Responses of a loblolly pine ecosystem to CO2 enrichment: a modeling analysis

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Summary   The development of the Free-Air CO_2 Enrichment (FACE) facilities represents a substantial advance in experimental technology for studying ecosystem responses to elevated CO_2. A challenge arising from the application of this technology is the utilization of short-term FACE results for predicting long-term ecosystem responses. This modeling study was designed to explore interactions of various processes on ecosystem productivity at elevated CO_2 on the decadal scale. We used a forest model (FORDYN) to analyze CO_2 responses—particularly soil nitrogen dynamics, carbon production and storage—of a loblolly pine ecosystem in the Duke University Forest. When a 14-year-old stand was exposed to elevated CO_2, simulated increases in annual net primary productivity (NPP) were 13, 10 and 7.5% in Years 1, 2 and 10, respectively, compared with values at ambient CO_2. Carbon storage increased by 4% in trees and 9.2% in soil in Year 10 in response to elevated CO_2. When the ecosystem was exposed to elevated CO_2 from the beginning of forest regrowth, annual NPP and carbon storage in trees and soil were increased by 32, 18 and 20%, respectively, compared with values at ambient CO_2. In addition, simulation of a 20% increase in mineralization rate led to a slight increase in biomass growth and carbon storage, but the simulated 20% increase in fine root turnover rate considerably increased annual NPP and carbon storage in soil. The modeling results indicated that (1) stimulation of NPP and carbon storage by elevated CO_2 is transient and (2) effects of elevated CO_2 on ecosystem processes—canopy development, soil nitrogen mineralization and root turnover—have great impacts on ecosystem C dynamics. A detailed understanding of these processes will improve our ability to predict long-term ecosystem responses to CO_2 enrichment.

Keywords: carbon dioxide increase, FACE, global change, mineralization, nitrogen, Pinus taeda, root turnover.

Introduction

The response of forest trees to elevated atmospheric CO_2 concentration has been investigated with a variety of experimental techniques, including controlled environmental chambers, greenhouses, branch bags, and open-top chambers (Eamus and Jarvis 1989, Mousseau and Saugier 1992, Ceulemans and Mousseau 1994). The CO_2 fertilization effect has been widely observed in these experiments (Koch and Mooney 1996), although the magnitude of response is highly variable, depending on other environmental factors including temperature, irradiance, water, and nutrients (Luo and Mooney 1999). Because most of these studies are based on short-term experiments with seedlings or branches of individual trees, it is difficult to derive a realistic estimate of longer term responses of natural forest ecosystems to elevated CO_2, including the fate of photosynthetically fixed carbon (C) in ecosystems and interactions between the C and nitrogen (N) cycles (Johnson and Ball 1996). For example, although there is substantial evidence that N has strong and positive effects on leaf photosynthesis and plant growth at elevated CO_2 (Bazzaz 1990, Thomas et al. 1994, Griffin et al. 1995, King et al. 1996), N limitations in natural ecosystems may constrain such effects (Norby et al. 1992, Comins and McMurtrie 1993, Diaz et al. 1993, Melillo et al. 1993, Schimel 1995).

Several long-term modeling studies have indicated a limited response to elevated CO_2 in nutrient-limited ecosystems (e.g., Rastetter et al. 1991), whereas other models have predicted a strong response (e.g., Comins and McMurtrie 1993, McMurtrie and Comins 1996). There are numerous processes that may supply additional nutrients to balance the increase in carbon input resulting from CO_2 enrichment, including nitrogen mineralization (Diaz et al. 1993), litter decomposition (Coûteaux et al. 1991, O'Neill and Norby 1996), and C:N ratios in soil organic matter and wood (McMurtrie and Comins 1996, Rastetter et al. 1997).

The Free-Air CO_2 Enrichment (FACE) experiment in the Duke University Forest, North Carolina (Ellsworth et al. 1995) provides an opportunity to examine ecosystem responses to elevated CO_2, particularly feedback between the C and N cycles. We have used the model FORDYN to examine how elevated CO_2 may affect the stand structure and physiology of this forest ecosystem. We calibrated the simulation model with photosynthesis and tree growth data from a three-year, open-

top chamber experiment with loblolly pine (*Pinus taeda* L.) conducted in the Duke Forest (Lewis et al. 1996, Tissue et al. 1996). The calibrated model was then used to analyze how the forest ecosystem would respond to elevated CO_2 under FACE conditions. In particular, we examined possible constraints to tree growth and C production and storage by soil N availability by simulating changes in N mineralization and root turnover rates.

Methods

Model description

The forest simulator FORDYN has been described in detail by Luan et al. (1996). Therefore, we only outline the FORDYN model here, but provide details on the main calculation procedure related to the carbon–nitrogen interactions affecting forest productivity at different scales. The FORDYN forest model is hierarchical and simulates forest dynamics by integrating (1) leaf photosynthesis, transpiration, and respiration; (2) growth processes such as carbon, nitrogen, and water translocation among tree parts; (3) forest succession; and (4) ecosystem processes including carbon, nitrogen and water cycling in the plant–soil system (Figure 1). The FORDYN model also extrapolates across multiple scales: for example, forest development is the aggregated result of individually located trees, each of which is driven by hourly climate change. The model treats each tree as leaf, wood (branch, stem, supporting root), and root (fine root) parts. Leaves are evenly distributed in each crown within a cylindrical shape and grouped into crown layers of equal height. Soil nitrogen and water are assumed to be homogeneously distributed.

