# GROSS PRIMARY PRODUCTIVITY IN DUKE FOREST: MODELING SYNTHESIS OF CO$_2$ EXPERIMENT AND EDDY–FLUX DATA

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*Abstract.* This study was designed to estimate gross primary productivity (GPP) in the Duke Forest at both ambient and elevated CO$_2$ (ambient + 200 μL/L) concentrations using a physiologically based canopy model. The model stratified the canopy of loblolly pine (*Pinus taeda* L.) forest into six layers and estimated photosynthesis in each layer according to the Farquhar submodel coupled with the Ball-Berry stomatal conductance submodel. The model was parameterized with a suite of physiological measurements, including leaf area index (LAI), leaf nitrogen (N) concentration, photosynthesis–N relationships, and stomatal conductance. The model was validated against measured leaf photosynthesis and canopy carbon (C) fluxes estimated from eddy-covariance measurements (ECM). Application of this model to simulate canopy C fixation from 28 August 1996, the onset of CO$_2$ fumigation, to 31 December 1998 suggested that elevation of atmospheric [CO$_2$] to ambient + 200 μL/L resulted in increase of canopy C fixation by 35% in 1996, 39% in 1997, and 43% in 1998. The modeled GPP and its response to elevated [CO$_2$] were sensitive to parameter values of quantum yield of electron transport, leaf area index, and the vertical distribution of LAI within the canopy. Thus, further investigation on those parameters will help improve the precision of estimated ecosystem-scale C fluxes. Furthermore, comparison between the modeled and ECM-estimated canopy C fluxes suggested that soil moisture, in addition to air vapor pressure, controlled canopy photosynthesis during the drought period.

*Key words: canopy; carbon sink or sequestration; Duke Forest, North Carolina (USA); forest; global change; gross primary productivity (GPP); loblolly pine; model; modeling; photosynthesis; Pinus taeda; stomatal conductance.*

## INTRODUCTION

The signing of the Kyoto Protocol requires the quantification of terrestrial carbon (C) sinks in various biomes (IGBP terrestrial carbon working group 1998). Among all terrestrial biomes, forests are widely considered to have the largest potential to act as sinks for atmospheric CO$_2$ (Kirschbaum and Fischlin 1996). As a consequence, much effort is currently being directed towards studies of forest C uptake, storage, and release. Two newly developed techniques in particular are providing insight in forest C dynamics. They are Free-Air CO$_2$ Enrichment (FACE), in which mature forest canopies are exposed to elevated levels of atmospheric carbon dioxide (Hendrey et al. 1999), and eddy-covariance, which is used to measure whole-ecosystem CO$_2$ exchange (e.g., Baldocchi and Meyers 1998). At the Duke Forest in North Carolina, USA, these two

experimental techniques have been installed in parallel, providing an unrivaled source of experimental data for quantifying forest C fluxes (Hendrey et al. 1999, Katul and Albertson 1999). In order to predict the future rate of forest C sequestration, the data gained from such experiments need be used to quantify two key parameters: gross primary productivity (GPP), which is the amount of C that flows into the forest ecosystem via canopy photosynthesis, and residence time of C in the ecosystems (Luo and Reynolds 1999). The former is the subject of this study.

Attempts have long been made to quantify ecosystem GPP. One of the modern approaches is the micrometeorological technique of eddy covariance, which measures net ecosystem C exchange (Baldocchi and Meyers 1998). Conceptually when combined with estimated or measured ecosystem respiration (e.g., the summation of plant and soil respiration), the net ecosystem C fluxes can be partitioned to quantify GPP in ambient [CO$_2$] conditions. However, it is infeasible to use the eddy-covariance method for quantifying GPP in elevated [CO$_2$] plots. Mesocosms often are used to measure can-

opy C fluxes (Bugbee 1992, Luo et al. 1999). Such measurements are highly accurate but only technically feasible in artificial, small-stature ecosystems. Allometric relationships between biomass and some simple, measurable variables such as diameter at breast height are often used to estimate aboveground forest net and/ or gross primary productivity (NPP and GPP, respectively) (Kinerson et al. 1977, DeLucia et al. 1999), but belowground productivity typically is ignored. Modeling synthesis of experimental measurements offers another viable approach to quantify GPP at both ambient and elevated [$CO_2$] scenarios (Wang et al. 1998). The accuracy of the modeled GPP, however, depends on extensive data sets for parameterization and validation.

Canopy models, which account for heterogeneity in direct vs. diffuse radiation, wind profile, and nitrogen (N) distribution within canopy, are often used to examine scaling issues from leaf to canopy levels (Reynolds et al. 1992, Norman 1993), to test various algorithms to represent eddy-covariance flux data (Amthor 1994, Baldocchi and Meyers 1998, Williams et al. 1998), to study canopy ecophysiology (Gutschick and Wiegel 1988, Hirosi and Bazzaz 1998), and to quantify GPP (Williams et al. 1997, Wang et al. 1998). With eddy-covariance measurements (ECM) of C fluxes, such models can now be tested and/or parameterized at the canopy scale. In addition, about 40 field $CO_2$ experiments have been conducted worldwide using either open-top chambers or FACE facilities. Synthesis of data from those experiments with flux-validated models to estimate GPP has the potential to make a critical contribution to prediction of terrestrial C sequestration in the present and a future, higher $CO_2$ atmosphere.

In this paper we used the canopy model MAESTRA (Medlyn et al. 1999), a development of the MAESTRO model (Wang and Jarvis 1990), to estimate canopy GPP for the ambient and elevated [$CO_2$] treatments in the Duke Forest FACE experimental site. The model was parameterized from leaf-scale gas exchange measurements and validated against the flux data at the ambient atmospheric [$CO_2$] environment. Since it is technically difficult to measure canopy fluxes in the elevated [$CO_2$] treatment plots, the model provides an effective means to estimate GPP in this treatment, allowing us to quantify the stimulation of total canopy C uptake by exposure to elevated [$CO_2$]. In addition, accurate model estimates of GPP depend on constraints of model parameters by experimental data. Where data are not available or measured with low precision, sensitivity analysis was carried out to evaluate variability in estimated GPP caused by the uncertainties in model parameterization. Finally, many smaller-scale experiments with plants in elevated [$CO_2$] indicate that trees may acclimate physiologically or structurally to growth at higher [$CO_2$] levels. Although there is little evidence of such acclimation in the Duke FACE experiment to date (e.g., Ellsworth et al. 1995, Ellsworth 1999, 2000,

Hymus et al. 1999, and Myers et al. 1999), we use the model to explore the potential impacts of such acclimation on estimated GPP.

## MATERIAL AND METHODS

### Site description

The Duke FACE experimental site is located in the Blackwood Division of the Duke Forest, North Carolina, USA (35.58' N, 79.8' W). The FACE technique (Hendrey et al. 1999) has been applied to three 30-m-diameter circular plots for exposure to elevated [$CO_2$] (ambient + 200 μL/L) and another three plots are exposed to ambient [$CO_2$]. The experiment started in August 1996 on a 14-yr-old loblolly pine (*Pinus taeda* L.) stand that wàs established from seedlings in 1983 following clear-cutting (Ellsworth et al. 1995). Loblolly pine trees were initially planted at 2.4 × 2.4 m spacing. The subcanopy is dominated by *Liquidambar styraciflua* L., *Liriodendron tulipifera* L., and *Acer rubrum* L. There are ~50 understory species (J. Mohan, *personal communication*) but measurements suggest that biomass and net primary productivity (NPP) of those species is only a small fraction in the whole forest ecosystem (DeLucia et al. 1999). Thus, we focused this modeling study on the loblolly pine for quantifying the whole ecosystem canopy C fluxes.

The climate at the FACE site can be characterized as warm and humid with a frost-free season of ~200 d. Daily average air temperature ranges from −5°C in winter to 30°C in summer (Fig. 1A) with annual average of 14.3°, 14.4°, and 15.6°C in 1996, 1997, and 1998, respectively. Average annual precipitation was 1064 mm over 1948–1998. It was 1116, 1062, and 1305 mm in 1996, 1997, and 1998, respectively, and relatively evenly distributed throughout the year (Fig. 1B). Total photosynthetically active radiation (PAR) on clear days ranged from 25 mol·m$^{-2}$·d$^{-1}$ in winter and nearly 60 mol·m$^{-2}$·d$^{-1}$ in summer (Fig. 1C). The soil at the site is of the Enon Series, a low-fertility Ultic Alfisol, derived from igneous rock, yielding an acidic (pH = 5.75), well-developed profile with mixed clay mineralogy (Andrews et al. 1999).

