments have evaluated root responses to the interactive effects of CO_2 and temperature. A 4-year open-top chamber experiment in Tennessee showed that both the main effects of elevated CO_2 and temperature on root turnover (productivity and mortality) of two deciduous tree species were statistically significant and additive; i.e. there were no interactive effects of CO_2 and temperature (Wan *et al.*, 2004). The combination of elevated CO_2 and temperature significantly increased fine-root biomass of Loblolly pine seedlings (*Pinus taeda*), but had no effect on Ponderosa pine seedlings (*P. ponderosa*; King *et al.*, 1996). By contrast, Soussana *et al.* (1996) and Kandeler *et al.* (1998) found significant reductions in root biomass under elevated CO_2 and temperature. Apparently, elevated CO_2 can sometimes compensate for the anticipated negative effects of increased temperature on root biomass (Bassow *et al.*, 1994; Wan *et al.*, 2004), possibly by reducing evapotranspiration and increasing soil moisture (Nelson *et al.*, 2004), by increasing the
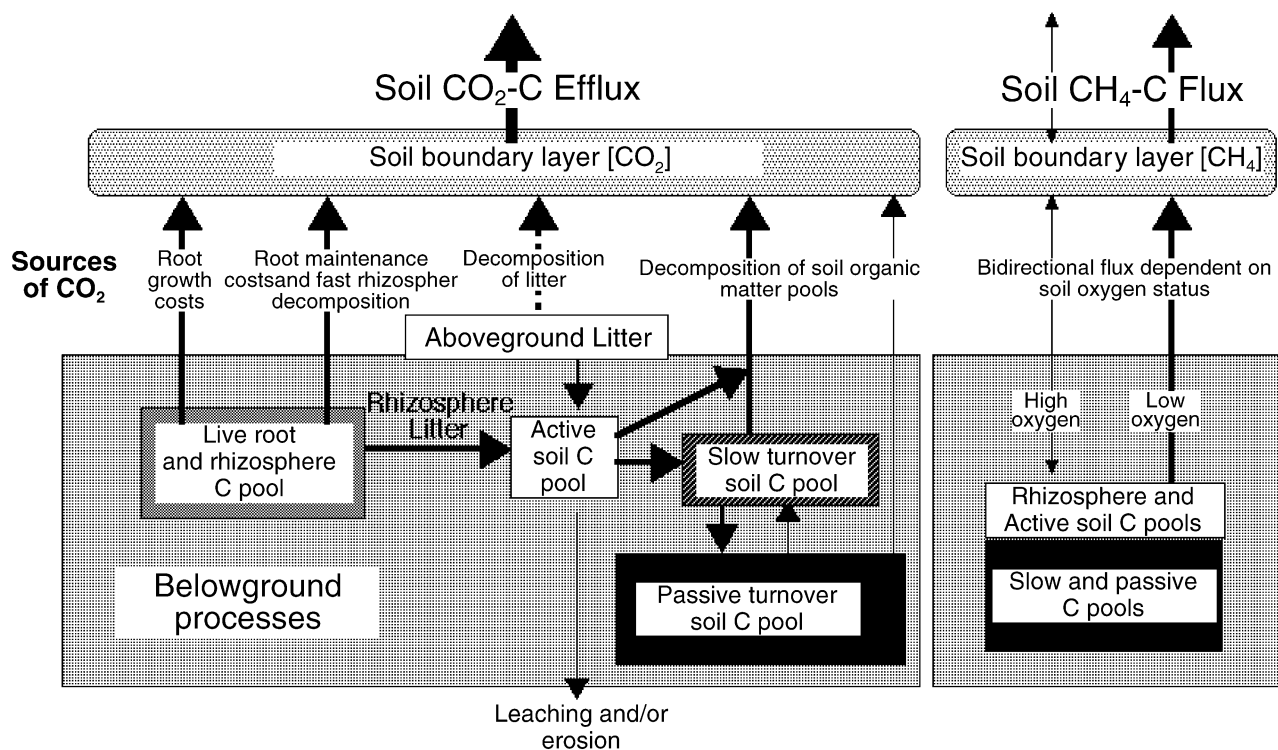
Fig. 2 Below-ground carbon cycle processes and components affected by elevated CO_2, warming, and their interactions. Although soil organic matter is a complex mixture of materials spanning a continuum of decomposability, we conceptualize three main pools, Active, Slow and Passive. The Active pool receives inputs from the rhizosphere and above-ground litter, and turns over on time scales of up to a few years. The Slow pool receives most inputs from the active pool, with remineralization of Passive C contributing small amounts, and turns over on decadal to century time scales. The Passive C pool consists of physically or chemically protected organo-mineral complexes, with turnover times of millennia. CO_2 efflux is derived from decomposition of the various C pools, including roots and litter, and varies with soil temperature, moisture, and plant phenology. Erosion of particulate organic matter and leaching of dissolved organic carbon are important fluxes in many systems. Decomposition of C pools in all soils produces both CH_4 and CO_2, with the ratio of the two regulated by O_2 and saturation. The CH_4/CO_2 ratio ranges from zero in dry upland soils where production is restricted to microsites, to perhaps 1/3 in permanently wet, hydric soils; in some systems the ratio varies seasonally or spatially. Methane production is more dependent on labile carbon pools than is CO_2 production, but there is generally less known about the contribution of various C pools to CH_4 production than CO_2 production.

