ELEVATED CO$_2$ DIFFERENTIATES ECOSYSTEM CARBON PROCESSES: DECONVOLUTION ANALYSIS OF DUKE FOREST FACE DATA

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Abstract. Quantification of the flux of carbon (C) through different pathways is critical to predict the impact of global change on terrestrial ecosystems. Past research has encountered considerable difficulty in separating root exudation, root turnover rate, and other belowground C fluxes as affected by elevated CO$_2$. In this study we adopted a deconvolution analysis to differentiate C flux pathways in forest soils and to quantify the flux through those pathways. We first conducted forward analysis using a terrestrial-C sequestration (TCS) model to generate four alternative patterns of convolved responses of soil surface respiration to a step increase in atmospheric CO$_2$. The model was then validated against measured soil respiration at ambient CO$_2$ before it was used to deconvolve the CO$_2$ stimulation of soil respiration. Deconvolved data from the Duke Forest free-air CO$_2$ enrichment (FACE) experiment suggest that fast C transfer processes, e.g., root exudation, are of minor importance in the ecosystem C cycling in the Duke Forest and were not affected by elevated CO$_2$. The analysis indicates that the fine-root turnover is a major process adding C to the rhizosphere. This C has a residence time of several months to ~2 yr and increases significantly with increased CO$_2$. In addition, the observed phase shift in soil respiration caused by elevated CO$_2$ can be only reproduced by incorporation of a partial time delay function in C fluxes into the model. This paper also provides a detailed explanation of deconvolution analysis, since it is a relatively new research technique in ecology.

Key words: carbon flux; carbon sink; CO$_2$; convolution and deconvolution; forest ecosystem; forward modeling; global change; inverse analysis; root exudation; root turnover; soil carbon processes; terrestrial-carbon sequestration (TCS).

INTRODUCTION

The rapid increase in atmospheric CO$_2$ concentration provides an urgent need to quantify potential carbon (C) sinks in terrestrial ecosystems. Estimation of terrestrial C sinks in various biomes has been conducted with both modeling and experimental approaches. In the past two decades, perhaps a dozen biogeochemical models have been developed to predict terrestrial C sequestration in response to rising atmospheric CO$_2$ (e.g., Parton et al. 1987, Rastetter et al. 1991, 1997, Comins and McMurtrie 1993, Mellilo et al. 1993, Luo and Reynolds 1999, Thompson and Randerson 1999). Most of those models share a common structure that partitions photosynthetically fixed C into several pools, even though the number of C pools in each model may vary (e.g., two pools in multiple-element limitation [MEL] model [Rastetter et al. 1997] vs. 12 pools in Carnegie–Ames–Stanford approach [CASA] [Thomp-

son and Randerson 1999] and terrestrial carbon sequestration [TCS] models [Luo and Reynolds 1999]). Modeling 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 and Reynolds 1999, Thompson and Randerson 1999). If photosynthetically fixed C is largely cycled through fast pathways, e.g., root respiration and root turnover, the capacity of an ecosystem to sequester C is small. If fixed C is largely cycled through slow pathways with decadal or longer residence times, such as woody biomass and soil organic matter (SOM), the C sequestration capacity is large. Accurate model parameter values for C cycling through different pathways are critical for making reliable predictions of terrestrial C sinks.

Experimental studies have been conducted using open-top chambers (OTC) and free-air CO$_2$ enrichment (FACE) techniques to quantify terrestrial C sinks in response to elevated CO$_2$ (Mooney et al. 1999). Many OTC and FACE studies in the past decades have indicated that ecosystems under elevated CO$_2$ have higher primary productivity than those under ambient CO$_2$ (Owensby et al. 1993, Norby 1996, DeLucia et al. 1999). Plant growth under elevated CO$_2$ usually results

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in increased root biomass and turnover (Rogers et al. 1999, Pregitzer et al. 2000). Increased fluxes of C to the soil in elevated CO_2 potentially alter rhizosphere C and N dynamics (Hungate et al. 1997, Hu et al. 1999, Allen et al. 2000). While a great deal of data has been accumulated on responses of C processes to elevated CO_2, it is still a major challenge to integrate experimental results into models that predict potential terrestrial C sequestration.

Integration of data into models has been done primarily in two approaches. One is that ecosystem models are used to explore long-term and large-scale consequences of short-term experimental observations. For example, experiments across several sites recently suggested that elevated CO_2 induced little change in litter quality (Norby and Contrufo 1998), which is contrary to early results and expectations (O'Neill and Norby 1996). The recent result has been incorporated into the CENTURY and generic decomposition and yield (G'DAY) models to examine the long-term implications for ecosystem C dynamics (Mooney et al. 1999). Similarly, long-term consequences of experimental results have been examined using models for stomatal conductance, foliage N concentration, N retranslocation, partitioning, C:N ratio in SOM, and soil exploration (Kirschbaum et al. 1994, Luo and Reynolds 1999).

Another approach to model–data integration is to estimate parameter values from measurements. According to the degree of difficulty, parameter estimation can be divided into three cases. The first case is that experimental data can be directly converted to parameter values. For example, specific rates of litter decomposition are usually derived directly from laboratory and field studies of litter decomposition (Parton et al. 1987), and C allocation to leaf and other plant compartments is generally estimated from measured biomass (Wang et al. 1998). The second case is that parameter values are not measurable in experiments due to limited technology, and they cannot be derived from process-level measurements. For example, root exudation, which is suspected to be an important pathway of transferring C to the rhizosphere (Norby et al. 1987, Ineson et al. 1996, Körner et al. 1996, Luo et al. 1997, Paterson et al. 1997, Hu et al. 1999), is not readily measurable in natural ecosystems. As a consequence, this C transfer pathway has been rarely included by any of the biogeochemical models. The third case is that process-level measurements are not easily converted into parameter values for modeling studies. For example, fine root biomass is a result of two simultaneous but counteracting processes: root growth and death. A given level of root biomass can be produced by numerous combinations of root growth and death rates (Luo et al. 1995). Similarly, microbial biomass is determined by the counteracting growth and death processes. All the three cases use a reductioinist approach.

Parameter estimation can also be done holistically when a measurable quantity represents a convolved product of several processes with distinguishable characteristics. For example, the soil surface respiration, the focus of this study, is the product of multiple rhizosphere processes including root exudation, respiration, and turnover, as well as aboveground litter decomposition, and soil organic decomposition. Those processes have distinctive response times to C perturbation. This study employed a deconvolution approach to an analysis of soil respiration observed at the Duke Forest FACE site. Deconvolution is a procedure to untangle a complex data set in order to quantify processes and/or mechanisms underlying observed phenomena. Deconvolution of soil respiration data allows us to evaluate the relative importance of those constituent processes in response to C perturbation under elevated CO_2. First, we describe the deconvolution approach since it is relatively new to the research field of ecology. Then we present the terrestrial carbon sequestration (TCS) model, which was first used to generate four alternative convolved responses of soil respiration to a step CO_2 increase. The four alternative patterns demonstrate the relative influence of various rhizosphere processes in determining responses of soil respiration to elevated CO_2. The TCS model was then validated against measured soil respiration at ambient CO_2 and was finally used to deconvolve the CO_2 stimulation of soil respiration.

Approach

This study considers an ecosystem as a general system with multiple processes operating simultaneously, but with each process having its own characteristic response time to perturbation. By definition, such a heterogeneous system should have output equal input when at a steady state. Observations at the steady state may provide a general description of the system's performance, but they do not help probe processes underlying the system's performance. A conventional approach in systems research is to perturb the system by altering inputs or other external variables. Observations of the system's responses to the perturbation can be used to differentiate a variety of processes according to their distinctive response times. Thus, the perturbation approach can be useful in probing the system's mechanisms in a way that the observations alone cannot achieve.

In the case of the Duke Forest free-air CO_2 enrichment (FACE) experiment, we have a perturbation that generates a large and abrupt increase in C influx. This perturbation will send additional C through various processes. Different processes possess different response times (or residence times)—the time of C remaining in an ecosystem from entrance via photosynthesis to exit via respiration (Thompson and Randerson 1999). Thus the release of the additional C back to the atmosphere will occur at different time scales. For ex-

Fig. 1. A schematic representation of rhizosphere C processes and their operational time scales. In general, the C cycling from fixation to release takes weeks through the fast pathways of root exudation and root respiration, one year or longer through the pathway of root turnover (defined as growth, death, and decomposition in this study), 2–4 years through needle turnover in the coniferous forest, decades through woody tissue turnover, and centuries or even millennia through the turnover of soil organic matter. Pretransformed time scale units were years.
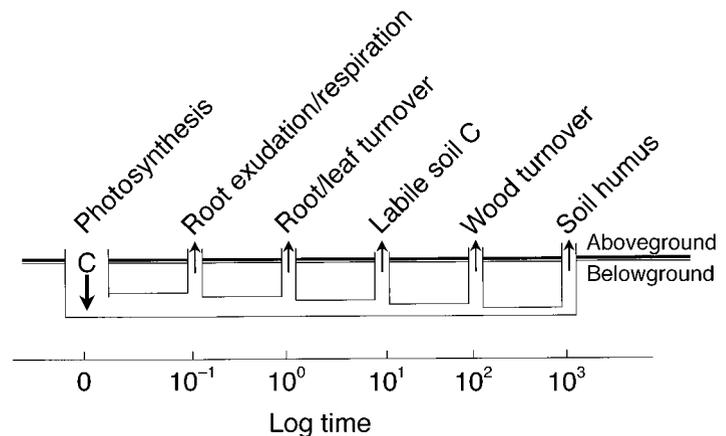
ample, belowground C cycling through the pathway of root exudation takes only a few weeks from photosynthesis to respiratory release (Cheng et al. 1994, Rouhier et al. 1996). In contrast, C cycling through the pathway of wood growth, death, and decomposition takes several decades from photosynthesis to respiratory release (Fig. 1).

While knowledge regarding individual C processes is fundamentally critical for prediction of terrestrial C cycling, some of the processes are extremely difficult to quantify. For example, root exudation generally can be measured only in hydroponic culture for its chemical composition (Bekku et al. 1997, Groleau et al. 1998). To the best of our knowledge, no methods are available to quantify the amount of root exudation in the field. Despite great efforts that have been made by the research community to understand root turnover in the field, quantification of this process is still unsatisfactory (Aber et al. 1985, Nadelhoffer and Raich 1992). On the other hand, it is relatively easy to measure soil respiration in natural ecosystems using infrared gas analyzers (Norman et al. 1992), although the accuracy of the measured respiration varies with many factors, including chamber pressure (Lund et al. 1999, Janssens et al. 2000).

