

# Exposure to an enriched CO<sub>2</sub> atmosphere alters carbon assimilation and allocation in a pine forest ecosystem

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## Abstract

We linked a leaf-level CO<sub>2</sub> assimilation model with a model that accounts for light attenuation in the canopy and measurements of sap-flux-based canopy conductance into a new canopy conductance-constrained carbon assimilation (4C-A) model. We estimated canopy CO<sub>2</sub> uptake ( $A_{nC}$ ) at the Duke Forest free-air CO<sub>2</sub> enrichment (FACE) study. Rates of  $A_{nC}$  estimated from the 4C-A model agreed well with leaf gas exchange measurements ( $A_{net}$ ) in both CO<sub>2</sub> treatments. Under ambient conditions, monthly sums of net CO<sub>2</sub> uptake by the canopy ( $A_{nC}$ ) were 13% higher than estimates based on eddy-covariance and chamber measurements. Annual estimates of  $A_{nC}$  were only 3% higher than carbon (C) accumulations and losses estimated from ground-based measurements for the entire stand. The C budget for the *Pinus taeda* component was well constrained (within 1% of ground-based measurements). Although the closure of the C budget for the broadleaf species was poorer (within 20%), these species are a minor component of the forest. Under elevated CO<sub>2</sub>, the C used annually for growth, turnover, and respiration balanced only 80% of the  $A_{nC}$ . Of the extra 700 g C m<sup>-2</sup> a<sup>-1</sup> (1999 and 2000 average), 86% is attributable to surface soil CO<sub>2</sub> efflux. This suggests that the production and turnover of fine roots was underestimated or that mycorrhizae and rhizodeposition became an increasingly important component of the C balance. Under elevated CO<sub>2</sub>, net ecosystem production increased by 272 g C m<sup>-2</sup> a<sup>-1</sup>: 44% greater than under ambient CO<sub>2</sub>. The majority (87%) of this C was sequestered in a moderately long-term C pool in wood, with the remainder in the forest floor–soil subsystem.

**Keywords:** Canopy stomatal conductance, Free air CO<sub>2</sub> enrichment, net ecosystem exchange, net primary productivity, plant canopy modelling, respiration

Received 3 October 2002; revised version received 11 April 2003 and accepted 24 April 2003

## Introduction

Attempting to reduce the rate at which atmospheric CO<sub>2</sub> increases, the Kyoto Protocol has transformed CO<sub>2</sub> emissions and sinks into valuable trading commodities (Steffen *et al.*, 1998). The size of the carbon (C) sink in terrestrial ecosystems and the contribution of different processes to its strength under current atmospheric concentrations are still uncertain (Schimel *et al.*, 2001). The uncertainty over the strength of the sink in a future CO<sub>2</sub>-enriched world is even greater (Houghton, 1997).

For example, despite some down-regulation of photosynthetic rates ( $A_{net}$ ) under elevated CO<sub>2</sub> (Rey & Jarvis, 1998; Jach & Ceulemans, 2000; Griffin *et al.*, 2001; Tissue *et al.*, 2001; Rogers & Ellsworth, 2002), CO<sub>2</sub> uptake of canopies is expected to increase. However, the amount of C stored in the biosphere does not necessarily increase with the assimilation of CO<sub>2</sub> in photosynthesis (Valentini *et al.*, 2000). Uncertainties in C balances hamper the establishment and implementation of policies aimed at regulating atmospheric CO<sub>2</sub> concentrations.

To reduce uncertainties in the C balances, studies often combine different approaches and methodologies to estimate C fluxes into and out of vegetation. The

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degree of confidence in these estimates is high when different methods produce similar results, thereby 'closing' the C budget for an ecosystem. For example, physiological and biophysical models of net canopy assimilation ( $A_{nC}$ ) and respiration by plants and microorganisms (Collatz *et al.*, 1991; Leuning *et al.*, 1998; Wang & Leuning, 1998) can be compared to C balances estimated by eddy covariance, biomass-based estimates of net primary productivity ( $NPP$ ) and chamber based estimates of respiration (Law *et al.*, 1999). Interestingly, the degree of closure in the C balance varies considerably among studies (Baldocchi *et al.*, 1996; Luo *et al.*, 1997; Law *et al.*, 2000). A lack of closure in the C balance for plants growing under ambient conditions of atmospheric CO<sub>2</sub> (CO<sub>2</sub><sup>a</sup>) is particularly troubling when the ultimate goal is to estimate C balances under elevated atmospheric CO<sub>2</sub> (CO<sub>2</sub><sup>e</sup>). The lack of closure in C balances under CO<sub>2</sub><sup>e</sup> suggests an incomplete understanding of key processes (including missing or neglecting appreciable pools and fluxes), improper model parameterization, errors in measurements, or erroneous gap-filling methodologies. These problems may cause a greater lack of closure under CO<sub>2</sub><sup>e</sup> with an impetus to search for an explanation where none is needed.