### Model structure and parameterization

We used the MAESTRA model to estimate photosynthetic $CO_2$ assimilation of the loblolly pine canopy at the Duke FACE site. The MAESTRA model (Medlyn et al. 2000) is an updated version of MAESTRO (Wang and Jarvis 1990), a three dimensional model of forest canopy radiation absorption, photosynthesis, and transpiration. The MAESTRO model has been applied to study canopy C fluxes of *Picea sitchensis* (Wang and Jarvis 1990), *Pinus radiata* (McMurtrie and Wang 1993), and *Betula pendula* (Wang et al. 1998). The major revision in the MAESTRA model is the incorporation of standard formulations of the mechanistic $C_3$ photosynthesis model of Farquhar et al. (1980) and the more empirical formulation of stomatal conduc-
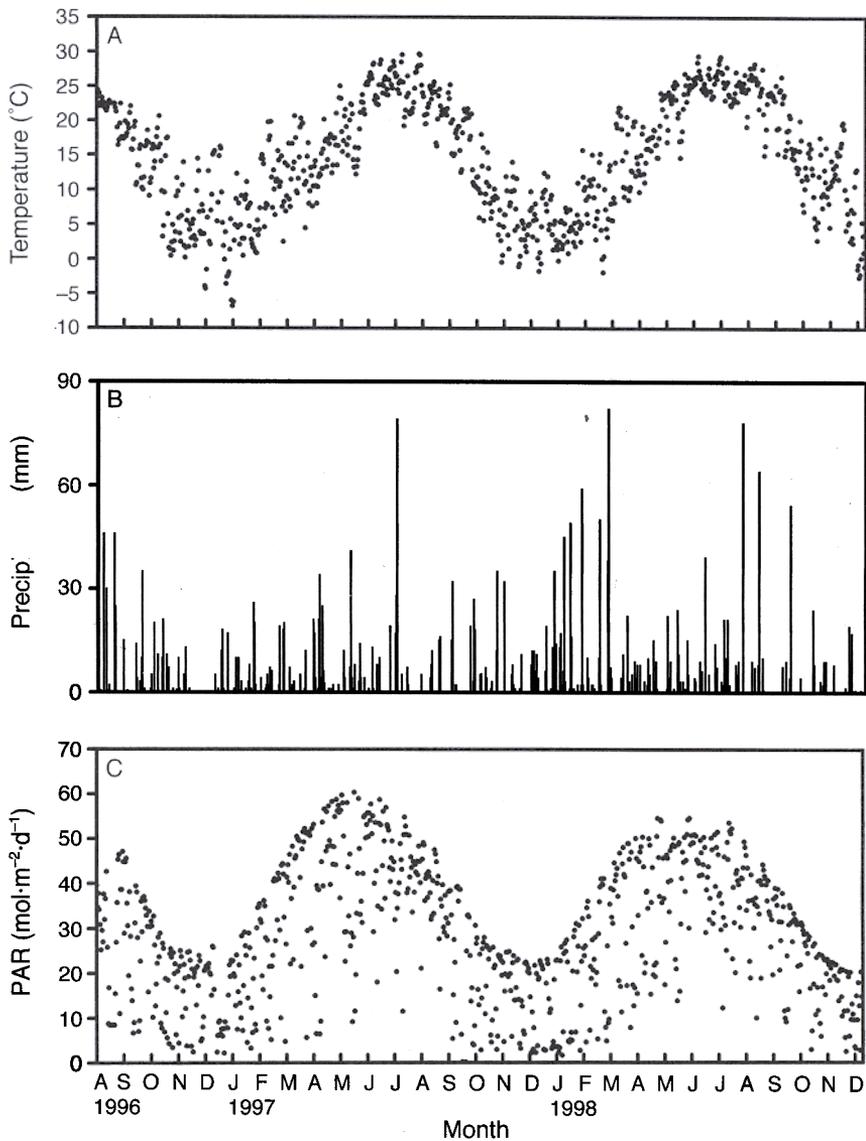
FIG. 1. Daily average values of three local climate measures recorded from August 1996 to December 1998 at the Duke Forest FACE site: (A) air temperature, (B) precipitation, and (C) daily total photosynthetically active radiation (PAR).

tance described by Ball et al. (1987) (Medlyn et al. 2000). In addition, changes were made to improve coding by modularization and flexible handing of input and output. The advantage of this degree of physiological detail is that complex interactions of CO$_2$ concentration, light, temperature, and air humidity can be accounted for realistically.

Leaf photosynthesis is estimated by the Farquhar photosynthesis model (Farquhar et al. 1980), in which photosynthesis is given by the minimum of

$$A_V = V_{cmax}(C_i - \Gamma^*)/(C_i + K_C(1 + O/K_O)) - R_d \quad (1a)$$

$$A_J = (J/4)(C_i - \Gamma^*)/(C_i + 2\Gamma^*) - R_d \quad (1b)$$

coupled to the Ball-Berry stomatal conductance model (Ball et al. 1987):

$$g_s = g_0 + g_1 A_n RH/C_a. \quad (2)$$

All the above and below symbols are defined in Table 1 together with units, values, and reference sources. The light dependence of $J$ is given by the non-rectangular hyperbola:

$$\theta J^2 - (a\alpha I + J_{max}) J + a\alpha I J_{max} = 0. \quad (3)$$

The temperature dependences follow the formulation given by Medlyn et al. (1999):

$$\Gamma^* = 36.9 + 1.88(T - 25) + 0.036(T - 25)^2 \quad (4a)$$

$$K_C = 404 \exp[59.4(T - 25)/298R(T + 273)] \quad (4b)$$

$$K_O = 0.248 \exp[36(T - 25)/298R(T + 273)]. \quad (4c)$$

The coefficients in the above equations are taken from

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TABLE 1. List of symbols, definitions, units, and values of variables used in the model of carbon uptake in a forest canopy.

| Variable | Definition | Unit | Value |
|---|---|---|---|
| $a$ | leaf radiation absorptance | dimensionless | |
| $A_v$ | leaf photosynthesis limited by carboxylation | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $A_J$ | leaf photosynthesis limited by RuBP regeneration | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $A_n$ | net photosynthetic rate, being the minimum of $A_v$ and $A_J$ | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $b$ | coefficient in Eq. 8 | dimensionless | |
| | coefficient in Eq. 8 | dimensionless | |
| $C_a$ | the atmospheric $CO_2$ concentration | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $C_i$ | intercellular $CO_2$ concentration | $\mu mol/mol$ | |
| $d$ | coefficient in Eq. 8 | dimensionless | |
| $E_{aJ}$ | Activation energy for RuBP regeneration (Eq. 5a) | kJ/mol | |
| $E_{av}$ | Activation energy for carboxylation (Eq. 5b) | kJ/mol | |
| $f_i$ | normalized leaf area density at canopy layer $i$ | $m^{-1}$ | |
| $g_1$ | empirical coefficients | dimensionless | |
| $g_0$ | empirical coefficients | $mol \cdot m^{-2} \cdot s^{-1}$ | |
| GPP | gross primary productivity | $g \, C \cdot m^{-2} \cdot yr^{-1}$ | , |
| $g_s$ | stomatal conductance | $mol \cdot m^{-2} \cdot s^{-1}$ | |
| $h$ | relative height of canopy layers in Eq. 8 | dimensionless | |
| $H$ | temperature dependent coefficient in Eq. 5a | kJ/mol | |
| | the instantaneous photon flux density | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $J$ | rate of electron transport | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $J_{max}$ | maximum electron transport rate | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $J_{max\,25}$ | $J_{max}$ at 25°C | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $K_C$ | Michaelis-Menten constants for $CO_2$ | $\mu mol/mol$ | |
| $K_O$ | Michaelis-Menten constants for oxygen | $mmol/mol$ | |
| LAI | leaf area index | dimensionless | |
| $N_{area}$ | area-based $N$ concentration in live leaves | $g/m$ | |
| $O$ | partial pressure of oxygen | $mol/mol$ | |
| $R$ | universal gas constant | $J \cdot mol^{-1} \cdot K^{-1}$ | |
| $R_d$ | leaf dark respiration rate | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $R_{d\,25}$ | $R_d$ at 25°C | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| RH | the relative humidity | dimensionless | |
| $S$ | crown shape | dimensionless | |
| $T$ | leaf temperature | °C | |
| $V_{cmax}$ | maximum RuBP carboxylase activity | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $V_{cmax\,25}$ | $V_{cmax}$ at 25°C | $\mu mol \cdot m^{-2} \cdot s^{-1}$ | |
| $Z$ | temperature dependent coefficient in Eq. 5a | $kJ \cdot K^{-1} \cdot mol^{-1}$ | |
| $\Gamma*$ | $CO_2$ compensation point | $\mu mol/mol$ | |
| $\alpha$ | the initial quantum yield of electron transport at low quantum density | dimensionless | |
| $\theta$ | the curvature | dimensionless | |