Measured soil respiration includes C produced by root respiration (including both fine and coarse roots) and microbial respiration in the rhizosphere (Fig. 1). Thus, a CO_2-induced change in soil respiration at elevated CO_2 is a convolved response, which is the integration of all the rhizosphere C production processes. The convolved response to elevated CO_2 depends on relative activities of those C processes. If the rapid C transfer pathways (e.g., root exudation, root respiration, and root turnover) contribute a substantial amount of C to soil respiration, the convolved response will manifest a large and rapid increase in soil respiration after the CO_2 fumigation. In the contrast, if the majority of C goes through the slow C pathways, the convolved response will not show up in the first few years after the CO_2 fumigation. Thus, the convolved response of

soil respiration to elevated CO_2 contains information about the relative importance of the rhizosphere C processes.

To extract the information on relative importance of individual rhizosphere C processes, this study uses a simulation approach to deconvolve the observed response of soil respiration to the step CO_2 increase at the Duke FACE site and then to quantify C fluxes through different pathways. This simulation approach is a compromise between ecological reality and mathematical feasibility. We have tried to be as realistic as possible. But at the same time, we are trying to simplify it to the extent that deconvolution is possible.

Methods

Experimental site and soil respiration measurements

The data set used in this deconvolution analysis is the measured soil surface respiration at the Duke Forest free-air CO_2 enrichment (FACE) site, North Carolina, USA. The FACE experiment is composed of six 30-m diameter plots in a 15-yr-old (in 1996) loblolly pine (*Pinus taeda* L.) plantation (Hendrey et al. 1999). In the three treatment plots, CO_2 concentration has been maintained at 200 μL/L (measured volumetrically) above ambient since August 1996; three control plots are fumigated with ambient air only. Soils at the site are of the Enon Series, a low-fertility Ultic Alfisol that is typical of many upland areas in the Southeast. Mean annual temperature is 15.5°C, and mean annual precipitation is 1140 mm.

Soil respiration was measured approximately once a month, using a portable infrared gas analyzer (EGM-1, PPSystems, Haverhill, Massachusetts, USA) equipped with soil respiration chambers (SRC-1). Measurements were taken during a one-to-two-minute interval during 1200–1500 h. Potential pressure changes were avoided while inserting the respiration chamber into the PVC coupling by adding a vent hole (1-cm diameter), which was plugged with a neoprene stopper during the measurements. Soil moisture was measured with four
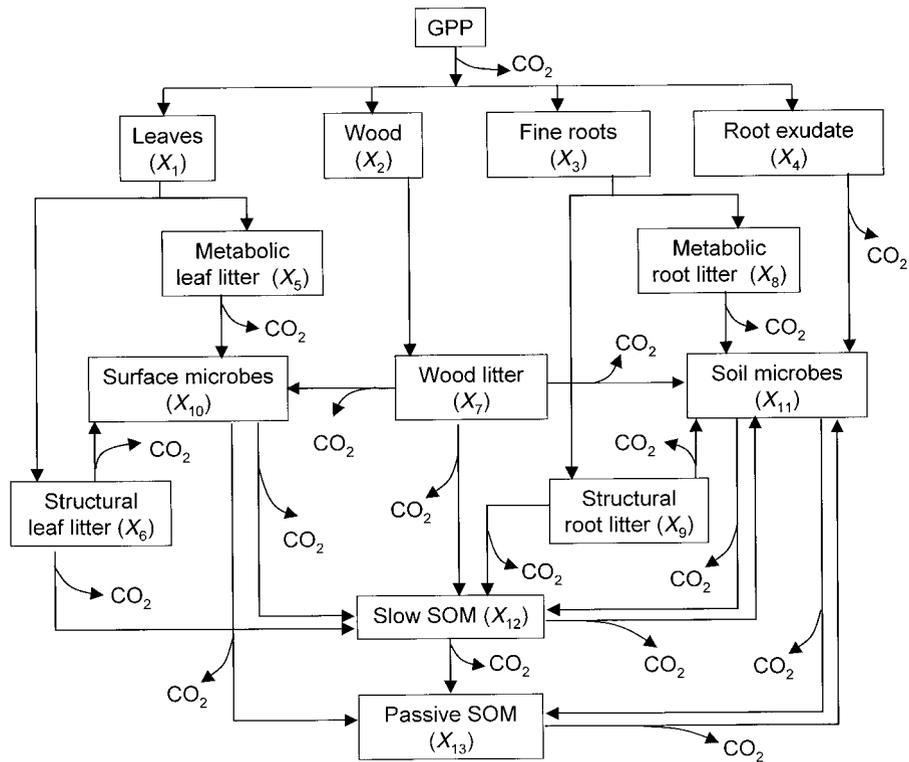
FIG. 2. Carbon pools and pathways of C flux in the terrestrial-C sequestration (TCS) model. SOM stands for soil organic matter.

probes in each plot, integrating the upper 30 cm of soil with a water content reflectometer (CS615 Campbell Scientific, Logan, Utah, USA). The measurements are converted to volumetric water content using calibration values for soil with medium electrical conductivity.

Model description

The terrestrial carbon sequestration (TCS) model developed by Luo and Reynolds (1999) was used as a template in this deconvolution study. By adding and subtracting transfer pathways, we evaluated the likelihood that individual processes are involved in C transfer in the rhizosphere. By increasing and decreasing parameter values, we evaluated the relative contributions of individual processes to rhizospheric C transfer.

The TCS model has been presented in detail by Luo and Reynolds (1999). We focus the description in this paper on the C processes related to the deconvolution analysis. The TCS model uses the canopy photosynthetic rates, which were estimated by a comprehensive canopy model validated with measured leaf photosynthesis and eddy-covariance measurements of canopy fluxes (Luo et al. 2001), as the input. The photosynthate is partitioned into five pools, which, in turn, provide C for plant respiration, leaf growth, wood growth, fine root growth, and exudation (Fig. 2). The plant respiration is determined by the C content in each of the plant pools (leaf, wood, and fine root) multiplied by

specific respiratory rates, equaling 0.625, 0.0625, and 0.625 $mg \cdot g^{-1} \cdot h^{-1}$ for leaves, woody, and fine roots, respectively. The coefficients were chosen so that ~43% of photosynthate is used for plant respiration according to a difference between net (DeLucia et al. 1999) and gross (Luo et al. 2001) primary productivities at the site.

After respiration, the rest of photosynthate is used for plant growth and root exudation. Carbon partitioning for growth among various parts of the plant is based on the nitrogen production relationship (Luo and Reynolds 1999). Since nitrogen content of leaves and fine roots was hardly affected by elevated CO_2 in the Duke FACE project (Finzi et al. 2001; R. Matamala, *unpublished data*) and had little seasonal variation (R. Thomas, *unpublished data*), the C partitioning for growth is virtually constant among plant parts. In the simulation of root exudation, a fraction of the total photosynthate is allocated to the root exudate pool. Dead plant material goes to litter pools. Leaf and fine root litter are each divided into metabolic and structural components according to their lignin content and the C:N ratio as specified by Luo and Reynolds (1999). Litter is decomposed by microbes, and part of the litter C is respired and part of it is converted to soil organic matter (SOM). The C transfer pathways are depicted in Fig. 2. The amount of C transferred among pools 5–13 is mathematically described as follows:

$$\Delta X_i = \sum_{j=1}^{13} a_{i,j}X_j - a_{i,i}X_i \qquad i = 5, \ldots, 13 \quad (1)$$

where ΔX_i is the change of C content per hour in pool i, X_i is the amount of C in pool i, $a_{i,j}$ is the transfer coefficient from pool j to i, and $a_{i,i}$ is the exit rate of C away from pool i. The coefficient $a_{i,j}$ is calculated in the following manner:

$$a_{i,j} = f_{i,j}E_{i,j}a_{j,j} \qquad i = 10, \ldots, 13;$$
$$j = 4, \ldots, 13 \quad (2)$$

where $f_{i,j}$ is the fraction of $a_{j,j}$ going to pool i: $f_{10,6} = f_{12,6} = f_{12,7} = f_{11,9} = f_{12,9} = 0.5$, $f_{10,7} = f_{11,7} = 0.25$, $f_{12,10} = f_{12,11} = 0.987$, $f_{13,10} = f_{13,11} = 0.013$, $f_{11,12} = 0.933$, $f_{13,12} = 0.067$, and $f_{i,j} = 1$ for all other values of i,j. $E_{i,j}$ is the conversion efficiency of substrate to microbial biomass from pool j to i, $E_{11,4} = 0.2$, $E_{10,5} = E_{11,8} = E_{11,9} = E_{11,12} = E_{11,13} = E_{12,9} = E_{13,12} = 0.45$, $E_{10,6} = E_{10,7} = E_{11,7} = E_{12,6} = E_{12,7} = 0.55$, and $E_{12,10} = E_{12,11} = E_{13,10} = E_{13,11} = 0.3$, according to Parton et al. (1987). Thus, CO_2 releases that result from litter and SOM decomposition are calculated by

$$F_{CO_2,i} = \left(1 - \sum_{j=10}^{13} f_{j,i}E_{j,i}\right)a_{i,i}X_i \qquad i = 4, \ldots, 13 \quad (3)$$

where $F_{CO_2,i}$ is C release from pool i. The modeled soil respiration is calculated by

$$F_{soil} = \frac{F_2}{2} + F_3 + \sum_{i=4}^{13} F_{CO_2,i} \quad (4)$$

where F_2 and F_3 are respiratory CO_2 release by woody tissue and fine root, respectively. This model assumes one half of plant woody tissue respiration originates belowground, which has been found to fit data best during model evaluation. Eq. 4 is called a mapping function to match the modeling estimates with measurements of soil respiration.

Forward analysis

Given the model structure described here and a set of parameter values, we used the TCS model to generate soil respiration in response to a step increase in CO_2 concentration. We call this procedure "forward analysis." We designed four scenarios as specified in Table 1 to examine influences of rapid-cycle processes on soil respiration. The integration of multiple rhizosphere processes to generate soil respiration is referred to convolution. Convolution provides a basis for identifying mechanisms that underlie the observed responses at the Duke FACE site. To the sake of simplicity, the forward analysis will not consider annual variations in soil temperature, moisture, and C influx.