The general relationship of carbon, nitrogen, and water cycling in a forest represented by FORDYN is shown in Figures 1A–C. The main symbols used in the figures and equations are listed in Table 1.

Leaf photosynthesis

Leaf photosynthesis Leaf photosynthesis is calculated according to the model of Farquhar and von Caemmerer (1982) as modified by Harley et al. (1992) and Luo et al. (1998). Leaf photosynthetic rate is co-limited by ribulose bisphosphate regeneration and ribulose-1,5-bisphosphate carboxylase-oxygenase activity as well as by leaf conductance. The temperature dependence and acclimation of photosynthesis are described by considering the temperature response of the two primary parameters, V_{cmax} and J_{max} (see Lewis et al. 1996), where V_{cmax} is maximum rate of carboxylation and J_{max} is maximum rate of electron transport. The N dependence of both V_{cmax} and J_{max} is represented as a linear relationship with leaf nitrogen content (Harley et al. 1992).

Leaf-level photosynthetic rate is integrated within the canopy profile (Luan et al. 1996) to derive the total gross photosynthetic rate of the forest stand. The net photosynthetic production of each tree is derived by aggregating gross photosynthetic rate and respiration rate, which includes growth and maintenance respiration rates of the tree parts.

Tree growth processes In FORDYN, the growth of each tree in the stand is driven by leaf carbon assimilation, N, and water
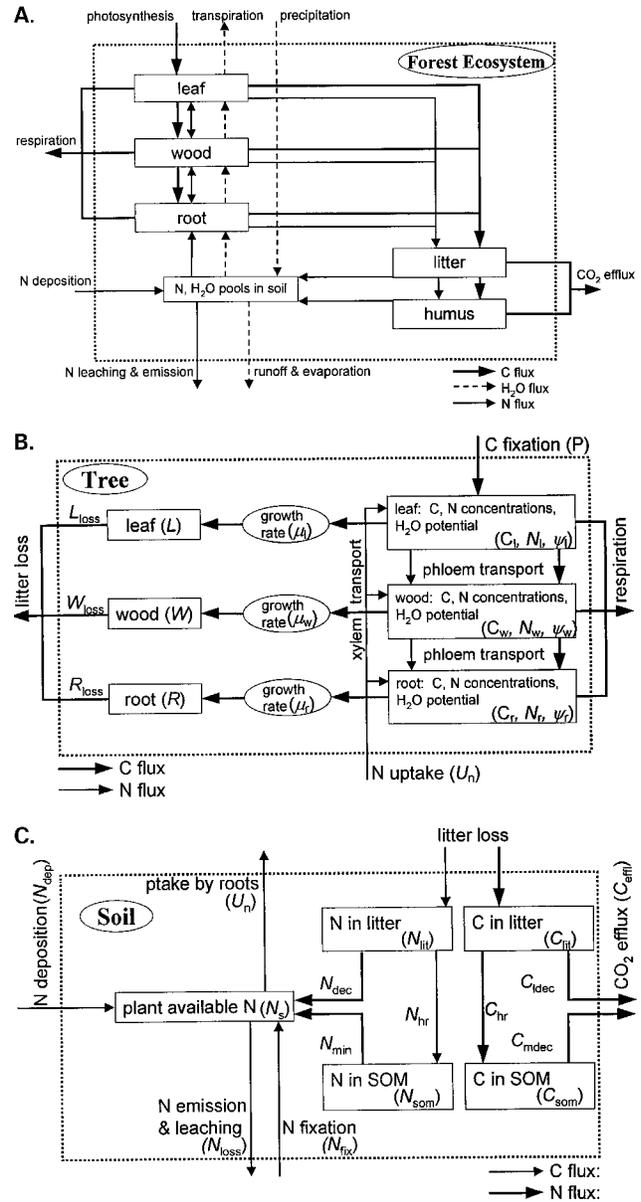

Figure 1. Dynamics of C, N, and H_2O in the FORDYN model. (A) C, N, and H_2O cycles in forest ecosystem; (B) C and N dynamics in plants; and (C) C and N dynamics in soil.

uptake through roots. The translocation of labile C, labile N, and water among different tree parts through the xylem and phloem (a Münch flow mechanism of phloem translocation of nitrogen) follows the approach of Dewar (1993). The growth of each tree part is a function of local N and C concentrations as well as water potential as shown in Figure 1B. For example, leaf biomass growth is given by:

$$dL/dt = k_lC_lN_lf(\Psi_l) - L_{lr}, \quad (1a)$$

where L is leaf biomass, C_l is leaf carbon concentration, N_l is leaf nitrogen concentration, and L_{lr} is leaf turnover rate. The effect of leaf water potential $f(\Psi_l)$ is a scalar (0–1) given by the

Table 1. Symbols and their definitions and units.

