VALIDITY OF EXTRAPOLATING FIELD CO_2 EXPERIMENTS TO PREDICT CARBON SEQUESTRATION IN NATURAL ECOSYSTEMS

Yiqi Luo[1,3] and James F. Reynolds[2]

[1]*Biological Sciences Center, Desert Research Institute, Reno, Nevada 89512 USA*
[2]*Department of Botany, Duke University, Durham, North Carolina 27708 USA*

Abstract. One of the ultimate goals of ecosystem carbon dioxide (CO_2) experiments is to infer the capacity of terrestrial ecosystems to sequester carbon (C) in a CO_2-enriched world. This modeling study examines C sequestration (C_{seq}) in natural ecosystems based on CO_2 experiments. Most experiments are conducted by a step increase in CO_2 concentration, whereas natural ecosystems are experiencing a gradual increase in atmospheric CO_2 (C_a). To examine the effects of a step vs. gradual CO_2 increase on ecosystem responses, we have developed a terrestrial C sequestration (TCS) model that focuses on C and nitrogen (N) interactions in regulating C_{seq}. We used the model to: (1) compare C_{seq} and N demand in response to the step vs. gradual increase in CO_2; (2) identify mechanisms underlying different ecosystem responses to the step vs. gradual CO_2 forcing; (3) examine key parameters in controlling C_{seq}; and (4) explore three hypothesized N supply mechanisms in regulating photosynthetic acclimation and C_{seq}.

Application of this model to simulate responses of a forest ecosystem with gross primary productivity of 1200 g $C \cdot m^{-2} \cdot yr^{-1}$ suggested that a step increase in CO_2 from 350 to 700 ppm resulted in C_{seq} of 263 g $C \cdot m^{-2} \cdot yr^{-1}$ in the first year. A gradual C_a increase led to the C_{seq} rates of 27 and 58 g $C \cdot m^{-2} \cdot yr^{-1}$ in 1987 and 2085 when CO_2 reached 350 and 700 ppm, respectively. The model predicted that N demand required to balance the additional C influx was 4.1 g $N \cdot m^{-2} \cdot yr^{-1}$ in the step CO_2 increase and only 0.6 and 1.7 g $N \cdot m^{-2} \cdot yr^{-1}$ in 1987 and 2085, respectively, in the gradual C_a increase. The contrasting differences in C_{seq} and N demand between the two increase scenarios reflected the nature of C fluxes that were controlled by the sizes of donor pools (i.e., donor-controlled system). Our modeling analysis of four ecosystems (forest with high productivity [HP]; grassland with HP; forest with low productivity [LP]; and grassland with LP) indicated that additional C influx and C relaxation time are the key parameters in determining ecosystem C_{seq}. The additional C influx varied with ecosystem productivity and N regulation, while C relaxation time differed between the forests and grasslands due to woody tissues and litter in the forests. We conclude that in spite of the fact that the step experiment is one of the most effective approaches in ecosystem studies, its results cannot be directly extrapolated to predict terrestrial C_{seq} in natural ecosystems responding to a gradual C_a increase. In order to develop predictive understanding from the step experiments, we need not only to improve experimental design and measurement plans, but also to develop new approaches, such as deconvolution and inverse modeling, for data analysis and interpretation.

Key words: deconvolution; Duke Forest, North Carolina; extrapolation of experimental results; global change; inverse modeling; net ecosystem productivity; photosynthesis; plant and soil carbon; relaxation time; residence times.

INTRODUCTION

The increase in the global atmospheric concentration of carbon dioxide (CO_2; C_a) represents an imbalance among the carbon (C) sources and sinks in the biogeosphere. Assessing the potential for terrestrial ecosystems to sequester C is a major challenge for earth system scientists. In an attempt to quantify the terrestrial C sink, ecosystem scientists use open-top chambers (OTC) and Free-Air CO_2 Enrichment (FACE) fa-

cilities to conduct experiments in intact ecosystems (see technology reviews in Mooney et al. 1991, Allen et al. 1992, Hendrey and Kimball 1994, Koch and Mooney 1996). In the past decade, OTCs have been successfully used in a variety of intact ecosystems, including a Chesapeake Bay salt marsh (Drake et al. 1996), tallgrass prairie in Kansas (Owensby et al. 1993), California annual grasslands (Field et al. 1996), and Tennessee deciduous forest (Norby et al. 1996). Field experiments using FACE technology have been conducted in an Arizona cotton field (Kimball et al. 1994), loblolly pine forest in North Carolina (Ellsworth et al. 1995), and pastureland in Switzerland (Jongen et al. 1995). FACE is currently being employed in nu-

merous other ecosystem types, e.g., the Nevada desert and Minnesota grassland.

The tremendous enthusiasm among ecologists for ecosystem CO$_2$ experiments, especially those using FACE technology, stems from the potential to understand changes in the function and structure of intact ecosystems in a CO$_2$-enriched world. When combined with other field experiments, these data will be invaluable for advancing our understanding of ecosystem responses to elevated CO$_2$. To date, ecosystem experiments have produced some intriguing results. For example, photosynthetic C fixation has been found to be sustainably stimulated in most ecosystems (Koch and Mooney 1996; Mooney et al. 1998), indicating that changes in various processes in natural ecosystems may supply adequate nutrients to balance the extra C input (Zak et al. 1993, McMurtrie and Comins 1996, Rastetter et al. 1997). Despite considerable changes in tissue chemistry of live biomass grown in elevated CO$_2$ (Luo et al. 1994), litter quantity has been found to exhibit little change (O'Neill and Norby 1996; but see Cotrufo and Ineson 1996). Results such as these are useful for regional and global modeling efforts (see VEMAP 1995, Sellers et al. 1997).

While manipulation of CO$_2$ concentration is an effective way to gain insights into ecosystem behavior, one fundamental question has yet to be carefully addressed about these experiments: Can the observed responses of ecosystems to a step increase in C$_a$ (the standard protocol in FACE and OTC experiments) be directly extrapolated to infer the response of an ecosystem to a gradual C$_a$ increase? Atmospheric CO$_2$ (measured volumetrically) has gradually increased from 280 ppm in the preindustrial time (Neftel et al. 1982, Friedli et al. 1986) to 350 ppm in 1987 (Keeling et al. 1995) and is expected to reach 700 ppm in 2085 (IPCC 1996). It is currently increasing at approximately 1.5 ppm/yr (Keeling et al. 1995). This increase is estimated to stimulate a 0.17–0.37% increase in ecosystem C influx (Luo and Mooney 1996), equivalent to an average of 3.3 g C·m^{-2}·yr^{-1} in a productive grassland or temperate forest ecosystem at a gross primary productivity (GPP) of 1200 g C·m^{-2}·yr^{-1}. With a step increase in CO$_2$ from 350 to 700 ppm, ecosystem C influx increases by 30–70%, equivalent to an average of 480 g C·m^{-2}·yr^{-1}, with GPP of 1200 g C·m^{-2}·yr^{-1} (Luo and Mooney 1996). In response to the large, abrupt increase in C influx in step experiments, ecosystem C and nitrogen (N) processes may experience changes that are different from those in response to small, gradual increases in C$_a$.

To explore the effect of a step vs. gradual increase in CO$_2$ concentration on ecosystem responses, we developed a terrestrial C sequestration (TCS) model. The TCS model combines the photosynthetic C influx model developed by Luo et al. (1994, 1996) with the soil C model used in CENTURY (Parton et al. 1987). The TCS model, which focuses on C and N interactions in

regulating ecosystem C$_{seq}$, is used here to: (1) compare C sequestration (C$_{seq}$) and N demand in response to a step vs. gradual increase in C$_a$; (2) identify key mechanisms and feedbacks that may be involved in mediating ecosystem response to step vs. gradual C$_a$ forcings; (3) elucidate important parameters that affect C$_{seq}$ by comparing four ecosystems differing in C influx and relaxation time (forests and grasslands with low or high productivity); and (4) examine three hypothesized mechanisms that potentially control N supply in response to additional C influx. We discuss the transient nature of ecosystem responses to a step C$_a$ increase, potentials and limitations of step experiments, and recommendations for result interpretation, experimental design, and measurements. This paper also calls for adoption and development of deconvolution analysis, a method widely used in other science disciplines for analyzing perturbation experiments.

MODEL DESCRIPTION

General structure

The terrestrial C sequestration (TCS) model consists of a C submodel and a N submodel, and is designed to emphasize interactions between C and N processes. The time step of TCS is 1 wk. The model was originally intended to simulate forest ecosystems, but was also modified, as described in the *Results* section, to simulate grasslands.

