Sustainability of terrestrial carbon sequestration: A case study in Duke Forest with inversion approach

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[1] A sound understanding of the sustainability of terrestrial carbon (C) sequestration is critical for the success of any policies geared toward stabilizing atmospheric greenhouse concentrations. This includes the Kyoto Protocol and/or other greenhouse strategies implemented by individual countries. However, the sustainability of C sinks and pools has not been carefully studied with either empirical or theoretical approaches. This study was intended to develop a conceptual framework to define the sustainability based on C influx and residence time (τ). The latter τ quantifies the capacity for C storage in various plant and soil pools. We estimated τ via inverse analysis of multiple data sets from a Free-Air CO_2 Enrichment (FACE) experiment in Duke Forest, North Carolina, United States. This study suggested that estimated residence times at elevated CO_2 decreased for plant C pools and increased for litter and soil pools in comparison to those at ambient CO_2. The ensemble of the residence times from all the pools at elevated CO_2, however, was well correlated with that at ambient CO_2. We then used the estimated residence times, combined with C influx, to simulate C sequestration rates in response to a gradual increase in atmospheric CO_2 concentration (C_a). The simulated C sequestration rate gradually increased from 69 g m^{-2} yr^{-1} in 2000 when C_a was 378 ppm to 201 g m^{-2} yr^{-1} in 2100 when C_a was at 710 ppm. Thus, the current evidence from both experimental observations and inverse analysis suggested that C sequestration in the forest ecosystem was likely to increase gradually as C_a gradually increases. The model projection of the C sequestration will improve as more data on long-term processes become available in coming years. In addition, such a modeled increase in terrestrial C sequestration is too small to balance the anthropogenic C emission. *INDEX TERMS:* 1615 Global Change: Biogeochemical processes (4805); 1620 Global Change: Climate dynamics (3309); 9350 Information Related to Geographic Region: North America; *KEYWORDS:* carbon residence time, Free-Air CO_2 Enrichment (FACE), inverse analysis, modeling, sustainability, terrestrial carbon sink

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1. Introduction

[2] Significant advances have recently been made in our understanding of the current role of terrestrial ecosystems in the global C cycle by the uses of eddy covariance techniques [*Valentini et al.*, 2000], inversion of atmospheric signals [*Fan et al.*, 1998], forest inventory [*Brown and Schroeder*, 1999; *Pacala et al.*, 2001], and simulation models [*Schimel et al.*, 2000]. Estimation from those various approaches suggests that current C sink in global terrestrial ecosystems ranges from 0.5 to 3.9 Gt C per year [*Schimel et al.*, 2001]. This current sink is responsible for removing from the atmosphere up to one third of the CO_2 emitted from fossil fuel combustion and tropical deforestation. By sequestering that amount of C, the terrestrial ecosystems help decrease the rate of accumulation of anthropogenic CO_2 in the atmosphere, and its associated

climate change. As international efforts are implemented to stabilize atmospheric CO_2 concentration (C_a) and climate change [*Wigley et al.*, 1996; *Azar and Rodhe*, 1997], it is imperative to assess the sustainability of terrestrial C sequestration.

[3] The latest report by the Intergovernmental Panel of Climate Change (IPCC) predicts that the terrestrial C sink will continue to sequester up to 5–10 Gt C yr^{-1} by the end of the twenty-first century [*Houghton et al.*, 2001]. The predicted increase in the current terrestrial sink is largely based on biosphere models, which primarily respond to gradually rising C_a. However, several physiological and ecological processes could alter such model predictions and potentially result in the saturation of the terrestrial C sink. For example, increased C storage in plant and soil pools under elevated CO_2 may result in immobilization of nutrients in plant biomass and soil organic matter, progressively leading to lower nutrient availability for plant uptake [*Gill et al.*, 2002]. Limited nutrient availability, in return, constrains C sequestration in terrestrial ecosystems. Photosynthetic responses to rising C_a are also diminishing at high levels of CO_2 concentration. Moreover, incorporation of the effects of warming on terrestrial C processes into global models predicts that terrestrial ecosystems will switch from C sinks to C sources in the middle of this century [*Cox et al.*, 2000; *Cramer et al.*, 2001; *McGuire et al.*, 2001] due to temperature stimulation of C releases from soil and plant pools.

[4] In addition to global change, the current C sink may be driven by other factors, including forest regrowth, woody plant encroachment, atmospheric nitrogen deposition, and C burial in sediment [*Pacala et al.*, 2001]. Some of the sink mechanisms will saturate while other sinks will quickly disappear. The C sink due to forest regrowth in regions of the eastern United States, for example, may decline quickly as forests reach maturity in coming decades [*Caspersen et al.*, 2000]. Thus, it is critical to understand the sustainability of (1) individual sink factors and (2) net sink resulting from the combined effects of multiple factors. If the expected increase in sink strength is not realized or current sinks disappear, atmospheric CO_2 growth will take place at a much faster pace than currently predicted, and policies devised to stabilize CO_2 concentrations will fall short in meeting their targets.

[5] To assess the sustainability of the current C sink, we need to evaluate how it varies with environmental forcing over time. This issue can be addressed by improving biosphere models via examination of model structure and estimation of parameter values because the future rates of C sequestration are ultimately predicted by those models. In the past decades, dozens of biogeochemical models have been developed to predict future terrestrial C sequestration [e.g., *Parton et al.*, 1987; *Luo and Reynolds*, 1999; *Cramer et al.*, 2001; *McGuire et al.*, 2001]. Most of the models share a similar structure that partitions photosynthetically fixed C into plant and soil pools. The model structure is robust and supported by experimental evidence. Variation in the predicted future C sinks among models largely results from differences in canopy C influx and transfer coefficients between pools as well as their responses to environmental variables. The transfer coefficients are inversely correlated with the C residence times (τ) in plant and soil pools. The latter τ, in turn, determines the capacity for C storage in terrestrial ecosystems. For a given canopy C influx rate, the longer τ is, the larger the capacity of the ecosystem to sequester C. For a given set of τ in plant and soil C pools, the larger the canopy photosynthetic C influx, the more C an ecosystem will sequester. Thus, to assess the sustainability of terrestrial C sequestration, we have to quantify both canopy photosynthesis and τ in future scenarios.

[6] This study was designed to address the issue of C sink sustainability. Since research on this subject is in its infancy, we intended to first establish a general framework for evaluating the sustainability based on C influx and τ. We then applied an inversion approach to the estimation of τ and its adjustments to global change. We evaluated the sustainability in reference to rising C_a because it is essential to understand individual factors before we can evaluate all the sink factors together. Specifically, we estimated parameter values of τ via an inverse analysis of six data sets collected from the Duke Forest in North Carolina, United States, where a Free-Air CO_2 Enrichment (FACE) experiment has been in progress since August 1996 [*Hendrey et al.*, 1999]. The estimated τ, in combination with photosynthetic C influx, was used to predict C sequestration rates in response to a gradual C_a increase as happening in the real world.

2. Conceptual Framework

[7] Many factors contribute to C sinks in terrestrial ecosystems, including CO_2 fertilization, nitrogen (N) deposition, climate change, forest regrowth, woody plant encroachment, accumulations of durable products and landfills, and burial in sediments [*Holland et al.*, 1999; *Archer et al.*, 2001; *McGuire et al.*, 2001; *Schimel et al.*, 2001]. These factors influence terrestrial C sequestration by altering either C influx into an ecosystem or its residence time (τ) or both. For instance, CO_2 and nitrogen fertilizations mainly stimulate C influx into ecosystems, whereas C burial in sediments and accumulations of durable products primarily extend τ. Woody encroachment may alter both C influx and τ. Thus, C influx and residence time are the two key parameters for quantifying the capacity of an ecosystem to sequester C.