Symbol	Definition	Units
A	Assimilation rate of carbon	$\mu mol\ m^{-2}\ s^{-1}$
C_{effl}	Carbon efflux from soil	$kg\ ha^{-1}\ day^{-1}$
C_i	Intercellular CO_2 concentration	$\mu mol\ mol^{-1}$
C_{hr}	Carbon transfer rate from litter to SOM	$kg\ ha^{-1}\ day^{-1}$
C_l	Leaf carbon substrate concentration	dimensionless
C_{ldec}	Carbon release from litter decomposition	$kg\ ha^{-1}\ day^{-1}$
C_{lit}	Carbon content in litter	$kg\ ha^{-1}$
C_{mdec}	Carbon release from humus decomposition	$kg\ ha^{-1}\ day^{-1}$
CN_{soma}	C:N ratio in litter	dimensionless
CN_{somb}	C:N ratio in humus	dimensionless
C_r	Carbon substrate concentration in root	dimensionless
C_{som}	Carbon pool size in soil organic matter	$kg\ ha^{-1}$
C_w	Carbon substrate concentration in wood	dimensionless
D_r	Decomposition rate of litter	$kg\ ha^{-1}\ day^{-1}$
J_{max}	Maximum electron transport rate	$\mu mol\ m^{-2}\ s^{-1}$
k_l	Leaf growth coefficient	dimensionless
L	Leaf biomass	$kg\ stem^{-1}$
L_g	Leaf biomass increment	$kg\ ha^{-1}\ day^{-1}$
L_{lr}	Leaf turnover rate	day^{-1}
L_n	Leaf nitrogen content	dimensionless
N_d	Nitrogen demand of all trees in the stand	$kg\ ha^{-1}\ day^{-1}$
N_{dec}	Nitrogen mineralization of litter	$kg\ ha^{-1}\ day^{-1}$
N_{dep}	Nitrogen deposition	$kg\ ha^{-1}\ day^{-1}$
N_{fix}	Nitrogen fixation by root	$kg\ ha^{-1}\ day^{-1}$
N_{hr}	Nitrogen transfer rate in humification	$kg\ ha^{-1}\ day^{-1}$
N_l	Leaf nitrogen concentration	$kg\ kg^{-1}$
N_{lim}	Nitrogen availability factor	dimensionless
N_{lit}	Nitrogen content in litter	$kg\ ha^{-1}$
N_{loss}	Nitrogen loss from emission and leaching	$kg\ ha^{-1}\ day^{-1}$
N_{min}	Humus mineralization rate	$kg\ ha^{-1}\ day^{-1}$
NPP	Net primary productivity	$kg\ ha^{-1}\ year^{-1}$
N_r	Nitrogen concentration in root	$kg\ kg^{-1}$
N_s	Nitrogen supply rate from soil	$kg\ kg^{-1}\ day^{-1}$
N_{som}	Nitrogen pool size in soil organic matter	$kg\ ha^{-1}$
N_u	Nitrogen uptake rate by root	$kg\ kg^{-1}\ day^{-1}$
N_w	Nitrogen concentration in wood	$kg\ kg^{-1}$
P	Net photosynthetic carbon production	$kg\ stem^{-1}\ day^{-1}$
R	Root biomass	$kg\ stem^{-1}$
R_f	Fine root biomass	$kg\ stem^{-1}$
R_g	Root biomass increment	$kg\ stem^{-1}\ day^{-1}$
R_{loss}	Root death	$kg\ stem^{-1}\ day^{-1}$
R_{lr}	Root turnover rate	day^{-1}
R_n	Root nitrogen concentration	dimensionless
T	Time	day
T_r	Temperature dependence of root activity	dimensionless
U_i	Specific N uptake rate of roots	$kg\ kg^{-1}\ day^{-1}$
U_n	Total N uptake rate by root in the stand	$kg\ ha^{-1}\ day^{-1}$
U_w	Total water uptake by roots in the stand	$kg\ ha^{-1}\ day^{-1}$
V_{cmax}	Maximum carboxylation rate	$\mu mol\ m^{-2}\ s^{-1}$
W	Wood biomass	$kg\ stem^{-1}$
W_g	Wood biomass increment	$kg\ stem^{-1}\ day^{-1}$
W_{loss}	Wood loss	$kg\ stem^{-1}\ day^{-1}$
W_n	Wood nitrogen concentration	$kg\ kg^{-1}$
μ_l	Leaf growth rate	$kg\ stem^{-1}\ day^{-1}$
μ_r	Root growth rate	$kg\ stem^{-1}\ day^{-1}$
μ_w	Wood growth rate	$kg\ stem^{-1}\ day^{-1}$
Ψ_l	Leaf water potential	MPa
Ψ_c	Threshold water potential for active growth	MPa
Ψ_r	Root water potential	MPa
Ψ_w	Wood water potential	MPa

equation:

$$f(\Psi_l) = \max(1 - \Psi_l/\Psi_c, 0), \tag{1b}$$

where Ψ_l is leaf water potential and Ψ_c is the threshold water potential for active growth. Leaf carbon concentration, C_l, is derived from leaf C assimilation and is consumed by growth (into structure), respiration, and transport to other tree parts. Leaf nitrogen concentration, N_l, is derived from upward N transport (from root to leaf) and is consumed by growth (into structure) and downward phloem translocation. Leaf water potential, Ψ_l, is established from upward water transport (with downward water potential gradient) from root to leaf (Dewar 1993). The time step dt for calculating tree growth is one day.