temperature optimum for photosynthesis (Long, 1991) or by providing carbohydrate supplies to support sustained root growth. Root responses will be partly determined by the growth stage of the experimental plants; larger positive responses may be detected in young systems where the soil volume is not fully occupied.

Root turnover and respiration rates are positively correlated with fine root N concentration (Ryan *et al.*, 1996; Pregitzer *et al.*, 1998, 2002; Eissenstat *et al.*, 2000), which is expected to decrease by 10–25% under elevated CO_2 (Curtis *et al.*, 1990; Berntson & Bazzaz, 1997; King *et al.*, 1997; Cotrufo *et al.*, 1998; Rogers *et al.*, 1999; Pregitzer *et al.*, 2000; Wan *et al.*, 2004). By contrast, elevated temperatures are reported to increase root N concentration (King *et al.*, 1997; Kandeler *et al.*, 1998; Wan *et al.*, 2004), presumably because mineralization and diffusion of N are stimulated at high temperatures (BassiriRad *et al.*, 1993; BassiriRad, 2000). Higher root N concentration could lead to greater fine-root mortality (Pregitzer *et al.*, 1998, 2002), which has the potential to alter rates

of microbial immobilization and modify soil N cycling (Zak *et al.*, 2000a).

Very few studies have reported responses of root N concentration to CO_2 and temperature interactions (King *et al.*, 1997; Loiseau & Soussana, 1999; Wan *et al.*, 2004). Wan *et al.* (2004) found that the interactions of elevated CO_2 and temperature significantly increased root N concentration, but King *et al.* (1997) found no interactive effects. Studies that measure separate rhizosphere respiration responses are required to assess how N concentration and root maintenance cost respond to the interactions of elevated CO_2 and temperature.

Microbial biomass and community structure

Most important biogeochemical processes in soil are microbially mediated, so it is imperative to understand how soil microbial biomass will respond to warming and enhanced CO_2. Although increased labile C input to soil under elevated CO_2 is expected to increase microbial C and N, increases, decreases, and neutral

responses have been found (Zak *et al.*, 2000b). Clear relationships with NPP are lacking, despite the strong relationship between plant productivity and microbial biomass when comparing different ecosystem types (Zak *et al.*, 1993). Negative and neutral microbial biomass responses may be explained by increased turnover rates if soil water content is high (Hungate *et al.*, 1997; Arnone & Bohlen, 1998), if grazing by soil organisms is stimulated (Jones *et al.*, 1998; Ronn *et al.*, 2002) or N availability is low (Diaz *et al.*, 1993). Microbial biomass generally responds positively to increased temperature, whereas responses to elevated CO_2 are highly idiosyncratic. Possibly, microbial response to the interaction of CO_2 and temperature would be dominated by the more ubiquitous temperature effect, or as shown below for mycorrhizas, the effects may offset one another. The community structure of free-living and symbiotic microbes is likely to mediate below-ground C cycle responses to elevated CO_2 and warming by regulating turnover rates of SOM pools and providing feedback pathways on C cycling, but very little work has been done in this area.