Only two free air CO<sub>2</sub> enrichment (FACE) experiments exist in maturing forests, providing data on forest response to elevated CO<sub>2</sub> in otherwise unaltered conditions. One experiment is in a pure stand of *Liquidambar styraciflua* L. (Norby *et al.*, 2001), and one in a planted stand of *Pinus taeda* L. that currently includes 48 woody species and a large number of species of herbaceous plants and vines (DeLucia *et al.*, 1999; Hamilton *et al.*, 2002). In both these experiments, the plot size precludes the use of eddy covariance to estimate biosphere-atmosphere water vapour and heat exchange under CO<sub>2</sub><sup>e</sup>, and the method cannot be used to quantify CO<sub>2</sub> flux because large quantities of CO<sub>2</sub> are emitted with FACE technology. A C balance of the CO<sub>2</sub><sup>e</sup> experimental plots can be assessed by comparing  $A_{nC}$  estimated from a physiological model with gross primary productivity ( $GPP$ ) estimated from the summation of biomass production and respiration. Although a number of studies have focused on different components of the C budgets at these sites (DeLucia *et al.*, 1999; Luo *et al.*, 2001; Oren *et al.*, 2001; Norby *et al.*, 2001; Finzi *et al.*, 2002; Hamilton *et al.*, 2002), the C balance of either site has not yet been verified using a combination of different approaches.

In this study, we linked a leaf-level CO<sub>2</sub> assimilation model (Katul *et al.*, 2000) with light models (Campbell & Norman, 1998; Stenberg, 1998) and sap-flux-based canopy conductance (Köstner *et al.*, 1992; Ewers & Oren, 2000) into a canopy-level model, hereafter

referred to as the canopy conductance-constrained CO<sub>2</sub> assimilation or 4C-A model. We tested the 4C-A model estimates of net photosynthesis ( $A_{net}$ ) against leaf gas exchange measurements under ambient and elevated CO<sub>2</sub>. Under CO<sub>2</sub><sup>a</sup> we modelled net canopy assimilation ( $A_{nC}$ ) and tested its prediction against independent measurements of net ecosystem exchange ( $NEE$ ) and net ecosystem production ( $NEP$ ), after accounting for respiration. We then used the model to assess the effect of CO<sub>2</sub><sup>e</sup> on C uptake and allocation to different components of the C budget. Unlike other ecophysiological models (e.g. Leuning, 1995; Lai *et al.*, 2000; Baldocchi & Meyers, 1998), the 4C-A model is unique in that it uses nearly continuous measurements of canopy conductance to constrain CO<sub>2</sub> uptake by different species under varying environmental conditions. This approach eliminates the uncertainties that typically affect modelled stomatal conductance, but retains the biochemical processes necessary to estimate intercellular CO<sub>2</sub>.

## Material and methods

### Study site

The site is located in Duke Forest, North Carolina, USA (35°58'N, 79°05'W). The average annual temperature is 15.5°C and the annual precipitation is 1140 mm. The soil is a moderately well-drained low-fertility acidic Hapludalf of the Enon Series with a clay pan at ca. 30 cm depth. The even-aged *P. taeda* L. forest was planted in a clear-cut opening in 1983, with additional tree species representing seed sources of pine and broadleaf species from the surrounding area. The main broadleaf species are *L. styraciflua* L., *Acer rubrum* L., *Ulmus alata* Michx., and *Cornus florida* L. Further details about the site can be found in Ellsworth (1999) and Schäfer *et al.* (2002). The FACE facility at Duke Forest (Hendrey *et al.*, 1999) was designed with six circular plots (30 m in diameter), three of which are under CO<sub>2</sub><sup>a</sup> and three under CO<sub>2</sub><sup>e</sup> (ambient + 200 µmol<sup>-1</sup> CO<sub>2</sub> mol<sup>-1</sup> air). Radial boardwalks oriented in north-to-south and east-to-west directions transverse each plot.

### Approach

We estimated canopy-level net daytime CO<sub>2</sub> uptake (in g C m<sup>-2</sup> ground s<sup>-1</sup>) based on the 4C-A model. Sap-flux-based conductance estimates were available for a 1.5 m wide strip on each side of the boardwalk (211 m<sup>2</sup> of a plot total of 707 m<sup>2</sup>), and thus we applied our estimates to this section only in each plot. We first verified our  $A_{nC}$  estimate for ambient plot 1 against

the sum of daytime values of (1) CO<sub>2</sub> uptake from the atmosphere measured with eddy covariance above the canopy in this plot ( $F_C^a$ ; Lai *et al.*, 2000), (2) respiration estimated based on temperature-respiration functions for the forest floor ( $F_C^{ff}$ ) and above-ground woody biomass (maintenance respiration,  $R_M$ , and construction respiration,  $R_C$ ), and (3) CO<sub>2</sub> depletion in the forest air volume from measurement of the CO<sub>2</sub> concentration profile between the forest floor and the position of the eddy-covariance system ( $\Delta S_C^a$ ). Following this verification step, we proceeded with a C balance, comparing the estimated  $A_{nC}$  for each plot with the sum of the annual utilization of C for growth, growth respiration, and maintenance respiration of the major biomass components.