Soil carbon and nitrogen cycling   In FORDYN, the available soil N is a dynamic pool with input from atmospheric deposition, root fixation, litter decomposition, and humus mineralization (Figure 1C). The soil mineral N pool is depleted by leaching, root uptake, immobilization, and soil CO_2 efflux (Bossel and Schäfer 1989). Thus, the potential N supply in the soil (N_s) is determined by deposition (N_{dep}), mineralization (from humus N_{min} and litter N_{dec}), nitrogen fixation (N_{fix}), and loss through root uptake (N_u) as well as leaching and emission (N_{loss}) (Figure 1C):

$$dN_s/dt = N_{dep} + N_{min} + N_{dec} + N_{fix} - N_u - N_{loss}. \tag{2}$$

Nitrogen uptake by roots (N_u) is determined by the amount of fine roots per tree (R_i where $i = 1,2, ..., n$, where n is the total number of trees in the stand), specific N uptake rate of roots (U_i), soil temperature effect (T_r, represented as a quadratic function of soil temperature where $0 < T_r < 1$, see Bossel and Shäfer 1989), and a N availability index (N_{lim}):

$$N_u = \sum_{i=1}^{n} (R_i U_i N_{lim} T_r), \tag{3}$$

where N_{lim} is expressed by relating soil N supply (N_s) to plant N demand (N_d):

$$N_{lim} = N_s/N_d. \tag{4}$$

And N_d is estimated by:

$$N_d = \sum_{i=1}^{n} (L_{gi} L_{ni} + W_{gi} W_{ni} + R_{gi} R_{ni}), \tag{5}$$

where L_g, W_g, and R_g are the biomass increments of leaf, wood, and root of each tree, respectively; and L_n, W_n, and R_n are the N contents of leaf, wood, and root of each tree, respectively.

Soil CO_2 efflux in the model (excluding root respiration) is determined by the decomposition of both litter and humus (Figure 1C). The release of CO_2 from both litter (C_{ldec}) and soil organic matter (C_{mdec}) is temperature dependent, and the soil temperature effect is a quadratic function of soil temperature.

Note also that C_{ldec} depends on the litter pool (C_{lit}) and decomposition rate (D_r) of litter; and C_{mdec} is a function of the soil organic pool size (C_{som}), soil organic matter mineralization rate (M_r), and soil temperature effect (a quadratic function).

Calibration and parameterization

We calibrated the components of leaf photosynthesis and tree growth in the FORDYN model based on results from an open-top-chamber (OTC) experiment on loblolly pine. Complete details of the experimental protocols for the OTC study have been described by Lewis et al. (1996) and Tissue et al. (1996). The OTC experiment was conducted in the Duke Forest from 1992 to 1995 with 3-m-diameter by 3-m-tall open-top chambers. There were three chambers for each of the three CO_2 treatments (ambient, ambient + 150 ppm, ambient + 300 ppm), three nitrogen treatments (low, medium, high), and three non-chambers plots. The nitrogen treatments were discontinued after two growing seasons because nitrogen was not limiting. We used the data to estimate some of the key parameters for FORDYN and to calibrate its performance for loblolly pine. Climate data used in the calibration were based on the 1993 values from the OTC experiment. The growing season was warm and humid with 200 frost-free days. Mean annual precipitation of 1150 mm was evenly distributed throughout the year.

Leaf photosynthetic parameters were obtained by fitting the Farquhar and von Caemmerer (1982) model to the observed A–C_i curves (Lewis et al. 1996) (Table 2). The predicted photosynthetic response to elevated CO_2 was compared to experimental observations from different seasons (Lewis et al. 1996) (Figures 2A and 2B). Predicted biomass growth was generally consistent with observed values ($r^2 = 0.98$) (Figures 2C and 2D).

We parameterized the soil carbon and nitrogen components of the FORDYN model with data from the Duke FACE experimental study. The Duke FACE experiment, which is located in a loblolly pine stand in the Duke Forest (35.58° N, 79.8° W), began in 1996 with six FACE rings (circular plots of 30-m diameter) within a stand of loblolly pine. Three rings were selected for exposure to elevated CO_2 and another three plots were exposed to ambient CO_2 concentration. Initial stand density in the model is based on FACE site stand conditions, with a mean of 1736 trees per hectare. Nitrogen deposition rate and C:N ratio in both litter and soil organic matter are based on measured values (A. Allen, Duke University, Durham, NC, unpublished) (Table 2). Carbon turnover rate of soil organic matter is based on measurements made by the radiocarbon technique (Harrison et al. 1995). Initial soil organic matter pool size was derived from the vertical distribution of the active soil organic matter (SOM) along the soil profile, in which most SOM is distributed within 2 m of the soil surface. The litter decomposition rate (0.3 g g^{-1} year^{-1}) was derived from a previous study of the loblolly pine stand (Kinerson et al. 1977).

Simulation scenarios

We used FORDYN to explore five scenarios in which tree

Table 2. Main parameters and initial values used in the simulation. See Table 1 for the definition of the parameters.