[8] C influx and residence time are not only useful for assessing how various factors influence C sequestration, but these parameters also represent the fundamental nature of ecosystem C processes [*Luo and Reynolds*, 1999; *Taylor and Lloyd*, 1992]. Since any C atom that enters an ecosystem from the atmosphere is eventually cycled back to the atmosphere, terrestrial ecosystems only have dynamic C storage. That is, the C-storage pools are transient. The transient C storage is determined by the duration of C atoms from the entrance to exit (i.e., their residence times, τ). The longer τ is, the higher the capacity of an ecosystem to store C. Note that the C-storage capacity defined by τ is not a concept of static pool sizes (e.g., a maximum amount of C an ecosystem can store) but a dynamic measure of transit time of C atoms from the entrance to the exit in the ecosystem. Even if the C-storage

capacity is the same in two environments (e.g., ambient and elevated CO_2) with identical transit times of C atoms, the amount of C that an ecosystem can store could be different due to different C influx. If elevated CO_2 increases C influx into an ecosystem but does not change C transit times, for example, the C sequestration rate of the ecosystem increases purely due to the fact that more C stays in the ecosystem for the same length of time. Thus, C sequestration in terrestrial ecosystems is determined by both the amounts of C entering an ecosystem and their residence times (τ). To evaluate the sustainability of terrestrial C sequestration, we need to examine the dynamics of both C influx and τ over time.

[9] The sustainability of photosynthetic C influx can be quantified according to sensitivity and acclimation [*Farquhar et al.*, 1980; *Luo et al.*, 1996]. Photosynthetic sensitivity is independent of growth environments and interspecific variation, and varies only with CO_2 concentration and temperature [*Luo*, 1999]. Photosynthetic acclimation (i.e., adjustment in photosynthetic capacity) may be caused by many factors [*Luo et al.*, 1994; *Mooney et al.*, 1999; *Norby et al.*, 1999], frequently related to nitrogen supply [*Peterson et al.*, 1999; *Sims et al.*, 1998]. Although there is no universal rule to predict acclimation, we can quantify adjustments in the photosynthetic capacity (i.e., upregulation, downregulation, or no change) under different growth environments when we measure photosynthetic responses to light and CO_2 concentration.

[10] In contrast to C influx, our ability to measure τ and its adjustments to global change is extremely limited [*Balesdent et al.*, 1988; *Bird et al.*, 1996; *Trumbore*, 2000]. To the best of our knowledge, no report has been published on τ adjustments in response to rising atmospheric CO_2. In this study, we employed an inversion approach to an analysis of multiple data sets obtained from the Duke FACE experiment to estimate τ at ambient and elevated CO_2 (i.e., τ_A and τ_E, respectively). Since the residence time measures the capacity of an ecosystem to store C, a comparison between τ_A and τ_E is indicative of adjustments in the C-storage capacity in response to elevated CO_2. The C-storage capacity is sustainable if the residence time at elevated CO_2 is equal to that at ambient CO_2 (i.e., $\tau_A = \tau_E$). When the residence time at elevated CO_2 decreases (i.e., $\tau_E < \tau_A$), the C-storage capacity becomes lower at elevated than at ambient CO_2. If the residence time at elevated CO_2 increases (i.e., $\tau_E > \tau_A$), the C-storage capacity increases in a high-CO_2 world.

[11] As discussed above, the capacity of an ecosystem to sequester C is determined by both the photosynthetic capacity and the C-storage capacity. In an ecosystem where neither the photosynthetic capacity nor the C-storage capacity changes at elevated CO_2, the C-sequestration capacity of that ecosystem is not altered by rising atmospheric CO_2. Thus, the amount of C sequestered by the ecosystem is primarily regulated by the forcing function (i.e., how fast C_a is rising). If either the photosynthetic capacity or the C-storage capacity or both decreases (i.e., down-regulated) at elevated CO_2, the ecosystem becomes less responsive to rising C_a and consequently sequesters less C than it would without down-regulation. If either the photosynthetic capacity or the C-storage capacity or both increases (i.e., up-regulation) at elevated CO_2, the ecosystem sequesters more C than it would without up-regulation.

3. Materials and Methods

3.1. Data Sources

[12] The data sets used in this inverse analysis are foliage biomass growth, woody biomass growth, litterfall, C content in the litter layers, C content in mineral soil, and soil respiration at the Duke FACE site in North Carolina, United States. The FACE experiment started in 1996 on a 15-year-old loblolly pine (*Pinus taeda* L.) plantation [*Hendrey et al.*, 1999] with six plots, each 30 m in diameter. The CO_2 concentration in the three treatment plots has been maintained at 200 ppm above ambient since August 1996, while three control plots have been 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 United States. Mean annual temperature is 15.5°C and precipitation is 1140 mm.

[13] Biomass of foliage and wood were estimated using an indirect method. Diameters at the breast height (DBH) of 203 canopy pine trees in the ambient and elevated CO_2 plots were measured once a month since March 1996. Starting in 1997, 112 subcanopy hardwood trees were also measured for DBH. We calculated the total biomass of the dominant pine trees (including woody roots, bole, branches, and foliage) from the measured DBH using a site-specific allometric equation [*Naidu et al.*, 1998]. Equations from the literature were used to convert the measured DBH to the total biomass for the subcanopy hardwoods [*DeLucia et al.*, 1999]. According to the site-specific allometric relationships, approximately 92.3% of the total biomass is woody biomass and the rest is foliage biomass. It was assumed that elevated CO_2 does not change the allometrical relationship [*DeLucia et al.*, 2002].

[14] Aboveground litter was collected from 12 replicate 40 × 40 cm baskets in each plot once per month between January and August and twice per month between September and December to avoid leaching leaf litter during the period of peak litterfall [*Finzi et al.*, 2001]. The collected litter was dried at 65°C for 4 days and weighed. Measured litterfall in an individual period varied due to extremely windy events. Since this modeling study did not simulate wind effects on litterfall, we lumped data to calculate the annual litterfall for inverse analysis.

[15] Measurements of C content in the forest floor and mineral soil were described by *Schlesinger and Lichter* [2001]. In each plot, we collected 16 soil samples in 1996 before CO_2 treatments and 12 samples in October 1999. Undecomposed plant materials on the soil surface in each of the samples were separated for measurement of C content in the surface litter layers. Mineral soil from 0 to 15 cm and from 15 to 30 cm depths were sieved to remove coarse roots and stored before measurement of C content using Dumas combustion of samples in a C and N analyzer (NA 1500 Series, Carlo Erba Instrumentazione, Milan, Italy). In this modeling analysis, we lumped soil C from the two layers together.

[16] Soil respiration was measured, approximately once a month, using a portable infrared gas analyzer (EGM-1, PP

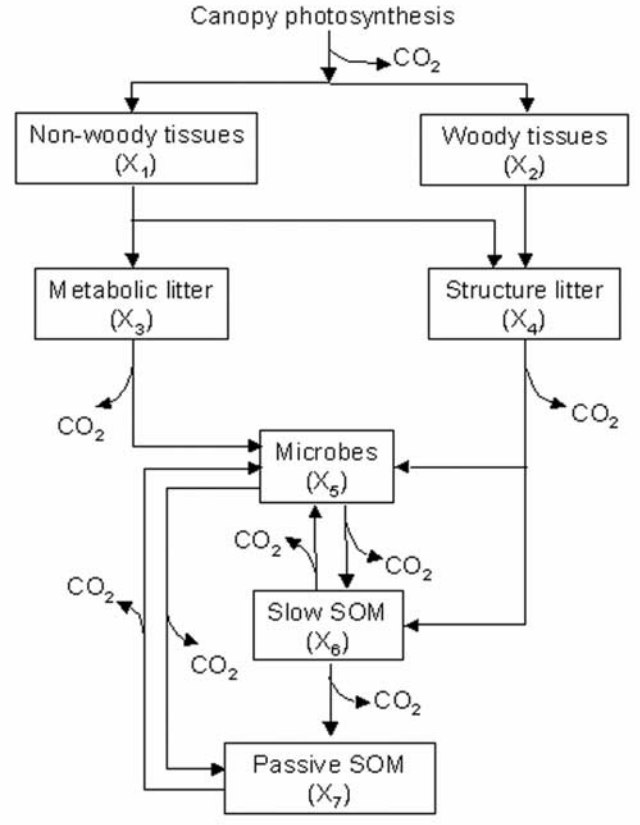

Figure 1. Schematic diagram of structure of C cycling processes in terrestrial ecosystems, from which we derived a matrix model of C transfer (i.e., equation (1)). The model includes seven pools, so the matrix A in equation (1) has 7×7 dimensions and the vectors X and B have 7 dimensions. SOM stands for soil organic matter.