Mycorrhizal processes

Mycorrhizas will modify plant, community and ecosystem responses to global change factors. Functions mediated by mycorrhizas include plant nutrient foraging, plant C allocation and architecture, changes in soil structure, and soil C storage (Rillig *et al.*, 2002; Staddon *et al.*, 2002). Changes in atmospheric CO_2 concentrations indirectly affect mycorrhizas through changes in C allocation from host plants to fungi (Sanders *et al.*, 1998; Treseder & Allen, 2000; Staddon *et al.*, 2002; Olsrud *et al.*, 2004), although mycorrhizal responses may be smaller when N availability is high (Treseder & Allen, 2000). Increased temperature may directly enhance arbuscular mycorrhizal (AM) colonization and development (Fitter *et al.*, 2000; Gavito *et al.*, 2003). Indirect temperature responses may be mediated via changes in plant photosynthesis rate, plant and soil nutrient concentrations, and soil moisture. For example, ericoid mycorrhizal colonization increased with soil temperature due to an increased below-ground C allocation associated with low soil moisture content (Olsrud *et al.*, 2004). In the same study, an interaction between elevated CO_2 and temperature increased plant water use efficiency, alleviating the soil moisture deficit and resulting in lower root and mycorrhizal densities compared to the effect of warming alone (Olsrud *et al.*, 2004). Another study reported decreased AM mycorrhizal colonization under elevated temperature, and concluded that the negative effects of temperature on soil water and root production might have been offset by increased plant nutrient availability (Monz *et al.*, 1994). Phosphorus uptake by AM mycorrhizas was stimulated by elevated temperatures more than by elevated CO_2, with no interaction, possibly because P uptake was not C limited (Gavito *et al.*, 2003).

Soil and C pool sizes and turnover rates

Soil organic matter is comprised of a complex array of compounds with variable reactivity or susceptibility to decomposition. SOM has often been conceptually divided into two or three compartments which decompose rapidly, slowly, or not at all; these compartments have been called the active (labile, microbial), slow (intermediate, unprotected) and passive (recalcitrant, protected) pools, respectively (e.g. Schimel *et al.*, 1985; Christensen, 1996, Fig. 2). Below-ground C pools can also include root biomass and litter or organic horizons lying above the mineral soil, each of which have different decomposition dynamics and responses to environmental change. Rapidly cycling, nonstructural carbohydrate pools, react quickly to disturbance or experimental manipulation, and can induce interannual variability in NEP (Hanson *et al.*, 2003a). Long-term net changes in C storage resulting from elevated CO_2 or temperature require changes in slow-turnover pools, those with mean residence times of decades or longer. Therefore, knowing only the bulk C content of soil is insufficient; sizes and turnover rates of specific identifiable pools are required for predicting responses to environmental change.

Elevated CO_2 has stimulated NPP in most experiments to date, but the fate of this C, especially the portion allocated below-ground, largely remains unknown. Studies have rarely found measurable changes in SOM pools using conventional C analyses (e.g. Tate & Ross, 1997; Van Kessel *et al.*, 2000; Leavitt *et al.*, 2001). This has been attributed to the difficulty in measuring a small increment of SOC against a large background (Hungate *et al.*, 1996). Stable C isotope labelling on both ambient and elevated CO_2 treatments during a FACE winter wheat experiment allowed detection of a net SOC increase of 5% over 2 years (Leavitt *et al.*, 2001). In a semiarid grassland, new C inputs to the bulk soil were roughly doubled by twice-ambient CO_2 over 4 years (Pendall *et al.*, 2004b). However, increased turnover rates of older SOM negated the gain of new C, resulting in no difference in NEP between ambient and elevated treatments during moist conditions (Pendall *et al.*, 2004a).

Warming often causes a rapid loss of labile substrates, which might make up *c.* 10% of the total SOM pool, followed by slower mineralization of intermediate SOM (Ineson *et al.*, 1998a,b; Loiseau & Soussana, 1999; Melillo *et al.*, 2002). A laboratory incubation experiment using Hawaiian soils and a ^{13}C label (derived from C_3-C_4 vegetation shift) suggested that intermediate and active SOM pools had similar sensitivity to warming (Townsend *et al.*, 1997).