Parameter	Value	Source
CN_{soma}	45	A. Allen (Duke University, Durham, NC, unpublished result)
CN_{somb}	14	A. Allen (unpublished result)
D_r	0.3 year^{-1}	Derived from Kinerson et al. (1977)
J_{max}	36 μmol m^{-2} s^{-1}	Derived from Lewis et al. (1996)
L_{lr}	0.002 day^{-1}	Estimated value
N_{dep}	8 kg ha^{-1} year^{-1}	W. Schlesinger (Duke University, Durham, NC, unpublished result)
R_{lr}	0.01 day^{-1}	Estimated value
U_i	0.05 kg kg^{-1} day^{-1}	From Johnson and Thornley (1987)
V_{cmax}	78 μmol m^{-2} s^{-1}	Derived from Lewis et al. (1996)
μ_r	0.02 day^{-1}	Estimated value

growth, carbon production and storage, and nitrogen dynamics respond to CO_2 enrichment: Scenario 1 (S1), ambient CO_2 (C_a = 350 ppm) throughout 24 years; Scenario 2 (S2), elevated CO_2 (C_a = 650 ppm) throughout 24 years; Scenario 3 (S3), ambient-to-elevated CO_2 with C_a = 350 ppm in the first 14 years and a step increase in C_a (C_a = 650 ppm) afterward, without changes in the mineralization and root turnover rates; Scenario 4 (S4), ambient-to-elevated CO_2 as in S3 but with the mineralization rate enhanced by 20% at elevated CO_2; and Scenario 5 (S5), ambient-to-elevated CO_2 as in S3 but with the root turnover rate increased by 20% at elevated CO_2.

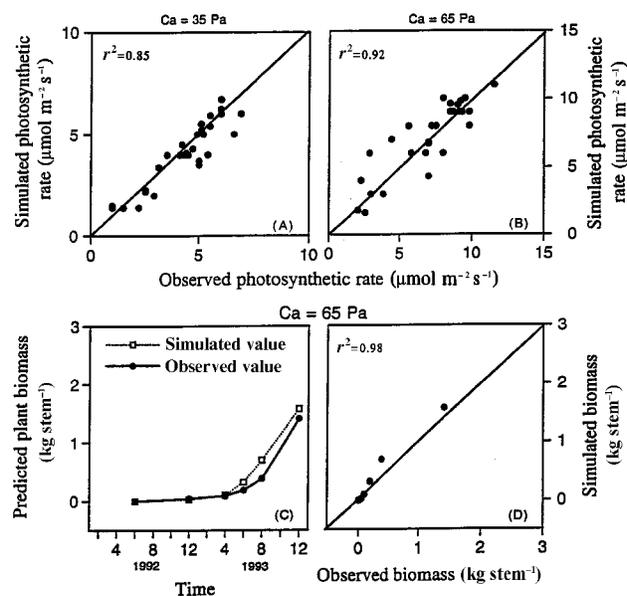Scenario 3, in which trees experience ambient CO_2 in the

Figure 2. Comparison of simulated photosynthetic rate and growth rate with measured results from Tissue et al. (1996). (A) Simulated photosynthetic rates versus observed values at ambient CO_2 condition; (B) predicted photosynthetic rates versus observed values at elevated CO_2; (C) and (D) predicted biomass growth versus observed value at elevated CO_2.

first 14 years and then are exposed to elevated CO_2 for 10 more years, was designed to predict medium-term dynamics of a natural loblolly pine stand subjected to elevated CO_2 concentrations. The time scale of this simulation study is within the time scale of the FACE experiment in the Duke University Forest. We also examined the potential effects of nitrogen mineralization and root turnover rates on CO_2 responses in S4 and S5. Both experimental and modeling studies have shown that soil nitrogen availability may constrain forest response to CO_2 enrichment in the long term (Zak et al. 1993, Rastetter et al. 1997, Luo and Reynolds 1999). In addition, a change in root turnover may have a profound influence on tree growth (allocation), nitrogen uptake, and turnover (Stulen and den Hertog 1993, Rogers et al. 1994). Model assumptions include (1) balanced initial soil nitrogen between plant uptake demand and soil supply; and (2) no water limitation.

Results and discussion

Simulated variation in tree growth patterns

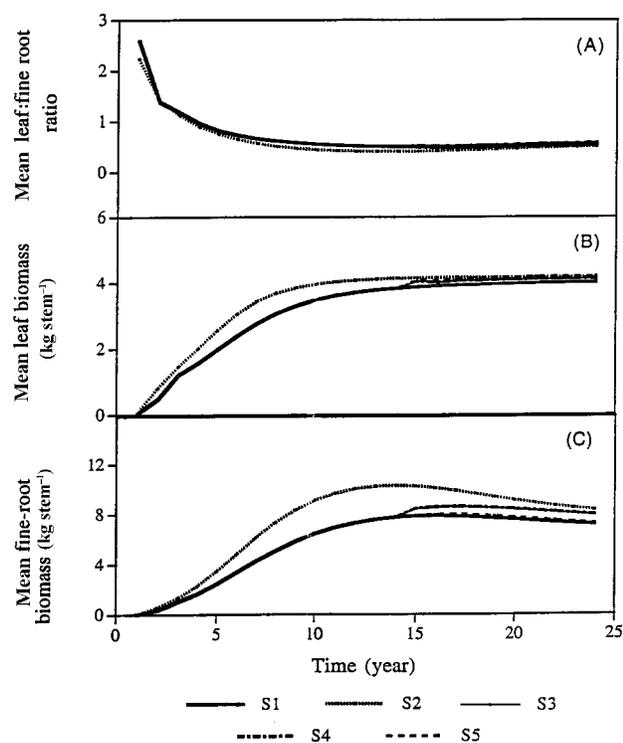Responses of leaf and root growth as well as leaf:fine root ratio