In the following sections we describe the components of the 4C-A model, the set of independent measured fluxes obtained for verifying it under ambient conditions, and then the measurements obtained for balancing its  $A_{nC}$  estimates against growth and respiration under both ambient and elevated CO<sub>2</sub> atmosphere.

### Modelling

At the leaf scale, net assimilation ( $A_{net}$  in  $\mu\text{mol CO}_2\text{ m}^{-2}$  projected leaf  $\text{s}^{-1}$ ) and stomatal conductance are related as follows (Katul *et al.* 2000):

$$A_{net} = g_{CO_2} c_a \left( 1 - \frac{c_i}{c_a} \right), \quad (1)$$

where  $c_a$  is external CO<sub>2</sub> concentration in  $\mu\text{mol mol}^{-2}$ ,  $c_i$  is the internal CO<sub>2</sub> concentration in  $\mu\text{mol mol}^{-1}$ , and  $g_{CO_2}$  is mean stomatal conductance to CO<sub>2</sub> ( $\text{mol m}^{-2}$  leaf  $\text{s}^{-1}$ ), calculated from mean stomatal conductance of water vapour corrected for the ratio of diffusivity of water vapour to CO<sub>2</sub> (1.6) assuming Fickian diffusion (for parameters, symbols, and units, see Table 1).

'Big-leaf' models that use a single canopy layer tend to underestimate  $A_{nC}$  due to non-linearity of the response to light of several photosynthetic processes (DePury & Farquhar, 1997; Friend, 2001). Thus, in order to estimate  $g_{CO_2}$  and  $C_i/C_a$  for calculating  $A_{nC}$ , we estimated the light regime in each of 16 1 m layers in the canopy and used this light as an input in modelling  $g_{CO_2}$  and  $C_i/C_a$ . There are several reasons as to why this approach is advantageous: (1) the integrated value of  $C_i/C_a$  from leaf to canopy is properly weighed by the conductance thereby resolving the interaction between  $C_i/C_a$  and  $g_{CO_2}$  while preserving the bulk canopy conductance; (2) variability in  $c_a$  across the canopy height can be explicitly incorporated in the up-scaling of  $C_i/C_a$ ; and (3) the physiological calculations are applied at the appropriate scale (i.e. leaf) prior to integration to the canopy level. In addition, modelled

long-term mean  $C_i/C_a$  can be tested against an independent estimate from  $\delta^{13}\text{C}$  measurements.

### Estimating the vertical profile of PPFD

The approach for estimating photosynthetic photon flux density ( $PPFD$  in  $\mu\text{mol m}^{-2}\text{ s}^{-1}$ ) at each layer in the canopy, and the proportion of foliage receiving different quantities of  $PPFD$  at each layer is described in the Appendix. Briefly: (1) incoming  $PPFD$  was partitioned into direct and diffuse components (Erbs *et al.*, 1982), (2) the seasonal dynamics of leaf area density profile was modelled separately for the *P. taeda* (Kinerson *et al.*, 1974; Pataki *et al.*, 1998) and deciduous broadleaf species, (3)  $PPFD$  was estimated in each layer at half-hourly intervals, accounting for direct and diffuse components, using the penumbral effect to partition the direct component into 10 light categories (Campbell & Norman, 1998; Stenberg, 1998), and (4) the proportion of foliage in each light category was estimated (Campbell & Norman, 1998; Stenberg, 1998).

In coniferous stands, penumbral effects redistribute direct light, enhancing photosynthesis of the more shaded foliage. During periods of high light this redistribution of direct light occurs without impact on the oversaturated sunlit foliage. The model calculates the proportion of leaf area for which direct beam radiation is obstructed by 0, 1, ..., 9 branches in each canopy layer, and the light intensity incident on the leaf surface in each of the 10 light categories. To the light intensity thus calculated, the amount of diffuse and scattered light is added, producing half-hourly estimates of total incident  $PPFD$  in each category. In summary, the model explicitly resolves the seasonal dynamics of leaf area profile and its effect on the entire light environment (and thus the canopy-integrated  $C_i/C_a$ ).

The ultimate goal of assembling this model is to estimate  $A_{nC}$  under CO<sub>2</sub>. Recent findings on *P. taeda* in this site showed that previous-year foliage in CO<sub>2</sub><sup>e</sup> plots has 75% the carboxylation capacity of that in CO<sub>2</sub><sup>a</sup> plots (Rogers & Ellsworth, 2002) and current-year foliage has ~90% that in CO<sub>2</sub><sup>a</sup> plots. We therefore accounted for the vertical distribution of current- and previous-year foliage by 'growing' the canopy in relation to the vertical pattern of seasonal needle elongation (see the Appendix).