Systems, Inc., Haverhill, Mass.) equipped with soil respiration chambers (SRC-1) [*Andrews and Schlesinger*, 2001]. Measurements were taken during a 1–2 min interval between 1200 and 1500 local time. Meanwhile, we measured soil moisture with four probes in each plot, integrating the upper 30-cm soil layer with a water-content reflectometer (CS615 Campbell Scientific, Logan, Utah) and soil temperature with thermocouples.

3.2. Mathematical Formulation

[17] To quantify τ, we first defined a C-transfer coefficient matrix, which measures the efficiency of C delivery to and storage in various plant and soil pools. In reference to the Duke Forest, we characterized the structure of C-cycling processes in the ecosystem as illustrated in Figure 1. Carbon enters into the ecosystem via photosynthesis. Part of the photosynthate is consumed by plant respiration. The rest is partitioned into the growth of nonwoody (i.e., leaf and fine roots) and woody biomass. Dead plant material goes to litter pools. Nonwoody litter has metabolic and structural components according to their lignin content and C/N ratio and is decomposed by microbes. Part of the litter C is respired and part of it is converted to soil organic matter (SOM) in slow and passive soil C pools. The C processes were mathematically converted to a matrix form,

$$\frac{dX}{dt} = \xi AX + Bu, \tag{1}$$

where X is a vector of C pool sizes (Figure 1), A is a matrix of transfer coefficients, ξ is an environmental scaler representing effects of soil temperature and moisture on C transfer between compartments [*Luo et al.*, 2001b], u is ecosystem C influx, B is a vector of partitioning coefficients of C to growth of woody and nonwoody tissues, and dt is a time step which was set to be 1 day in this analysis. In the model, we lumped fine roots and leaves together as one nonwoody pool because they have similar residence times and this allowed us to reduce the number of parameter values to be estimated.

[18] The critical parameter in equation (1) for evaluating the sustainability of the C sink is the transfer matrix A that quantifies the capacity of C delivery to and storage in each of the pools. Variation in A in response to global change represents adjustments in the C-storage capacity. Values of A were determined by inverse analysis of data from the Duke FACE experiment.

3.3. Constraints and Parameterization

[19] Results of inverse analysis depend on initial values, constraints, prior information, and optimal criteria [*Tarantola*, 1987]. Since the Duke FACE experiment provided comprehensive data sets for most ecosystem C processes, estimation of C-transfer coefficients can be relatively well constrained. The initial values of C pool sizes of nonwoody biomass, woody biomass, metabolic litter, structural litter, microbes, slow SOM, and passive SOM were expressed in vector X_0 as

$$\mathrm{X}_0 = (469 \quad 4100 \quad 64 \quad 694 \quad 123 \quad 1385 \quad 923)',$$

where prime ($'$) is a mathematical symbol for transposition to a column vector. These initial values were selected according to newly collected data at the Duke FACE site, particularly for the C content in foliage, and wood [*DeLucia et al.*, 1999; *Naidu et al.*, 1998], fine roots [*Matamala and Schlesinger*, 2000], microbes [*Allen et al.*, 2000], aboveground litter and soil C in mineral layers [*Finzi et al.*, 2001; *Schlesinger and Lichter*, 2001]. The matrix A in equation (1) has non-zero elements for those connections between pools as illustrated in Figure 1 and zero for all the other elements, which were

$$\mathrm{A} = \begin{pmatrix} -\mathrm{a1,1} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -\mathrm{a2,2} & 0 & 0 & 0 & 0 & 0 \\ 0.712\mathrm{a1,1} & 0 & -\mathrm{a3,3} & 0 & 0 & 0 & 0 \\ 0.288\mathrm{a1,1} & 1.0\mathrm{a2,2} & 0 & -\mathrm{a4,4} & 0 & 0 & 0 \\ 0 & 0 & 0.45\mathrm{a3,3} & 0.275\mathrm{a4,4} & -\mathrm{a5,5} & 0.42\mathrm{a6,6} & 0.45\mathrm{a7,7} \\ 0 & 0 & 0 & 0.275\mathrm{a4,4} & 0.296\mathrm{a5,5} & -\mathrm{a6,6} & 0 \\ 0 & 0 & 0 & 0 & 0.004\mathrm{a5,5} & 0.03\mathrm{a6,6} & -\mathrm{a7,7} \end{pmatrix}. \tag{4}$$

The diagonal elements ($a_{i,i}$, i = 1, 2, . . ., 7) quantify the fraction of C left in its own pool after each time step. The off-diagonal, non-zero elements quantify C transfer from one pool to another, varying with lignin and nitrogen (N) content [*Parton et al.*, 1987]. Since lignin and N content in litter were not affected by elevated CO_2 in the Duke Forest [*Finzi et al.*, 2001], those elements were assumed to be the same between the two CO_2 treatments. Their values were estimated according to lignin and N content [*Luo and Reynolds*, 1999; *Luo et al.*, 2001b].

[20] Variable u in equation (1) is the canopy photosynthetic rate. The annual photosynthetic C influx into the ecosystem was estimated by a mechanistic canopy model MAESTRA as described by *Luo et al.* [2001a]. Vector B determines C partitioning between nonwoody and woody tissues according to a N-production relationship [*Luo and Reynolds*, 1999]. Since the N content in leaves, fine roots, and wood was hardly affected by elevated CO_2 in the Duke Forest [*Ellsworth*, 2000; *Matamala and Schlesinger*, 2000] and had little seasonal variation [*Myers et al.*, 1999], the C partitioning was assumed to be identical between the two CO_2 treatments. The vector B was

$$B = (0.25 \quad 0.30 \quad 0 \quad 0 \quad 0 \quad 0 \quad 0)'.$$

The partitioning vector indicates that 25% of canopy photosynthate (i.e., u) was allocated for nonwoody tissue growth and 30% for woody tissue growth. The remaining 45% of u was not incorporated into plant and soil C pools, but rather consumed by plant respiration. The portion for plant respiration was chosen according to the estimates for the study site [*DeLucia et al.*, 1999; *Lai et al.*, 2002; *Luo et al.*, 2001a]. Overall, available data from the Duke FACE experiment helped constrain the inverse problem of equation (1) into a search for only seven diagonal elements in the matrix A.

3.4. Observation Operator and Optimization Procedure

[21] This study used six data sets to search for A. The six data sets are measured woody biomass, C content in the forest floor, C content in mineral soil, foliage biomass, litterfall, and soil respiration at ambient and elevated CO_2, respectively. Each of the data sets was denoted by Q_o^j, where j = 1, 2,., 6 and t indicates time dependence. For each $Q_o^j(t)$, we defined an observation operator $Q^j(A)$ as

Woody biomass	(0	1	0	0	0	0	0)
C in forest floor	(0	0	0.75	0.75	0	0	0)
C in mineral soil	(0	0	0	0	1	1	1)
Foliage biomass	(0.75	0	0	0	0	0	0)
Litterfall	$(0.75a_{1,1}$	$0.75a_{2,2}$	0	0	0	0	0)
Soil respiration	$(0.25a_{1,1}$	$0.25a_{2,2}$	$0.55a_{3,3}$	$0.45a_{4,4}$	$0.7a_{5,5}$	$0.55a_{6,6}$	$0.55a_{7,7})$.