Figure 3. Predicted tree growth in various simulation scenarios. (A) Leaf:fine root ratio; (B) leaf biomass; and (C) fine root biomass. S1-S5 represent five simulation scenarios. Scenario 1 (S1) is at ambient CO_2 ($C_a = 350$ ppm) from the beginning of forest regrowth to the end of simulation for 24 years. Scenario 2 (S2) is at elevated CO_2 ($C_a = 650$ ppm) for 24 years. Scenario 3 (S3) is ambient-to-elevated CO_2 with $C_a = 350$ ppm in the first 14 years followed by a step increase in C_a ($C_a = 650$ ppm). Scenario 4 (S4) is ambient-to-elevated CO_2 as in S3 but with the mineralization rate enhanced by 20% at elevated CO_2. And Scenario 5 (S5) is ambient-to-elevated CO_2 as in S3 but with the root turnover rate increased by 20% at elevated CO_2.

in the five scenarios were examined over a 24-year period (Figure 3). In S2, where the ecosystem is exposed to elevated CO_2 from the beginning of regrowth, leaf biomass growth is increased by 28.8% in response to elevated CO_2 compared with that at ambient CO_2 at Year 8 (Figure 3B). The CO_2 stimulation gradually diminishes at Year 10 after leaf biomass (and leaf area index) reaches its maximum value. Elevated CO_2 also significantly increases fine root biomass growth (45.7% higher than at ambient CO_2 at Year 13, Figure 3C). The slight decline in fine root biomass after Year 15 is partly caused by increased root death and partly by a shift in biomass allocation to woody tissue with stand development. The differential increases in fine root versus leaf biomass growth results in reduced leaf:fine root ratio (Figure 3A). The modeling results suggest reduced responsiveness of leaf growth to CO_2 enrichment in a closed forest canopy, although strong positive responses of leaf growth to elevated CO_2 have been observed in short-term CO_2 enrichment studies with seedlings and saplings (Hogan et al. 1991, Tissue et al. 1996).

In S3 (ambient-to-elevated CO_2), which mimics the Duke FACE experiment, the leaf:root ratio decreases by 8%, leaf biomass increases by about 2.5% (Figure 3B), and root biomass increases by 11% compared with values for S1 (ambient CO_2 throughout the 24 years of simulation) (Figure 3C). A comparison of results for S3, where nitrogen mineralization rates were held constant, with those for S4, where mineralization rates were increased by 20%, indicates that, in S4, leaf growth slightly increased (from 4.11 to 4.13 kg stem^{-1}, Figure 3B) as did root biomass (7.8 to 8.0 Kg stem^{-1}, Figure 3C), leading to a 1.5% decrease in leaf:fine root ratio (Figure 3A).

When we simulated an enhanced root turnover rate of the roots at elevated CO_2 (S5), we found a slight increase in leaf growth (1.9%; from 4.11 to 4.19 kg stem^{-1}, Figure 3B) but decreased root biomass (6.8%; from 7.8 to 7.3 kg stem^{-1}, Figure 3C) compared to S3. Thus, there is a 7% increase in the leaf:fine root ratio (Figure 3A). The enhanced root turnover rate reduces root biomass and increases litter production, both of which contribute to higher soil organic matter decomposition and mineralization.

In all four elevated CO_2 scenarios (S2–S5), both leaf and root growth show a positive response, with roots being more sensitive to changes in CO_2 concentration than leaves. These patterns are similar to several observations in the field (e.g., Norby et al. 1992, Rogers et al. 1994).

Net primary productivity (NPP) and carbon storage

Elevated CO_2 (S2–S5) led to higher annual net primary productivity (NPP) and carbon storage compared with ambient CO_2 (S1) (Figure 4). If forest regrowth is exposed to elevated CO_2 through all 24 years (i.e., S2), annual NPP is always higher than at ambient CO_2 (S1) (Figure 4A). Annual NPP initially increases by 13% in S3, 14% in S4, and 28% in S5 compared with NPP in S1 (Figure 4A).

The predicted 13% increase in NPP in S3 is similar to preliminary findings of an approximately 12% increase in NPP in the first year of the Duke FACE experiment (E. DeLucia, University of Illinois, Champaign–Urbana, personal comm.).
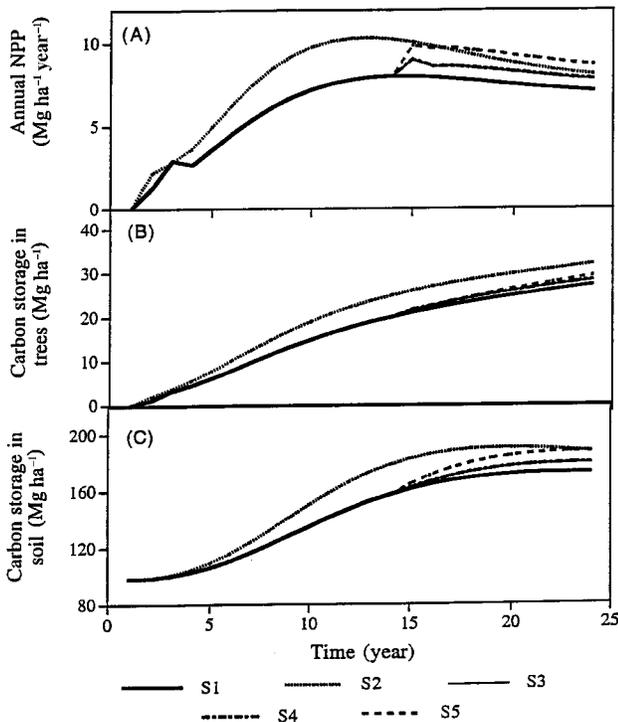
Figure 4. Predicted carbon production and storage of a forest ecosystem in various simulation scenarios. (A) Annual net primary production (NPP); (B) total carbon storage in trees; and (C) total carbon storage in soil (including carbon pools in both litter and soil organic matter). See Figure 3 for definition of S1–S5.