Temperature–CO_2 experiments focusing on changes in below-ground C pool sizes and turnover rates have rarely been reported in the literature, reflecting the largest gap in our understanding of below-ground process responses to climate change. In a warming–CO_2–N experiment in tunnels with ryegrass swards, particulate organic matter increased under elevated CO_2, warming increased turnover rates, and the interaction of CO_2 and warming strongly enhanced 'old' pool C decomposition (Loiseau & Soussana, 1999). In a shortgrass

steppe study in which CO_2 concentrations were doubled, an interesting feedback was noted in that the Q_{10} for decomposition was lower under elevated CO_2 than ambient CO_2 (Pendall *et al.*, 2003). This reduced temperature sensitivity under elevated CO_2 suggests that substrate quality was diminished and/or that microbial community composition had shifted toward a greater importance of fungi, which have lower temperature response than bacteria.

Soil respiration and its components

Soil respiration – the diffusive flux of CO_2 (and CH_4) from the soil boundary layer into the atmosphere – is a functional and commonly used term. However, it is far too vague for use in below-ground process studies because there is no single process that defines what is measured (Fig. 2; Hanson *et al.*, 2000). Under conditions that do not disturb the soil's natural surface boundary layer and microenvironment, measurements of CO_2 and CH_4 efflux from the soil surface are assumed to be in equilibrium with a wide range of below-ground biological processes. Those processes include autotrophic respiration associated with the growth and maintenance of roots and mycorrhizal fungi, rhizosphere microbial respiration tightly coupled to the supply of labile plant carbohydrates, and the respiration of heterotrophic decomposers. Because of the methodological difficulty in separating autotrophic root respiration from heterotrophic respiration by rhizosphere microbes, we define these combined processes as 'rhizosphere' respiration; 'decomposition', then, is the portion of the total soil CO_2 efflux that can be measured separately from the rhizosphere using mechanical or isotopic approaches (Hanson *et al.*, 2000).

Autotrophic (rhizosphere) and heterotrophic respiratory processes are likely to respond to elevated temperature and CO_2 in different ways, and determination of the separate sources in multifactor studies is essential to a predictive understanding of ecosystem responses to global change. The majority of studies, however, have examined the effects of CO_2 or warming on the total efflux rather than attempting to separate the components. Pajari (1995) studied *Pinus* spp. responses at 550 ppm CO_2 and a 2–3°C increase in temperature in open-top chambers, and found that increased soil respiration under elevated CO_2 was sometimes counteracted by increasing temperatures. Possibly, an indirect effect of warming led to drier soils, limiting respiration rates. Edwards & Norby (1999) evaluated the response of soil respiration under *Acer* to +300 ppm CO_2 and +4°C and found greater total soil respiration under each treatment, but the heterotrophic soil component was only increased by temperature and root growth/activity was increased by both. Decomposition was more strongly stimulated by elevated CO_2 and warming together than by elevated CO_2 alone, but this interaction was dependent on adequate N supply in ryegrass swards (Loiseau & Soussana, 1999). Litter decomposition, rhizosphere respiration, and mineral soil respiration increased in experimental *Pseudotsuga*

spp. mesocosms exposed to +200 ppm CO_2 and +4°C (Lin *et al.*, 1999). The decomposition component of soil respiration was only significantly affected by temperature, while rhizosphere respiration responded to both CO_2 and temperature.

Substrate availability, regulated by NPP, will ultimately limit the response of soil CO_2 efflux to altered conditions, regardless of the respiratory pathway. A key issue to consider is to what degree the increased supply of labile substrates under elevated CO_2 enhances decomposition of pre-existing organic matter (i.e. 'priming'), and whether warming interacts with CO_2 to suppress or stimulate the priming effect. Over 2–3 yr of elevated CO_2, both wheat and shortgrass steppe showed increased decomposition under elevated CO_2, or priming (Pendall *et al.*, 2001, 2003), but forest ecosystems with larger SOM pools may not show a priming effect. Norby *et al.* (2002) concluded that in forests, much of the C allocated below ground under elevated CO_2 was entering a fast turnover pool, and insufficient experimental duration prevented build-up of mineral soil C to support a measurable increase in baseline heterotrophic decomposition rates. In wetlands, a portion of the plant carbon that enters the fast turnover pool is emitted as CH_4 (Whiting & Chanton, 2001).