The observation operator maps modeled pool size $X(A)(t)$ to compare with data set $Q_o^j(t)$ as expressed in a cost function $J(A)$,

$$J(A) = \sum_{j=1}^{m} \nu_j \left[\sum_{i=1}^{n_j} \left(Q^j(A)X(A)(t_{i,j}) - Q_0^j(t_{i,j}) \right)^2 \right] \quad (2)$$

where $t_{i,j}$, for $i = 1, 2, \ldots, n_j$, represent observation times for the jth data set; n_j is the number of data points, equal to 58, 2, 2, 58, 5, and 56 for woody biomass, C content in the forest floor and mineral soil, foliage biomass, litterfall, and soil respiration, respectively; m is the number of data sets, equaling 6; ν_j is a weighing factor for data set j toward the evaluation criteria,

$$\nu_j = \frac{p_j}{m} \frac{1}{V(Q_0^j)} \quad (3)$$

where p_j is a proportional value of data set j contributing to the overall evaluation, $V(Q_o^j)$ is the variance of the observation data set Q_o^j. In this study, we assumed $p_j = 1$ for all six data sets.

[22] We used the Levenburg-Marquardt minimization method in combination with a quasi-Monte Carlo algorithm to search for the diagonal elements of the matrix A [*Dennis and Schnabel*, 1983; *White and Luo*, 2002]. The Levenburg-Marquardt minimization method was used for the fundamental decent step. However, because of the apparent shape of the function, we couple this method with a quasi-Monte Carlo search. The algorithm proceeded by using the Levenburg-Marqurdt method to reduce the cost function until the reduction was smaller than a prescribed tolerance. A quasi-Monte Carlo method was then used to generate points within the neighborhood of the current point. If the function was sufficiently reduced by a generated point, it was taken to the new point. The algorithm then repeated. If, after a prescribed number of generated points, the function was not reduced, then the algorithm terminated.

3.5. Photosynthetic Carbon Influx in the Forward Model Simulations

[23] To simulate the long-term terrestrial C sequestration in response to a gradual increase in C_a, we quantified photosynthetic sensitivity (ℓ) to rising C_a as

$$\ell = \frac{1}{k_1} \frac{0.7C_a - 35.7}{0.7C_a + k_2} \quad (4)$$

where k_1 and k_2 are coefficients that were chosen to be 0.2176 and 540.34 so that $\ell = 1$ when C_a = 280 ppm and $(\ell_{560} - \ell_{360})/\ell_{360} \times 100 = 40$, where ℓ_{360} and ℓ_{560} are the relative photosynthetic sensitivity at 360 and 560 ppm of C_a. The modeled 40% increase in photosynthesis at elevated CO_2 in comparison with that at ambient CO_2 was a match with the observations [*Ellsworth*, 2000]. The equation is a modified form of the Farquhar photosynthesis model [*Farquhar et al.*, 1980] and quantifies the sensitivity component of photosynthetic responses to rising C_a [see *Luo et al.*, 1996]. The sensitivity ℓ was multiplied by 1436 g C m^{-2} yr^{-1} to compute annual gross primary productivity, which was used as input for the forward model simulation of ecosystem C sequestration.

4. Results and Discussion

4.1. Gross Primary Productivity and Model Inputs

[24] Ecosystem C processes in the model were driven by canopy C influx. We used the mechanistic model MAESTRA [*Luo et al.*, 2001a] to estimate canopy photosynthesis.

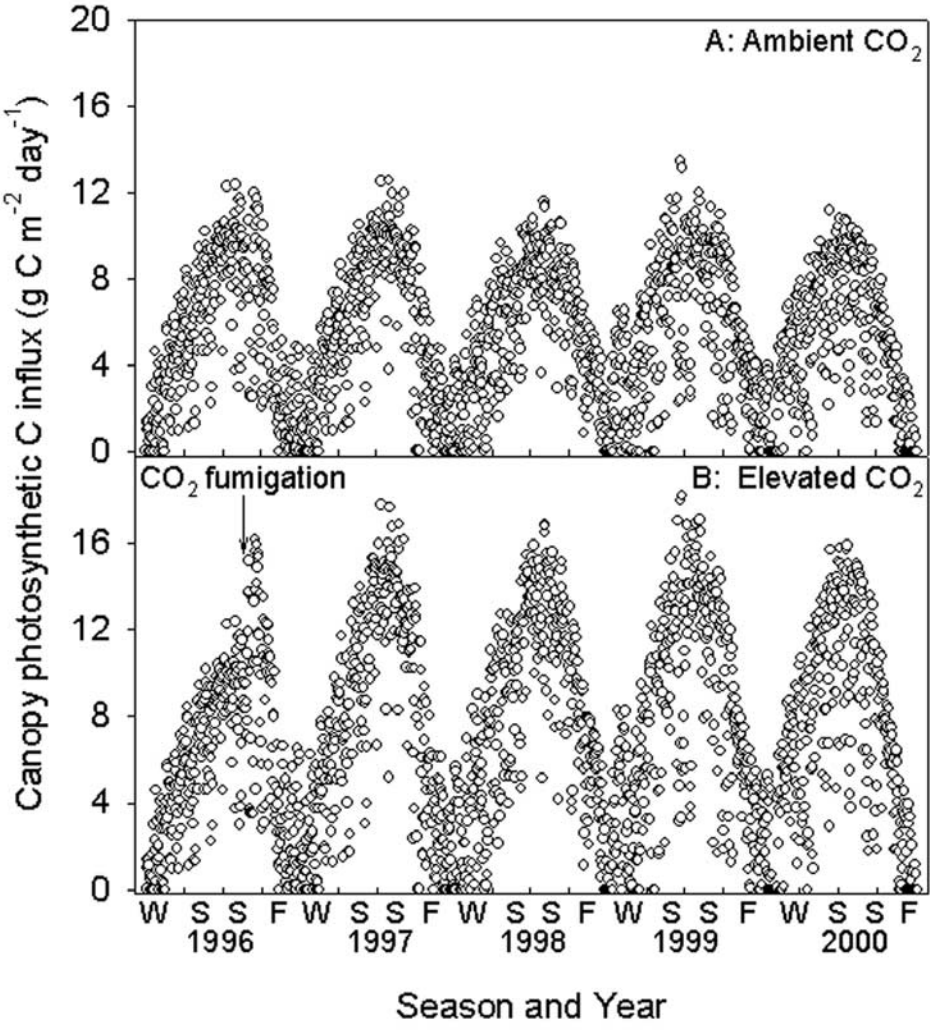

Figure 2. Canopy photosynthetic carbon influx at ambient and elevated CO_2 from 1996 to 2000. The carbon influx was estimated with a mechanistic model MEASTRA and amounted to around 1800 g C m^{-2} yr^{-1} at ambient CO_2 and 2500 g C m^{-2} yr^{-1} at elevated CO_2. The estimated C influx was used as input into the model for the inverse analysis. Letters W, S, S, and F on *X* axis stand for winter, spring, summer, and fall, respectively.