Note: Values can be constants, model input or output, calculated from an equation, or estimated by model simulation.
† Value from Hymus et al. (1999).
‡ Values derived from measured vertical distribution of leaf area (D. Ellsworth, *unpublished data*) and a defined crown shape.
§ Values from Badger and Collatz (1977) and Farquhar et al. (1980).
‖ Values derived from data by Ellsworth (2000).
¶ Value from J. Lewis (*unpublished data*).
# Values derived from relationship between transmittance and LAI data (D. Ellsworth, *unpublished data*) with a prescribed crown type.
†† Value at ambient [$CO_2$]. At elevated $CO_2$ $\alpha = 0.15$, 25% higher than that at ambient [$CO_2$].
‡‡ Value from Walcroft et al. 1997.

Badger and Collatz (1977), Jordan and Ogren (1984), and von Caemmerer et al. (1994). The temperature dependences of $V_{cmax}$ and $J_{max}$ are given by

$$J_{max} = J_{max\,25}\exp[E_{aj}(T - 25)/(298RT)]$$
$$\times (\{1 + \exp[(298Z - H)/(298R)]\}$$
$$\div \{1 + \exp[(Z[T + 273] - H)$$
$$\div (R[T + 273])]\}) \quad (5a)$$

$$V_{max} = V_{cmax\,25}\exp[E_{av}(T - 25)/298R(T + 273)]. \quad (5b)$$

The above temperature dependence equations resulted in overestimated photosynthesis when temperature is below 10°C. In this simulation, we assume that both

$J_{max}$ and $V_{cmax}$ are linearly reduced to 0 between 10° and 5°C as per Ellsworth (2000).

The parameters $V_{cmax\,25}$ and $J_{max\,25}$ are linearly related to area-based leaf N concentration ($N_{area}$, in grams per square meter) (Field 1983, Luo et al. 1994). The following relationships were determined from experimental measurements with loblolly pine (Ellsworth 1998):

$$V_{cmax\,25} = 25.3N_{area} + 28.6 \quad (6a)$$

$$J_{max\,25} = 53.1N_{area} + 60.0. \quad (6b)$$

The leaf dark respiration rate $R_d$ is given by

$$R_d = R_{d\,25}\exp(0.07(T - 25)). \quad (7)$$

Eqs. 1–7 are analytically solved for $A_n$, $g_s$, and $C_i$ using

a method presented by Leuning (1995). When the light level is below the light compensation point, $A_n$ is negative and $g_s$ becomes $<g_0$ or even negative. This modeling study assumes that $g_s = g_0$ below the light compensation point.

The canopy is represented by an array of semi-ellipsoidal tree crowns in an area of 25 × 25 m$^2$ plot. Each crown is divided into six horizontal layers with each layer divided into 12 gridpoints of equal volume (Wang and Jarvis 1990). Each layer is specified by a number of physical and physiological properties, including radiation, temperature, leaf area, and leaf N content. The trees were assumed to be evenly spaced because the loblolly pine forest was established as a plantation. Leaf area index (LAI) was measured from August 1996 to December 1998 using optical techniques (LI-COR LAI-2000, LI-COR, Lincoln, Nebraska, USA). The measurements indicated that canopy LAI displays a strong seasonal variation, but less year-to-year variation, and no significant changes with respect to [CO$_2$] treatments in the first 2.5 yr of CO$_2$ exposure (D. Ellsworth, *unpublished data*). The measured monthly mean values of LAI were 2.63, 2.63, 2.63, 2.67, 2.83, 3.63, 4.50, 4.67, 4.43, 4.00, 3.50, and 2.83 from January to December at both ambient and elevated [CO$_2$] treatments. A continuously changing leaf area for each day was obtained using the linear interpolation of the monthly mean LAI.

Mean leaf area density within the crown was calculated as leaf area per unit crown volume in each layer according to Wang et al. (1990). In October 1997 the vertical distribution of leaf area was measured at points every 2 m through the canopy (D. Ellsworth, *unpublished data*). The measured leaf area distribution was divided by the volume of the crown in each canopy layer, calculated using a semi-ellipsoid approximation, to obtain leaf area density in that layer. The leaf area density was then normalized using the total leaf area density for the crown. The normalized leaf area density ($f_i$, where $i$ represents the $i$th canopy layer) was then fitted to a beta function,

$$f_i = dh^b(1 - h)^c \qquad (8)$$

resulting in 0.16, 0.66, 1.16, 1.50, 1.56, and 1.04 m$^{-1}$ at the midpoint of the six canopy layers from the top to the bottom. Note that $f_i$ in this individual tree-based model differs from functions of leaf area density calculated in other models, due to the need to consider the volume of crown defined by a particular crown shape.

The MAESTRA model alters the light extinction coefficient by varying leaf incidence angle distribution defined by the ratio of horizontal to vertical axes ($S$, crown shape) of the semi-ellipsoidal crown. If $S = 1$, there is a spherical leaf angle distribution. The mean leaf angle is ~57° and light extinction coefficient is 0.5. From simultaneously measured transmittance and LAI (D. Ellsworth, *unpublished data*), a value for the

canopy extinction coefficient of 0.67 was estimated, corresponding to a mean leaf incidence angles of 45° and $S = 1.64$ (Wang and Jarvis 1988). N content per unit projected leaf area in the six layers from the top to the bottom of the canopy were 2.10, 2.10, 1.92, 1.73, 1.55, 1.37 g/m, which were derived from measured N content per unit total surface leaf area (D. Ellsworth, *unpublished data*) times the ratio of total to projected leaf area (equaling 2.36). Since no apparent seasonal variation in leaf *N* was observed (R. Thomas, *personal communication*), this modeling study used a single *N* profile in the canopy for the whole simulation period.

Environmental variables that drive model simulations are radiation, air temperature, air humidity, wind speed, and atmospheric CO$_2$ concentration above the canopy. All the variables were recorded at the FACE site (Fig. 1), and the recorded data were used in the model simulations. Missing data of relative humidity from late 1996 to early 1997 were filled using dewpoint temperature that was assumed to be the minimum daily temperature. The input radiation was PAR, and near infrared (NIR) and thermal radiation were estimated from PAR, with their distribution within the canopy as described by Wang and Jarvis (1990). The wind speed in canopy was assumed to decay exponentially with canopy depth with extinction coefficient equaling 0.4. The generated wind profile is similar to that predicted by the second-order closure model of Katul and Albertson (1999). The MAESTRA model assumed that air humidity, temperature, and CO$_2$ concentration were uniformly distributed within the canopy and identical to their values above the canopy. The time step in the model simulation is 1 h.