The forward analysis is based on an initial steady-state C balance in the TCS model. That is, the pool sizes and flux coefficients between pools are chosen so that C efflux from the modeled ecosystem equals the C influx, and the C pool size does not change during

TABLE 1. Definition of five scenarios used in this study. Scenarios I–IV were used in the forward analysis, and scenarios I–V were used in the inverse analysis.

Scenario	Description
I	All rhizospheric processes are active in C transfer to the rhizosphere. The state variable values are listed in the second column of Table 2. In this scenario, it is assumed that 10% of photosynthate is transferred to the rhizosphere via root exudation.
II	No C transfer to the rhizosphere via the pathway of root exudation, but all the other processes are active as in scenario I.
III	(1) No root exudation and (2) downregulation in specific root respiration rates at elevated CO_2, to the extent that the total root respiration in elevated CO_2 is the same as in ambient CO_2.
IV	(1) No root exudation, (2) no CO_2-induced increase in root respiration, and (3) no CO_2-induced increase in root turnover.
V	Partial time delay function to account for the observed phase shift in soil respiration caused by elevated CO_2. See *Methods: Inverse analysis* for further description.

the simulation period at ambient CO_2. We obtained the steady-state values of pool sizes by using the MATLAB program (The MATH WORK, Natick, Massachusetts, USA) of matrix operation. Let

$$\frac{d\mathbf{X}}{dt} = \mathbf{A}\mathbf{X} + \mathbf{B}u = \mathbf{0} \quad (5)$$

Then

$$\mathbf{X} = -\mathbf{A}^{-1}\mathbf{B}u. \quad (6)$$

where $\mathbf{X}$ is a vector of C pools with 13 dimensions in scenario I with root exudation and 12 dimensions in the other three scenarios (Table 2). $\mathbf{A}$ is the matrix of C transfer coefficients with 13 × 13 dimensions in scenario I and 12 × 12 dimensions in the other three scenarios. $\mathbf{A}^{-1}$ is the inverse of matrix $\mathbf{A}$. Elements in matrix $\mathbf{A}$ are $a_{i,j}$, where i and j indicate row and column in the matrix. Nonzero elements are those with connections between pools in Fig. 2, and their values are defined in Table 1 and Eq. 2. The other elements in matrix $\mathbf{A}$ all are zero. $\mathbf{B}$ is the vector of distribution coefficients of input function u with 13 dimensions, equaling 0.173 for the first three elements, 0.1 for the fourth element, and 0.0 for the rest, in scenario I; and 12 dimensions, equaling 0.19 for the first three elements and 0.0 for the rest, in the other three scenarios. The summation of distribution coefficients in all the scenarios equals 0.54, a fraction of C influx used for biomass growth. The function u indicates a photosynthetic C influx of 3.6 g $C \cdot m^{-2} \cdot d^{-1}$, a mean daily value with the annual total of 1314 g $C \cdot m^{-2} \cdot yr^{-1}$ under ambient CO_2 (Luo et al. 2001). The function u increases by 40% under elevated CO_2.

Estimated pool sizes (vector $\mathbf{X}$) differ between scenarios I and II due to different distribution coefficients

TABLE 2. Steady-state carbon pools and their values (in units of no. grams C per square meter) used in the forward and inverse analysis, with and without root exudation.

	Forward analysis		Inverse analysis	
Carbon pool	Exudation	No exudation	Exudation	No exudation
Standing leaf biomass (X_1)	387	424	312	350
Standing wood biomass (X_2)	5109	5937	4450	5000
Standing fine root biomass (X_3)	260	285	196	220
Root exudate (X_4)	21	0	19	0
Leaf metabolic litter (X_5)	65	72	62	70
Leaf structural litter (X_6)	207	230	205	230
Wood litter (X_7)	594	660	445	500
Root metabolic litter (X_8)	72	79	62	70
Root structural litter (X_9)	196	216	205	230
Microbial biomass at soil surface (X_{10})	137	156	142	160
Microbial biomass in bulk soil (X_{11})	150	145	120	135
Slow SOM† (X_{12})	3621	4125	3382	3800
Passive SOM† (X_{13})	2489	2846	2225	2500

† SOM, soil organic matter.

(Table 2). In order to create scenario III, we ran the TCS model to generate C release via root respiration at ambient CO_2, which was used as the input in the simulation run for the elevated CO_2 treatment. Thus the root respiration was assumed identical at the two CO_2 treatments. By doing so, we assume that the specific root respiration rate is downregulated to the extent that the increase in the root respiration due to the increase in root biomass is completely compensated. To create scenario IV, we ran the TCS model to generate hourly values of root biomass at ambient CO_2, which was used as the input in the simulation run for the elevated CO_2 treatment. In this way, the root turnover rate at elevated CO_2 was set identical to that at ambient CO_2.

With the estimated pool sizes, we ran the TCS model to generate the quantity of C released from each of the 13 C pools at ambient and elevated CO_2, respectively. Dividing C release at the elevated CO_2 by the total soil respiration at ambient CO_2 defines the relative contributions of each pool to the soil respiration. Adding all the relative contributions from each pool, we generate convolved C release curves, which are the soil respiration. The latter is experimentally measurable, whereas the former components are not measurable but are what we want to quantify.

Inverse analysis

While the forward analysis was designed to generate soil respiration from a given model structure and a set of parameter values, the inverse analysis was used to evaluate model structure and parameter values by deconvolving the observed responses of soil respiration to elevated CO_2. By doing so, we can infer what processes may be important in C transfer to the rhizosphere. In this case study, the forward analysis involves convolution because multiple rhizosphere processes were integrated to generate soil respiration, whereas the inverse analysis involves deconvolution inasmuch

as observed soil respiration was disaggregated into its constituent processes. In other words, the forward analysis asks what the model can tell us about the rhizosphere complexity, and the inverse analysis asks what the data can tell us about that same system. Combining the two approaches, we tried to probe mechanisms operating in the rhizosphere.

The inverse analysis is based on the theory of the Laplace transformation with a set of first-order differential equations, which usually can adequately describe ecosystem C processes (Bolker et al. 1998). Because transfer coefficients vary with diurnal and seasonal changes in temperature and soil moisture, we cannot analytically solve the inverse problem to obtain a simple solution. Rather, we used a simulation approach to conduct the deconvolution. Operationally, the inverse analysis is different from the forward analysis in the following aspects. First, in the inverse analysis parameters of decomposition and transfer coefficients are functions of temperature and moisture. Second, the steady-state values of pool sizes were derived by running the model several times. Third, the model that was used for the inverse analysis has been validated against experimental data of soil respiration under the ambient CO_2 treatment.

The modification of C transfer coefficients by temperature (F_T) and moisture functions (F_W) was done according to the following equation:

$$a'_{i,j} = a_{i,j} F_T F_W \tag{7}$$

where F_T describes temperature effects on plant respiration or decomposition of litter and soil organic matter as

$$F_T = 0.5 \times 2.2^{(T-10)/10} \tag{8}$$

where 0.5 is the relative effect when temperature is at 10°C. Soil temperature T at depth of 5 cm is estimated by the following equation:

$$F(5, t) = T_{mean} + A_0 e^{-5/D} \sin\left[\omega(t - 8) - \frac{5}{D}\right] \quad (9)$$

where t is time (measured in hours), T_{mean} is the mean daily soil surface temperature, which is assumed to be mean daily air temperature recorded at the FACE site, A_0 is the amplitude of the temperature fluctuations (equaling half of the difference between maximum and minimum temperatures), D is the damping depth (equaling 12 cm), and ω is $\pi/12$. F_W represents the effects of soil water content (W) on plant respiration or decomposition of litter and soil organic matter as follows:

$$F_W = \begin{cases} 1.0 - 5.0(0.2 - W) & W < 0.2 \\ 1 & W \geq 0.2. \end{cases} \quad (10)$$

Soil water content is a mean value of soil moisture measurements from six FACE plots, since CO_2 effects on volumetric soil moisture content were not statistically significant (K. V. R. Schäfer, *unpublished data*). To avoid abrupt changes in estimated F_W after rains, we used five-day moving averages of W to drive the model.

In the inverse analysis, we repeatedly ran the TCS model for a period of three years at ambient CO_2, and we adjusted the values of $a_{i,j}$ until the pool sizes by the end of three-year simulation were roughly equal to those at the beginning. In scenario I, the addition of the root exudation pathway reduces C fluxes into other pools. Thus the smaller C fluxes require smaller pool sizes to reach a steady state. Using the similar approach to the one described here, we obtained quasiequilibrium steady state pool sizes, as listed in Table 2.

In addition to examining the four scenarios, as in the forward analysis (Table 1), we used this inverse analysis to explore the potential for another mechanism (i.e., a partial time delay function; scenario V) to influence ecosystem C fluxes. Scenario V was added to account for the observed phase shift in the seasonal variation in soil respiration at elevated CO_2. We created a new C pool, named as temporal labile C in soil (TLCS), which receives a small fraction of C from rhizosphere pools if the C pool sizes at elevated CO_2 are ≥30% of that at ambient CO_2. Respiratory C loss from the TLCS pool was determined by the amount of C in the TLCS pool multiplied by a specific rate. The latter is further modified by a seasonality function (p):

$$p = \sin\left[\frac{3.14(d + 180)}{182.5}\right] + 1.2 \quad (11)$$

where d is the Julian day. This function was created for the sake of fitting data.

Parameterization and sensitivity analysis

In this study, four separate sets of pool size values were required for scenario I and II, in forward and inverse analysis, respectively. Since scenario II in the inverse analysis was most representative of the observations in the field, pool sizes in that scenario were parameterized primarily from experimental data. As discussed in Luo and Reynolds (1999), parameterization of the TCS model is based on measurements from Binkley and Johnson (1991) for C and N pool sizes. The values for C pool sizes were revised in this study based on newly collected data at the Duke FACE site, particularly for the C content in leaves and wood (Naidu et al. 1998), fine roots (Matamala and Schlesinger 2000), microbial biomass (Allen et al. 2000), and leaf and aboveground wood litter (Finzi et al. 2001). With the C pool sizes given in that scenario (Table 2), values of C transfer coefficients between pools were achieved by adjustment while running the model several times (Table 3). Once the C transfer coefficients in scenario II of the inverse analysis were determined, the same values of the coefficients were used in scenario I while pool sizes were readjusted. This study assumes the simplest scenario: specific rates of C transfer are not affected by root exudation, which does changes C partitioning among pools. In the forward analysis, the C transfer coefficients in scenario II were first empirically adjusted so that pool sizes were similar to those in scenario II of the inverse analysis. Given the transfer coefficients, the steady-state pool sizes were determined using the MATLAB program for both scenarios I and II of the forward analysis. Residence time of root exudates is assumed to be 57.5 d in the forward analysis and 50 d in the inverse analysis. The latter is further modified by soil temperature and moisture.