The latter varied from 0 g C m^{-2} d^{-1} in the winter when the temperature was normally below 5°C to 12 g C m^{-2} d^{-1} in the summer at ambient CO_2 and 18 g C m^{-2} d^{-1} at elevated CO_2. (Figure 2). The annual gross primary productivity (GPP), which is the sum of daily canopy photosynthesis, was approximately 1800 g C m^{-2} yr^{-1} at ambient CO_2 and 2500 g C m^{-2} yr^{-1} at elevated CO_2. The modeled GPP was similar to that estimated by *Lai et al.* [2002] at ambient CO_2, lower than the estimate of *Hamilton et al.* [2002], and higher than that estimated by *Luo et al.* [2001a]. The estimated GPP was used as model inputs for the inverse estimation of residence times.

4.2. Data-Model Comparisons

[25] Data-model comparisons help illustrate how well the model represents ecosystem C processes and therefore how effectively the existing data constrain the parameter estimation. Results in Figure 3 indicate that our matrix model adequately simulated C fluxes in the forest ecosystem. Modeled woody biomass and soil C were highly correlated with observations at both ambient and elevated CO_2, with determinant coefficients R^2 being more than 0.99 for both data sets (Figures 3a and 3b). In both the cases, the modeled and observed data were distributed tightly to their 1:1 lines, indicating that our model accurately reproduced observed biomass growth and soil C accumulation. The high precision of the model's reproduction of the observed biomass was largely due to an extremely low variation in biomass estimates using the allometric relationship [*DeLucia et al.*, 1999; *Hamilton et al.*, 2002; *Naidu et al.*, 1998]. The precise reproduction of observed soil C by the model was partly because we had data of only two points in time (one before the CO_2 fumigation and the other at 3 years after the fumigation)

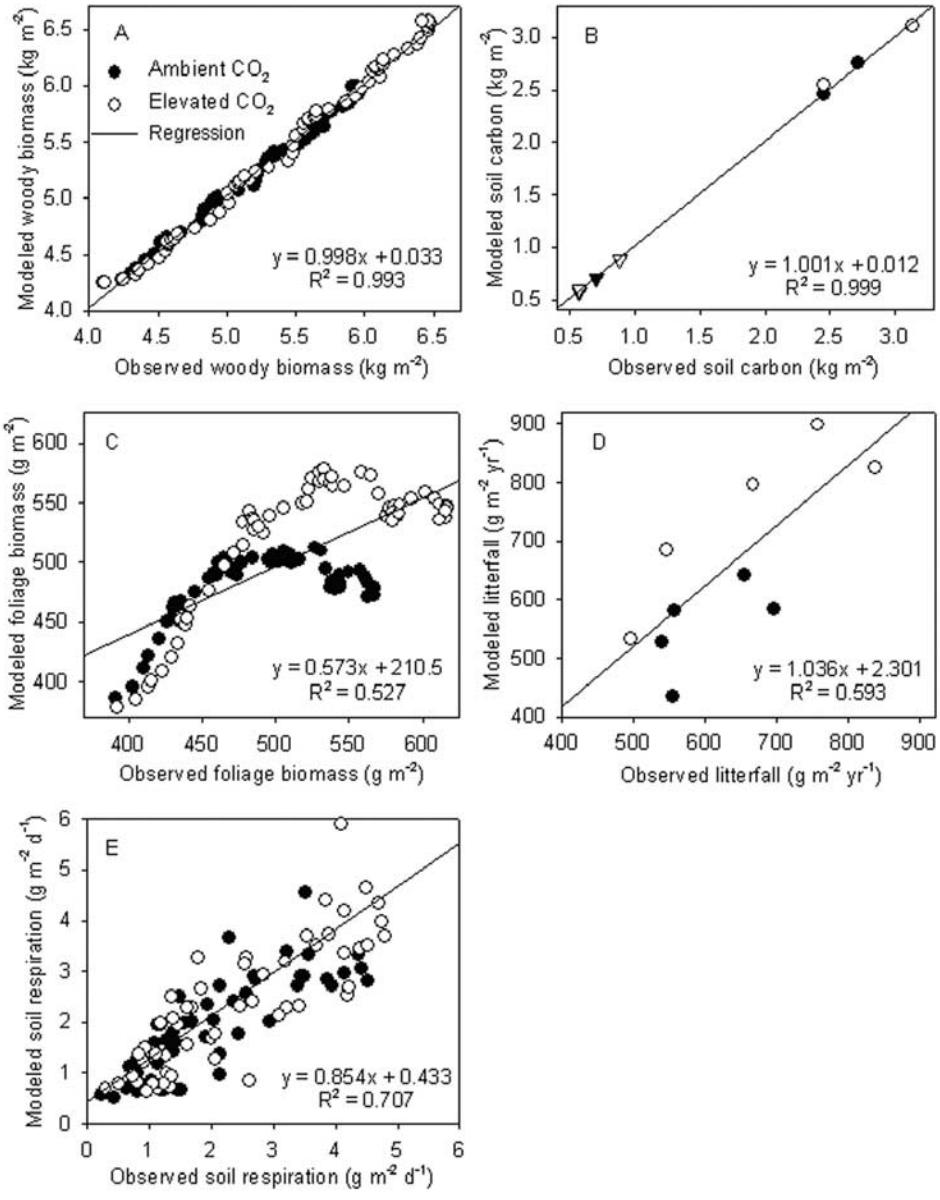

Figure 3. Comparison of measured and modeled (a) woody biomass, (b) C in the forest floor and in mineral soil, (c) foliage biomass, (d) litterfall, and (e) soil respiration at ambient and elevated CO_2 at the Duke FACE site. The solid circles represent data at ambient CO_2 and the open circles represent data at elevated CO_2. In Figure 3b, circles represent C in mineral soil and triangles represent C in the forest floor. Data points in each panel equal numbers of observations at ambient plus those at elevated CO_2. Litterfall was observed approximately at a monthly interval but is represented in Figure 3d by yearly values from 1996 to 2000 to avoid extreme data points due to episodic events (e.g., windy weather). We used mean values, for all the six data sets, averaged from the three control rings for ambient CO_2 and the three fumigated rings for elevated CO_2.

for the C content in the forest floor and in the mineral soil [*Schlesinger and Lichter*, 2001].

[26] Both observed and modeled woody biomass increased from approximately 4400 g C m^{-2} before the CO_2 treatment in August 1996 to nearly 6000 g C m^{-2} at ambient CO_2 and to ~6500 g C m^{-2} at elevated CO_2 by the end of 2000 (Figure 3a). Elevated CO_2 resulted in 20–25% increases in biomass growth rates from 1997 to 2000 [*DeLucia et al.*, 1999; *Hamilton et al.*, 2002]. Observed C content in the forest floor litter layers was 183 g C m^{-2} higher at elevated CO_2 than that at ambient CO_2 after 3 years of CO_2 fumigation from 1996 to 1999 [*Schlesinger and Lichter*, 2001]. During the same period, the forest floor in the ambient CO_2 plots likely accumulated about 44 g C m^{-2}

Table 1. Estimated Exit Rates of Carbon From and Residence Times in Seven Pools at Ambient and Elevated CO_2 at Duke Forest[a]

	Exit Rate, g kg^{-1} d^{-1}		Residence Time, Years	
Pool	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2
Nonwoody biomass	1.7600	2.1700	1.557	1.263
Woody biomass	0.1001	0.1410	27.369	19.429
Metabolic litter	21.4680	22.6800	0.128	0.121
Structural litter	0.8450	0.9650	3.242	2.839
Microbial biomass	8.5340	2.5340	0.321	1.081
Slow soil organic matter	0.0898	0.0558	30.523	49.134
Passive soil organic matter	0.0031	0.0027	885.027	1031.368

[a]The seven pools are defined in Figure 1.

yr^{-1}, leading to the total C accumulation of 132 g C m^{-2} over 3 years. Thus, the C accumulation in the forest floor was nearly 140% higher at elevated than at ambient CO_2 (Figure 3b). The observed C content in the mineral soil was 397 g C m^{-2} higher at elevated than ambient CO_2 over 3 years. However, this difference was not statistically significant due to high variability [*Schlesinger and Lichter*, 2001].