### Estimating the vertical profile of stomatal conductance

We employed the following approach to estimate stomatal conductance in leaves positioned along the canopy: (1)  $PPFD$  was calculated for each category at half-hourly intervals at each layer and combined with stomatal conductance- $PPFD$  response functions of sun-type and shade-type foliage derived from leaf gas exchange measurements (CIRAS-1, PP-systems, Ellsworth, 1999, 2000; Naumburg & Ellsworth, 2000) to

**Table 1** Parameters and their definition used in the model

Parameter	Definition	Unit
$\overline{c_i/c_a}$	Long-term mean $C_i/C_a$ based on $\delta^{13}\text{C}$	Dimensionless
$\beta$	Silhouette to leaf area ratio	Dimensionless
$\Pi$	Clumping factor	Dimensionless
$\rho$	Density of water at 4 °C	998 kg m <sup>-3</sup>
$\kappa$	Zenith angle	
$\Gamma^*$	CO <sub>2</sub> compensation point	$\mu\text{mol mol}^{-1}$
$\tau_b$	Light transmission coefficient for direct radiation	Dimensionless
$\tau_d$	Light transmission coefficient for diffuse radiation	Dimensionless
$\tau_s$	Light transmission coefficient for scattered radiation	Dimensionless
$\alpha_p$	Leaf absorptivity of PPFD	Dimensionless
$\Delta S_C^a$	Change in atmospheric CO <sub>2</sub> storage in forest air volume	$\text{g C m}^{-2} \text{ground s}^{-1}$
$a, b, s, y_0$	Fitting parameters	
$A_{\text{nC}}$	Canopy net assimilation	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$A_{\text{net}}$	Leaf net assimilation	$\mu\text{mol m}^{-2} \text{leaf s}^{-1}$
$B_S$	Standing biomass	$\text{g C m}^{-2} \text{ground a}^{-1}$
$c$	Transmission coefficient	Dimensionless
$c_a$	Atmospheric CO <sub>2</sub> concentration	$\mu\text{mol mol}^{-1}$
$CE$	Carboxylation efficiency	
$CE_{\text{max}}$	Maximum light saturated $CE$	$\mu\text{mol m}^{-2} \text{s}^{-1}$
$c_i$	Substomatal cavity CO <sub>2</sub> concentration	$\mu\text{mol mol}^{-1}$
$D$	Water vapour pressure deficit of air	kPa
$DIC$	Dissolved inorganic carbon	$\text{g C m}^{-2} \text{ground a}^{-1}$
$DOC$	Dissolved organic carbon	$\text{g C m}^{-2} \text{ground a}^{-1}$
$E_C$	Canopy transpiration	$\text{mmol m}^{-2} \text{ground a}^{-1}$
$E_L$	Canopy transpiration per unit leaf area	$\text{mmol m}^{-2} \text{leaf s}^{-1}$
$F_C^a$	Atmospheric CO <sub>2</sub> flux	$\text{g C m}^{-2} \text{ground s}^{-1}$
$F_C^{\text{ff}}$	Forest floor CO <sub>2</sub> efflux	$\mu\text{mol m}^{-2} \text{s}^{-1}$
$f_{\text{sl}}$	Sunlit fraction of foliage	
$g_{\text{CO}_2}$	Leaf-level stomatal conductance to CO <sub>2</sub>	$\text{mol m}^{-2} \text{leaf s}^{-1}$
$g_{\text{crit}}$	Critical conductance	$\text{mol m}^{-2} \text{leaf s}^{-1}$
$GPP$	Gross primary productivity	$\text{g C m}^{-2} \text{ground s}^{-1}$
$G_S$	Canopy stomatal conductance to water vapor	$\text{mmol m}^{-2} \text{leaf s}^{-1}$
$G_{\text{SCO}_2}$	Canopy stomatal conductance to CO <sub>2</sub>	$\text{mmol m}^{-2} \text{leaf s}^{-1}$
$g_{\text{sh}}$	Stomatal conductance to CO <sub>2</sub> for shaded foliage	$\text{mol m}^{-2} \text{leaf s}^{-1}$
$g$	Stomatal conductance to CO <sub>2</sub> for sunlit foliage	$\text{mol m}^{-2} \text{leaf s}^{-1}$
$G_{\text{Sref}}$	Reference $G_S$ at 1 kPa	$\text{mmol m}^{-2} \text{leaf s}^{-1}$
$G_V$	Universal gas constant corrected for water vapour	$0.462 \text{ kPa m}^3 \text{K}^{-1} \text{kg}^{-1}$
$I_b$	Direct radiation	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$I_{bi}$	Direct radiation in layer $i$	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$I_C$	Light compensation point	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$I_d$	Diffuse radiation	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$I_{di}$	Diffuse radiation in layer $i$	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$I_{\text{ex}}$	Extraterrestrial radiation	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$I_o$	Total incoming radiation	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$I_{\text{sc}}$	Scattered radiation in layer $i$	
$I_S$	Light saturation point	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$k$	Probability of light category (for <i>P. taeda</i> )	
$K_{\text{be}}$	Light extinction coefficient for direct radiation	Dimensionless
$K_d$	Light extinction coefficient for diffuse radiation	Dimensionless
$K_T$	Clearness index	Dimensionless
$L$	Leaf area index	$\text{m}^2 \text{m}^{-2}$
$LOC$	Lack of closure	
$L_t$	Leaf area density	$\text{m}^2 \text{m}^{-2}$
$L_{ti}$	Cumulative leaf area density in layer $i$	
$M_0, x_0$	Fitting parameter	