The C submodel simulates photosynthetic C fixation, C partitioning among 12 pools, and respiratory release from plants, detritus, and soil organic matter (SOM) (Fig. 1). Photosynthetic C fixation is determined by two components: sensitivity and acclimation (Luo et al. 1994, 1996). Sensitivity is due to the competition between carboxylation and oxygenation of ribulose bisphosphate (RuBP) catalyzed by Ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) as described by Farquhar et al. (1980). This assumes that photosynthesis is limited either by Rubisco (P_1) or by the light-driven regeneration of RuBP (P_2):

$$P_1 = V_{cmax}\frac{C_i - \Gamma}{C_i + k_c(1 + O/k_O)} - \rho \qquad (1)$$

$$P_2 = J\frac{C_i - \Gamma}{4.5C_i + 10.5\Gamma} - \rho \qquad (2)$$

where V_{cmax} is the maximum RuBP carboxylase activity, C_i is the intercellular CO$_2$ concentration, Γ is the CO$_2$ compensation point without dark respiration, k_c and k_O are the Michaelis-Menten constants for CO$_2$ and oxygen, O is the partial pressure of oxygen at the site of carboxylation, ρ is dark respiration, and J is the rate of electron transport, which varies with the maximum electron transport rate J_{max} and light availability. Units and values of these parameters are listed in Table 1.

Photosynthetic acclimation is strongly correlated with CO$_2$-induced changes in area-based leaf N con-
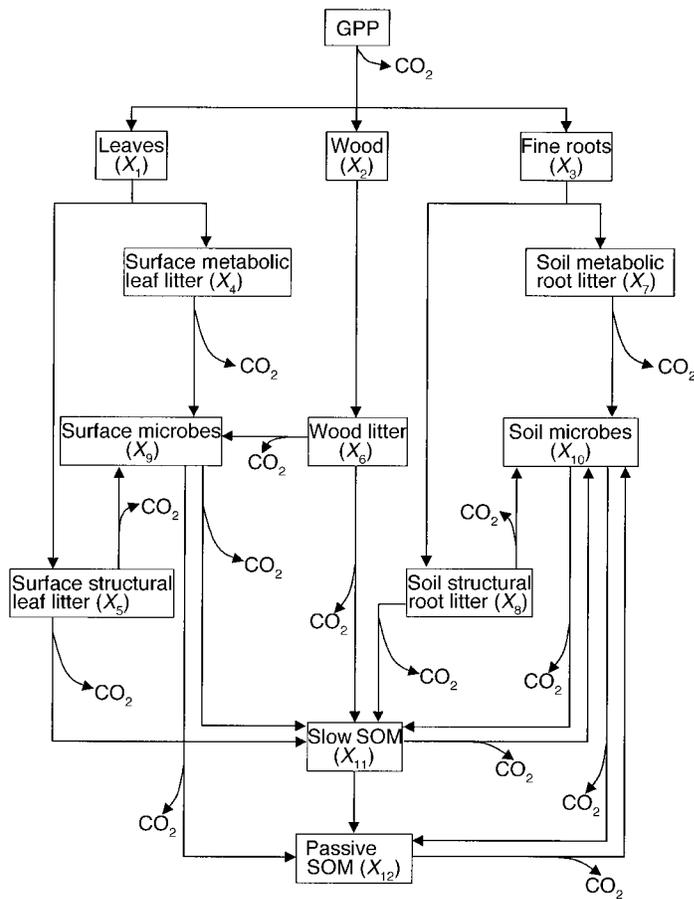
Fig. 1. Schematic representation of the Terrestrial Carbon Sequestration (TCS) model. X_1–X_{12} represent the amount of carbon in each pool.

centration (Luo et al. 1994, 1998) and the N-photosynthesis relationship is simulated according to Field (1983) and Harley et al. (1992) as:

$$V_{cmax} = k_1 n_a + k_2$$

$$J_{max} = k_3 n_a + k_4$$

$$\rho = k_5 n_a + k_6 \qquad (3)$$

where k_1 through k_6 are constants (Table 1). Eqs. 1–3 are used to calculate CO_2 stimulation of GPP as regulated by ecosystem N dynamics.

Photosynthetically fixed C is allocated to three pools: leaves, woody tissues, and fine roots. The allocation coefficients vary with N concentration in leaves and fine roots. The ratio of fine roots to leaves (R/L) is estimated from experimental measurements of ponderosa pine in response to three CO_2 and two N treatments (J. T. Ball, *personal communication*):

$$R/L = a_0 - a_1 n_{r+1} \qquad (4)$$

where a_0 and a_1 are constants (Table 1) and n_{r+1} is the averaged N concentration in fine roots and leaves. Eq. 4 accounts for an increase in the R/L ratio as root and leaf N concentration decreases.

Litter of leaves and fine roots are partitioned to metabolic and structural litter pools (Parton et al. 1987):

$$F_m = 0.85 - 0.016 \frac{L_s}{n} \qquad (5)$$

where F_m is the fraction of total leaf or root litter that goes to metabolic pools; L_s is lignin content (Table 1); and n is the N concentration of leaf or root litter. Dead wood flows to wood litter pool at the soil surface and litter C flows into microbial pools and then to slow and passive SOM pools (Fig. 1). As in CENTURY, the TCS model also has two microbial pools, one on the soil surface and the other in bulk soil.

Decomposition of litter and SOM is calculated as

$$\frac{dX_i}{dt} = K_i X_i \qquad (6)$$

where X_i is the amount of C in the ith pool, $i = 4, 5, \ldots, 12$; and K_i is the loss rate parameter for the ith state variable, which varies with temperature and moisture (Parton et al. 1987). The rate of decomposition of structural litter (K_5, K_6, and K_8) is a function of lignin content:

$$K_i^a = K_i e^{-3.0 L_s} \qquad (7)$$

TABLE 1. List of symbols, definitions, units, and values of variables used in the model.

Variable	Definition	Units	Values
a_0	Coefficient in Eq. 4		1.036
a_1	Coefficient in Eq. 4		0.043
b	Coefficient in Eq. 8 for slow SOM		0.0003†
	Coefficient in Eq. 8 for passive SOM		0.00003†
c_1	Coefficient in Eq. 10		1.0001‡
c_2	Coefficient in Eq. 10		0.0003‡
c_3	Coefficient in Eq. 10		1.0‡
c_4	Coefficient in Eq. 10		2.0‡
C_i	Intercellular CO_2 concentration	μmol/mol	
C_i/C_a	Intercellular/ambient CO_2 concentration		0.7
F_m	Fraction of leaf or root litter to metabolic pools		
GPP	Preindustrial gross primary productivity	g C·m^{-2}·yr^{-1}	1200
J	Rate of electron transport	μmol·m^{-2}·s^{-1}	
J_{max}	Maximum electron transport rate	μmol·m^{-2}·s^{-1}	
k_1	Constant in Eq. 3		35.7§
k_2	Constant in Eq. 3		12.4§
k_3	Constant in Eq. 3		92.55§
k_4	Constant in Eq. 3		13.85§
k_5	Constant in Eq. 3		0.775§
k_6	Constant in Eq. 3		−0.238§
k_c	Michaelis-Menten constants for CO_2	μmol/mol	25.6‖
k_o	Michaelis-Menten constants for oxygen	mmol/mol	41.9‖
K_4	Decomposition coefficient for metabolic leaf litter	g C·g^{-1}·wk^{-1}	0.0068
K_5	Decomposition coefficient for structural leaf litter	g C·g^{-1}·wk^{-1}	0.00178
K_6	Decomposition coefficient for wood litter	g C·g^{-1}·wk^{-1}	0.006285
K_7	Decomposition coefficient for metabolic root litter	g C·g^{-1}·wk^{-1}	0.0064
K_8	Decomposition coefficient for structural root litter	g C·g^{-1}·wk^{-1}	0.00206
K_9	Decomposition coefficient for surface microbes	g C·g^{-1}·wk^{-1}	0.01625
K_{10}	Decomposition coefficient for soil microbes	g C·g^{-1}·wk^{-1}	0.0106
K_{11}	Decomposition coefficient for slow SOM	g C·g^{-1}·wk^{-1}	0.000858
K_{12}	Decomposition coefficient for passive SOM	g C·g^{-1}·wk^{-1}	0.0000478
K_i^a	Actual rates of K_5, K_6, K_8, K_{11}, and K_{12}	g C·g^{-1}·wk^{-1}	
L_s	Lignin content for wood litter		0.35¶
	Lignin content for fine root and leaf litter		0.084¶
M_e	Microbial assimilation efficiency:		
	Soil structural, metabolic C, slow and passive SOM		0.45
	Surface structural litter		0.55
	Stabilizing lignin into slow SOM		0.7
n	N concentration in leaf or root litter	g/g	
n_a	Area-based N concentration in live leaves	g/g	
n_{r+1}	N concentration in leaves and fine roots	g/g	
$N_{T,e}$	Total available N at elevated CO_2		
$N_{T,a}$	Total available N at ambient CO_2		
O	Partial pressure of oxygen	mol/mol	0.21
P_1	Leaf photosynthesis limited by carboxylation	μmol·m^{-2}·s^{-1}	
P_2	Leaf photosynthesis limited by RuBP regeneration	μmol·m^{-2}·s^{-1}	
R/L	Ratio of fine roots to leaves		
V_{cmax}	Maximum RuBP carboxylase activity	μmol·m^{-2}·s^{-1}	
X_i	Amount of carbon in the ith pool, $i = 1, 2, \ldots 12$	g C/m^2	see Table 2
Γ	CO_2 compensation point	μmol/mol	42‖
$\eta_{e/a}$	Ratio of root biomass at elevated to ambient CO_2		
ρ	Dark respiration	μmol·m^{-2}·s^{-1}	