### Validation and sensitivity analysis

Validation of the model was done using measurements of leaf-level photosynthetic rates and canopy photosynthesis. Measurements of leaf photosynthesis were described in detail by Ellsworth (1999, 2000). The eddy-covariance technique measured net ecosystem exchange of C (Katul and Albertson 1999) as the difference between canopy photosynthesis and ecosystem dark respiration. The latter is the summation of plant and soil respiration. Ecosystem dark respiration during the daytime was estimated from nighttime respiration of the entire ecosystem with $Q_{10} = 1.9$ (Andrews et al. 1999) for the difference between averaged night temperature and temperature at a particular hour during daytime. Averaged nighttime respiration was used as a base value for each day whereas daytime ecosystem respiration was calculated individually for each 1-h time step. Since the accuracy of eddy-covariance measurements (ECM) at night depends on wind speed, we excluded nearly 28% of data points of ECM when wind speed was $<0.4$ m/s. Note that modeled net leaf photosynthesis was compared with leaf-level measurements, whereas modeled canopy photosynthesis was validated against the estimated GPP from

FIG. 2. Modeled (open circles) and measured (solid circles) diurnal variation in photosynthetic rate of leaves at the top canopy at ambient [$CO_2$] on (A) 1 February 1997, (B) 8 April 1997, (C) 8 August 1997, (D) 30 September 1997, and (E) 18 November 1997.
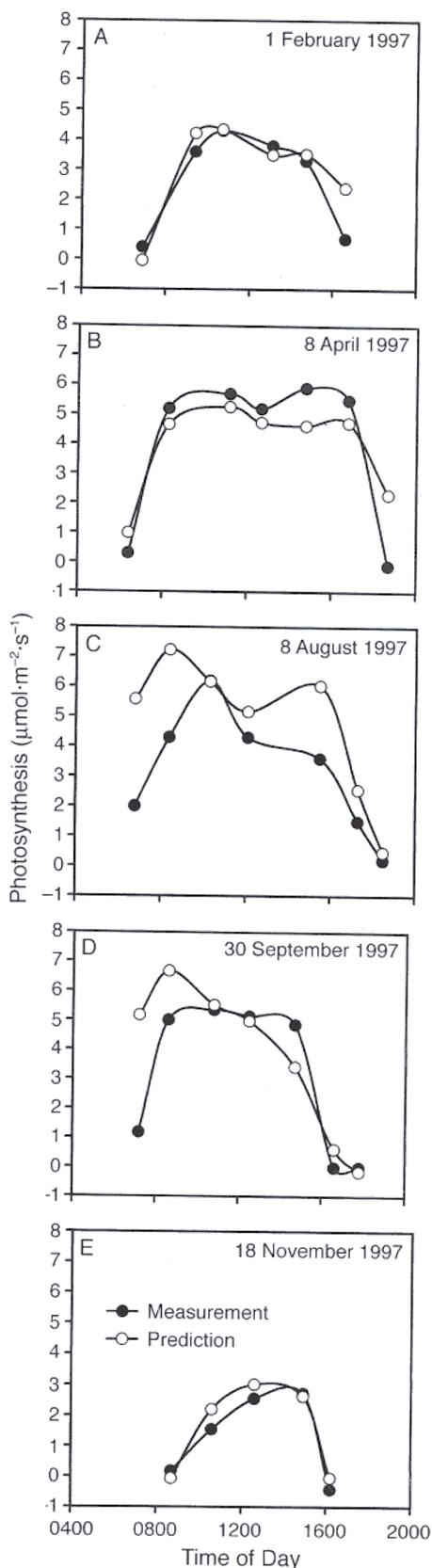
ECM. The latter were made above one control plot of the FACE project with the ambient $CO_2$ treatment starting in July 1997.

We did sensitivity analysis (SA) on accuracy of modeling estimates of GPP, motivated by the fact that predicting terrestrial C sequestration requires a minimal uncertainty. SA was done on three types of parameters. The first type of parameters are those measured at the Duke FACE site. The sensitivity analysis was used to assess the variability in GPP caused by the variation in parameter values. That type of parameters include: (1) the slope ($g_1$); and (2) intercept ($g_0$) of the Ball-Berry model; and (3) area-based N concentration ($N_{area}$); (4) carboxylation at 25°C ($V_{cmax\,25}$); (5) electron transport at 25°C ($J_{max\,25}$); and (6) total canopy leaf area (LA). The ranges of parameter values were chosen according to either measurements or variance in published results. For example, the 4.0–7.0 range of $g_1$ may be too broad for loblolly pine but does envelop all the reported variation (Baldocchi and Meyers 1998). The 15% changes in the $V_{cmax\,25}$ and $J_{max\,25}$ are within the ranges reported in Wullschleger (1993) and were done by altering both the coefficients in Eqs. 6a and 6b, respectively.

The second type of parameters are those not measured in the FACE project but with the potential to affect canopy C fluxes based on our prior knowledge. Those parameters include (1) curvature of assimilation-to-radiation response curve ($\theta$) and (2) initial quantum yield of electron transport at low quantum flux densities ($\alpha$, quantum yield hereafter). The values of $\theta$ and $\alpha$ were from Walcroft et al. (1997). The sensitivity analysis was done to evaluate the necessity of measuring those parameters in the FACE project in the future.

The third type of parameters were examined with the maximal theoretical ranges or quantitatively different patterns. They include (1) total vs. projected area (T:P) ratio of needles; (2) crown shape ($S$); (3) uniform vertical N distribution within the canopy; (4) uniform vertical LA distribution; and (5) vertical distribution of relative leaf density ($b$, $c$). The area ratio varied from T:P = 2.36 in the base case to T:P = 3.14 for a cylindrical shape. Crown shape varied from $S = 1.64$ (more planophile) to $S = 1.00$ (spherical), corresponding to the light extinction coefficient of 0.67 and 0.50, respectively. In the uniform $N$ distribution, the area-based N concentration is set to $N_{area} = 1.68$, the mean $N_{area}$ by conserving total canopy N. The uniform LA distribution has the same LAI as in the base case. By switching coefficients $b$ and $c$ in Eq. 8, the vertical

distribution of relative leaf density changed from an upright cone to the inverse cone. Note that temperature parameters in calculation of carboxylation ($V_{cmax}$), electron transport ($J_{max}$), and $CO_2$ compensation point ($\Gamma^*$) were not analyzed because of the lack of alternative values for pine species.

Results from the accuracy sensitivity analysis were reorganized to evaluate relative importance of $CO_2$-induced acclimation on GPP. The variables used in the sensitivity analysis of acclimation include: (1) $N_{area}$; (2) canopy leaf area index (LAI); (3) $g_1$; (4) quantum yield $\alpha$. Those parameters were chosen to reflect often-observed variation in $CO_2$ experiments. The reorganization was done to calculate $CO_2$ enhancement of GPP at elevated $CO_2$ divided by that in the base case of ambient $CO_2$. Acclimation of the quantum yield from $\alpha = 0.12$ (no change from the base case of the ambient [$CO_2$]) to $\alpha = 0.20$ (66.7% higher than that in the ambient [$CO_2$]) is within the range of experimental data (Hymus et al. 1999).

### RESULTS

#### Predicted and measured leaf photosynthetic rates

The diurnal courses of photosynthetic rate of leaves at the top of the canopy calculated from the model were validated against data collected at the Duke Forest FACE site at both ambient (Fig. 2; Ellsworth 2000) and elevated [$CO_2$] treatments (Fig. 3) in 1997. In comparison with the measurements at ambient [$CO_2$], the model overestimated the leaf photosynthesis at a few time points including 0800 and 1500 on 8 August, and 0800 on 30 September. Model estimates were lower than the measurements at ambient [$CO_2$] from 1000 to 1800 on 8 April and 1600 on 30 September (Fig. 2). At elevated [$CO_2$], the model overestimated the leaf photosynthesis at 1500 on 8 August and 18 November and underestimated the leaf photosynthesis at 0900 and 1100 on 8 April and at 1500 on 30 September (Fig. 3). Overall, the model slightly underestimated the leaf photosynthesis in the high range and overestimated the photosynthesis in the low range (Fig. 4).

#### Predicted and measured canopy C flux

We compared canopy C influx rates between the model predictions and estimates from eddy-covariance measurements (ECM) from 1 August to 31 December 1997 (Figs. 5–8). In order to provide an overall picture of goodness of fit between the model and data, we averaged hourly values of canopy C uptake in each month from August to December 1997 (Fig. 5). Modeled values were excluded from the calculation of the monthly averages of canopy C fluxes for those hours when eddy-covariance data were not available. As a result, from 10 to 23 data points were used for calculating the monthly averages for each hour.