A sensitivity analysis of TCS model was carried out under the four scenarios (I–IV) to examine influences of the transfer coefficient values on estimated soil respiration. Low and upper limits were chosen for each of the parameters yielding the variation range (VR). We designed 10 sensitivity tests (ST's), as specified in Table 3, together with parameter values. The time interval in all the simulations is one hour.

RESULTS

Convolution of rhizosphere C processes

In the scenario that all the rhizosphere C processes are actively involved in C transfer (Scenario I), soil respiration is depicted by the bold line that gradually increases over a period of 10 yr (Fig. 3). It increases by 10.3%, 15.7%, 19.3%, and 26.9% by the end of the first, second, third, and 10th year of the CO_2 fumigation, respectively. Carbon release through the process of root exudation increases quickly to ~4.3% of the total soil respiration at ambient CO_2 a few months after the onset of the CO_2 experiment. The contribution of C release through root exudation remains at that level in the rest of 10-yr simulation. The contribution of root respiration to soil respiration becomes substantial in the first (2.8%) and second year (4.1%), and stabilizes in the third year at 4.5%. Carbon release through the

TABLE 3. Parameterization of specific rates of C exit from the donor pools in the forward analysis (FA), inverse analysis (IA), and 10 sensitivity tests.

Donor pool	Symbol	FA	IA	Sensitivity test (g·g^{-1}·h^{-1}) [$\times$ 10^4]				
				1	2	3	4	5
Leaf	$a_{1,1}$	0.613	0.882	0.381	0.533	0.685	0.837	0.989
Wood	$a_{2,2}$	0.044	0.063	0.023	0.041	0.059	0.078	0.096
Fine root	$a_{3,3}$	0.913	1.313	0.285	0.609	0.932	1.256	1.579
Exudate	$a_{4,4}$	7.246	8.333	2.083	4.167	6.250	8.333	10.417
Leaf metabolic litter	$a_{5,5}$	2.480	3.565	2.283	4.110	5.936	7.763	9.589
Leaf structural litter	$a_{6,6}$	0.405	0.451	0.228	0.411	0.594	0.776	0.959
Wood litter	$a_{7,7}$	0.374	0.734	0.228	0.411	0.594	0.776	0.959
Root metabolic litter	$a_{8,8}$	2.096	3.013	2.283	4.110	5.936	7.763	9.589
Root structural litter	$a_{9,9}$	0.498	0.555	0.228	0.411	0.594	0.776	0.959
Surface microbes	$a_{10,10}$	1.083	1.557	1.142	1.484	1.826	2.169	2.511
Soil microbes	$a_{11,11}$	1.308	1.880	1.142	1.484	1.826	2.169	2.511
Slow soil C	$a_{12,12}$	0.053	0.076	0.023	0.041	0.059	0.078	0.096
Passive soil C	$a_{13,13}$	0.003	0.003	0.001	0.001	0.002	0.003	0.003

Note: Numerical values reported for sensitivity tests have been multiplied by 10^4, for presentation purposes.

† LL and UL are the lower and the upper limits, respectively, for each of the specific transfer coefficients. Percentages in test definitions of sensitivity tests 7–10 define parameter values as LL plus percentage variation range (UL − LL) in each of the tests. Definitions of sensitivity tests 1–6 are as follows: (1) all with lower limits; (2) all with lower limits + 20% variation range; (3) all with lower limits + 40% variation range; (4) all with lower limits + 60% variation range; (5) all with lower limits + 80% variation range; (6) all with upper limits. The forward analysis (FA) and inverse analysis (IA) are both defined with parameter values as in the control run.

pathway of root turnover is not substantial in the first year (1.1%), becomes larger in the second (2.2%) and third years (2.8%), and remains at 3.3% in year four and afterward. Beyond year four, the increase in soil respiration is attributed to increased aboveground litterfall, microbial biomass, and soil organic matter. In short, processes that affect pools with shorter residence times contribute to the increase in soil respiration soon after the initiation of the CO_2 experiment and vice versa.

If we assume that no C goes through the pathway of the root exudation, the percentage change in soil respiration at elevated CO_2 is predicted to follow trajectory II (Fig. 4). By the end of the first year of the CO_2 fumigation, the percentage change in soil respiration is predicted to be 6.3%, instead of 10.3% as in scenario I. Since the contribution of root exudation to percentage change in soil respiration is constant from year 2 and beyond (Fig. 3), trajectory II is approximately parallel to trajectory I one year after the CO_2 fumigation. Thus, the observed soil respiration in the first year of the CO_2 experiment can be used as a signal to differentiate whether or not the root exudation is an important pathway of C transfer to the rhizosphere.

Similarly, we can change the assumption about the specific root respiration to explore possible signals from experimental measurements. If the specific root respiration is downregulated in elevated CO_2 to the extent that the increase in root respiration caused by increased root biomass is completely compensated, the total root respiration is the same in elevated CO_2 as in ambient CO_2. The percentage change in soil respiration at elevated CO_2 is predicted to follow trajectory III (Fig. 4), leading to a 4.5% increase of soil respiration by the end of the first year of the CO_2 fumigation. In

the rest of the 10-yr simulation, the soil respiration is proportionally lower than in trajectories I and II. If we further assume that root growth in elevated CO_2 is the same as in ambient CO_2, the fine-root turnover is identical at the two CO_2 levels. The percentage change in soil respiration at elevated CO_2 is predicted to follow trajectory IV (Fig. 4), and it increases by 1.4%, 3.5%, 7.5%, and 10.4% by the end of the first, second, fifth, and 10th years of the CO_2 experiment. Under that scenario, we expect the measurements of soil respiration will not show many statistical differences between the two CO_2 treatments in the FACE experiment for several years. Note that since CO_2 stimulation is a relative value, relaxation of the assumption on steady-state pool sizes hardly affects the pattern showed in Figs. 3 and 4.

In summary, we used the four hypothetical scenarios to generate trajectories of soil respiration at elevated CO_2. The trajectories were used to identify mechanisms underlying observed soil respiration.

Measured soil respiration and model validation

Measured midday soil respiration at the Duke FACE site displayed a strong seasonal variation, 0.05 g C·m^{-2}·h^{-1} in the winters of 1996–1997 and 1997–1998 and 0.4 g C·m^{-2}·h^{-1} in the three summers during 1996–1998 (Fig. 5a). Elevation of CO_2 concentration did not result in a statistically significant difference in soil respiration in the first experimental year after the FACE experiment (August 1996–July 1997), but led to significant increases of 33.3% and 45.6% in the second and third experimental years, respectively, of the FACE experiment (Fig. 5 and Table 4). (The experimental year is defined in this study as a period from August through the following July [Table 4] for the convenience of comparison between the forward and inverse analysis

TABLE 3. Extended.

Sensitivity test (g·g^{-1}·h^{-1}) [× 10^4]					Test definition†			
6	7	8	9	10	7	8	9	10
1.142	0.381	0.381	1.142	1.142	LL	LL	UL	UL
0.114	0.041	0.041	0.096	0.096	20%	20%	80%	80%
1.903	0.932	0.932	1.256	1.256	40%	40%	60%	60%
12.500	2.083	12.500	12.500	2.083	LL	UL	UL	LL
1.142	0.776	0.776	0.594	0.594	60%	60%	40%	40%
11.416	9.589	9.589	4.110	4.110	80%	80%	20%	20%
1.142	1.142	1.142	0.228	0.228	UL	UL	LL	LL
11.416	2.283	11.416	11.416	2.283	LL	UL	UL	LL
1.142	0.411	0.959	0.959	0.411	20%	80%	80%	20%
2.854	1.826	2.169	2.169	1.826	40%	60%	60%	40%
2.854	2.169	1.826	1.826	2.169	60%	40%	40%	60%
0.114	0.096	0.041	0.041	0.096	80%	20%	20%	80%
0.004	0.004	0.001	0.004	0.004	UL	LL	LL	UL

in this study and will be called "year" hereafter. We also present results based on calendar year in Table 5 in order to help establish a common basis with other studies from the same FACE site.) The ratio of measured soil respiration at elevated CO_2 to that at ambient CO_2 is within the range 0.80–1.20 in the first year, 1.2–1.4 (except for an outlier of 2.23) in the second year, and 1.4–1.6 in the third year (Fig. 5b). Exclusion of the outlier of 2.23 results in an increase of 28% in the second year. It appears that the CO_2 stimulation of soil respiration itself has seasonal variation, highest in the autumn (August–November) in both 1997 and 1998 and lowest in the spring (February–May). Similar trends in CO_2-induced changes in soil respiration over time show on the calendar year (Table 5).

The measured soil respiration at ambient CO_2 was used to validate the TCS model. The model can ade-
quately reproduce the seasonal variation in measured midday soil respiration (Fig. 6). The model underestimates soil respiration in the fall of 1996 and overestimates it in the spring of 1997. Plotting modeled (y) against measured (x) soil respiration results in a regression line $y = 0.858x + 0.021$, with a determinant coefficient $R^2 = 0.868$.