† Values used only when feedback between N mineralization and photosynthetic acclimation is examined (Fig. 7C, D).
‡ Values used only when feedback between soil exploration and photosynthetic acclimation is examined (Fig. 7E, F).
§ Values from Field (1983) and Harley et al. (1992).
‖ Values at temperature of 25°C.
¶ Values from Baldock and Preston (1995), Preston et al. (1990), and van Ginkel et al. (1996) at ambient CO_2.

where $i = 5$, 6, or 8. The decomposition rate for the microbial material (K_{10}) is a function of the soil texture. The decomposition of slow and passive SOM (K_{11} and K_{12}) is affected by root biomass:

$$K_i^a = K_i(1 + b\eta_{e/a}) \qquad (8)$$

where b is a coefficient (Table 1) and $\eta_{e/a}$ is the ratio

of fine root biomass from the elevated CO_2 treatment relative to that from the control treatment. Eq. 8 accounts for experimental findings that the decomposition of slow and passive SOM may increase or decrease due to more root-associated microbial activity (Clarholm 1985, Körner and Arnone 1992, Diaz et al. 1993, Zak et al. 1993).

Respiration from litter and soil C pools (R_i, $i = 4$,
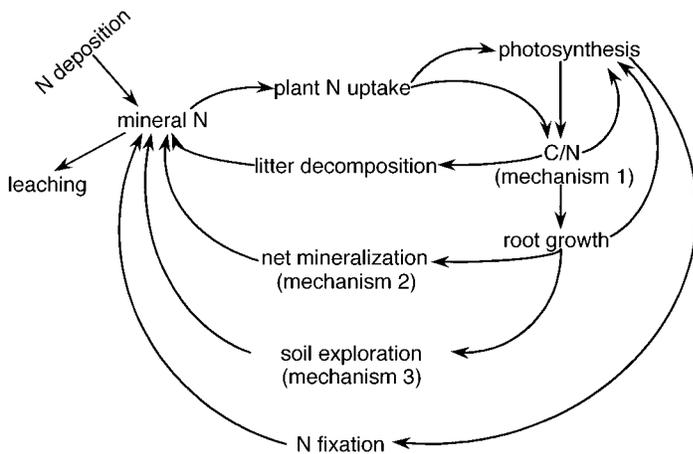
FIG. 2. N and C interactions in the TCS model in regulating ecosystem C_{seq} (see *Model description* for explanation).

5, . . . , 12) is proportional to the flow of C from each pool times a fraction equal to $(1 - M_e)$:

$$R_i = (1 - M_e)\frac{dX_i}{dt} = (1 - M_e)K_iX_i \qquad (9)$$

where M_e is the microbial assimilation efficiency of each pool (Table 1).

The N submodel has an identical structure to the C flow submodel (Fig. 1) with an additional mineral N pool. N flows are assumed to be coupled stoichiometrically with C flows and are equal to the product of the C flow rate and the C/N ratio of the state variables receiving C. Either mineralization or immobilization of N can result from C flow, depending on the initial C/N ratio of material, the C/N ratio of pools receiving C, and the fraction of the C flow lost as CO_2 respiration. The model assumes that all C flows between belowground pools are a result of microbial activity, and that microbial respiration is associated with each of these flows, except litterfall. The model allows for variation in the C/N ratio in each pool.

Extensive experimental evidence suggests that greater root biomass may facilitate soil exploration (e.g., Norby et al. 1986, van Veen et al. 1991, Johnson et al. 1996). To account for this possibility, we use an empirical equation to simulate soil exploration by expanded rooting systems:

$$N_{T,e} = N_{T,a}\left(c_1 - \frac{c_2}{c_3 + c_4\eta_{e/a}}\right) \qquad (10)$$

where $N_{T,e}$ and $N_{T,a}$ are total available N at elevated and ambient CO_2, respectively, and coefficients c_1 through c_4 are constants (Table 1). This equation simulates a diminishing increase in total available N with increasing root biomass.

Ecosystem C and N interactions

The TCS model represents ecosystem C and N interactions via processes of photosynthesis, adjustments in tissue C/N ratio, litter decomposition, net mineral-

ization, and rhizosphere expansion for soil exploration (Fig. 2). We investigate three of these mechanisms: (1) adjustments in C/N ratio of live biomass in leaves, wood, and fine roots; (2) net mineralization; and (3) soil exploration. When photosynthetic C fixation is stimulated by elevated CO_2, the C/N ratio in leaves, and possibly in fine roots and woody tissues, increases. Increased C/N results in downregulation of photosynthesis followed by reduced C influx into the ecosystem. Increased photosynthesis may also stimulate root growth in order to acquire additional nutrients through two mechanisms: (1) expansion of root systems into spaces where previously no roots existed (soil exploration), and (2) stimulation of net mineralization. Soil exploration is described in Eq. 10 and stimulation of net mineralization by Eq. 8.

Limitations

To focus on long-term C and N dynamics in response to rising C_a, we substantially simplified leaf and canopy physiology. We do not explicitly consider short-term interactions between photosynthesis and stomatal conductance, and the effects of temperature and humidity on these processes. Although photosynthetic acclimation varies with environmental conditions and species, photosynthetic sensitivity is independent of interspecific variation and growth environments (Luo and Mooney 1996, Luo et al. 1996). While stomatal conductance strongly fluctuates, the C_i/C_a ratio itself is relatively constant ($\sim$0.7) across various species groups and environmental conditions (Wong et al. 1985a, b, c). These findings suggest that photosynthetic sensitivity and C_i/C_a ratio are scale independent and may be used to predict long-term, large-scale C influx stimulated by rising C_a (Luo 1999). While the effects of short-term interactions and environmental effects on long-term C and N dynamics may be important (e.g., Nikolov et al. 1995), this is beyond the scope of the work presented here.

We also do not consider C and N interactions as-

TABLE 2. Comparative values of C and N pool sizes in Duke Forest, North Carolina, from experimental measurements vs. the TCS model.

	Experimental data				TCS model parameter		
Component	C (g/m²)	N (g/m²)	C/N	Compartment	C (g/m²)	N (g/m²)	C/N
Plant							
Foliage	381.2	8.3	45.9	Leaf	400	8.9	45
Branch	779.5	3.6	216.5	Wood	5000	14.3	350
Bole	3909	8.6	454.5	Fine roots	200	3.3	60
Root	1283.5	2.9	442.6				
Litter							
O horizons	3150	45	70.0	Leaf structure	800	10.0	80
Wood	0	0	...	Leaf metabolic	400	10.0	40
				Wood	1500	4.3	350
				Root structure	800	10.0	80
				Root metabolic	400	8.0	50
Soil horizons							
Ap (0–20 cm)	1389.3	82.9	16.8	Microbe (surface)	160	16.0	10
E (20–35 cm)	599.4	84.9	7.1	Microbe (bulk)	270	33.8	8
Bt1 (35–60 cm)	920	...	...	Slow SOM	3800	253.3	15
Bt2 (60–80 cm)	576.1	...	...	Passive SOM	2500	227.3	11
Total	12 988	236.2		Total	16 230	599.2	

Notes: Experimental data are from the Integrated Forest Study project (Binkley and Johnson 1991). Parameter values for the model are at equilibrium.

sociated with litter decomposition. First, many experimental studies suggest minor (if any) changes in litter quality and decomposition at elevated CO$_2$ (O'Neill and Norby 1996, but see Cotrufo and Ineson 1996). Second, implications of CO$_2$-induced changes in litter quality for ecosystem C and N dynamics have been recently examined by Mooney et al. (1999). Numerous other processes that may play a significant role in short- vs. long-term responses of ecosystems to elevated CO$_2$ include N fixation by plants and free-living organisms, leaching of dissolved N and C, fire, hurricanes, or land use disturbance and atmospheric N deposition. They are also outside of the scope of this study.