[27] The modeled foliage biomass appeared to deviate systematically from the observed values largely due to the discrepancy between the model assumption of a faster turnover of leaves than wood and the indirect estimation of foliage biomass from DBH. Based on prior knowledge, the model assumed that the longevity of leaves (together with fine roots) was on a scale of years. Consequently, we only allowed the model to search for a C transfer coefficient within a range from 0.00137 to 0.0137 g g^{-1} d^{-1} (i.e., 0.5 to 5.0 years of residence time) for the nonwoody tissue pool. The estimated transfer coefficient stabilized the modeled foliage biomass at 480–500 g C m^{-2} at ambient CO_2 and 540–570 g C m^{-2} at elevated CO_2, after an initial biomass increase in 1996 and 1997. On the other hand, the observed foliage biomass that was estimated indirectly from DBH showed a steady increase in tree biomass, an expected increase because the trees in the Duke Forest were growing. Accordingly, the foliage biomass indirectly derived from the DBH data showed continuous increases from 390 g C m^{-2} in July 1996 to 570 g C m^{-2} at ambient CO_2 and to ~610 g C m^{-2} at elevated CO_2 by the end of 2000 [*Hamilton et al.*, 2002]. Thus, the modeled transient increases followed by stabilized foliage biomass resulted in a systematic deviation from the observed continuous biomass increases (Figure 3c). In addition to the indirect method of estimating foliage biomass from DBH, we also estimated it from canopy light interception (D. Ellsworth, unpublished data, 2001) and litter fall [*Finzi et al.*, 2001]. The light interception method showed a year-to-year change in foliage biomass that was similar to modeling results. The seasonal variability in estimated foliage biomass from canopy light interception was extremely high so that it could not be accurately represented by the present model. Incorporation of foliage phenology into the model may help reproduce the seasonal variability but complicates the inverse analysis. The litter fall method estimated a much higher foliage biomass than either the DBH or light interception method. To improve the fit between the modeled and observed foliage biomass, it is essential not only to modify the model, but also to develop better methods for measuring foliage biomass.

[28] Observed litterfall ranged from 540 to 600 g C m^{-2} yr^{-1} at ambient CO_2 and from 500 to 840 g C m^{-2} yr^{-1} at elevated CO_2 (Figure 3d) [*Finzi et al.*, 2001]. Observed soil respiration varied from 0.23 to 4.5 g C m^{-2} d^{-1} at ambient CO_2 and from 0.29 to 4.79 g C m^{-2} d^{-1} at elevated CO_2 (Figure 3e) [*Andrews and Schlesinger*, 2001]. Modeled soil respiration and litterfall were less well correlated with observed data than woody biomass and soil carbon, largely because of high variability in the measurements. This variability resulted from scattered points in the original data.

4.3. Estimation of Carbon Residence Times as Affected by Elevated CO_2

[29] The six data sets in Figure 3 were used to estimate one set of the seven diagonal elements of matrix A, each at ambient and elevated CO_2. The diagonal elements ($a_{k,k}$, $k = 1, 2, \ldots 7$) are related to exit rates of C from individual pools as $1 - a_{k,k}$, which in turn are inversely proportional to C residence times in individual pools [i.e., $\tau_k = 1/(1 - a_{k,k})$]. The ensemble of (hereinafter denoted by τ for simplicity) for all the C pools represents the capacity of an ecosystem to retain C in plant and soil pools. A comparison of τ_E at elevated CO_2 with τ_A at ambient CO_2 enabled us to assess how the C-storage capacity in the ecosystem was affected by elevated CO_2.

[30] The estimated C exit rates were the highest from metabolic litter pools at both ambient and elevated CO_2 (Table 1), being 21.5 and 22.7 g kg^{-1} d^{-1}, respectively. They were the lowest from passive soil organic matter (SOM) pools, being 0.0031 and 0.0027 g kg^{-1} d^{-1}, respectively, at ambient and elevated CO_2. The estimated τ_A ranges from 0.13 years for the metabolic litter pool to 885 years for the passive SOM pool at ambient CO_2 (Table 1). It ranges from 0.12 years for the metabolic litter pools to 1031 years for the passive SOM pool at elevated CO_2. The estimated τ_E was longer than τ_A for soil C pools, largely due to soil C accumulation at elevated CO_2 that was proportionally larger than that at ambient CO_2 over the first 3 years of the CO_2 experiment (Figure 3b) [*Schlesinger and Lichter*, 2001]. The time course of soil respiration was also suggestive of a higher C accumulation in soil pools at elevated than ambient CO_2 [*Luo et al.*, 2001b]. In contrast, the estimated τ_E for the foliage biomass pool was 1.26 years, nearly 0.3 years shorter than τ_A. This result was supported by the observation that elevated CO_2 had little effect on standing leaf biomass (1.1% in 1998) [*Hamilton et al.*, 2002], but increased litterfall by 25% [*Finzi et al.*, 2001],

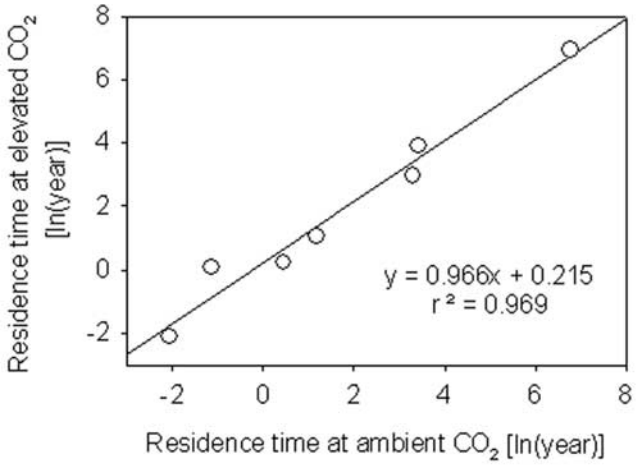

Figure 4. Comparison of the estimated residence times at elevated CO_2 (τ_E) with those at ambient CO_2 (τ_A). The seven data points represent residence times for each of the seven C pools as defined in Figure 1. The estimated residence times were well correlated between the two CO_2 treatments with a regression line $\ln(\tau_E) = 0.966 \ln(\tau_A) + 0.215$ and a determinant coefficient $R^2 = 0.969$. This result indicated that elevated CO_2 scarcely induced adjustments in residence times, suggesting a sustainable capacity of the ecosystem to store additional C.

leading to an increased leaf turnover rate. τ_E for the woody biomass pool was 19.4 years, 7.7 years shorter than τ_A, attributable to proportionally less stimulation in biomass growth than in C fluxes at elevated CO_2. Plotting estimated τ_E from the seven plant and soil C pools against τ_A in a natural logarithmic scale yielded a close relationship with $\ln(\tau_E) = 0.966 \ln(\tau_A) + 0.215$ with $R^2 = 0.969$ (Figure 4). It suggests that the C-transit time (i.e., overall C-storage capacity) in the Duke Forest ecosystem was similar between ambient and elevated CO_2. More C flowing into the forest at elevated CO_2 resulted in more C respired and more C stored in plant and soil pools, proportionally.

[31] Overall, we observed sustained photosynthetic stimulation at leaf and canopy levels [*Ellsworth*, 2000; *Lai et al.*, 2002; *Luo et al.*, 2001a; *Myers et al.*, 1999], which resulted in sustained stimulation of wood biomass increment [*Hamilton et al.*, 2002] and a larger C accumulation in the forest floor at elevated CO_2 than at ambient CO_2 [*Schlesinger and Lichter*, 2001]. Greater C influx in the elevated CO_2 plots, with little change in τ, resulted in an approximately proportional distribution of additional C among the plant and soil pools in the Duke Forest.