Predictions were generally consistent with measurements. The model overestimated midday canopy C
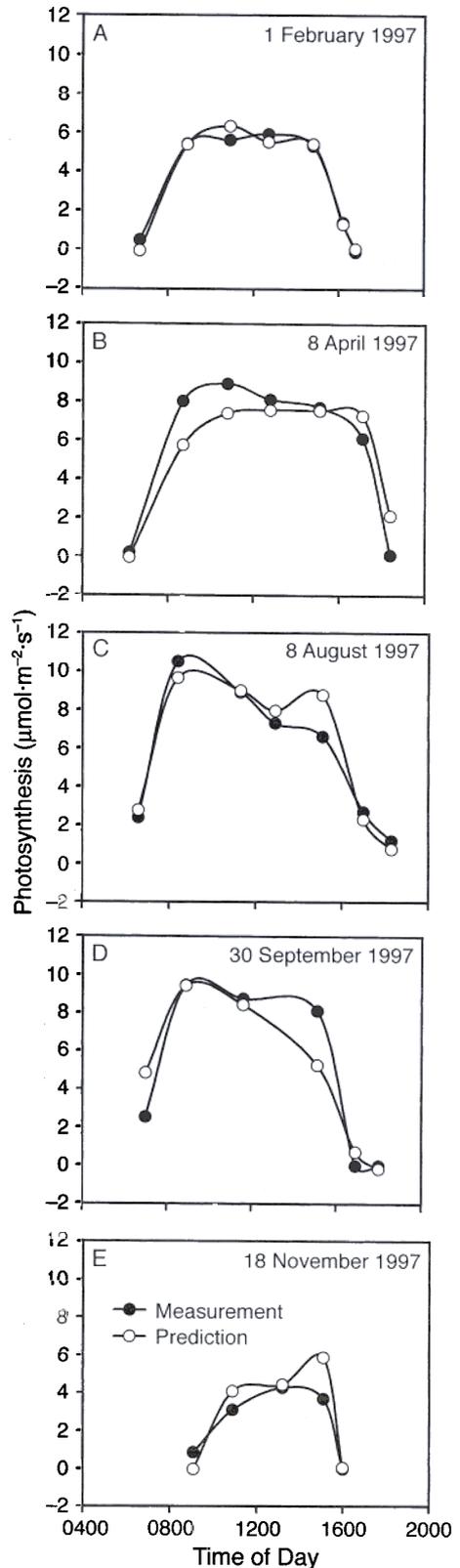


FIG. 3. Modeled (open circles) and measured (solid circles) diurnal variation in photosynthetic rate of leaves at elevated (ambient + 200 μL/L) $CO_2$ concentration from 1 February to 18 November 1997.
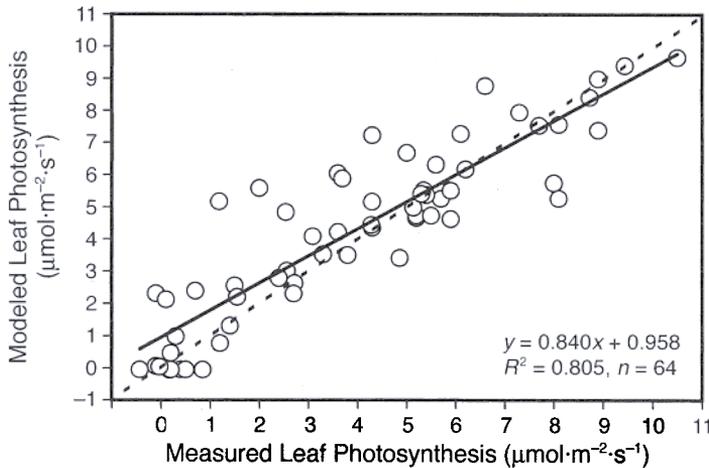
FIG. 4. Comparison of modeled with measured leaf photosynthetic rates using data presented in Figs. 1 and 2. The solid line is the regression indicating model-predicted net photosynthesis: $y = 0.958 + 0.84x$, where $x$ is measured net photosynthesis, with determination coefficient $R^2 = 0.805$ and sample size $n = 64$ iterations. The dotted line is the 1:1 line.

fluxes in August 1997 (Fig. 5) due to the severe drought stress in the late part of the month (Ellsworth 1999). Indeed, the MAESTRA model overpredicted canopy C fluxes by 15% in comparison to data from ECM during the severe drought period from 26 August to 6 September 1997. On the most severe drought day of 30 August 1997, the measured midday canopy photosynthesis averaged 0.273 g $C \cdot m^{-2} \cdot h^{-1}$, 47% lower than the model prediction. In addition, the model tended to underestimate the canopy C fluxes in early morning and overestimate the fluxes in late morning (Fig. 5). Toward noon, the difference disappears. Overall, the cumulative error during the period of 5 mo is <1.0% of the total of the fluxes from ECM.

Plotting predicted hourly values of canopy C fluxes against estimates from ECM demonstrates a correlation between the model and data (Fig. 6) with a determination coefficient of $R^2 = 0.717$ and a regression equation $y = 0.855x + 0.020$, where $y$ is the model predictions and $x$ is the estimates from ECM. The considerable deviation of this regression from a 1:1 line partly results from the fact that the model does not predict any negative values of canopy gross photosynthesis whereas some of estimated gross C fluxes from ECM were negative, reflecting uncertainties in the ecosystem respiration estimates.

Predicted daily total of canopy C uptake was consistent with the estimates from ECM during the period from 1 August to 31 December 1997 (Fig. 7). Both predicted and measured canopy C fluxes decreased from 9 g $C \cdot m^{-2} \cdot d^{-1}$ in early August to ~2 g $C \cdot m^{-2} \cdot d^{-1}$ in December 1997. Plotting model predictions against the estimates from ECM yields a regression line $y = 0.958x$, where $x$ is the estimates from ECM and $y$ is the model predictions, with $R^2 = 0.851$ (Fig. 8).

### Predicted annual GPP at ambient and elevated [CO₂]

The dynamics of gross C uptake through the loblolly pine forest canopy at ambient and elevated [CO₂] dur-

ing the period from 28 August 1996, the onset of $CO_2$ fumigation, to 31 December 1998 are shown in Fig. 9. Daily canopy C uptake ranged from 0 g $C \cdot m^{-2} \cdot d^{-1}$ in the winter on some exceptionally cold days to 8 g $C \cdot m^{-2} \cdot d^{-1}$ in the summer at the ambient [CO₂]. At elevated [CO₂] it ranged from 0 g $C \cdot m^{-2} \cdot d^{-1}$ in the winter to nearly 12 g $C \cdot m^{-2} \cdot d^{-1}$ in the summer. Summation of the daily values leads to estimates of the annual gross primary productivity (GPP) in the loblolly pine forest (Table 2). The annual GPP was estimated to be 1224 and 1695 g $C \cdot m^{-2} \cdot yr^{-1}$ at ambient and elevated [CO₂], respectively, in 1997. It was 1250 and 1786 g $C \cdot m^{-2} \cdot yr^{-1}$ at ambient and elevated [CO₂], respectively, in 1998. The canopy C influx from 28 August to 31 December 1996 was estimated to be 337 and 456 g $C \cdot m^{-2} \cdot yr^{-1}$ at ambient and elevated [CO₂], respectively. Accordingly, elevated [CO₂] increased GPP by 35% in 1996, 39% in 1997, and 43% in 1998. The larger $CO_2$ stimulation in 1998 than the two previous years likely resulted from higher annual temperature and more precipitation (Fig. 1). The $CO_2$ enhancement in canopy C flux also varied with season, being higher in summer and lower in winter (Fig. 10). The seasonal variation is consistent with theoretical prediction that the $CO_2$ stimulation of photosynthetic C fixation increases with temperature (Long 1991).