Parameterization

We used data from a site in Duke Forest in North Carolina, where a FACE experiment is currently being conducted, to parameterize the TCS model (Table 2). Duke University acquired this forest in the 1960s. Prior to this, the land was used for farming and no records were kept of soil treatments and vegetation. The data shown in Table 2 were collected from a 23-yr-old loblolly pine plantation (Binkley and Johnson 1991, Johnson et al. 1995) close to the current FACE site. To parameterize TCS, we made several adjustments. First, we included C from branch, bole, and part of the roots as live wood C and we assigned a fraction of the measured root C to fine roots. Second, we adjusted the C content in litter and soil C pools to reflect a more mature forest since the 23-yr-old pine plantation was in the early-to-middle stage of succession and we assume that litter and SOM C pools have not reached an equi-

librium. The forest does not have wood litter, whereas a mature forest may have a substantial amount of C in the wood litter. The measured C amount in the O horizons is assumed to be a mixture of both soil surface litter and SOM. In addition, we parameterized TCS with more C in the slow and passive soil C pools, in part because the experimental measurements are only down to 80 cm. The relative sizes of slow and passive C pools are based on Schimel et al. (1994). Values of C/N ratios are set based on experimental data and those used in the CENTURY (Parton et al. 1987) and G'DAY models (Comins and McMurtrie 1993).

Once the pool sizes and C/N ratios in the model were set, we determined values of parameters. Ecosystem photosynthetic C influx in preindustrial time was assumed to be 1200 g C·m^{-2}·yr^{-1}, a typical value for temperate forests. Specific respiration coefficients were set to 0.0209 g·g^{-1}·wk^{-1} for leaves, 0.0105 g·g^{-1}·wk^{-1} for fine roots, and 0.00105 g·g^{-1}·wk^{-1} for woody tissues, so that ~50% of photosynthate is respired by plants. The initial leaf mass of 400 g C/m^2 is equivalent to a leaf area index (LAI) of 4, assuming leaf mass per unit area (LMA) is 100 g C/m^2. During the simulation, we assume that an increase in LMA is proportional to the increase in leaf C pool size, leading to no change in LAI. The maximal increase in LMA, which was ~40%, is within the range of observations (Luo et al. 1994). Longevity was set to 2 yr for leaves, 1 yr for fine roots, and 25 yr for wood. Decomposition rates K_i were obtained by running the model until a steady state was reached after a 1000-yr run. The values of K_4 through K_{12} are listed in Table 1.
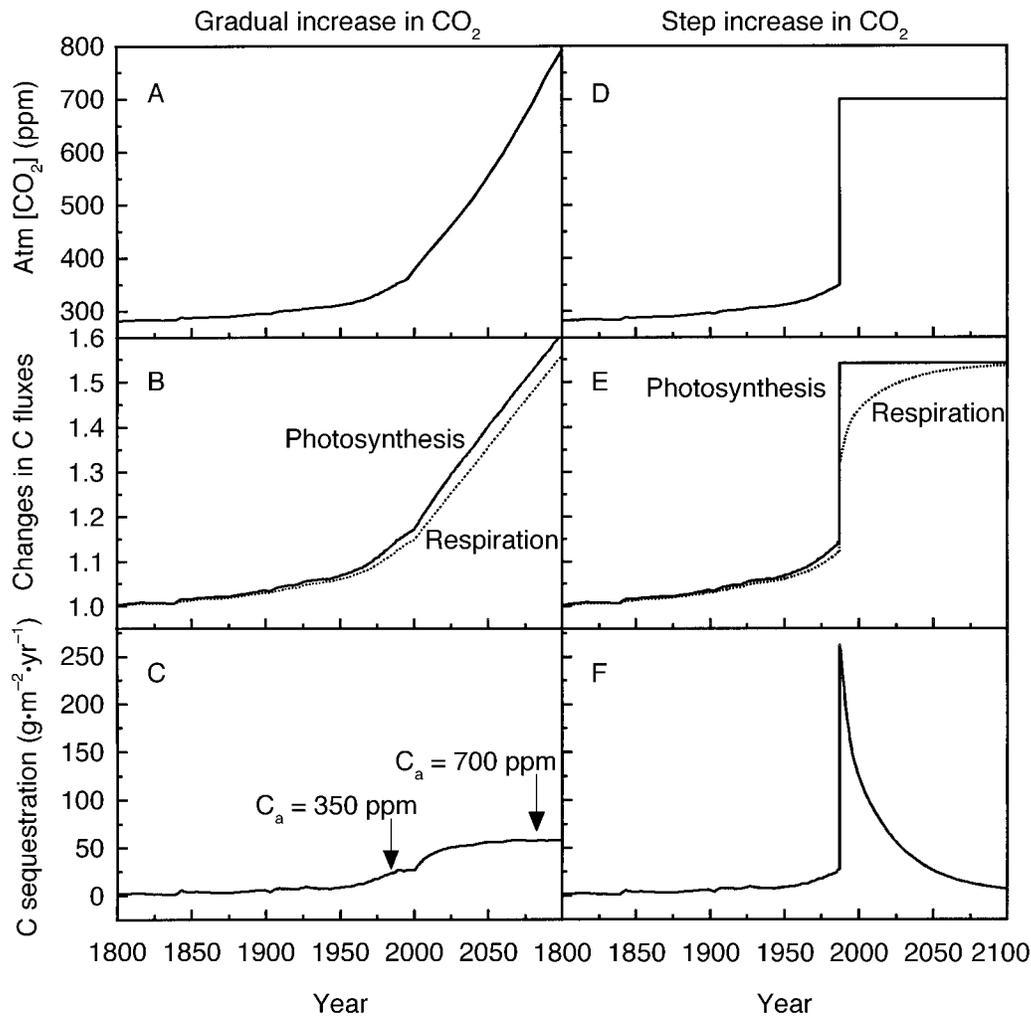
FIG. 3. Comparative ecosystem C dynamics in response to a step vs. gradual increase in atmospheric CO_2 (C_a). (A) C_a gradually increases from 280 ppm in 1800 to 793 ppm in 2100 in the natural world. (B) In response to the gradual increase in C_a, both photosynthesis and respiration increased gradually. (C) The rate of ecosystem C_{seq} gradually increased. (D) C_a gradually increased to 350 ppm in 1987 and then was elevated to 700 ppm to mimic CO_2 experiments using FACE or OTC facilities. A constant CO_2 level was assumed at 700 ppm for 113 yr for the purpose of illustrating long-term C and N dynamics. (E) In response to the step CO_2 increase, photosynthetic C fixation increased immediately, but respiratory C release increased slowly. The constant photosynthesis after the CO_2 treatment resulted from assumed constant LAI and no environmental disturbance. (F) The rate of C_{seq} was high right after the step increase in CO_2 and then declined.

RESULTS

Forest ecosystem response to a step vs. gradual increase in CO_2

The IPCC business-as-usual scenario for increasing atmospheric CO_2 concentration (C_a) is shown in Fig. 3A. In response to this gradual increase in C_a, both photosynthetic C influx and respiratory efflux in the forest ecosystem increase, but with a delay in respiratory C release (Fig. 3B). The difference between influx and efflux is the rate of C sequestration (C_{seq}). In 1987 this was 27 g $C·m^{-2}·yr^{-1}$ (when C_a = 350 ppm) and is predicted to be 58 g $C·m^{-2}·yr^{-1}$ in 2085 (when C_a = 700 ppm) (Fig. 3C). (Note: This is based on a GPP of 1200 g $C·m^{-2}·yr^{-1}$ in preindustrial time). In

contrast, ecosystem C influx increases to 154% of the preindustrial level in response to a step increase in C_a from 350 to 700 ppm in 1987, which mimics OTC and FACE C_a experiments (Fig. 3D, E). Ecosystem C efflux via plant and microbial respiration increases to 132% of the preindustrial level of C efflux in the first year of the step increase and gradually approaches the level of C influx in the next 100 yr or so (Fig. 3E). The difference between C influx and efflux abruptly increases from 27 to 263 g $C·m^{-2}·yr^{-1}$ immediately after the step C_a increase, and then gradually declines (Fig. 3F).