**Table 1** (Continued)

Parameter	Definition	Unit
$N$	Nitrogen concentration	$\mu\text{mol mol}^{-1}$
$NEE$	Net ecosystem exchange	$\text{g C m}^{-2} \text{ground s}^{-1}$
$NEP$	Net ecosystem productivity	$\text{g C m}^{-2} \text{ground a}^{-1}$
$NPP$	Net primary productivity	$\text{g C m}^{-2} \text{ground a}^{-1}$
$PPFD$	Photosynthetic photon flux density	$\mu\text{mol m}^{-2} \text{ground s}^{-1}$
$R_A$	Autotrophic respiration	$\text{g C m}^{-2} \text{ground s}^{-1}$
$R_C$	Construction respiration	$\text{g C m}^{-2} \text{ground s}^{-1}$
$R_E$	Ecosystem respiration	$\text{g C m}^{-2} \text{ground s}^{-1}$
$R_H$	Heterotrophic respiration	$\text{g C m}^{-2} \text{ground s}^{-1}$
$R_M$	Maintenance respiration	$\text{g C m}^{-2} \text{ground s}^{-1}$
$T_a$	Air temperature	$^{\circ}\text{C}$
$T_{\text{stem}}$	Stem temperature	$^{\circ}\text{C}$
$V_{\text{cmax}}$	Maximum RubisCO capacity	$\mu\text{mol m}^{-2} \text{leaf s}^{-1}$
$x$	Leaf angle distribution	Dimensionless

estimate conductance. Shade-type foliage was foliage exposed to direct light less than 35% of the time. (2) Stomatal conductance was scaled to the layer based on  $L$  of each foliage type in each  $PPFD$  category, summed for all layers, and expressed as the relative contribution of stomatal conductance in each type within each layer to that of the total canopy. (3) Relative conductance was multiplied by the sap-flux-scaled canopy stomatal conductance ( $G_S$ ), repartitioning  $G_S$  between foliage types among layers.

Over the 3 years in which  $A_{nC}$  was estimated based on the 4C-A model, sap flux-scaled conductance was available for 55 991 (i.e. 86% recovery) half-hourly daytime values for *P. taeda*, and 28 603 (65%) for the hardwoods. Many of the missing data (~80%) represent conditions in which  $G_S$  calculated from sap-flux measurements incur large error (i.e.  $D < 0.6$  kPa, based on Ewers & Oren, 2000). The remaining proportion of missing data represents instrument or power failure, or when hardwoods are not in leaf.

#### Estimating the ratio of internal-to-external $\text{CO}_2$ concentration

The ratio of  $\text{CO}_2$  concentration in the stomatal cavity relative to the concentration at the leaf surface ( $c_i/c_a$ ) can be modelled after Katul *et al.* (2000). The  $c_i/c_a$  was calculated separately for  $PPFD < I_S$  and  $PPFD > I_S$  where  $I_S$  is the light saturation point of the mean leaf carboxylation efficiency ( $CE$ ), considering  $CE$  as the initial slope of the  $A_{\text{net}} - c_i$  curve. Under conditions of  $PPFD > I_S$ ,  $c_i/c_a$  was calculated separately for  $g_{\text{CO}_2}$  less than a critical conductance ( $g_{\text{crit}}$ ) and for  $g_{\text{CO}_2} \geq g_{\text{crit}}$  stem. Critical conductance is the conductance in which  $c_i$  reaches sufficiently high values so  $\delta A_{\text{net}}/\delta g_{\text{CO}_2} \rightarrow 0$ . The critical conductance is calculated based on Katul

*et al.* (2000) as

$$g_{\text{crit}} = \frac{CE \times \overline{c_i/c_a} - (CE \times \Gamma^*)/c_a}{1 - \overline{c_i/c_a}}, \quad (2)$$

where  $\Gamma^*$  is the  $\text{CO}_2$  compensation point (not considering mitochondrial respiration) calculated from the  $A_{\text{net}} - c_i$  curve measured *via* leaf gas exchange measurements (Ellsworth 1999, 2000, Herrick & Thomas 1999, 2001), and  $\overline{c_i/c_a}$  is the long-term mean  $c_i/c_a$  ratio obtained from  $\delta^{13}\text{C}$  measurements. Although this approach describes the biochemical processes less realistically than models based on Farquhar *et al.* (1980), it preserves the key biochemical mechanisms linking  $c_i$  to  $A_{\text{net}}$ . Furthermore, the uncertainty added with increasing numbers of model parameters can degrade performance when compared to leaf gas exchange measurements (Katul *et al.*, 2000), a factor that is likely to be particularly troublesome in studies aimed at long-term estimates of gas exchange.