### Sensitivity of GPP to model parameters

Among the parameters examined (Table 2), predicted GPP was most sensitive to quantum yield of electron transport ($\alpha$, see Eq. 3). For a change from $\alpha = 0.12$–0.15 mol/mol at ambient [CO₂] and from $\alpha = 0.15$–0.20 mol/mol at elevated [CO₂], predicted GPP increased on average by 19% and 25%, respectively, over the study period of 2.5 yr. Predicted GPP was also sensitive to changes in total canopy leaf area (LA), the curvature in the assimilation-to-light response curve ($\theta$), the total vs. projected needle areas ratio (T:P), the slope in the Ball-Berry model ($g_1$), and the vertical distribution of relative leaf density ($b$, $c$), and area-
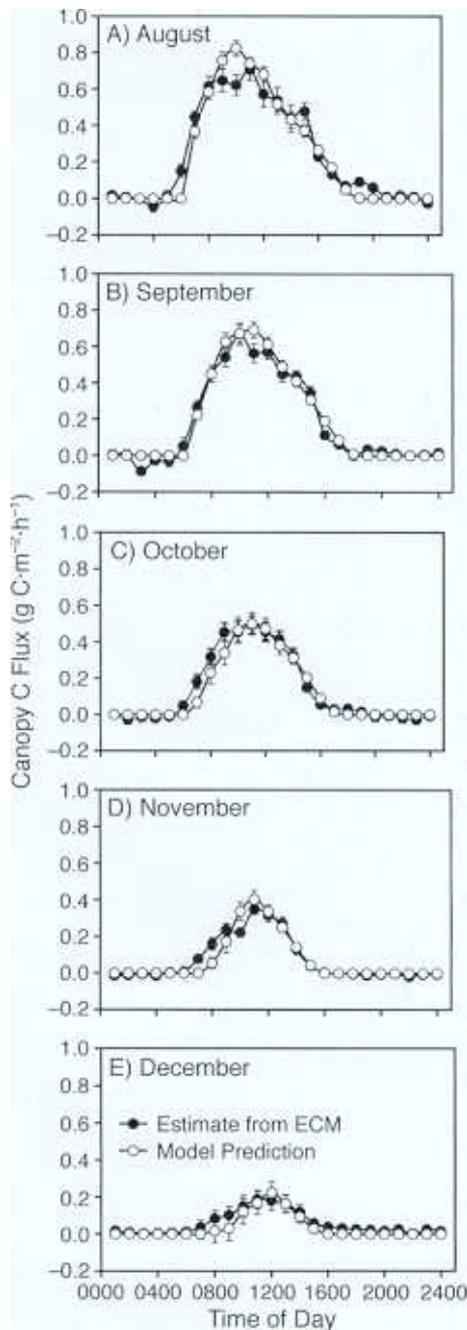
FIG. 5. Diurnal variation in canopy C fluxes estimated from eddy-covariance measurements (solid circles) and predicted from the model (open circles) from August to December 1997.

based leaf N ($N_{area}$). On the other hand, the sensitivity analysis indicated changes in the intercept in the Ball–Berry model ($g_0$), maximal electron transport ($J_{max\ 25}$), maximal carboxylation rate ($V_{cmax\ 25}$), light extinction coefficient by changing needle angle distribution ($S$), and canopy N distribution had small impacts on GPP.

### Potential effects of CO$_2$ acclimation on GPP

Of the potential acclimation responses considered, the most significant was a change in the quantum yield of electron transport ($\alpha$) (Fig. 11). If $\alpha$ was assumed to be identical between ambient and elevated [CO$_2$] treatments, GPP was estimated to increase by <20% at elevated [CO$_2$] in comparison to that at ambient [CO$_2$]. On the other hand, if quantum yield at elevated [CO$_2$] treatment was set to be $\alpha = 0.20$, 66.7% higher than that at ambient [CO$_2$] treatment, GPP was estimated to increase by >70% at elevated [CO$_2$] in comparison to that at ambient [CO$_2$]. The predicted response of GPP to elevated [CO$_2$] was also sensitive to potential acclimatory adjustments in LAI; a 10% increase or decrease in LAI causes approximately a 10% change in predicted CO$_2$ stimulation effects on GPP. Changes in area-based leaf N and $g_1$ (the slope of the Ball-Berry model) had smaller effects on GPP.

### DISCUSSION

Synthesis of both leaf- and canopy-level measurements using a physiologically based model in this study suggested that the loblolly pine forest at Durham, North Carolina, USA fixes 1200–1300 g C·m$^{-2}$·yr$^{-1}$ at the ambient [CO$_2$]. The estimated annual GPP is in the upper range of GPP for temperate forests given by Whittaker (1975), which was from 600 to 1200 g C·m$^{-2}$·yr$^{-1}$, largely because the loblolly pine grows in one of the most productive regions in North America (Ellsworth, *in press*). Our estimates are well within the range of GPP from 302 to 2404 g C·m$^{-2}$·yr$^{-1}$ across the Oregon transect from high-plateau mountain juniper to coastal Sitka spruce (Williams et al. 1997). In addition, the estimated GPP in this study is comparable to measured and modeled net primary productivity
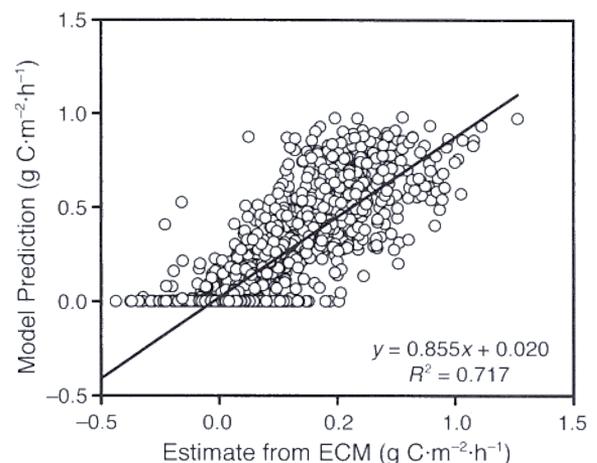


FIG. 6. Comparison of modeled with measured hourly values of canopy C fluxes. The solid line is the regression indicating model-predicted hourly photosynthesis: $y = 0.020 + 0.855x$, where $x$ is measured hourly net photosynthesis, with determination coefficient $R^2 = 0.717$.
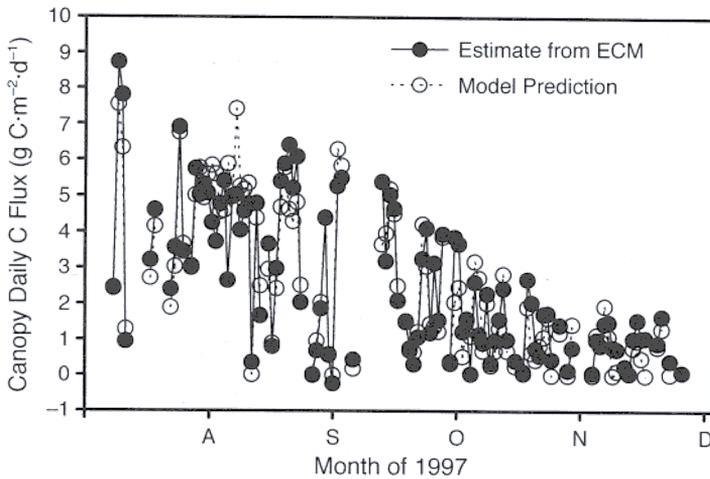
FIG. 7. Time course of predicted (open circles) and measured (solid circles) canopy daily C fluxes from August to December 1997. The x-axis labeling represents the end of the month indicated.

(NPP) in other studies (Teskey et al. 1987, McNulty et al. 1996, DeLucia et al. 1999). In the same Duke Forest FACE site, DeLucia et al. (1999) found that NPP at ambient $[CO_2]$ was 655 and 665 g $C \cdot m^{-2} \cdot yr^{-1}$ in 1997 and 1998, respectively, accounting for 54% of the estimated GPP in this study. McNulty et al. (1996) predicted loblolly pine productivity in the southern United States with the PnET-IIS model, which ranges from 120 to 930 g $C \cdot m^{-2} \cdot yr^{-1}$ with 540 g $C \cdot m^{-2} \cdot yr^{-1}$ in Chatham, North Carolina, the nearest to the Duke Forest. It accounts for ~45% of the estimated GPP in this study.