The demand for N in order to balance the additional C influx also differs between the step and gradual increases in C_a. When C_a is abruptly doubled, an eco-
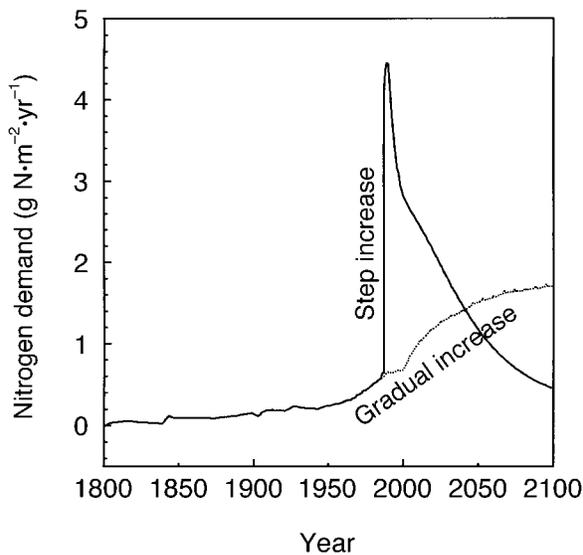
FIG. 4.   N demand to balance extra C storage in an ecosystem in response to a gradual (dotted line) vs. step (solid line) increase in CO_2. In response to the gradual increase in CO_2, the N demand gradually increased to 0.6 g $N·m^{-2}·yr^{-1}$ in 1987 and 1.7 g $N·m^{-2}·yr^{-1}$ in 2085. In response to the step increase in CO_2, the N demand was 4.1 g $N·m^{-2}·yr^{-1}$ in the first year, slightly increased in years 3 and 4, and then declined.

system C_{seq} rate of 263 g $C·m^{-2}·yr^{-1}$ (Fig. 3F) requires an additional 4.1 g $N·m^{-2}·yr^{-1}$ (Fig. 4) to balance the C and N relationships. When C_a gradually increases to 350 and 700 ppm in 1987 and 2085, ecosystem C_{seq} can be balanced by supplying an additional 0.6 and 1.7 g $N·m^{-2}·yr^{-1}$, respectively (Fig. 4). Notice that the N demand increases from 4.1 g $N·m^{-2}·yr^{-1}$ in year 1 of the step CO_2 increase to 4.5 g $N·m^{-2}·yr^{-1}$ in year 3. In addition, the decline in N demand is not as sharp as the decline in the C sink. The slight increase in the first few years, followed by the slow decline, is a result of C reallocation from pools with high C/N ratios (live woody tissue and litter) to pools with low C/N ratios (soil organic matter).

Determination of ecosystem responses to CO_2

The different responses of C_{seq} and N demand to a step vs. gradual C_a increase in the TCS model reflect the nature of ecosystem C processes that can be characterized by three key terms: compartmentalization, donor-controlled transfer, and sequential linearity. It is obvious that photosynthetically fixed C goes to distinctive compartments, including leaves, roots, and woody tissues, litter, and SOM. Thus, C processes are highly compartmentalized. In each of the compartments, C release through either plant or microbial respiration is controlled by sizes of donor pools, and hardly at all by products of respiration, leading to a donor-controlled system. CO_2-induced adjustments in C partitioning and transfers between compartments, how-

ever, may complicate the system. In addition, the majority of the photosynthetically fixed C sequentially transfers from one compartment to another (Fig. 1), following a first-order linear function as described by Eq. 6 (also see Bolker et al. 1998). For example, C transferred from the plant to the litter compartments cannot go back to plants internally. Only a small fraction (usually <5%) of GPP can be recycled through loops from slow and passive SOM compartments to the soil microbial compartment (Fig. 1).

In this simulation study, the pool sizes (given in Table 2) and flux coefficients (given in Table 1) result in an equilibrated influx–efflux system, with GPP equaling 1200 g $C·m^{-2}·yr^{-1}$. Without changing anything else, an increase in pool sizes above those given in Table 2 will lead to net C effluxes from the ecosystem; alternatively, decreases in pool sizes will lead to net C influx, i.e., C sequestration. Rising atmospheric CO_2 stimulates photosynthetic C influx. Hence, without changes in rates of litter and SOM decomposition and C allocation coefficients, the additional C influx must result in an increase in pool sizes. In response to a gradual increase in CO_2, pools are gradually built up (Fig. 5A). Accordingly, respiratory C effluxes from the pools gradually increase, tracking the increase in photosynthesis (Fig. 5C). Since each C pool has a specific C turnover time, increases in pool sizes and fluxes vary; the faster the turnover is, the faster the pool size is built up and the smaller the time lag between effluxes and influx. For example, metabolic pools of leaf and root litter have a high turnover rate and thus accumulate quickly, whereas the passive SOM turns over very slowly and accumulates slowly (Fig. 5A, B). Consequently, C efflux from the metabolic pool tracks C influx, but the C efflux from the passive SOM substantially lags behind the influx (Fig. 5C, D). In response to a step increase in CO_2, C influx abruptly increases to 154% of the preindustrial GPP. Although pool sizes are built up quickly (Fig. 5B) and C effluxes increase rapidly (Fig. 5D), the time lag creates a large gap between C influx and efflux, leading to a large C_{seq} in the first few years of the step CO_2 increase (Fig. 3F).

Comparison of ecosystems

We used the TCS model to simulate C_{seq} and N demand in two pairs of ecosystem types: forests and grasslands, with low and high productivity (LP and HP, respectively). The HP forest is used as a "control" ecosystem with the model structure presented in the *Model description* section, parameters in Tables 1 and 2, and results in Figs. 3 and 4. The LP forest differs from the HP forest only by its preindustrial GPP, equaling 600 instead of 1200 g $C·m^{-2}·yr^{-1}$. The grasslands differ from forests in several ways: no live woody tissue, no dead wood litter, and leaf longevity reduced to 1 yr. Parameters that control C and N fluxes in the grasslands are identical to those in the forests, whereas some of the pool sizes were adjusted to achieve steady
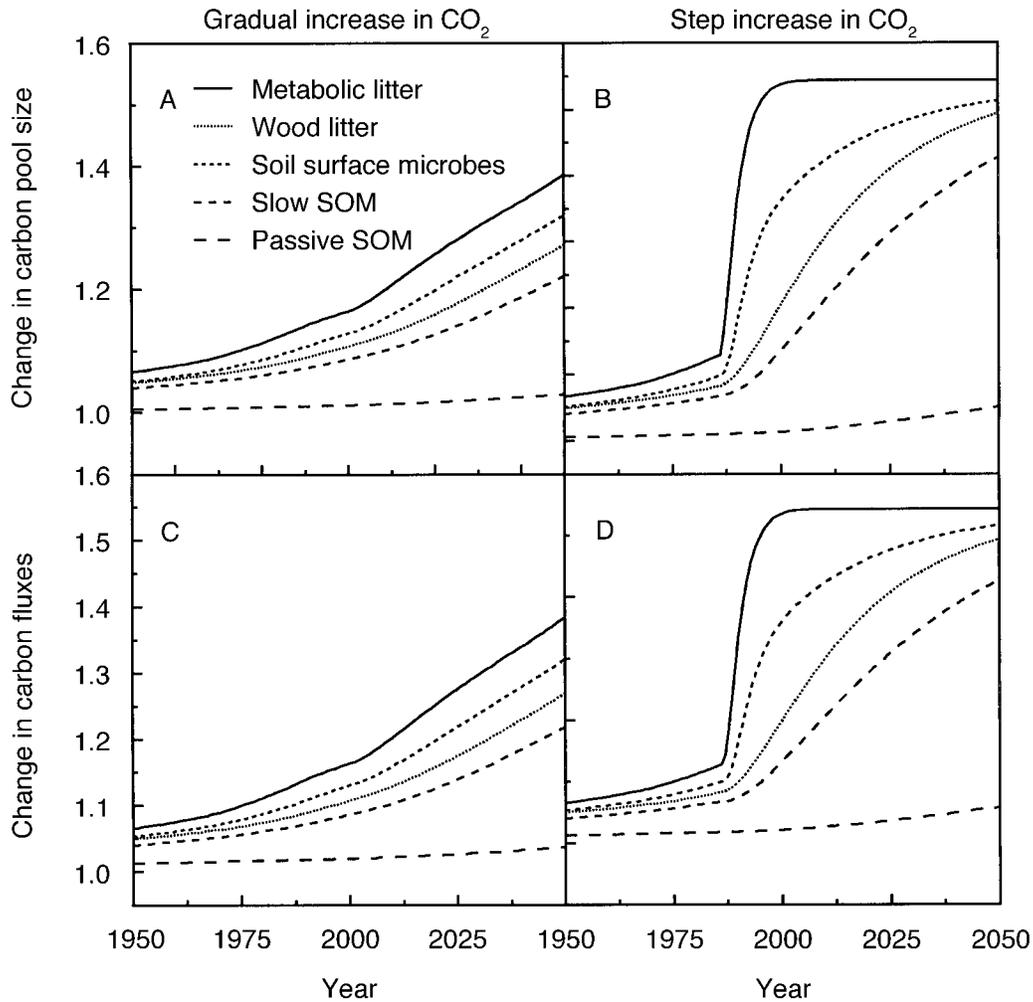
FIG. 5. Changes in C pool sizes in response to a gradual (A) and step (B) increase in CO_2 and changes in C fluxes in response to a gradual (C) and step (D) increase in CO_2. Selection of five pools (metabolic litter, wood litter, soil surface microbes, slow and passive SOM) is for the purpose of illustration.

TABLE 3. Comparison of ecosystem C and N dynamics in response to a step vs. gradual (Grad.) increase in atmosphere CO_2.