Deconvolution of rhizosphere C processes

The forward analysis indicates that the increase of soil respiration during the first year is primarily caused by C released by root exudation and respiration, in the second year by root turnover in addition to root exudation and respiration, in the third year by aboveground litterfall in addition to the other three pathways. Experimental data show that soil respiration increased by 3.8%, 28.0%, and 45.6% in the first, second, and third years of the CO_2 experiment (Table 4). A qualitative comparison between listed processes and observed increases in Table 4 suggests that the increases in root
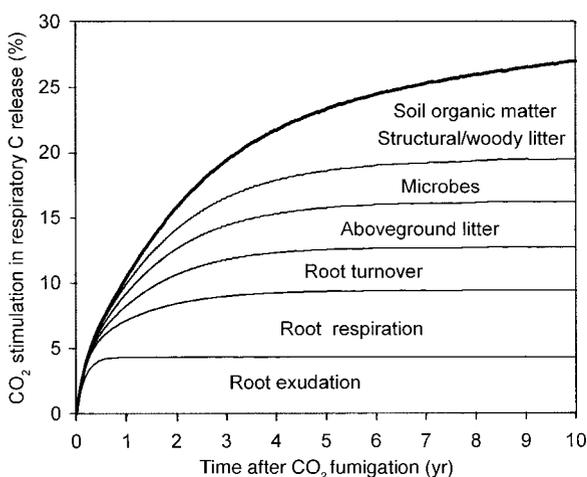
FIG. 3. Modeled temporal variations in percentage CO_2 stimulation of respiratory C release at elevated CO_2, relative to that at ambient CO_2 from each of the C pathways. The bold line is a convolution of all the soil C release processes in response to elevated CO_2. The convolved response is soil surface respiration, which is measurable. All the processes are difficult to measure but are what we want to quantify.
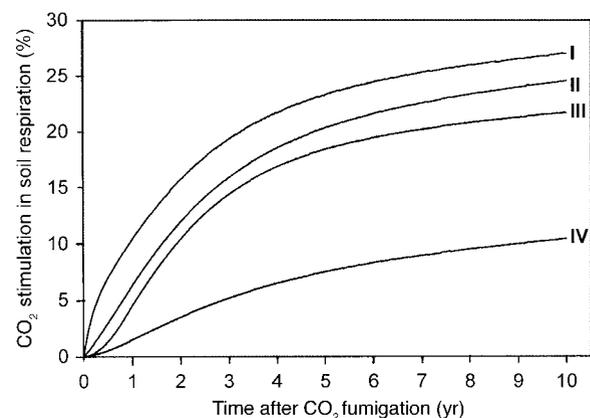
FIG. 4. Four trajectories of convolved responses of soil respiration to elevated CO_2. The four trajectories correspond to the first four scenarios listed in Table 1 and are used to identify mechanisms underlying observed soil respiration at the Duke Forest free-air CO_2 enrichment (FACE) site.
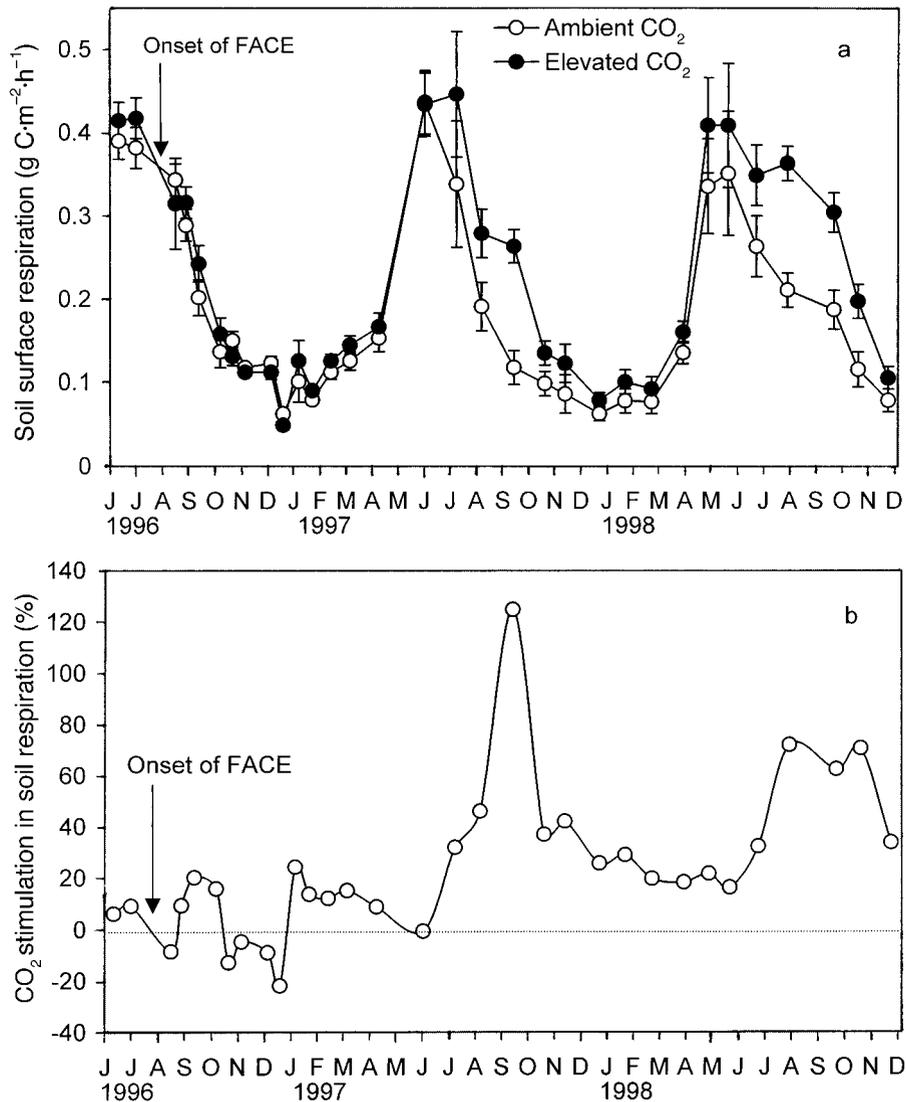
FIG. 5. (a) Measured midday values of soil respiration at the Duke Forest free-air CO_2 enrichment (FACE) experiment, and (b) percentage changes in soil respiration at elevated CO_2, compared to that at ambient CO_2, during June 1996–December 1998. Elevated CO_2 resulted in little change in the first year but significantly increased in soil respiration in the second and third years of the FACE experiment. It also appears that elevated CO_2 caused a phase shift in soil respiration, being highest in the autumn (August–November) and lowest in the spring (February–May).

TABLE 4. Observed CO_2 stimulation in soil respiration and associated mechanisms during the three experimental years of the free-air CO_2 enrichment (FACE) project at the Duke Forest.

Experimental year	Period	Observed change (%)	Possible mechanisms
1	August 1996–July 1997	3.8	(1) root exudation and (2) root respiration
2	August 1997–July 1998	28.0†	(1) root exudation, (2) root respiration, and (3) root turnover
3	August 1998–July 1999	45.6‡	(1) root exudation, (2) root respiration, (3) root turnover, and (4) aboveground litter

† The abnormal large CO_2 stimulation of 125% on 13 October 1997 (see Fig. 5) was not included. With that value, the mean observed change was 33.3% in the second growing season.

‡ The mean change during the period August 1998–December 1998 was 63.9%, due to the high values in the autumn.

TABLE 5. Calendar-year-based increases in soil respiration under conditions of elevated CO_2 as observed by experimental measurements and predicted by the terrestrial-C sequestration (TCS) model with five simulation scenarios at the Duke Forest free-air CO_2 enrichment (FACE) project.

Calendar year	Period	Observed change (%)	Simulation scenario				
			I	II	III	IV	V
1	August–December 1996	3.0	8.8	2.2	0.6	0.5	3.5
2	January–December 1997	23.2	17.5	9.3	4.9	3.5	22.1
3	January–December 1998	35.5	25.5	19.1	13.0	9.3	37.1

exudation and root respiration may be of minor importance in C transfer to the rhizosphere, whereas root turnover and aboveground litterfall are the major processes delivering C to soil. Mindful of this qualitative evaluation, we conducted the inverse analysis to quantify the relative contributions of each of those C processes to soil respiration.