These initial increases in NPP are followed by a decline over time, down to less than 10% after two years. This pattern has also been reported in other modeling studies (Rastetter et al. 1991, Comins and McMurtrie 1993), and is attributed partly to soil nitrogen limitation and partly to the nature of donor-controlled processes in terrestrial ecosystems (Luo and Reynolds 1999). In S5, however, the increase in NPP is maintained for a longer time because increased root turnover resulted in increased soil N availability.

In general, increased carbon fixation in response to elevated CO_2 results in increased C storage in trees (cf. S1 with S2–5, Figure 4B). In S2, total C storage in trees is substantially increased, and in S3, there is a 4% increase in C storage after 10 years of exposure to elevated CO_2 (Figure 4B). Enhanced N mineralization (S4) increases C storage in trees by a small amount (0.2%) by the end of the simulation compared to the scenario with no mineralization changes (S3). Increased root turnover (S5) led to a 4% increase in stored C in trees compared with S3.

Increased carbon fixation in response to elevated CO_2 also results in increased C storage in the soil (i.e., litter and soil organic matter, Figure 4C). Simulated litter production is small in the first several years of CO_2 enrichment, but becomes substantial five years later. Thereafter, C input by litter production exceeds C release from soil respiration, leading to a rapid increase in soil carbon storage. The ambient-to-elevated CO_2

scenario (S3) led to a 9.2% increase in total C storage in soil after 10 years of CO_2 enrichment compared with S1. Enhanced N mineralization (S4) hardly increases C storage in soil compared with S3. Enhanced root turnover rate (S5) increases C storage in the soil by 4.7% after 10 years of CO_2 enrichment compared with S3 (Figure 4C).

Soil nitrogen availability and plant nitrogen demand

Plant–soil nitrogen cycling is a major process in determining the long-term responses of the ecosystem to CO_2. In Figure 5, we examined soil N dynamic processes by comparing the soil N availability index (N_{lim}, Equation 4) and N demand by trees over 24 years for each of the five simulation scenarios. The value of N_{lim}, which is the ratio of soil N supply to N demand by tree growth, was initially set at 1 in all simulations. The index declines quickly during the first 10 years of forest development in all the scenarios (Figure 5A). This sharp decline in N_{lim} during the first three years is a result of a sudden increase in N demand (Figure 5B) and is one of the major causes of reduced stimulation in forest NPP (Figure 4A). Enhanced nitrogen mineralization in S4 slightly increases soil N availability (1%) compared with S3. On the other hand, enhanced root turnover rate (S5) increases soil N availability by 5% compared with S3 (Figure 5A), because of more litter production.

After 10 years of forest regrowth, N_{lim} stabilizes at a low value, whereas simulated plant nitrogen demand is fairly dynamic over the 24 years of simulation in all scenarios (Figures 5A and 5B). Nitrogen demand increases in the first 10 years, reaches a maximum at 12 years, and then declines (Figure 5B). The N demand in S2 is 34.2% higher than in S1 at Year 12 and 6.5% higher at Year 24. Scenarios 3–5 result in approximately 3% increases in demand at Year 24 compared with S1.
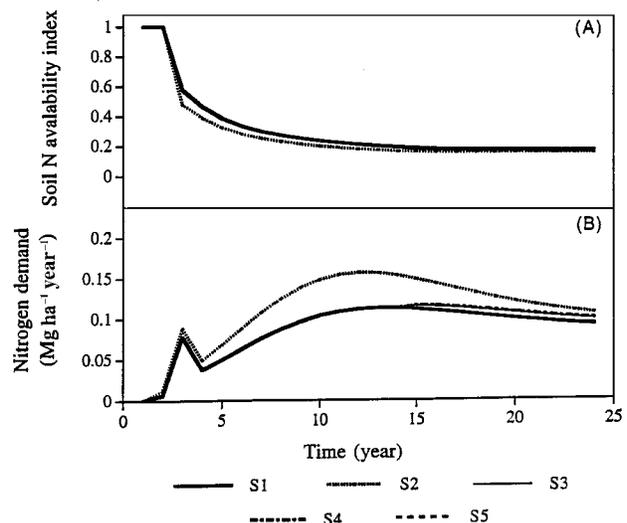

Figure 5. Responses of soil nitrogen availability and nitrogen demand under various simulation scenarios. (A) Soil nitrogen availability index; (B) plant nitrogen demand. See Figure 3 for definition of S1-S5.

Soil N availability versus NPP

To explore the dependence of NPP on soil nitrogen availability, we simulated mean annual NPP over 10 years with a series of fixed soil nitrogen availability indices (Figure 6A). These simulations show a positive response of forest production to soil nitrogen supply, consistent with both theoretical (Ågren 1988, Ingestad 1991) and experimental studies (Cole and Rapp 1981). In addition, elevated CO_2 positively interacts with soil nitrogen in determining annual NPP (Figure 6A). As the soil nitrogen availability index changes from 0.4 to 1, annual NPP at elevated CO_2 increases from 30 to 98% over 10 years compared with values at ambient CO_2. This positive interaction between CO_2 and nitrogen has been observed in several open-top chamber experiments with loblolly pine (Thomas et al. 1994, Griffin et al. 1995, King et al. 1996).