Thus, for conditions in which  $PPFD < I_S$ , or  $PPFD \geq I_S$  and  $g_{\text{CO}_2} < g_{\text{crit}}$ ,

$$\frac{c_i}{c_a} = \frac{g_{\text{CO}_2} + (CE \times \Gamma^*)/c_a}{CE + g_{\text{CO}_2}}. \quad (3)$$

The  $c_i/c_a$  can be estimated from this relationship when the  $A_{\text{net}} - c_i$  curve is approximately linear for the range of external  $\text{CO}_2$  concentration. This condition was satisfied for both sun- and shade-type foliage initiated under both  $\text{CO}_2^s$  and  $\text{CO}_2^d$  in our stand (Ellsworth, 1999; Herrick & Thomas, 2001). For conditions in which  $g_{\text{CO}_2} \geq g_{\text{crit}}$ ,  $g_{\text{CO}_2}$  is set to equal  $g_{\text{crit}}$ , and  $c_i/c_a$  is calculated based on Eqn (3).

The  $\Gamma^*$  in Eqns (2) and (3) is similar in a large variety of  $\text{C}_3$  species and environmental conditions; thus, a single base value may be used for both *P. taeda* and the broadleaf species vertically through the canopy (Wilson

*et al.*, 2000). The base value of  $\Gamma^*$  is corrected for temperature based on Katul *et al.* (2000). In contrast, maximum  $CE$  ( $CE_{\max}$ ) is 75% higher in sun- than in shade-type foliage, increases with  $PPFD$ , and shows seasonal dynamics that approximately reflects the changing temperature.

In each foliage type of *P. taeda*, the maximum carboxylation capacity ( $V_{C_{\max}}$ ), measured *via* leaf gas exchange under saturating light conditions, has a distinctly large seasonal course deviating ~20% above and below the annual mean (Ellsworth, 2000). The seasonal course is just as pronounced in the foliage of some deciduous broadleaf species, with a pattern resembling that of *L* (Wilson *et al.*, 2000). The seasonal dynamics in  $CE_{\max}$  is primarily driven by the dynamics in  $V_{C_{\max}}$ , because both are fitted to the actual or to the temperature and kinetic coefficient-corrected relationship between  $A_{\text{net}}$  and  $c_i$ :

$$\begin{aligned} \text{in } P. \text{ taeda foliage : } CE_{\max} &= 0.4716 \\ &\times \log(0.00249 \times (V_{C_{\max}} \\ &+ 0.9915)), \end{aligned} \quad (4)$$

$$\begin{aligned} \text{in } L. \text{ styraciflua foliage : } CE_{\max} &= 0.00079 \\ &\times (V_{C_{\max}}) + 0.0099. \end{aligned} \quad (5)$$

We approximated the seasonal dynamics of  $CE_{\max}$  for *P. taeda* using a sine wave function with minima (0.8 of the long-term mean; see the mean in Table 2) in January 31 and maxima (1.2 of the mean) in July 31, approximately at the time of year in which temperature minima and maxima occurred during the study (Schäfer *et al.*, 2002). The  $CE_{\max}$  for the hardwood species after bud break was set to 0.1 of the maximum value obtained in June (Herrick & Thomas, 2001), increasing to the maximum in June and decreasing to 0 thereafter with the entire dynamics set to mimic that of *L*.  $CE_{\max}$  is discounted to actual  $CE$  by accounting for the incident  $PPFD$ . Thus,  $CE$  was set to zero at the photosynthetic light compensation point ( $I_c$ ) of each species (Table 2), increasing linearly with  $PPFD$  until  $CE_{\max}$  is reached at the point in which photosynthetic rate was nearly saturated with respect to light ( $I_s$ ; Table 2). Any further increase in photosynthesis with  $PPFD > I_s$  is related to an increase in  $g_{CO_2}$  with light.

For the shade-type foliage of the broadleaf species, we used the leaf-area-weighted mean of the physiological parameters of four species measured at the site, including the dominant broadleaf species *L. styraciflua* (Naumburg & Ellsworth, 2000). Broadleaf sun-type foliage was almost exclusively *L. styraciflua*, for which we used locally measured parameters (Herrick & Thomas, 2001).

**Table 2** Parameters (mean and standard error in parenthesis) used for calculating canopy net assimilation and respiration under ambient (CO<sub>2</sub><sup>a</sup>) and elevated (CO<sub>2</sub><sup>b</sup>) conditions