Variable	Forest, HP		Grassland, HP		Forest, LP		Grassland, LP	
	Step	Gradual	Step	Gradual	Step	Gradual	Step	Gradual
C influx (g C·m^{-2}·yr^{-1})	480	4.8	480	4.8	240	2.4	240	2.4
C_{seq} (g C·m^{-2}·yr^{-1})	262.8	58.0	249.3	28.3	131.4	29.0	124.6	14.1
Total C_{seq} (g C/m^2)	7566	6861	3770	3430	4404	4222	1834	1773
N demand (g N·m^{-2}·yr^{-1})	4.09	1.67	6.13	1.41	2.23	0.83	2.78	0.71
Total N demand (g N/m^2)	216.8	181.8	108.4	90.9	192.8	173.7	92.0	83.91
Relaxation time (yr)	21.6		9.6		21.6		9.6	

Notes: Simulation ecosystems are forests and grasslands with low productivity (LP) and high productivity (HP). The LP and HP ecosystems have GPP values of 600 and 1200 g C·m^{-2}·yr^{-1}, respectively. Additional ecosystem C influx, C sequestration (C_{seq}), and N demand are the values in the year when CO_2 concentration rises to 700 ppm (1987 in the step CO_2 increase and 2085 in the gradual increase). Total C_{seq} and N demand are the cumulative values during the 300 yr of simulations. Relaxation time is defined by the time required for annual C_{seq} to decline to $1/e$ of the value in the first year of the step CO_2 increase, where e is the base of natural logarithms (2.7183).
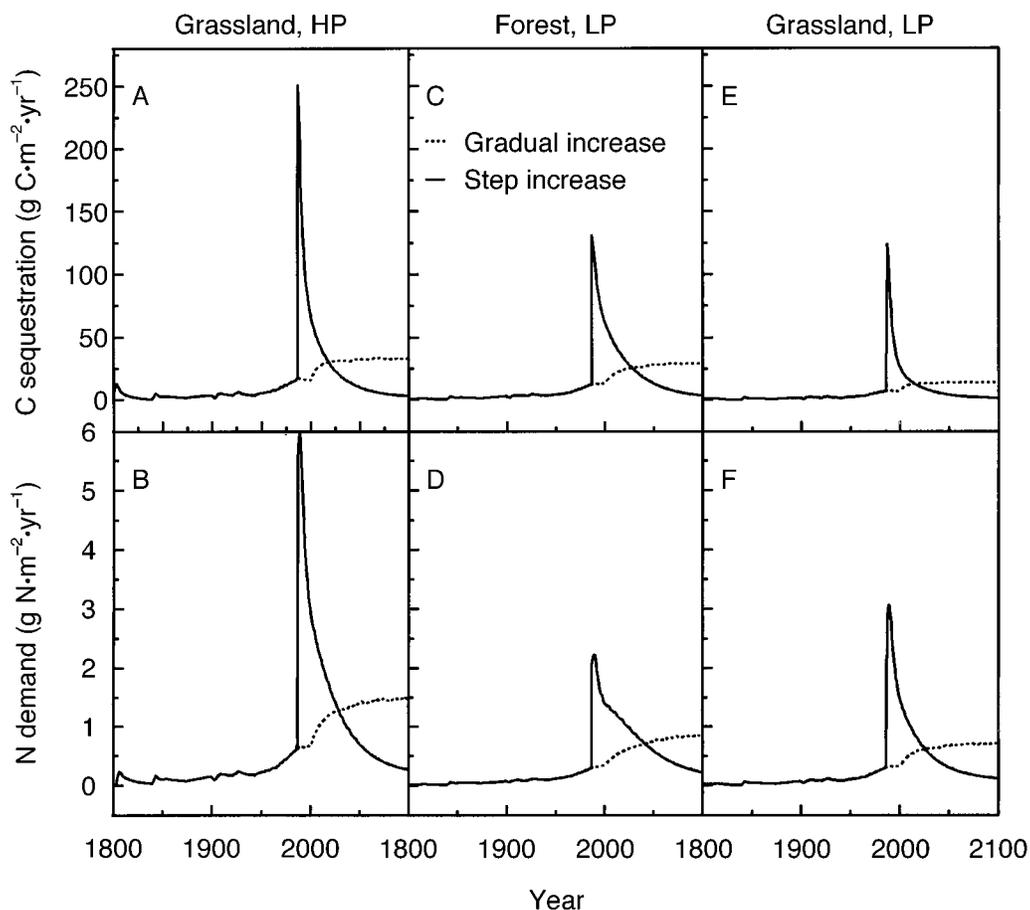
Fig. 6. Comparative simulation studies between grasslands and forests were used to illustrate that C relaxation time and additional photosynthetic C influx (in response to an increase in CO_2) determined the capacity of an ecosystem to sequester C (HP = high productivity; LP = low productivity). (A) Ecosystem C_{seq} and (B) N demand in an HP grassland; (C) C_{seq} and (D) N demand in an LP forest; (E) C_{seq} and (F) N demand in an LP grassland. Dotted lines represent the responses to the gradual increase in CO_2 and solid lines represent the responses to step increase in CO_2.

state before CO_2 treatments. The LP and HP grasslands have a GPP of 600 and 1200 g $C·m^{-2}·yr^{-1}$, respectively. When we assume no photosynthetic acclimation in either forests or grasslands, LP ecosystems gain an additional C influx of 240 g $C·m^{-2}·yr^{-1}$ in the step C_a increase from 350 to 700 ppm in 1987 and 2.4 g $C·m^{-2}·yr^{-1}$ with a gradual C_a increase to 700 ppm in 2085. By comparison, both HP ecosystems gained additional C influx of 480 g $C·m^{-2}·yr^{-1}$ in the step and 4.8 g $C·m^{-2}·yr^{-1}$ with a gradual increase (Table 3). To facilitate comparisons, we use the relaxation time (RT), which is the time from the onset of the step C_a experiment to the point at which C_{seq} declines to $1/e$ (e = 2.7183, the base of the natural logarithm) of the initial value (following a similar definition in physical chemistry, see Laidler and Meiser 1982). For reference, the control ecosystem (HP forest), RT is 21.6 yr (Table 3 and Fig. 3F).

In the HP grassland, the C_{seq} rate is 16 and 28 g $C·m^{-2}·yr^{-1}$ as C_a increases gradually to 350 ppm in

1987 and 700 ppm in 2085 (Fig. 5A). In response to a step increase in C_a, the rate is 249 g $C·m^{-2}·yr^{-1}$ in the first year with an RT of 9.6 yr (Fig. 6A and Table 3). The demand of N supply to balance the C_{seq} when C_a gradually increases to 350 and 700 ppm, is 0.7 and 1.41 g $N·m^{-2}·yr^{-1}$, respectively (Fig. 6B and Table 3). The N demand is 6.1 g $N·m^{-2}·yr^{-1}$ in the first year of the step CO_2 increase, higher than that in the HP forest because woody C pools in the forest have higher C:N ratio than the grasslands. In the LP forest, the C_{seq} rate in response to the gradual increase in CO_2 slowly increases to 29 g $C·m^{-2}·yr^{-1}$ in 2085 when C_a reaches 700 ppm (Fig. 6C), similar to that in the HP grassland (Fig. 6A). However, the rate in response to the step increase is 131 g $C·m^{-2}·yr^{-1}$ in the first year, approximately one-half of the equivalent rate in the HP grassland. The N demand is 0.83 and 2.23 g $N·m^{-2}·yr^{-1}$ at 700 ppm in response to a gradual and a step C_a increase, respectively (Fig. 6D). The N demand in the LP forest is much smaller than that in the HP grassland. In the

LP grassland, the C_{seq} and N demand in response to the gradual increase (Fig. 6E, F) are one-half of those in the LP forest or the HP grassland. The C_{seq} in the first year of the step C_a increase, however, is similar to that in the LP forest but declines much faster than in LP forest due to shorter relaxation time (Table 3).

This comparison of ecosystems reveals that C_{seq} in the first few years of a step increase in C_a is more closely related to the additional input of C via photosynthesis, whereas the C_{seq} in response to a gradual increase in C_a is determined by both the ecosystem C relaxation time and the amount of the additional C influx. Thus, near-term (3–5 yr) results from the step CO_2 experiments may not be a good indicator of the long-term C_{seq} capacity in natural ecosystems in response to a gradual C_a increase.

Ecosystem N dynamics and photosynthetic acclimation

When the C:N ratio in live biomass pools is adjusted without any other changes, the ecosystem is not responsive to an increase in CO_2. Photosynthetic C influx is strongly limited by N (Fig. 7A). The C_{seq} rate ranges from 0 to 2.5 g $C \cdot m^{-2} \cdot yr^{-1}$ in response to a gradual increase in C_a (Fig. 7B); the rate increases to 120 g $C \cdot m^{-2} \cdot yr^{-1}$ in the first year of the step C_a increase and becomes negative or very low in subsequent years.