Annual GPP were predicted to increase by 40% when atmospheric $CO_2$ concentration was elevated to ambient + 200 μL/L. The high $CO_2$ stimulation in GPP largely resulted from sustained high stimulation in leaf photosynthesis (Ellsworth 2000). The estimated 40% increase in GPP in the Duke Forest caused by a 200-μL/L $[CO_2]$ increase is considerably smaller than the modeling estimate of the 110% increase in birch tree canopy C fluxes caused by a 350-μL/L $[CO_2]$ increase by Wang et al. (1998). However, that study was conducted on individual trees growing in open-top chambers, and a large increase in leaf area was observed in the elevated $CO_2$. A mesocosm study with continuous measurements of whole-canopy gas exchange demonstrated that elevation of 350-μL/L $[CO_2]$ resulted in a 53% increase in canopy carbon fluxes (Luo et al. 2000) while little leaf-level physiological acclimation was found (Sims et al. 1999). There have been few other open-top chambers or FACE studies in which elevated $[CO_2]$ effects on GPP have been estimated, against which we could compare our estimates.

Even with extensive data sets at both leaf and canopy levels for model parameterization and validation in this study, estimated GPP still has substantial uncertainties that are much higher than the precision required to quantify global terrestrial C sequestration. Among the three types of parameters examined in this study, most

have <10% effects on GPP except the quantum yield of electron transport (α) (Table 2). In order to improve precision of estimation of GPP in future, we need to make measurements to derive α as well as the curvature in the assimilation-to-light response curve (θ). During this modeling study, we found no species-specific data available to parameterize temperature functions of carboxylation ($V_{cmax}$), electron transport ($J_{max}$), and $CO_2$ compensation point (Γ*) for loblolly pine. The parameter values used in this study were from measurements of herbaceous species (e.g., Badger and Collatz 1977, Jordan and Ogren 1984). Model testing indicated that those functions generated temperature responses that were larger than experimental observations (*data not shown*).

There is considerable research emphasis on evaluating short- and long-term physiological acclimation to elevated $CO_2$ because acclimation has the potential to either amplify or dampen the initial $CO_2$ stimulation of
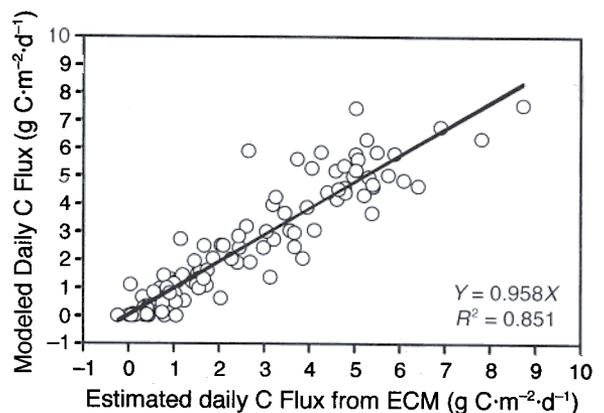


FIG. 8. Comparison of modeled with measured daily values of canopy C fluxes. The solid line is the regression indicating model-predicted daily C fluxes: $y = 0.958x$, where $x$ = measured daily C fluxes with $R^2 = 0.851$.
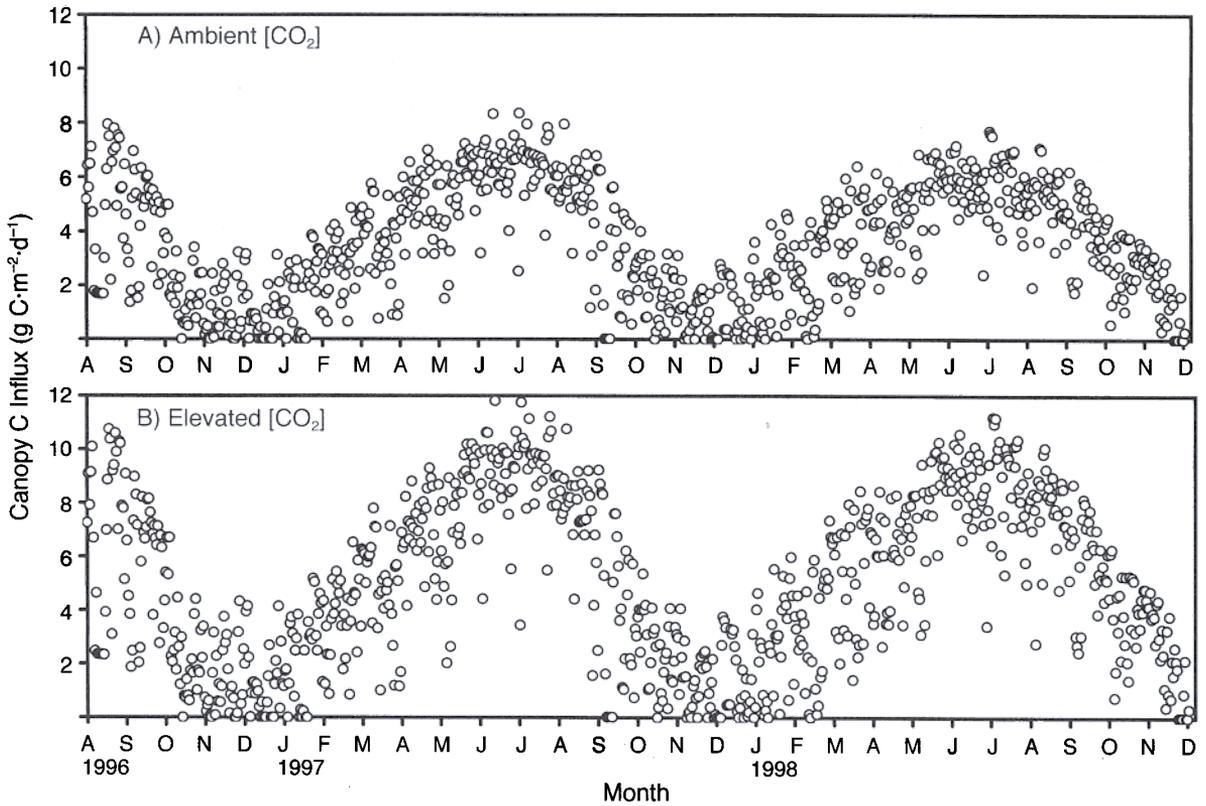
FIG. 9.  Modeled daily canopy C fluxes at (A) ambient and (B) elevated [CO$_2$] from August 1996 to December 1998.

photosynthetic C fixation (Strain and Cure 1985, Luo and Reynolds 1999). The short-term acclimation is primarily regulated by a combination of biochemical downregulation and morphological upregulation (Luo et al. 1994, 1998, Sims et al. 1998, Medlyn et al. 1999). The long-term acclimation is predicted to be caused mainly by constraints in ecosystem N availability

(Comins and McMurtrie 1993, Rastetter et al. 1997). Accordingly, most of the measurements have focused on evaluation of photosynthesis–N relationships and related enzyme activities (Huxman et al. 1998, Myers et al. 1999, Peterson et al. 1999). Our modeling analyses suggested that variation in $N_{area}$ by 10%, or $V_{cmax}$ and $J_{max}$ by 15%, resulted in much less change in GPP
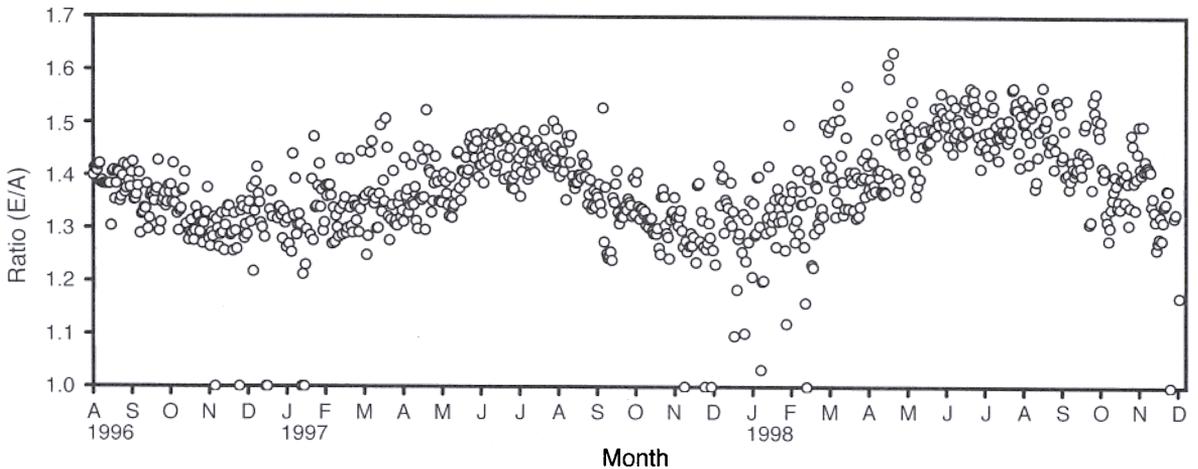


FIG. 10.  Ratio of modeled daily canopy C fluxes at elevated (E) CO$_2$ concentration relative to that at ambient (A) CO$_2$ concentration from August 1996 to December 1998, demonstrating predicted CO$_2$ stimulation of GPP.