		<i>Pinus taeda</i>		<i>Liquidambar styraciflua</i>	
		Sun	Shade	Sun	Shade
<i>Leaf</i>					
$\beta$		0.5			1.0
$\alpha_p$				0.83	
$c$		0.4			Not applicable
$\Pi$				0.5	
$CE_{\max}$	CO <sub>2</sub> <sup>a</sup>	0.07 (0.002)	0.04	0.062	0.035 (0.0003)*
	CO <sub>2</sub> <sup>b</sup>	0.07† (0.002)	0.04†	0.062	0.033 (0.0012)*
		0.05‡ (0.002)	0.03‡		
$\overline{C_i/C_a}$	CO <sub>2</sub> <sup>a</sup>			0.69 (0.01)	
	CO <sub>2</sub> <sup>b</sup>	0.68 (0.02)	0.77 (0.01)	0.65 (0.02)	
$I_s$		700	400	700	400
$I_c$		35	20	27	15
<i>Wood</i>					
$N$		Branch	Stem	Branch	Stem
$CO_2$	CO <sub>2</sub> <sup>a</sup>	2.3 (0.3)	0.95 (0.04)	4.0	1.8
	CO <sub>2</sub> <sup>b</sup>	2.1 (0.1)	0.89 (0.07)	3.0	1.4

Parameter values of *L. styraciflua* are provided because this species dominated the broadleaf component at the site. Parameters definitions and units are provided in Table 1. Centred values represent both foliage types or both species.

\*Leaf area weighted  $CE$  for four species that were measured; see text for details.

†Current-year foliage.

‡Previous-year foliage.

The effect of CO<sub>2</sub><sup>b</sup> on  $CE_{\max}$  was accounted for by a change proportional to that observed in  $V_{C_{\max}}$ . For *P. taeda*, a reduction in  $CE_{\max}$  for previous-year foliage was 25% (Rogers & Ellsworth, 2002) and for current-year foliage up to 10%. This effect was captured through a linear reduction in  $CE_{\max}$  for current-year foliage beginning at the initiation of needle elongation, reaching 10% when needle elongation of all flushes is completed, and remaining at this level until the end of the year, at which point the now previous-year foliage decreases linearly, reaching the 25% mark by the time of bud break and remaining at this level until senescence. For the broadleaf species the effect of CO<sub>2</sub><sup>b</sup> on  $CE_{\max}$  was not significant in most studies (Herrick & Thomas, 1999; Naumburg & Ellsworth, 2000), but has recently

been shown to cause an ~13% reduction in  $CE_{\max}$  for *L. styraciflua* (Ellsworth, unpublished).

#### Estimating canopy net assimilation

The net assimilation rate per unit of leaf surface ( $\text{mmol m}^{-2}\text{leaf s}^{-1}$ ) calculated according to Eqn (1) in each light category was scaled to canopy  $A_{\text{nC}}$  using the leaf area in each category ( $\text{g m}^{-2}\text{ ground}^{-1}\text{ s}^{-1}$ ).  $A_{\text{nC}}$  was summed across all light categories in each canopy layer for each species, and was then expressed for each species type or for the entire canopy.

#### Measurements

##### Measurements of sap flux and environmental variables

Sap flux (Granier, 1987) and environmental variables used in calculating and modelling  $G_S$  were measured continuously in each plot from May 1997 to December 2000. Detailed information on sampling, calculations, and modelling are provided in Schäfer *et al.* (2002, in review). Of special relevance to this study, *PPFD* was measured with a sensor mounted to the central tower above the canopy of one plot (Q190, LiCor, Lincoln, NE, USA). Stem temperature ( $T_{\text{stem}}$  in °C) in four cardinal directions was measured in one tree and on the north side of two additional trees, soil temperature was measured at 10–15 cm depth at each plot (M 841/S1, Siemens, Germany) and air temperature ( $T_a$  in °C) was also measured in each plot at two-thirds of the height of the canopy (Vaisala HMP35C or HMP45C, Helsinki, Finland). These temperature measurements were used to estimate  $R_M$  and  $F_C^{\text{ff}}$  (Maier *et al.* 1998, Butnor *et al.*, 2003). All measurements were sampled every 30 s and 30 min averages were stored in a data logger (21X or 23X, Campbell Scientific, Logan, UT, USA).

##### Estimating biomass production and respiration components

Based on previous studies, it was assumed that allometric relationships are not affected by elevated  $\text{CO}_2$  (Norby *et al.*, 2001; Pataki *et al.*, 1998; DeLucia *et al.*, 2002), justifying the use of the same relationship under ambient and elevated  $\text{CO}_2$  conditions. We further verified that allometry is not altered by growth under  $\text{CO}_2^{\text{s}}$  by measuring height and diameter of *Pinus taeda* ( $n = 121$  under  $\text{CO}_2^{\text{s}}$  and 102 under  $\text{CO}_2^{\text{a}}$ ), *Liquidambar styraciflua* ( $n = 53$  and 66), *Cornus florida* ( $n = 20$  and 12), and *Ulmus alata* ( $n = 39$  and 34) trees; the relationship of height and diameter at 1.4 m above ground did not differ between the treatments for any species (minimum  $P > 0.3$ ).