Elevated CO_2 has been shown to increase CH_4 emissions from a variety of wetland ecosystems (Dacey *et al.*, 1994; Vann & Megonigal, 2003; and references therein), sometimes dramatically. This response effectively amplifies CO_2 radiative forcing by converting a portion of the CO_2 to CH_4, a gas with a warming potential that is 8–21 times higher on a mole basis. Ecosystem respiration as CO_2 flux in peatlands appears more responsive to temperature than to changes in water table, while CH_4 fluxes in these systems are strongly responsive to water table fluctuations (Updegraff *et al.*, 2001). Interactions between elevated CO_2 and temperature on CH_4 emissions have not been investigated.

Decomposition of SOM is linked to N mineralization, providing feedbacks to NPP. Elevated CO_2 appears to have little effect on soil N mineralization (Norby *et al.*, 2001), but several studies have shown that soil warming can cause increased soil N mineralization and possibly nitrate leaching (Van Cleve *et al.*, 1990; Peterjohn *et al.*, 1994; Hobbie, 1996; Lükewille & Wright, 1997; Verburg *et al.*, 1999; Rustad *et al.*, 2001). In N-limited ecosystems, warming may relieve nutrient limitations on NPP under elevated CO_2 by increasing N mineralization (Shaver *et al.*, 2000). Litter decomposition is partly dependent on C : N ratios, which may be increased by elevated CO_2 and reduced by warming, but litter bag studies have so far shown little effect of these manipulations (Norby *et al.*, 2001).

Methodological Limitations and Suggestions for Improvements

Net ecosystem production

The long-term effects of elevated CO_2 and warming on C cycling may be predicted from changes in NEP, the difference

between gross primary production (GPP) and ecosystem respiration (R_e). If lateral transfers are ignored, NEP can be formulated as the difference between NPP and decomposition (R_h):

$$NEP = GPP - R_e = NPP - R_h \qquad \text{Eqn 1}$$

Often, decomposition is estimated from generic temperature response functions or mass loss over long periods and large regions. This approach severely restricts a mechanistic interpretation of responses to elevated CO_2 and warming, and more careful evaluation of drivers of decomposition rates is required to develop better predictive ability. A mass balance approach for estimating NEP in forest ecosystems that accounts for nonsteady state conditions is:

$$NEP = (NPP_A - R_{WD}) + (\Delta C_{FR} + \Delta C_{CR} + \Delta C_{soil} - \Delta C_{litter}) \qquad \text{Eqn 2}$$

Where NPP_A is above-ground net primary production, R_{WD} is the respiration from woody debris, ΔC_{FR} is the net change in fine root C, ΔC_{CR} is the difference between the net growth of live coarse roots and the decomposition of coarse roots attached to stumps, ΔC_{soil} is the net change in mineral soil C, and ΔC_{litter} is annual fine litter fall (Law *et al.*, 2003). The biometric approaches are extremely labour intensive, destructive, and still may miss a portion of C allocated below-ground. Where a stable isotope signal is present, NEP estimates may be constrained by using changes in $\delta^{13}C$ of SOM to estimate rhizodeposition (Pendall *et al.*, 2004b) and $\delta^{13}C$ of soil respiration to partition decomposition (Pendall *et al.*, 2003, 2004a).

Total below-ground C allocation

A simple budget approach can be used to estimate total below-ground C allocation (TBCA), the sum of C allocated below-ground for root and mycorrhizal respiration and turnover, and root exudates (Raich & Nadelhoffer, 1989, modified by Giardina & Ryan, 2002):

$$TBCA = F_s - F_A + \Delta(C_{soil} + C_{litter} + C_{roots}) \qquad \text{Eqn 3}$$

Where F_s is soil respiration and F_A is above-ground litter fall. Generally, these fluxes are evaluated over at least a year. Estimates of TBCA are useful for determining the total plant contribution to below-ground inputs (Giardina & Ryan, 2002; Giardina *et al.*, 2003), for examining large-scale patterns in those inputs (Raich & Nadelhoffer, 1989; Davidson *et al.*, 2002), and for constraining other estimates of below-ground activity based on measurements of the individual components (e.g. root turnover and respiration). Recently developed isotopic methods for evaluating root input and turnover rates (Gaudinski *et al.*, 2001; Matamala *et al.*, 2003) should be

applied cautiously because these estimates are sensitive to the presence of pre-treatment nonstructural carbohydrates (Luo, 2003).