Carbon allocation in response to CO_2 enrichment and soil nitrogen conditions was examined by comparing the leaf:fine root ratio after 10 years of forest growth to fixed soil nitrogen availability indices. The results are shown in Figure 6B. A high soil nitrogen availability index led to a high leaf:fine root ratio, but elevated CO_2 reduced the ratio at all soil nitrogen availability indices. The predicted decrease in leaf:fine root ratio at elevated CO_2 is consistent with experimental results reported by Rogers et al. (1994).

Long-term versus short-term responses

Our results suggest that long-term forest responses to atmospheric CO_2 enrichment differ from short-term measured responses. These conclusions are consistent with other modeling studies (e.g., Comins and McMurtrie 1993, McMurtrie and Comins 1996, Rastetter et al. 1997, Luo and Reynolds 1999). Leaf biomass, for example, undergoes fast growth in the first 10 years of simulated forest regrowth (Figure 3B) but slows
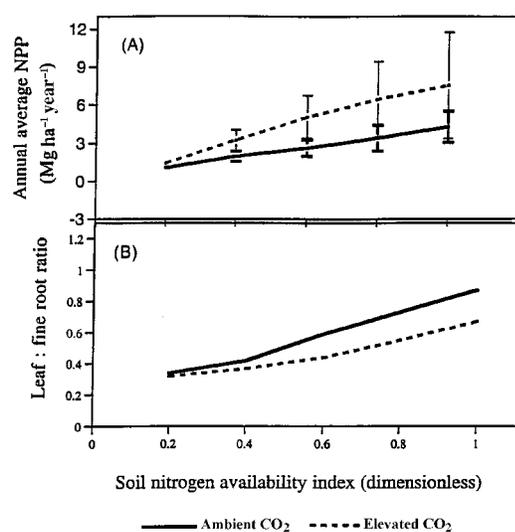

Figure 6. Response of tree growth to change in the soil nitrogen availability index at ambient and elevated CO_2. (A) Predicted annual average NPP and (B) leaf:root ratio at a series of fixed soil nitrogen availability indices (Equation 4) after 10 years of simulated tree growth.

down afterward. Similarly, fine root biomass rapidly accumulates in the first 15 years and then slightly declines (Figure 3C). As a consequence, the responsiveness of plant growth to elevated CO_2 is much higher in the early stages of forest development than in the later stages. In S2, for instance, mean leaf biomass increases by 34% at Year 5 of simulated forest regrowth compared with that in S1 (Figure 3B). Over the long-term (i.e., at Year 24), CO_2 enrichment (S2) led to only a 6% increase in leaf biomass (Figure 3B) compared with leaf biomass in S1.

Factors contributing to the large response to enhanced CO_2 in the early stages of forest stand development, as well as to the small responses in the later stages, include canopy development and soil N feedback. There is substantial evidence that leaf growth responds positively to elevated CO_2 in short-term studies (Hogan et al. 1991, Tissue et al. 1996). However, it is still unclear how canopies will respond to elevated CO_2 over a longer time and whether the "optimum" leaf area index (LAI) will be altered. Our results indicate that leaf growth slows down in a closed canopy exposed to elevated CO_2. Canopy development at elevated CO_2 will not only affect tree growth and NPP but also litter production and carbon storage (Norby et al. 1996). Current studies of canopy development in the FACE facility will help elucidate these responses.

Long-term responses of the forest ecosystem to elevated CO_2 may also be affected by nitrogen feedback. Previous studies have demonstrated that the change in N allocation in plants (Kirschbaum et al. 1994), the shift in C:N ratio in soil organic matter and wood (McMurtrie and Comins 1996), the change in net gross N mineralization ratio (Zak et al. 1993, Rastetter et al. 1997), and the change in the total amount of N in the ecosystem (McKane et al. 1997) are all important factors regulating long-term forest responses to CO_2 enrichment. Our modeling study with FORDYN shows that a 20% increase in root turnover rate results in a substantial increase in NPP and carbon storage in trees and soil, whereas the increase in mineralization produced a smaller enhancement in a CO_2 enriched environment. Models provide a convenient means to assess impacts of individual processes on ecosystem productivity and carbon storage. However, elevated CO_2 presumably induces changes in a suite of processes in natural ecosystems to balance the carbon and nitrogen relationship, potentially leading to additional carbon production and storage.

Conclusions

We used the hierarchical forest model FORDYN to examine tree growth and ecosystem carbon and nitrogen dynamics at different time scales. Our simulations suggest that estimation of long-term forest responses to CO_2 enrichment may be considerably affected by canopy development and soil nitrogen availability. A closed canopy may reduce the responsiveness of tree growth and ecosystem carbon storage to elevated CO_2, whereas forests in the early stage of canopy development are likely to be highly responsive to increaing atmospheric CO_2 concentration. Both increased nitrogen mineralization and root turnover rates in response to elevated CO_2 can stimulate tree growth and carbon storage. Enhanced root turnover rate re-

sulted in more carbon storage in trees than in soil. A detailed understanding of the nitrogen processes through both FACE experiments and modeling analyses will enhance our ability to predict long-term ecosystem responses to CO_2 enrichment.

Acknowledgments

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