In the simulation studies of C_a-induced changes in net mineralization and soil exploration, we defined parameter values (Table 1) so the photosynthetic response to a gradual increase in C_a would be minimally limited by N supply (Eqs. 8 and 10). We then used that set of model parameters to predict responses of photosynthesis and C_{seq} to the step increase in C_a. In response to a stimulation of N mineralization by increasing root growth in elevated C_a, the TCS predicted a slight decline in ecosystem photosynthesis in the first couple of years, then a reversal, reaching a peak during year 13 (Fig. 7C); afterwards, photosynthesis cycles down and up, again. The C_{seq} rate reaches 210 g $C \cdot m^{-2} \cdot yr^{-1}$ in the first year of the step CO_2 increase and then declines (Fig. 7D). When the rooting system expands in elevated CO_2, photosynthesis is downregulated to the lowest level in year 3 of the step experiment and then steadily increases to the end of the simulation (Fig. 7E). The C_{seq} rate is 200 g $C \cdot m^{-2} \cdot yr^{-1}$ in the first year of the step CO_2 increase, and then quickly declines to 60 g $C \cdot m^{-2} \cdot yr^{-1}$ (Fig. 7F).

DISCUSSION

Transient responses: model predictions and experimental data

Our modeling results show that ecosystem responses to a step increase in atmospheric CO_2 concentration are transient. Predicted C sequestration (C_{seq}) reaches the highest level in the first year of a step C_a increase and then declines in all cases we examined. These responses are consistent with other modeling studies (e.g., Comins and McMurtrie 1993, McMurtrie and Comins 1996, Rastetter et al. 1997, Thornley and Cannell 1997, Cannell and Thornley 1998). Rastetter et al. (1997) found that net primary productivity (NPP) increased from 450 to 750 g $C \cdot m^{-2} \cdot yr^{-1}$ in the first year of a step CO_2 increase and then rapidly declined to a range from 450 to 550 g $C \cdot m^{-2} \cdot yr^{-1}$ within 10 yr, depending on adjustments in N supply. Similarly, Comins and Mc-Murtrie (1993) predicted an initial increase in NPP from 680 to 970 g $C \cdot m^{-2} \cdot yr^{-1}$, followed by a decline to 750 g $C \cdot m^{-2} \cdot yr^{-1}$ within the 10 yr of a step CO_2 increase. Cannell and Thornley (1998) used the Hurley Pasture Model to study short- vs. long-term responses of grassland to step increases in CO_2 and found a strong, short-term transient response (30% increase in system C) under N-rich conditions, but a "prolonged" (long-term) and much greater (~50% increase) response under N-poor conditions. Similar transient responses have been reported for other environmental driving variables as well. Reynolds and Leadley (1992) examined the effects of changes in season length on arctic plants by imposing step (single-year) vs. gradual (over a 50-yr period) changes. For a step change in season length from 90 to 110 d, they found an increase of 19% in net gas exchange, but only 1% when the increase was gradual.

In general, the transient behaviors predicted by these models are unconfirmed by experiments. This is due to at least three reasons. First, experiments are usually conducted within a time frame of 3–10 yr and measurements are biased toward fast, responsive processes, such as photosynthesis, litterfall, and microbial biomass. Modeling scenarios, on the other hand, can readily include both short-term and long-term processes and can simulate ecosystem responses to step increases in CO_2 over decades or centuries, where transient responses are more apparent. Second, predicted transient changes in NPP or ecosystem C_{seq} are often small, ~5–10%, which is relatively insignificant given the background of natural variability. Third, current limitations in technology prevent us from direct and accurate measurements of whole-ecosystem C_{seq}. As a consequence, few data sets are available for comparison with model predictions.

While no direct experimental data are available to validate the predictions presented here, we argue that the structure of TCS, and hence its behavior, is a direct consequence of existing experimental evidence. As illustrated in Fig. 5, ecosystem C dynamics in TCS are donor-controlled, i.e., C flux is proportional to the size of the donor pool (see Eq. 6). This effectively governs the transient nature of ecosystem responses to step increases in CO_2. This behavior, however, can be complicated by other factors, e.g., climatic variability, canopy development, and C and N interactions. If a step increase in C_a, for example, stimulates canopy development, C influx may increase for years, which will
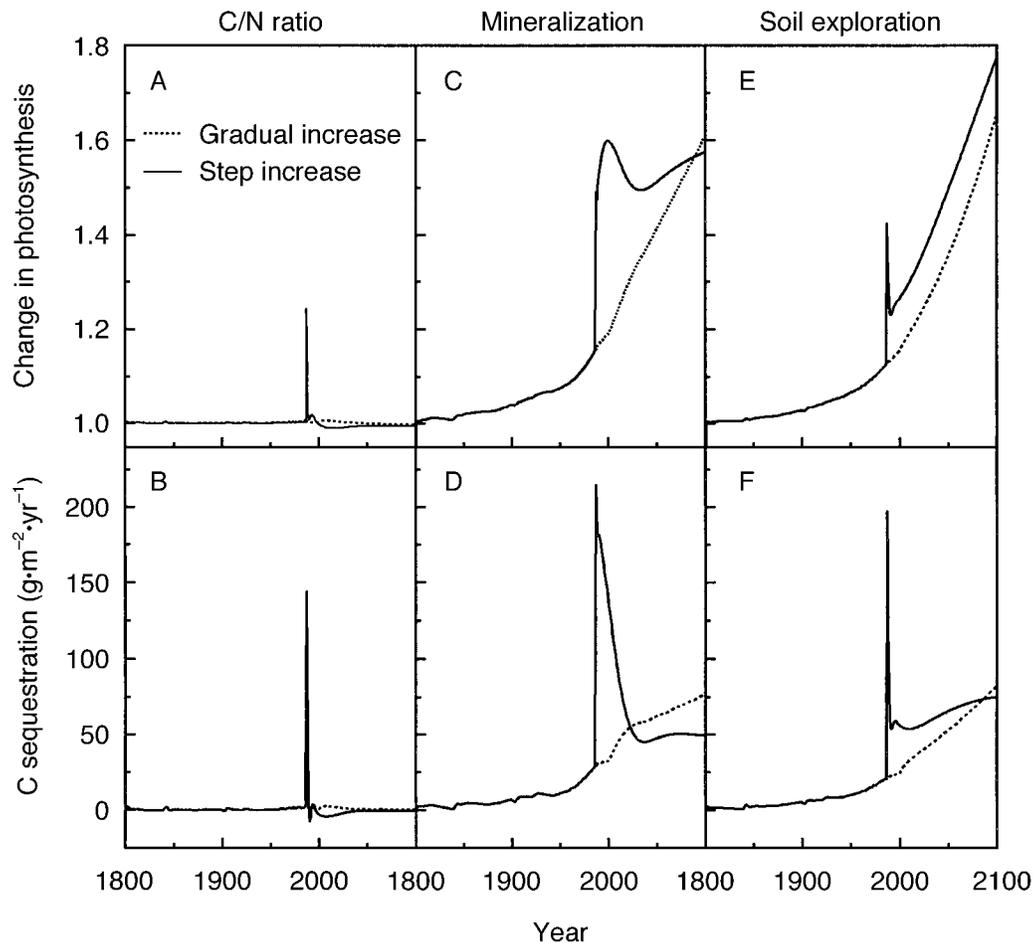
Fig. 7. Three mechanisms of N supply to balance the additional C influx in response to a gradual and step increase in CO$_2$ in regulating photosynthetic acclimation (A, C, and E) and C$_{seq}$ (B, D, and F). Panels A and B show effects of adjustment in C/N ratio in live biomass. Panels C and D show effects of increased N mineralization. Panels E and F show effects of soil exploration. Dotted lines represent the responses to the gradual increase in CO$_2$ and solid lines represent the response to a step increase in CO$_2$.

reduce the magnitude of subsequent decline in C$_{seq}$. This complication likely occurs in step CO$_2$ experiments, especially those conducted in the early stage of ecosystem succession. In addition, if increased C pool sizes lead to a reduction in the transfer coefficients out of the donor pools, the extent of the transience may also be reduced. In short, sustainable C$_{seq}$ occurs only when (1) flux coefficients decrease in proportion to increases in donor pool sizes; or (2) ecosystem C influx increases in proportion to the donor pool sizes; or (3) a combination of (1) and (2). These possibilities may occur in the first few years of CO$_2$ experiments, but it is almost impossible (over a long period) for ecosystem C influx to continue increasing and/or for the flux coefficients to continue decreasing in proportion to the increase in C pool sizes. Thus, we conclude that C$_{seq}$ will inevitably decrease over a long period of time after the onset of a step CO$_2$ experiment.