Heterotrophic and autotrophic respiration

A key question is whether autotrophic and heterotrophic processes respond differently to warming and elevated CO_2; the heterotrophic flux is also required for estimates of NEP and thus C sequestration. Mechanical separation techniques of the respired sources have involved measurements of total soil CO_2 flux, then rhizosphere and litter respiration, with determination of heterotrophic respiration from soil by difference (Ryan *et al.*, 1997; Law *et al.*, 2001), girdling (Högberg *et al.*, 2001), or root exclusion (Edwards & Norby, 1999). Stable isotope methods allow partitioning rhizosphere respiration and decomposition for elevated CO_2 experiments where isotopically distinct CO_2 is added (Pataki *et al.*, 2003) and in areas that have transitioned between C_3 and C_4 cover (Rochette *et al.*, 1999). This approach requires a minimum $\delta^{13}C$ offset of about 4–5‰ between the currently growing biomass and pre-existing soil organic matter, which is not often found in C_3-dominated ecosystems unless a tracer has been added.

Below-ground C pools and turnover rates

The total amount of C in soil is very large in comparison to annual inputs or losses, and so for short duration experiments (< 5 years), changes in labile C pools are easier to detect than in longer-lived pools. Density separation results in a light fraction, which is recent, partially decomposed plant residue, and a heavy fraction, which is composed of older, organo-mineral complexes (Khanna *et al.*, 2002). Particle size separations have shown that organic matter in smaller size classes, associated with silt or clay, has lower turnover rates than larger, particulate organic matter (POM; Balesdent, 1996). Physical separation methods, however, often do not result in pools, that can be directly comparable to conceptual categories used in process models (W. Parton, personal communication).

Changes in soil C pool sizes and turnover rates in elevated CO_2 and warming experiments should be evaluated at a finer level of detail than has generally been done, possibly applying a combination of physical or chemical separation methods and stable isotope analyses, to better quantify small changes attributable to experimental conditions (e.g. Loiseau & Soussana, 1999). A limitation in most elevated CO_2 experiments is that a stable isotope tracer is present on the elevated, but not ambient, treatment, eliminating the possibility of comparing treatment effects without additional labelling (e.g. Leavitt *et al.*, 2001). Radiocarbon tracers provide important insights into climatically driven changes in turnover times, and can be applied to systems lacking a stable isotope label (Trumbore, 1997).

Data Synthesis using Models

In the past two decades, dozens of biogeochemical models have been developed to study ecosystem response to rising atmospheric CO_2 and global warming (e.g. Parton *et al.*, 1987; Comins & McMurtrie, 1993; Rastetter *et al.*, 1997; Luo & Reynolds, 1999; Thompson & Randerson, 1999; McGuire *et al.*, 2001). Most of those models share a common structure that partitions photosynthetically fixed C into several pools. Although model complexity varies with numbers of pools and fluxes, modelling studies generally suggest that the predicted capacity of ecosystem C sequestration is strongly regulated by the residence time of C in these pools (Schimel *et al.*, 1994; Joos *et al.*, 1996; Luo & Reynolds, 1999; Thompson & Randerson, 1999). Thus, residence times of C in each of the pools, and their differential temperature sensitivities, are critical parameters for our predictive understanding of below-ground responses to elevated CO_2 and warming. Verification of model results has been done by comparing SOC measurements over long-term (3–5 decades) field experiments with modelled output, showing generally good performance (Izaurralde *et al.*, 2002). Although some below-ground models are constrained by available C stocks (e.g. Century (Parton *et al.*, 1988) and Rothamsted (Jenkinson, 1990)) model performance of the mechanisms underlying C cycling dynamics at shorter time steps has rarely been evaluated.