The inference on key processes and their relative contributions was made by simulation analysis using the validated TCS model. Using the model we examined four scenarios (Table 1) of C transfer into rhizosphere. Comparison of modeled with measured changes in soil respiration in the first year after CO_2 fumigation reveals that scenario II provides the closest
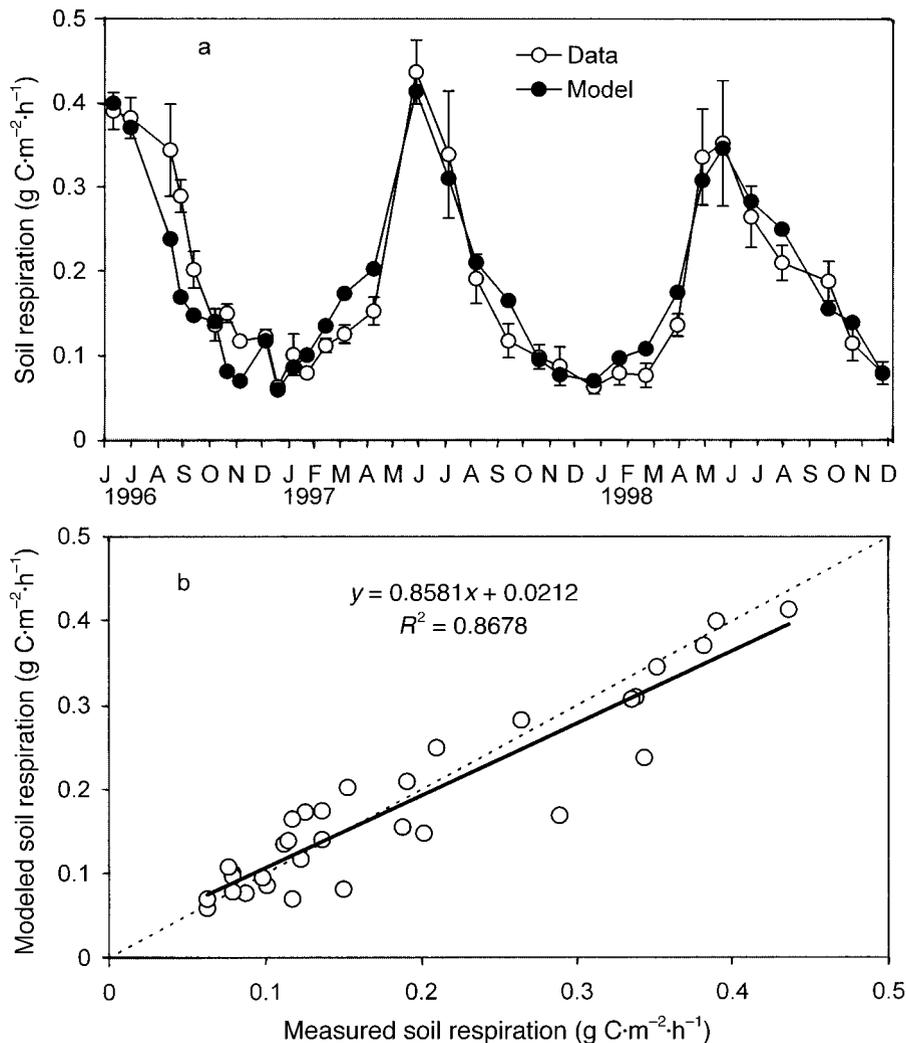
FIG. 6.   (a) Modeled vs. measured midday values of soil respiration at the Duke Forest free-air CO_2 enrichment (FACE) experiment at ambient CO_2 and (b) correlation between the modeled and measured soil respiration values. The terrestrial-C sequestration (TCS) model can adequately reproduce the seasonal variation in soil respiration at ambient CO_2 by considering seasonal variations in soil temperature, soil moisture, root growth, and C supply.
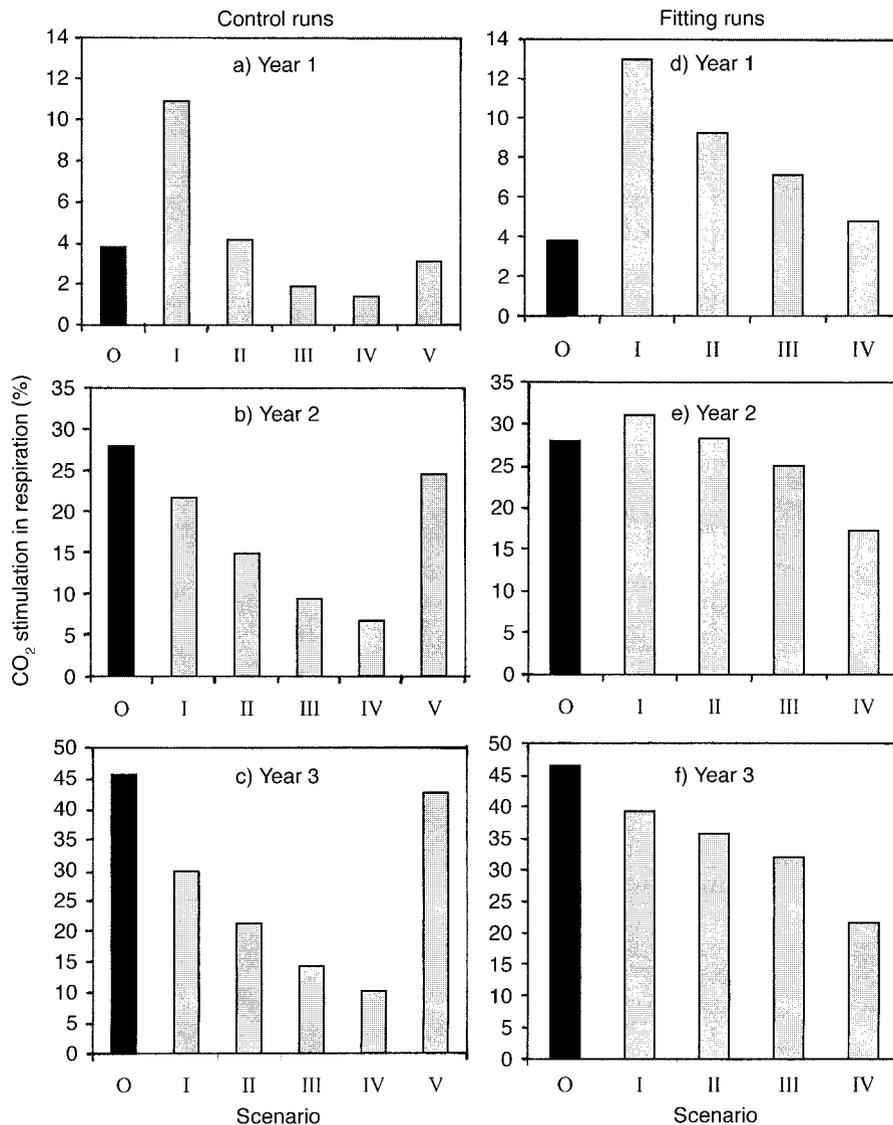
FIG. 7. Percentage CO_2 stimulation of soil respiration from experimental observations (O, black bars) and model simulations with scenario I–V (gray bars) in years 1–3. (a)–(c) Results of "control runs" of the model, with the parameter values in Tables 2 and 3. (d)–(f) Results of "fitting runs" of the model, using the upper limits of parameter values for the fast-turnover pools and lower limits for the slow-turnover pools. The fitting runs were created to best reproduce observed changes in soil respiration in year 2. The control runs suggest that root exudation may not be a primary mechanism to transfer C to the rhizosphere in the first year.

match between the modeled and measured respiration (4.0% vs. 3.8%; Fig. 7a). Scenario I provides a considerable overestimation (10.9%), whereas scenarios III and IV result in an underestimation (2.0% and 1.0%, respectively). Thus, it is likely that root exudation is not a primary mechanism to transfer C to the rhizosphere.

Measured soil respiration in the second and third years is partially explained by the four scenarios (Fig. 7b and c). Model simulations with root exudation (scenario I) and without root exudation (scenario II) result in 22.8% and 14.9% increases in year 2 and 30% and

21% increases in year 3 in soil respiration. Model simulations without CO_2-induced increases in root respiration (scenario III) or root turnover (scenario IV) lead to 9.4% and 6.7% increases in year 2 and 14.0% and 10.0% increases in year 3. The observed increases in soil respiration are 28.0% in year 2 and 45.6% in year 3. In order to reproduce the observed increase in soil respiration at elevated CO_2, we created "fitting runs" using the upper limits in the sensitivity tests of specific exit rates from donor pools of leaf biomass ($a_{1,1}$), root biomass turnover ($a_{3,3}$), exudate ($a_{4,4}$), metabolic leaf and root litter ($a_{6,6}$ and $a_{8,8}$, respectively), and soil sur-
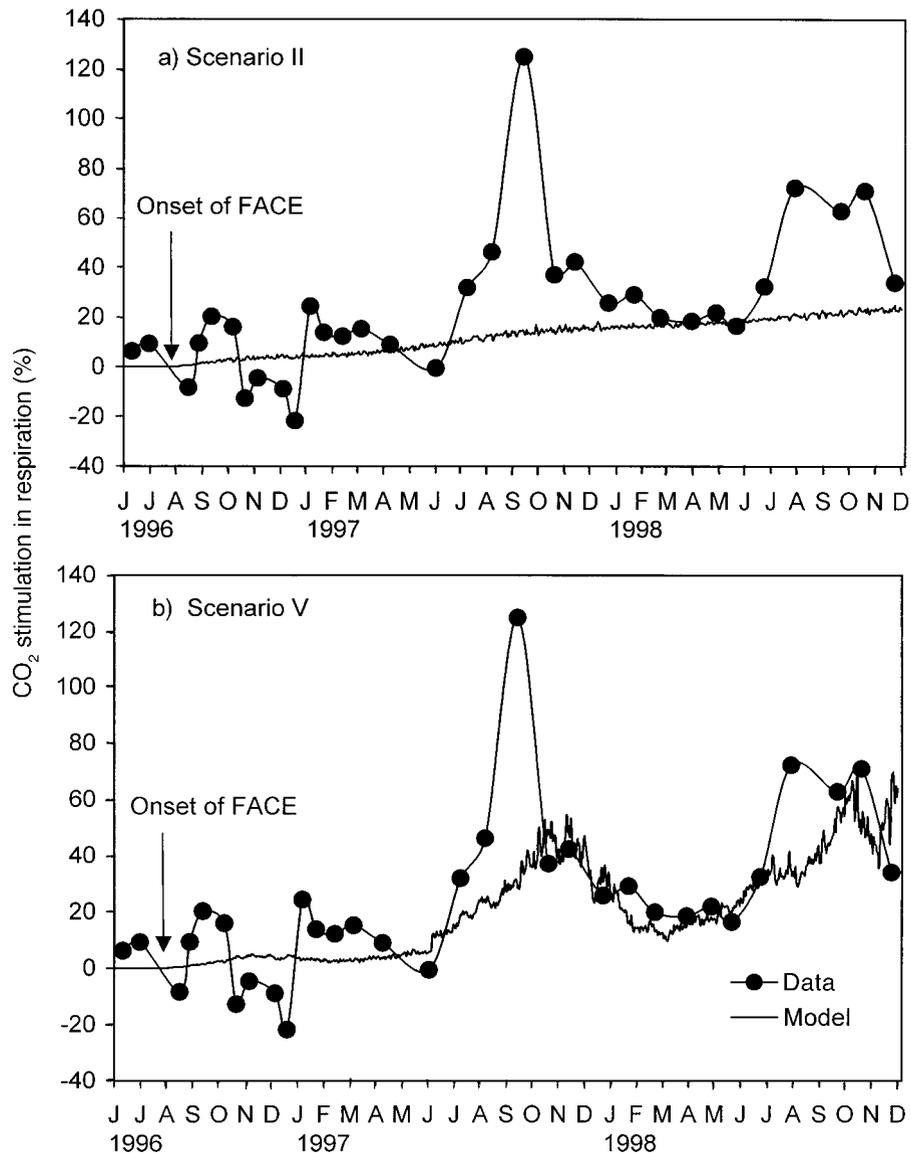
FIG. 8. Temporal variations in observed vs. modeled CO_2 stimulation in soil respiration with (a) scenario II and (b) scenario V. Scenario II results in a gradual increase of the CO_2 stimulation in soil respiration, whereas scenario V with a partial time delay function can better reproduce the observed phase shift in soil respiration caused by elevated CO_2 in the Duke Forest.

face and soil microbes ($a_{10,10}$ and $a_{11,11}$, respectively), along with the lower limits for the other C exit rates (Table 3). The fitting runs with scenario II estimate a 28.3% increase in soil respiration at elevated CO_2 in the second year, which is highly comparable for the observed 28% increase (Fig. 7e). However, the estimated CO_2 stimulation in soil respiration in the first year with either scenario I or II is several-fold higher than the observations (13% and 9.3% vs. 3.8%; Fig. 7d), due to exceedingly rapid C cycling through the fast turnover pools in the fitting runs.