Step experiments: limitations and potentials

Comparison of the ecosystem responses to a step vs. gradual increase in CO$_2$ (Figs. 3, 5, 6, and Table 3) suggest that C$_{seq}$ obtained in step CO$_2$ experiments cannot be considered a direct estimate of the potential of ecosystems to sequester C in the next century, when C$_a$ will gradually double. Predicted C$_{seq}$ in the first year of a step C$_a$ experiment is significantly higher than when C$_a$ is gradually increased to 700 ppm: i.e., approximately fivefold higher in the forests and ninefold higher in grasslands (with either LP or HP). In addition, ecosystem C$_{seq}$ at any point of time after the initiation of a step CO$_2$ increase is not equivalent to that in response to a gradual increase up to 700 ppm. C$_{seq}$ declines with time in response to a step increase but slowly increases in response to a gradual increase in CO$_2$. The predicted slow increases in C$_{seq}$ is consistent with other modeling studies at regional and global scales (Friedlingstein et al. 1995, Gifford 1996).

Similarly, C and N interactions are strikingly different between the step and gradual CO_2 increases (Figs. 4, 6, 7, and Table 3). In response to a gradual increase, N demand also increases gradually to balance the additional C sink. A step increase in CO_2 leads to abrupt increases in N demand. Predicted N demand ranges from 2.2 to 6.1 g $N \cdot m^{-2} \cdot yr^{-1}$ in the first year of a step CO_2 increase, 2.5–4.5 times the corresponding N demand in response to a gradual increase. In addition, by examining the two N supply mechanisms (net mineralization and soil exploration), we found different responses of C and N dynamics between the two scenarios (Fig. 7C–F). When the two mechanisms are adjusted to the point where enough N is supplied to sustain the CO_2 stimulation of photosynthesis in response to the gradual increase, responses to the step increase are different. The increase in net mineralization leads to sustainable ecosystem photosynthesis but declining C_{seq}. Soil exploration in elevated CO_2 results in strong down-regulation of photosynthesis in the first 5 yr, but a sustainable C_{seq} after year 5.

Despite the fact that C_{seq} estimates from step experiments in C_a cannot be directly extrapolated into the next century, the step experiment is one of the most powerful approaches for conducting manipulative experiments in terrestrial ecosystems. Atmospheric CO_2 concentration is currently increasing by ~1.5 ppm/yr (Keeling et al. 1995), a signal that is much too small for field experiments to detect a response. Hence, step CO_2 experiments using OTC and FACE technologies provide a large input signal or pulse that allows us to trace ecosystem responses over a short time frame. (Such pulse signals are routinely employed in complex systems studied in physics and chemistry [Laidler and Meiser 1982].) Observations of responses to this perturbation, including their subsequent relaxation times, can be used to differentiate and characterize underlying processes and, consequently, effectively quantify C fluxes between the various pools in the soil–plant–atmosphere system.

Recommendations for data interpretation, experimental measurements and design

Given (1) that a step increase in CO_2 is one of the best approaches for manipulative CO_2 experiments and (2) that measurements from these experiments cannot directly be extrapolated to predict ecosystem responses to a gradual increase in C_a, the challenge lies in correct analysis and interpretation of experimental results as well as in improved experimental design and measurements.

As illustrated in Table 3 and Figs. 3 and 6, simple comparison of C_{seq} in the first few years of the step experiments could be seriously misleading in predicting long-term effects of rising C_a. While statistical comparison between treatments is a valid method to determine whether or not observed difference is caused by random errors, such comparison may provide little information on whether or not an ecosystem has responded to elevated CO_2. For example, consider two studies, one initiated three years ago and the other a few months ago. Measurements may show a significantly increased belowground respiration in elevated CO_2 for the study initiated three years ago, but no change in the more recent one. The differences between the two studies are likely to be the consequence of time-dependent C transfer. It usually takes months or longer to transfer additional fixed C in elevated CO_2 from aboveground to belowground through root turnover and litterfall before respired. In other words, it may be too soon to observe any changes in belowground respiration in a study initiated just a few months ago. Thus, simple statistical comparison between the two studies without the context of temporal dynamics provides few insights.

The temporal dynamics of C processes can be represented by relaxation time (Table 3, Figs. 3 and 6). The relaxation time is related to ecosystem C residence time, which is determined by partitioning coefficients among C pools and turnover time in each pool. The latter can be calculated by the pool sizes relative to the efflux from the pools. Thus, essential parameters for developing predictive understanding of C_{seq} are C partitioning, pool sizes, and fluxes in addition to photosynthetic C fixation. As shown in Fig. 5B and D, different C pools and fluxes respond to elevated CO_2 differentially. Metabolic litter pools and fluxes responded to elevated CO_2 much faster than slow SOM pool and flux, reflecting their positions along the C transfer sequence and C residence time in individual pools. In order to quantify the residence time, it is imperative to observe time courses of fluxes and other variables after perturbation by a step CO_2 increase.

Improved experimental design can help characterize temporal dynamics of ecosystem C processes. Currently most of the CO_2 experiments utilizing FACE and OTC facilities follow a holistic approach—that is, to design experiments in ecosystems as natural as possible and then to observe their responses (Mooney et al. 1991). Since observed responses cannot simply be extrapolated to the natural world, it is necessary to quantify components and mechanisms underlying these observed responses. To accomplish that, we argue for a reductionistic approach that should parallel holistic CO_2 experiments. To achieve both goals of holistic observation of ecosystem responses and reductionistic analysis of components, the experimental design has to help reduce or exclude complications inherent in natural ecosystems. These complications include partial closure of canopy and rooting systems in experiments with seedlings or saplings of trees (Johnson and Ball 1996, Norby et al. 1996), ecosystem development in young stands of forests, episodic events in deserts, highly variable climatic conditions in grasslands (Owensby et al. 1993, Field et al. 1996). Those factors will obscure actual effects of elevated CO_2 and cause tre-

mendous difficulties in data analysis (Hungate et al. 1996) if not experimentally controlled.

The need for new analysis approaches

Manipulative experiments are commonly practiced in ecosystem studies in addition to field CO$_2$ experiments, for example: the addition of sulfur and/or N to experimental plots (e.g., Abrahamsen and Stuanes 1980), the addition of iron to lakes (e.g., Carpenter et al. 1995), ozone fumigation of experimental plots (Pell et al. 1992), and soil warming experiments (e.g., Harte and Shaw 1995). These experiments have a common goal: to extrapolate experimental results based on step changes of environmental variables to predict ecosystem responses to gradual changes in the natural world. All step change experiments fundamentally utilize the same ''perturbation–response'' approach. Treatments of step changes in N, ozone, and temperature are used to generate a perturbation in material or energy fluxes into ecosystems. As in most systems research, observations from the perturbation experiments reflect the reactions of the system to perturbations, and therefore cannot be directly extrapolated. Experimental results must be analyzed to characterize processes and mechanisms underlying the observations before we are able to predict future responses.

Analysis of the perturbation experiments has rarely been discussed in the literature of ecology. It has, however, been extensively explored in other fields, e.g., global C cycling (Enting 1985, Enting and Mansbridge 1991), seismology and tectonics (Loke and Barker 1995, Mohan and Rai 1995), hydrology (Mishra and Parker 1989), and acoustics (Pitre and Davis 1995). These analyses often involve deconvolution of experimental results (Dewar 1992, Dimri 1992). The deconvolution procedure usually starts with experimentally observed responses and then identifies mechanisms and/or constituent processes underlying the observations, using either analytic and/or inverse modeling approaches. The concepts and procedures developed in other scientific disciplines may be extremely useful in ecological studies. It will remain a challenge for ecologists to apply those approaches and to address critical issues associated with perturbation experiments.

CONCLUSIONS

This study was designed to answer the question: can step CO$_2$ experiments be extrapolated to predict future carbon sequestration in natural ecosystems? Our analysis suggests:

1) Ecosystem C processes possess three intrinsic characteristics: compartmentalization, donor-controlled transfer, and sequential linearity. These characteristics predetermine a long-term transient response: a step increase in CO$_2$ concentration will inevitably result in a pulse increase in C sequestration in the first few years, followed by a decline.

2) This transient response can be complicated by short-term feedbacks: (1) an increase in C influx and/or (2) a decrease in decomposition coefficients, resulting from canopy development and N feedback.

3) The transient response to a step CO$_2$ increase is strikingly different from ecosystem responses to a gradual increase in atmospheric CO$_2$ and, therefore, cannot be directly extrapolated to predict carbon sequestration in natural ecosystems.

4) While observations from the step experiments cannot be directly extrapolated, processes and mechanisms can. These processes include photosynthetic C influx, C partitioning to various pools, and C turnover times in each of the pools.

5) To quantify these processes, measurements of their time courses become essential.

6) Rigorous analysis of step experiments requires not only statistical but also other new approaches, such as deconvolution and inverse modeling.

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