TABLE 2. Sensitivity analysis on influences of model parameters on accuracy of estimated GPP.

| Model parameters | GPP (g C·m⁻²·yr⁻¹) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Ambient | | | Elevated | | | E/A | | | Type† |
| | 1996 | 1997 | 1998 | 1996 | 1998 | 1998 | 1996 | 1997 | 1998 | |
| | 322 | | 1135 | 442 | | 1655 | 1.38 | 1.41 | 1.46 | |
| | 354 | | 1381 | 472 | | 1918 | 1.33 | 1.35 | 1.39 | |
| | 336 | | 1242 | 455 | | 1773 | 1.36 | 1.38 | 1.43 | |
| | 324 | | 1213 | 438 | | 1726 | 1.35 | 1.38 | 1.42 | |
| | 346 | | 1275 | 470 | | 1827 | 1.36 | 1.39 | 1.43 | |
| | 332 | | 1239 | 451 | | 1773 | 1.36 | 1.39 | 1.43 | |
| | 339 | | 1256 | 458 | | 1791 | 1.35 | 1.38 | 1.43 | |
| | 331 | | 1232 | 445 | | 1750 | 1.35 | 1.38 | 1.42 | |
| | 341 | | 1263 | 464 | | 1811 | 1.36 | 1.39 | 1.43 | |
| | 354 | | 1307 | 485 | | 1889 | 1.37 | 1.40 | 1.45 | II |
| | 337 | | 1250 | 379 | | 1475 | 1.13 | 1.16 | 1.18 | II |
| | 403 | 1443 | 1504 | 572 | | 2259 | 1.42 | 1.45 | 1.50 | II |
| | 352 | 1303 | 1302 | 479 | | 1859 | 1.36 | 1.38 | 1.43 | III |
| | 313 | 1138 | 1160 | 423 | | 1656 | 1.35 | 1.38 | 1.43 | |
| | 361 | 1309 | 1338 | 489 | | 1912 | 1.36 | 1.39 | 1.43 | |
| | 332 | 1204 | 1228 | 449 | | 1755 | 1.35 | 1.39 | 1.43 | II |
| | 333 | 1209 | 1241 | 451 | | 1771 | 1.35 | 1.39 | 1.43 | III |
| | 344 | 1251 | 1279 | 466 | | 1827 | 1.35 | 1.38 | 1.43 | III |
| | 369 | 1315 | 1357 | 500 | | 1940 | 1.36 | 1.39 | 1.43 | III |

*Notes:* The base case used parameter values as specified in *Model structure and parameterization* and Table 1. T:P is the ratio of total to projected leaf area. A combination of *b* and *c* defines vertical distribution of relative foliage density. Other symbols are defined in Table 1. Values in parentheses are those in the base case. E/A is the ratio of GPP at elevated [CO₂] to that at ambient [CO₂]. GPP in 1996 is during the period from 28 August, the onset of the CO₂ fumigation, to 31 December.

† Type refers to three types of parameters: I, those that were measured at the Duke FACE site; II, not measured but may affect GPP; III, those sites examined with qualitatively different patterns or theoretical values.

than variation in LAI and quantum yield of electron transport ($\alpha$) did. Thus, further studies of leaf- and canopy-level light utilization will be fruitful.

This modeling study suggested that soil moisture, in addition to air vapor pressure, controlled canopy C fluxes during drought periods. Precipitation in the Raleigh-Durham area, North Carolina is relatively evenly distributed over seasons. In 1997, a major rainfall of 124 mm on 23–25 July was followed by a long period of drought until the middle of September. As a result, volumetric soil moisture content dropped below 0.15 in late August and early September 1997 (Ellsworth 1999). Such low soil moisture is known to control canopy conductance as evidenced from sapflux measurements by Oren et al. (1998). The MAESTRA model, which regulated stomatal conductance by air humidity only, led to overprediction of canopy C fluxes (Fig. 5). Although the overestimation did not result in a signif-
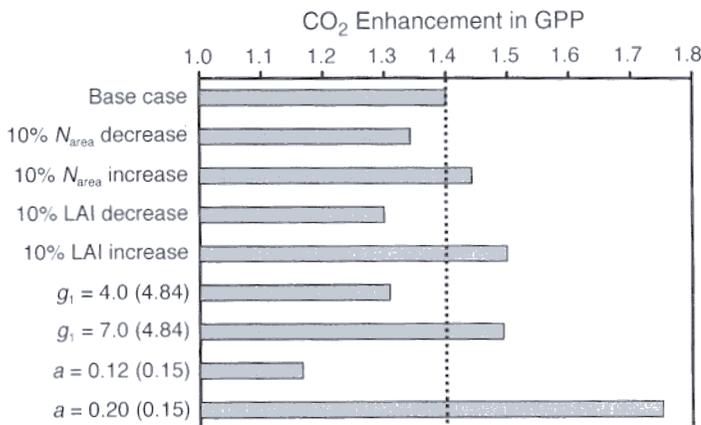


FIG. 11. Sensitivity analysis of acclimation effects on estimated GPP. The ratios of GPP at elevated [CO₂] to GPP at ambient [CO₂] are shown. Symbols are defined in Table 1. Values in parentheses are those in the base case.

icant error in the annual GPP in this study, the control of canopy gas exchange by soil moisture warrants further investigation.

Quantification of annual GPP provides a critical parameter toward prediction of C sequestration in the forest ecosystem. However, the capacity of C sinks in the terrestrial ecosystems is also dependent on residence time, that is, the duration of the fixed C to remain in the system (Luo and Reynolds 1999). The overall residence time of C varies with partitioning of assimilated C between the different pools, yet this partitioning is very poorly quantified. Although allocation of C to some pools, such as aboveground biomass, is fairly readily measured, allocation to other pools, particularly those below ground, is difficult to estimate experimentally. Development of innovative approaches to quantification of C fluxes through various pathways below ground and then estimation of whole-ecosystem C residence time becomes imperative for advancement in our predictive understanding of terrestrial C processes (Luo et al., *in press*).

In summary, this study used an ecophysiological approach to estimation of annual GPP, which was traditionally estimated by measurements of biomass combined with respiratory coefficients and root/shoot ratio. Our estimate of GPP in the Duke Forest is 1200–1300 g C·m$^{-2}$·yr$^{-1}$ in the ambient conditions, consistent with the estimates using the biomass approach. However, our ecophysiogical approach offers the possibilities to probe physiological determinants of GPP and to examine impacts of climatic change on ecosystem productivity. Indeed, our analysis suggests that elevation of atmospheric CO₂ concentration to ambient + 200 μL/L resulted in an ~40% increase in GPP. Quantum yield of electron transport has been found most critical in determination of GPP. This finding points to the same parameter as in remote sensing studies, indicating that prior knowledge of the apparent quantum efficiency of canopies, together with remotely sensed data of vegetation indices, determines time-integrated estimates of photosynthesis across landscapes (Waring et al. 1995). Finally, this study indirectly suggested that soil moisture, in addition to air vapor pressure, controlled canopy C fluxes during drought periods. The superposition of these two stomatal controls deserves further investigation using both modeling and experimental approaches.

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