The model simulation with scenario II shows a gradual increase of the CO_2 stimulation in soil respiration, whereas the measured data indicate a rather strong seasonal variation due to a phase shift of soil respiration caused by elevated CO_2 toward autumn (Fig. 8a). With scenario V (the partial time delay function), the TCS model can generate a seasonal variation in the CO_2 stimulation of soil respiration, which is more comparable to the observed values (Fig. 8b) than scenario II (Fig. 8a). In addition, the modeled increases in soil respiration at elevated CO_2, compared to that at ambient CO_2, are 3.1%, 24.5%, and 42.6% in the three growing seasons, respectively. The modeled increases with scenario V are similar to field observations (Table 4, Fig. 7a–c). On the calendar year, model performances are

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similar to those on the experimental year, inasmuch as scenario V fits the experimental data best (Table 5).

The 10 sensitivity tests consistently indicate that root exudation contributes most to the CO_2 stimulation of soil respiration in the first year, whereas CO_2 effects on soil respiration in second and third years are most sensitive to changes in root turnover and root respiration caused by the CO_2-induced biomass increase (Fig. 9). The modeled CO_2 stimulation in soil respiration is less sensitive to changes in parameter values with either scenario I or II. However, it is highly sensitive to parameter values in scenario III or IV, having less CO_2 stimulation with slower turnover (longer residence time) and more CO_2 stimulation with faster turnover (shorter residence time). The high sensitivity of the CO_2 stimulation to parameter values with scenario III and IV suggests that the C pathway through increased root biomass and turnover is critically important in adding C to the rhizosphere.

DISCUSSION

The rhizosphere is a complex system that has usually been studied with direct measurements of root biomass, microbial activities, and mineralization. In the past decades, isotope labeling with ^{13}C, ^{14}C, and ^{15}N has been also used to track C and N movements within this system. This study made a first attempt to add another tool to untangle the complexity by examining distinctive response times of various processes that add C to the rhizosphere. Our analysis suggests that (1) root exudation may not be a very important process to transfer C from plants to the rhizosphere in the Duke Forest, at least in the first experimental year after the CO_2 fumigation, (2) increased root biomass and turnover is a major process to deposit C in the rhizosphere, and (3) the observed phase shift in annual variation of soil respiration caused by elevated CO_2 can not be reproduced by a regular biogeochemical model unless a partial time delay function is incorporated into the model.

Root exudation

Root exudation is a process that transfers organic and inorganic chemical compounds from the inside of roots to the rhizosphere, possibly resulting from the positive pressure inside roots (Kramer and Boyer 1995). The chemical compounds of exudates could be important for phytoremediation (Schier and McQuattie 1998) and soil nutrient dynamics (Wang and Zabowski 1998). Although the chemical compounds of exudates can be measured in hydroponic studies (Bekku et al. 1997, DeLucia et al. 1997, Groleau et al. 1998), it is still not feasible to measure the amount of exudates in natural ecosystems. Since exudates often contain appreciable amounts of sugar and nutrient compounds, root exudation is often speculated as one of the major processes of transferring C to the rhizosphere when plant or ecosystem C or N budgets can not be balanced. For example, when their data did not support the direct

transfer of N and phosphorus (P) between N-fixing plants and non-N-fixing plants via arbuscular mycorrhiza, Ikram et al. (1994) presumed that root exudation was likely the pathway. Similarly, when an isotopic approach cannot fully explain the effects of nutritional status on plant transpiration efficiency in relation to biomass production, the root exudation was suspected to cause the discrepancy (Guehl et al. 1995). Root exudation was also considered as one of the major causes of discrepancies between estimated C allocation belowground and the sum of root respiration and root production in a *Pinus radiata* forest (Ryan et al. 1996)

Root exudation is frequently invoked in the CO_2 research community when measured increments in photosynthetically fixed C at elevated CO_2 can not be balanced by combined increases in respiration, plant biomass and soil C content (Norby et al. 1987, Körner et al. 1996, Luo et al. 1997, Cheng et al. 2000). For example, a 41% increase in C fixation in an alpine grassland was accompanied by little biomass increase (Körner et al. 1996), leading to locally missing C. It is often speculated that the disproportional increases in photosynthesis and plant biomass at elevated CO_2 result from several processes, including root exudation (Rouhier et al. 1996, Luo et al. 1997). Similarly, Ineson et al. (1996) hypothesized that a portion of the measured soil C gain in a short-term (186-d) study of birch seedling growing at both ambient and elevated CO_2 was attributable to root exudation and turnover. Root exudation is often considered one of the primary processes influencing microbial activities and ecosystem nutrient dynamics in elevated CO_2 environments (Zak et al. 1993, Rouhier et al. 1996, Paterson et al. 1997, Hu et al. 1999).

Despite the potential importance of root exudation to ecosystem C and N cycling, to the best of our knowledge, no report has been published on the amount of C delivered through that pathway in the field. This study attempts to quantify root exudation by deconvolving C transfer pathways. According to the kinetics of the rhizosphere C processes, root exudation contributes to the increase in soil respiration primarily in the first few months after the onset of CO_2 experiments (Darrah 1996; Fig. 3). The mean increase of 3.8% in soil respiration in the first year of the CO_2 fumigation in the Duke Forest free-air CO_2 enrichment (FACE) site suggested limited root exudation in the loblolly pine forest (Table 4, Fig. 7a). In addition, experimental measurements since the second year of CO_2 fumigation suggested that the specific rate of fine-root respiration was hardly affected by elevated CO_2 and that total fine root respiration increased in elevated CO_2, compared to that in ambient CO_2, due to increased root biomass (Matamala and Schlesinger 2000). The increased total root respiration and root turnover offered direct evidence that scenarios III and IV did not occur in the Duke Forest. It also offered indirect evidence that the small increase in soil respiration in the first year of the
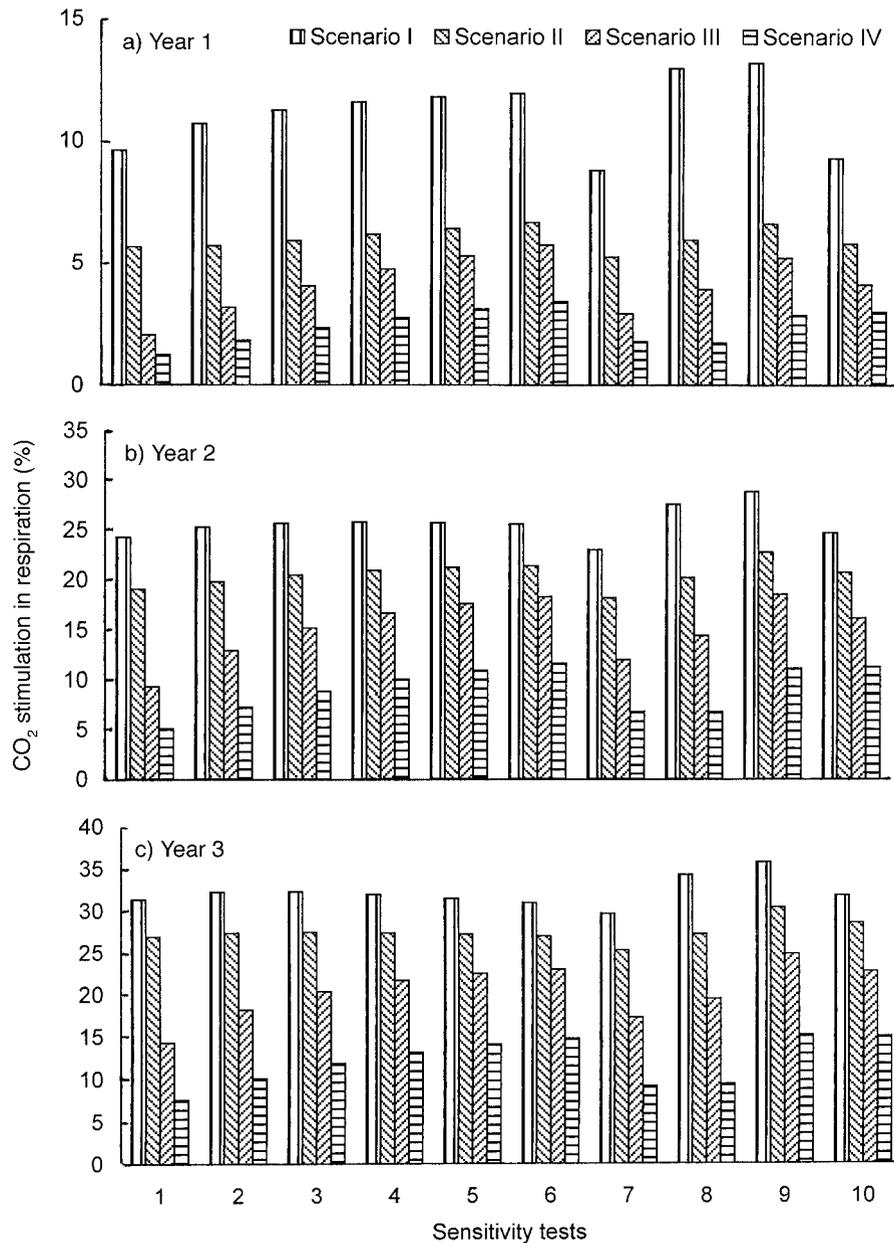
FIG. 9. Percentage CO_2 stimulation of soil respiration from 10 model sensitivity tests with scenarios I–IV in years 1–3. The sensitivity tests indicate that root exudation contributes most to the CO_2 stimulation of soil respiration in the first year, and root turnover in the second and third years. The latter is critically important in adding C to the rhizosphere.

CO_2 experiment was unlikely caused by root exudation. However, root exudation may be an important pathway of C transfer to the rhizosphere in other ecosystems. For example, measured soil respiration in a mesocosm experiment with sunflower plants was unchanged in the first 35 d and gradually increased up to 35% by the end of a 58-d exposure to elevated CO_2, in comparison to that in ambient CO_2 (Hui et al. 2001). The substantial increase in soil respiration can hardly be explicable other than by root exudation and respiration. Isotope-labeling experiments also suggest that root exudation

is potentially important in transferring C to the rhizosphere (Cheng et al. 1994, Rouhier et al. 1996).