[32] The inversion method focused on the time courses of the six observed variables, whereas the study by *Schlesinger and Lichter* [2001] emphasized whether measured C contents in the forest floor and mineral soil were statistically significant. Due to high variation in soil C data, the measured C content in the mineral soil was not statistically different between ambient and elevated CO_2 after 3 years of treatments. However, the large increments in C contents in litter layers and mineral soil at elevated CO_2 became signals that were picked up by the inverse analysis, leading to the inference that elevated CO_2 slightly increased τ in soil pools. In a future study, we may employ the Bayesian approach to incorporate statistical variability in measured soil C into the inverse analysis for assessment of variation in estimated τ values.

[33] Inverse analysis provides an effective method to evaluate CO_2-induced adjustments in τ (i.e., the C-storage capacity) in plant and soil pools. Plant physiological ecologists have long developed a method for evaluating photosynthetic adjustment (i.e., acclimation) to elevated CO_2. In response to rising C_a, instantaneous photosynthetic rate usually increases. But long-term growth under elevated CO_2 may lead to acclimation of photosynthetic capacity upward or downward (i.e., up- or down-regulation). The down-regulation of the photosynthetic capacity is usually associated with limitation by N or other resources, whereas the up-regulation generally results from enhanced leaf morphological growth [*Luo et al.*, 1994]. In contrast, soil scientists did not have any measures to quantify adjustments in the C-storage capacity in response to elevated CO_2. Estimation of τ at ambient and elevated CO_2, using the inversion approaches, offers a way to do so. In this study, for example, we found that the C-storage capacity at elevated CO_2 decreased in plant pools but increased in litter and soil pools in comparison to that at ambient CO_2. The overall C-storage capacity in the whole ecosystem was scarcely altered at elevated CO_2.

[34] By combining the estimated τ in various pools with estimates of photosynthetic acclimation, we were able to examine adjustments of the full ecosystem C cycle in response to elevated CO_2. At the Duke Forest FACE site, experimental data suggested little photosynthetic acclimation at elevated CO_2 [*Myers et al.*, 1999; *Ellsworth*, 2000]. This study suggested that the ensemble of τ from all the plant and soil pool at elevated CO_2 was similar to that at ambient CO_2. Thus, the C-sequestration capacity through the entire C cycle at the Duke Forest FACE site was scarcely adjusted to elevated CO_2. The change in environmental forcing via rising C_a led to increased photosynthetic C influx into the ecosystem. A small portion of the increased C influx at elevated CO_2 was proportionally stored in various plant and soil pools.

4.4. Carbon Sequestration in Response to Rising Atmospheric CO_2 Concentration

[35] One of the primary goals of the FACE study is to extrapolate results from a step CO_2 increase experiment to predict C sequestration in the real world where C_a is gradually increasing. The FACE experiment in the Duke Forest imposed a step increase in CO_2 concentration, leading to a step increase in ecosystem C influx [*Luo*, 2001]. Photosynthetically fixed C passes through the processes of plant respiration, biomass growth, litter fall and decomposition before being released back to the atmosphere. Thus, respiratory C release is gradually increasing in response to the step increase in CO_2 concentration. The contrasting pattern between the step increase in C influx and the gradual increase in C release [*Luo*, 2001] results in a spike of C sequestration immediately after the initiation of a FACE experiment followed by a gradual decline. Such a time course of C sequestration under FACE is different from that

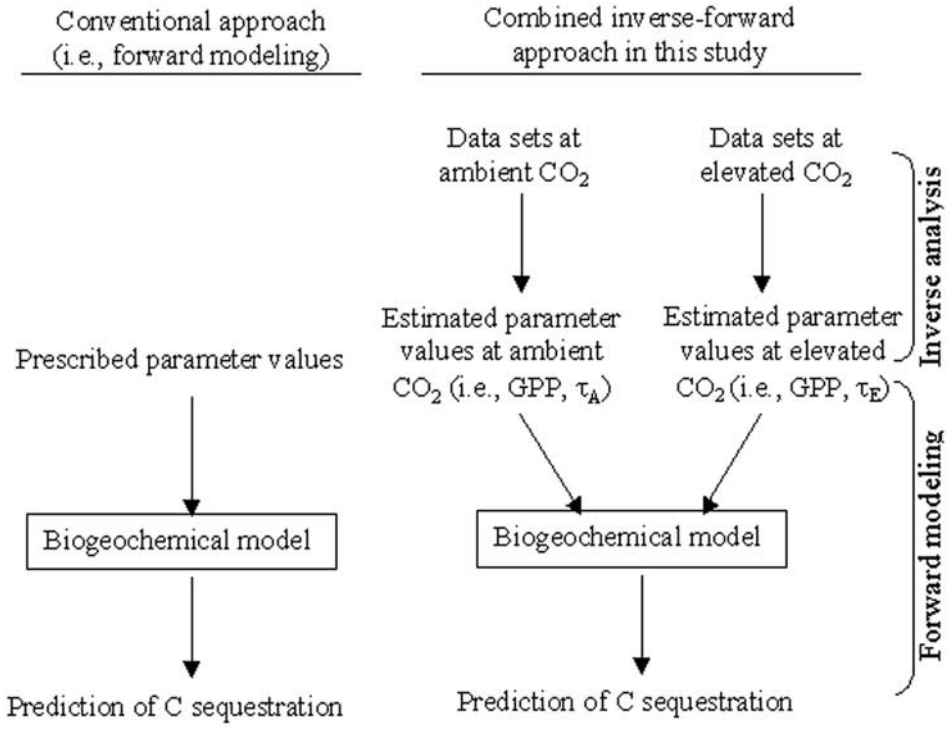

Figure 5. Illustration of the inverse-forward modeling approach used in this study in comparison with the conventional approach of forward modeling. The conventional approach to prediction of C sequestration is usually based on prescribed parameter values whereas the inverse-forward approach first estimates parameter values of gross primary productivity (GPP) and residence times from experimental results and then assesses effects of elevated CO_2 on the C-storage capacity before simulates C sequestration in the forest ecosystem.

in the real world, where atmospheric CO_2 concentration is gradually increasing [*Luo and Reynolds*, 1999]. As a consequence, measured C pool changes at elevated CO_2 cannot be directly extrapolated to predict C sequestration rates in the real world.

[36] However, various data sets from FACE experiments can be used to derive parameter values that are then incorporated into models to simulate future C sequestration rates in terrestrial ecosystems (Figure 5). Specifically, the simulation of C sequestration requires two sets of parameters: C influx and residence times. The short-term, step CO_2 increase in FACE experiments can exert an effect on either C influx or residence times that is different from the long-term, gradual CO_2 increase in the real world. The way in which the effect of the step CO_2 increase on C influx differs from that of the gradual CO_2 increase is on the acclimation component of the photosynthetic processes, whereas the sensitivity component of the photosynthesis is independent of CO_2 growth environments [*Luo et al.*, 1996]. Since photosynthetic acclimation in the Duke FACE experiment was not observed so far, we can extrapolate the observed photosynthetic sensitivity directly from the FACE experiment to simulate C influx in response to a gradual CO_2 increase using equation (4). The difference in the effect of the step CO_2 increase on residence times versus that of the gradual CO_2 increase is through changes in C allocation to different pools and/or changes in C exit rates from individual pools. Analysis in this study indicated that neither C allocation nor exit rates were altered much in the Duke FACE experiment (Table 1 and Figure 4). Thus, the estimated residence times can be directly used to simulate forest C sequestration in response to a gradual CO_2 increase.