Most terrestrial biogeochemistry models simulate exchanges between vegetation and soils that may influence the response of below-ground processes to changing CO_2 and temperature over time, and thus lead to CO_2 and temperature interactions (e.g. Cramer *et al.*, 1999). These interactive effects are related to feedbacks mediated by another variable such as soil moisture, N availability, or litter quality. In most terrestrial biogeochemistry models, warming decreases soil moisture whereas elevated CO_2 increases it (e.g. Century, Pan *et al.*, 1998; PnET, Aber *et al.*, 1995). The changes in soil moisture have the potential to influence decomposition differentially along moisture gradients with larger relative effects in semiarid regions than in more mesic regions (Pan *et al.*, 1998). The magnitude of these interaction effects depends on how hydrology is simulated and the assumed sensitivity of below-ground processes to soil moisture. Interactions between CO_2 and nitrogen deposition have also been shown to influence modelled NEE, particularly when the effects of variable N availability during disturbance cycles are considered (Thornton *et al.*, 2002).

Several terrestrial biogeochemistry models have incorporated the consequences of potential changes in litter quality on C sequestration into their simulations. The Century model allows C : N of leaf biomass to increase by 20% with a doubling of atmospheric CO_2, which decreased decomposition rates and N availability (Parton *et al.*, 1995). In a sensitivity study with the Terrestrial Ecosystem Model, McGuire *et al.* (1997) showed that the amount of soil organic C stored across the globe was sensitive to potential changes in vegetation and litter C : N ratios associated with a doubling of atmospheric CO_2, as a result of both increased litter inputs and decreased sensitivity of decomposition to temperature caused by reduced litter quality. Field litter bag studies, however, rarely confirm model predictions of altered decomposition rates attributable to altered litter C : N ratios (Norby *et al.*, 2001), suggesting another area for model validation.

Models should distinguish CO_2 fluxes from roots versus heterotrophs, and respiration from surface organic and litter layers versus mineral soil horizons because the temporal dynamics of temperature, moisture, and nutrients vary spatially. C losses associated with the growth of new root tissues (root construction costs) should be modelled separately from seasonal temperature patterns as they can drive arbitrarily high estimates of temperature sensitivity (Boone *et al.*, 1998; Hanson *et al.*, 2003b). A few studies have attempted to reconcile modelled and measured values of decomposition and autotrophic respiration. Law *et al.* (2001) compared field estimates of annual heterotrophic respiration and autotrophic respiration from foliage, wood and roots (scaled up chamber measurements), ANPP, BNPP, and eddy flux measurements of total ecosystem respiration and NEE with Biome-BGC model outputs. The multiple measurements helped to identify areas for improvement in model assumptions, such as C allocation and fine root turnover rates. Pendall *et al.* (2003) compared decomposition simulated with an abiotic, empirical model with decomposition rates partitioned using stable isotopes, and found reasonably good agreement at ambient and elevated CO_2, allowing simulation of decomposition for additional growing seasons which lacked isotope data.

Synopsis

Recent improvements in below-ground techniques, such as estimation of root turnover rates, evaluation of 'new' C inputs and below-ground C allocation, partitioning soil respiration into root and microbial components, identification of C pools with distinct residence times, and increased attention to mycorrhizas, are bringing us closer to understanding below-ground C cycling. Responses of soil C pools with turnover times of decades or longer will ultimately determine the net impact of climate change on below-ground C storage. The limited body of experimental evidence suggests that soil C cycling and decomposition may increase dramatically when warming and elevated CO_2 are combined. Long-term (decadal) responses will depend on whether substrate availability will be stimulated to the same degree, and whether substrate quality will be altered sufficiently to impact residence times of C pools. With few exceptions, however, current experiments do not adequately capture responses of slow pool C to altered environmental conditions.

Application of more standardized experimental methods in the field and laboratory would facilitate cross-site comparisons.

Below-ground C dynamics could be evaluated more precisely using isotope pulse labelling or soil transplanting approaches in long-term (5–10 years), multifactor experiments. If experimental treatments are imposed on moisture gradients, responses mediated by soil water content may be detected. However, as the complexity and duration of experiments increase, the systems may become so perturbed that it is difficult to discriminate treatment effects from experimental artefacts. Intercomparable techniques for quantifying labile and slow C pool sizes have been in development, but quantifying residence times of these pools has been more difficult. Improved understanding of how the longer-lived C pools will react to anthropogenic climate change also requires validation of improved models.

Acknowledgements

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