Seasonal variations in soil C processes

It is commonly observed that soil respiration displays strong seasonal patterns (Schlesinger 1977, Singh and Gupta 1977, Hanson et al. 1993, Luo et al. 1996, Hättenschwiler and Körner 1997). Seasonal variations in soil respiration coincided with the seasonal variations in soil temperature and soil water content in temperate deciduous forest (Hanson et al. 1993, Davidson

et al. 1998) and in a sub-humid grassland (Knapp et al. 1998). The seasonal variations were primarily regulated by water availability in arid grasslands (Wildung et al. 1975) and a Mediterranian grassland in California (Luo et al. 1996). The seasonal variability in soil respiration usually can be predicted by empirical models that integrate the temporal dynamics of soil temperature, soil moisture, and root growth (Hanson et al. 1993, Luo et al. 1996). In the Duke FACE site, the seasonal variation in soil respiration itself at ambient CO_2 can also be well reproduced by the TCS model by considering seasonal variations in soil temperature, soil moisture, root growth, and C supply (Fig. 6).

Compared to that under ambient CO_2, soil respiration under elevated CO_2 at the Duke FACE site showed a phase shift in its seasonal variation by approximately one month, so that the CO_2 stimulation in soil respiration was highest during August–November and lowest during February–May (Fig. 5b). The phase shift caused by elevated CO_2 can hardly be explained by soil variation in temperature and moisture, because neither of them significantly changed in elevated CO_2, either (Andrews and Schlesinger 2001; K. V. R. Schäfer, *unpublished data*). In addition, measurements of fine root growth and death did not show an obvious shift in seasonal dynamics caused by elevated CO_2 (Matamala and Schlesinger 2000). The phenology of aboveground growth rates showed a seasonal variation, high in spring and low in fall (DeLucia et al. 1999), which mirrors the seasonal pattern of the CO_2 stimulation of soil respiration. However, the phenological pattern of growth was not differentiated between the two CO_2 treatments, providing no obvious mechanisms to explain the observed phase shift.

The difficulty in explaining the observed phase shift is also reflected in the model simulation. With a conventional model structure of ecosystem C processes, the TCS model cannot reproduce the observed seasonal variation in the CO_2 stimulation (Fig. 8a). With the addition of a time delay function, the model can create seasonal variations (Fig. 8b). While the exact mechanisms for the time delay function are unknown, several processes may contribute to delay in respiratory C release, including (1) altered longevity of fine roots (Pregitzer et al. 2000), (2) ecophysiological controls of soil processes (Crane et al. 1999; Cardon et al., *unpublished manuscript*), (3) shifting in microbial communities (Ringelberg et al. 1997, Hu et al. 1999), (4) shifting microbial decomposition of new versus old soil organic C (Cardon et al. 2001), and (4) seasonal changes in the relative C supplies from labile vs. recalcitrant C pools. For example, Z. G. Cardon et al. (unpublished manuscript) have recently utilized seasonal flushes of new shoots on *Quercus rubra* as a measure of rhythmic controls of C allocation between shoots and roots and demonstrated that belowground microbial biomass and soil respiration were mirror images of the aboveground shoot growth. At the Duke FACE site, it might be pos-

sible that some plant physiological ''strategies'' are at play. For example, in the autumn of the first experimental year, trees might respond to elevated CO_2 by growing more root tissues to explore for nutrients. In the following spring, trees added more new shoots and needles. It would not be until the autumn of the second experimental year that root exudation might become important, leading to the phase shift in soil respiration in years 2 and 3. Although that strategy could provide a sounder explanation than any established models for the observed phase shift, it is yet a challenge to provide experimental confirmation of the strategy, due to a lack of methods for direct measurements of root exudation.

Uncertainties in experimental data can mask mechanisms underlying observed responses of soil respiration to elevated CO_2. The data set used in this study was obtained by measurements with an infrared gas analyzer (IRGA), which has been widely used to measure soil respiration in the past decades. Infrared gas analyzer measurements are generally consistent with Bowen-ratio apparatus (Norman et al. 1992, Dugas 1993), but were substantially higher than the alkaline absorption methods in the Duke Forest (Andrews 1999). In addition, the IRGA measurements are very sensitive to changes in chamber pressure (Lund et al. 1999). Quantification of C fluxes through different pathways by deconvolution heavily relies on accuracy of data. In addition, the difficulty in explaining the observed phase shift raises a question. Is the phase shift just a site-specific phenomenon at the Duke Forest, or is it a general pattern across various ecosystems? To answer that question we need systematic, accurate measurements of soil respiration in other FACE and open-top chamber (OTC) experiments.

Prediction of the forest carbon sequestration

Carbon storage in terrestrial ecosystems occurs when photosynthetic C influx is larger than respiratory C release. At the Duke FACE site, both leaf-level measurements (Ellsworth 1999) and canopy-modeling synthesis (Luo et al. 2001) indicate a step increase in ecosystem C influx by ~40%, which has been maintained since the CO_2 fumigation in August 1996. The respiratory C release at the soil surface was unchanged in the first experimental year and considerably increased in the second and third years at the elevated CO_2, in comparison to that at ambient CO_2 (Fig. 5). Preliminary results of tree respiration measurements indicate little CO_2 effect on specific respiration rates in trunks and needles (J. Hamilton and E. DeLucia, *personal communication*), leading to little changes in the aboveground respiratory C release in the first year and increases in the second and third years due to the increased aboveground biomass in elevated CO_2 (DeLucia et al. 1999). Integration of the three components yields a large C sequestration in the first experimental year, followed by smaller net C storages in the second and third years. This dynamic pattern of C sequestra-

tion is qualitatively similar to that predicted by the early version of the TCS model in Luo and Reynolds (1999).

Prediction of terrestrial C sequestration depends on proper model structure and parameterization of critical processes. Deconvolved data in this study indicate the minor importance of root exudation in C transfer to the rhizosphere. Since root exudation expedites C releases back into the atmosphere, an ecosystem with low exudation, such as the Duke Forest, consequently has a high capacity of carbon sequestration. Although it may be unimportant in the Duke Forest, root exudation may be significant in other ecosystems. Quantification of exudation using isotope labeling and deconvolution is critical for our prediction of ecosystem C sequestration.

In addition to quantification of the flux of C through individual pathways, model structure has to be rigorously examined against data. If the observed phase shift in soil respiration caused by elevated CO_2 at the Duke Forest is a general pattern across ecosystems, for example, modelers should ask a question: is a typical biogeochemical model adequate to represent a real ecosystem? The majority of those models share a similar structure, including compartmentalization, donor pool-controlled C transfer, and sequential linearity (Luo and Reynolds 1999). This type of model was first developed decades ago (Jenkinson and Rayner 1977, Parton et al. 1987) and is now widely used for quantification of global and regional C sequestration as well as for policy making (Schimel et al. 2000). Examination of the fundamental model structure against data will help reduce uncertainties in global predictions.

Deconvolution as a systems approach

The deconvolution analysis is a systems approach to rhizosphere complexity. It focuses on systems-level performance and underlying processes. Traditionally, the rhizosphere is studied using process-based measurements of microbial biomass, root biomass, and mineralization as well as application of isotope labeling. While those measurements are essential and help substantially to advance our understanding, difficulties in separating root vs. microbial processes necessitate new approaches to rhizosphere complexity. This study is the first attempt to apply the deconvolution analysis to soil respiration data, showing its potential in untangling biocomplexity in soil. Indeed, this deconvolution analysis has reached conclusions that no other approaches could, even if some of the conclusions may be tentative. Root exudation, for example, has become a frequently invoked process in the CO_2 research community in particular and ecosystem ecology in general. This study, for the first time, provides a reasonable theoretical base combined with experimental data to quantify root exudation. Although we have not provided a sound explanation of the seasonal variation in CO_2 stimulation in soil respiration, the comparison between the TCS model and measured soil respiration

represents our effort to confront theory with data. The discrepancy between the observations and model should stimulate research on this issue in the future.

Deconvolution and inverse analysis are quantitative methods to confront data with theory and/or challenge theory with data with a mathematical rigor. Although they have not been extensively discussed in the literature of ecology, their applications have been made to issues in plant ecophysiology (Tabrizi et al. 1998), population ecology (Wood 1997), community ecology (Clark et al. 1999), and ecosystem ecology, as in this study. For example, Clark et al. (1999) applied the inverse analysis to the issue of multiple seed sources contributing to a given location. The seed rain from these multiple sources is a smoothed version of individual seed shadows, making it difficult to assign recovered seeds to specific sources. Using the inversion approach, they statistically estimated the individual seed shadows using a model with two elements of the seed shadow together with a distribution of error.

Like any new method, the deconvolution approach needs future testing and further development. The analysis presented in this paper was implemented with a simulation approach. Parameter estimation can be made with other mathematical techniques, such as optimizations. Such approaches lies in realm of mathematical inverse theory (White and Luo 2001). These methods will allow us to estimate most likely parameter values for C transfer pathways from observed data, as well as providing probabilities that will be useful in making predictions (Luo et al., *unpublished manuscript*). In addition, successful applications of deconvolution heavily depend on the right data sets, which have to be generated from appropriate experimental design and data collection plans with a high accuracy of measurements.

Conclusions

Despite the fact that a large amount of data has been accumulated from free-air CO_2 enrichment (FACE) and open-top chamber (OTC) experiments, it is still a great challenge to integrate experimental results into models that predict terrestrial C sequestration. This study is based on the conception that credible predictions rely on proper model structure and parameterization. The structure of existing models needs to be challenged against and parameter values derived from experimental data. This procedure of data–model integration for the purpose of improvement of models is called inverse analysis.

The data–model integration may be difficult in the cases where processes in a model and observations are mismatched. Observations often are convolved responses of multiple processes. In this case, deconvolution is a procedure to evaluate relative importance of different processes in determining the observed responses. This study focused on observed soil respiration in response to elevated CO_2 in the Duke Forest,

which is a convolution of multiple rhizosphere processes, including root exudation, respiration, and turnover, as well as aboveground litter turnover and the decomposition of soil organic matter. Deconvolution of the observed soil respiration was accomplished with a simulation approach. That is, by adding and subtracting C transfer pathways from the model, we evaluated the likelihood that individual processes are involved in C transfer to the rhizosphere. By increasing and decreasing parameter values of C processes, we evaluated the relative contributions of individual processes to rhizospheric C transfer. Deconvolved data suggest the minor importance of root exudation. Root biomass growth and turnover are critically important in delivering C to the rhizosphere in the Duke Forest.

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