[37] To illustrate the general nature of C dynamics in response to a gradual C_a increase, we simplified our matrix model (equation (1)) by using a time step of 1 year without considering temperature and moisture effects on C processes. The sole driving variable in the model was C_a that was based on the IS92a scenario from 2000 to 2100 [*Houghton et al.*, 1992] (Figure 6a). We chose parameter values in equation (4) so as to increase photosynthetic C influx by 40% at 560 ppm CO_2 relative to that at 360 ppm as observed in the FACE experiment (Figure 6b). Using estimated τ, we calculated the steady state pool sizes in the 7 compartments for simulating the rate of C sequestration in response to a gradual C_a increase [*Luo et al.*, 2001b].

[38] The time courses in Figure 6c show C sequestration rates that were purely caused by rising C_a. A comparison between the two lines indicates the effect of residence times (between τ_A and τ_E). Using τ_A, the C sequestration rate increased from 69 g m^{-2} yr^{-1} in 2000 when C_a was 378 ppm to 201 g m^{-2} yr^{-1} in 2100 when C_a was at

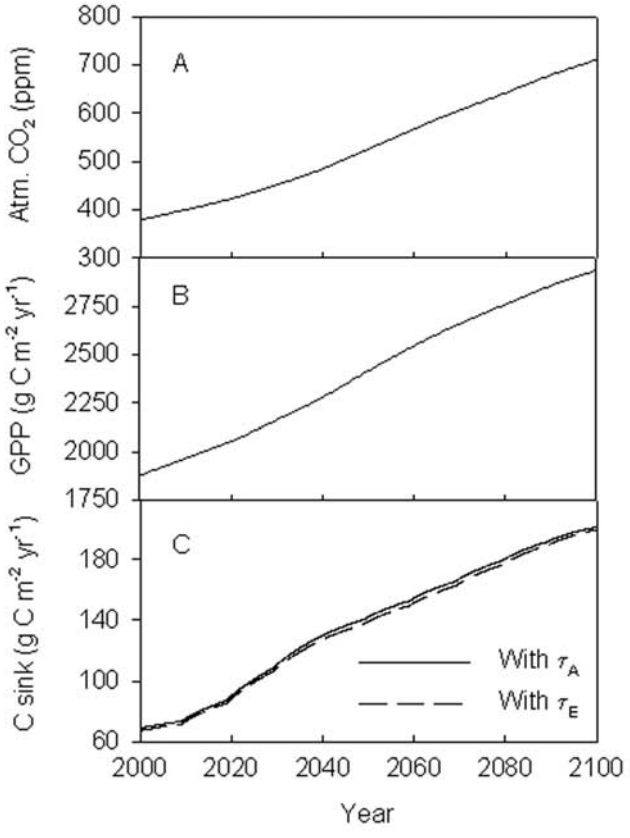

Figure 6. Time courses of (a) atmospheric CO_2 concentration, (b) projected canopy photosynthesis, and (c) C sequestration rates in the Duke Forest using estimated residence times at ambient (τ_A, solid line) and elevated CO_2 (τ_E, dashed line) from 2000 to 2100. The minor decrease in the estimated τ_E at elevated CO_2, particularly in the plant C pools, resulted in a slightly lower C sequestration rate than that at ambient CO_2. The projected C sequestration resulted only from rising C_a while observed C sequestration in the Duke Forest may be caused by multiple factors, including rising C_a, forest regrowth, and nitrogen deposition. Although this analysis simulated C sequestration for 100 years, the model assumes the tree longevity (i.e., residence time for the woody tissue) averages 20–30 years.

710 ppm. Since the ensemble of τ_E at elevated CO_2 was slightly lower than that at ambient CO_2, the C sequestration rate in response to the gradual increase in C_a by using τ_E was also slightly lower than that by using τ_A.

[39] The trend of C sequestration in this study was similar to that projected by six dynamic global vegetation models from 2000 to 2100 [*Cramer et al.*, 2001]. However, the traditional ecosystem models usually use prescribed parameter values (Figure 5). This study derived parameter values from a multiple data set at the specific forest site, which were then used to simulate C sequestration in response to rising C_a. If we can derive parameter values for τ and C influxes at a variety of sites in different vegetation and soil types, we may have the potential to improve predictions of regional and global C sinks [*Barrett*, 2003].

[40] It is noteworthy that the modeled C sequestration rates in Figure 6c are subject to uncertainties from a few sources. First, we used five years of data for estimation of τ that varies from a few months to hundreds of years. In general, the accuracy of estimated parameters values is high for those fast turnover pools but relatively low for the slow turnover pools. As more data become available, the uncertainty in the estimated τ for the long-term pools may decrease. Second, the simulated trend of C sequestration rates was based on C emission scenario IS92a. The third IPCC report presents seven emission scenarios. In the emission scenarios under which C_a growth decelerates in the future, C sequestration rates are expected to be lower. Third, this modeling analysis assumed that stimulation of photosynthetic C influx by elevated CO_2 was maintained at a level of 40%, according to recent experimental observations [*Ellsworth*, 2000]. If N limitation as observed in the prototype ring in the Duke Forest [*Oren et al.*, 2001] results in photosynthetic down-regulation, the predicted C sequestration would decrease. Nonetheless, the current trajectory in the Duke FACE experiment showed little sign of photosynthetic down-regulation.

5. Summary

[41] To assess the sustainability of terrestrial C sink, we need to quantify three capacities and their adjustments to environmental forcing. Those capacities are canopy photosynthetic capacity, C-storage capacity, and C-sequestration capacity. The canopy photosynthetic capacity is determined by leaf photosynthetic capacity and leaf area index. The C-storage capacity can be quantified by ecosystem residence times (τ). The C-sequestration capacity in an ecosystem is jointly determined by the canopy photosynthetic capacity and the C-storage capacity. The C-sequestration capacity is maintained in a future global change scenario only if neither the canopy photosynthetic capacity nor the C-storage capacity is up-or down-regulated. In that case, the future rate of terrestrial C sequestration is primarily determined by environmental forcing functions. Possible forcing functions are the rising of atmospheric CO_2 concentration, forest regrowth, woody plant encroachment, and nitrogen deposition.

[42] While plant physiological ecologists have examined the canopy photosynthetic capacity under various global change scenarios, this study focused on quantification of τ and its adjustment to elevated CO_2 in Duke Forest using an inversion approach. Our analysis of multiple data sets from the FACE experiment suggested that C sequestration in the Duke Forest would continue to increase as C_a gradually increases. That continuous increase in C sequestration resulted partly from sustained canopy photosynthetic capacity and a steady growth of C_a as predicted in emission scenario IS92a. The steady C_a growth overcompensated for a C_a-induced decrease in photosynthetic sensitivity, so that stimulated C influx into the ecosystem led to increased C sequestration. In addition, the predicted increase in C sequestration in the Duke Forest was associated with little changes in τ. The latter conclusion was consistent with our observations that biomass growth and soil C accumulation

steadily increased at elevated CO_2 compared to that at ambient CO_2 from 1996 to 2000.

[43] While the estimated parameter values of τ were relatively well constrained by comprehensive data sets for most of the ecosystem C processes in the Duke Forest, our projection of the future C-storage capacity improves as more data on long-term processes, particularly SOM formation and decomposition, become available in coming years. If elevated CO_2 induces reduction in τ in long-term C pools, the C-storage capacity would be down-regulated. Nonetheless, current evidence suggests that the forest ecosystem would continue to sequester C from the atmosphere, as C_a is gradually increasing.

[44] By addressing the sustainability issue, we also illustrated that inverse analysis of multiple data sets from FACE experiments could facilitate extrapolation of results from a step CO_2 experiment to predict ecosystem responses to a gradual CO_2 increase in the real world and assist evaluation of CO_2-induced adjustments in C transfers among plant and soil pools.

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