Broadleaf individuals 12–125 mm in diameter at 1.4 m above ground were harvested in 1998 and 1999 in order to develop allometric equations for estimating  $L$ ,  $L$  profile, and above-ground biomass components of the

prevailing broadleaf species in the stand. The individuals were harvested in the stand but outside of the experimental plots. The species were *Lirodendron tulipifera* (seven individuals), *A. rubrum* (seven; Naumburg & Ellsworth, 2000), *L. styraciflua* (15), *C. florida* (10), and, *U. alata* (7; Schäfer *et al.*, in review), species comprising 48–98% of the broadleaf basal area in the six experimental plots. For *P. taeda*, allometric equations were available for the site (Naidu *et al.*, 1998; Pataki *et al.*, 1998).

For the broadleaf species, harvest date was timed to the period of full leaf expansion, after stem growth was mostly completed, and before leaf senescence. After cutting at ground level, the height, base of crown, position of each branch along the stem, and its diameter were recorded. Then, the biomass was partitioned into leaf, branches and stem components, dried (wholly for individuals <45 mm, or subsampled, 1 week; 80 °C), and weighed. Specific leaf area was determined on a subset of leaves from each branch (individuals <45 mm) or every third branch (larger individuals). A relationship of sapwood-to-leaf area ratio vs. diameter at 1.4 m (Schäfer *et al.*, in review) was generated for each species. Standing biomass of each component was estimated from diameter measured on all trees in the measurement plots in November of each year (1998–2000), and the allometric relationships with diameter derived from biomass harvests. The biomass and leaf area of each species in the study for which allometric relationships were not developed at the site were estimated based on relationships developed for the species with the closest resemblance.

For *P. taeda*, estimates of stem, branch, and root biomass were based on Naidu *et al.* (1998), and needle biomass and area were based on Pataki *et al.* (1998). *P. taeda* comprise at least 80% of the basal area in each measurement plot.

*NPP* was calculated as the difference of current- to previous-year standing biomass augmented with fine root turnover (Matamala & Schlesinger, 2000). To this value we added litterfall of *P. taeda* (Finzi *et al.*, 2001), representing needle turnover, and the estimated leaf biomass produced by the broadleaf species.

To estimate maintenance respiration of branches and stems ( $R_M$ ), standing biomass was incremented reflecting the stem growth dynamics (Oren *et al.*, 2001), and  $R_M$  was estimated based on the biomass, stem temperature and nitrogen concentration (see Table 2) after Maier *et al.* (1998) and Maier (2001). Maintenance respiration of coarse roots was calculated based on soil temperature, nitrogen content, and root biomass (Maier, unpublished results). Maintenance respiration of foliage, calculated only over night-time hours, was estimated using air temperature as a proxy of leaf

temperature, assuming the canopy is well coupled (Phillips *et al.* 1997), based on relationships developed on site under each CO<sub>2</sub> treatment for *P. taeda* and *L. styraciflua*, the latter being used as a surrogate for all other broadleaf species (Hamilton *et al.*, 2001). Fine root respiration was taken from previously published values of Matamala & Schlesinger (2000).

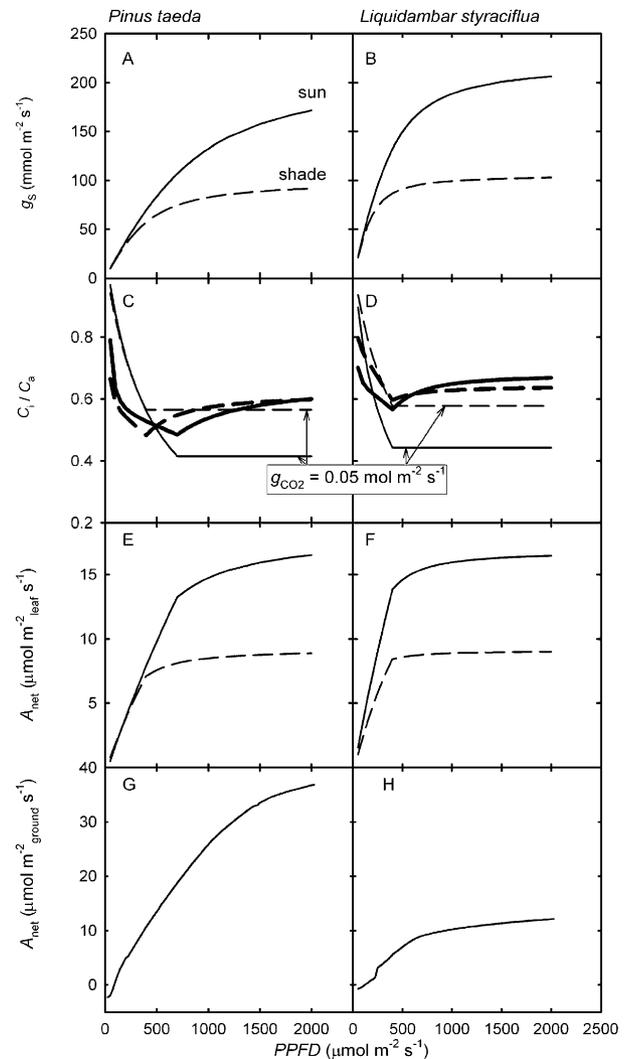
Construction respiration was calculated for each organ separately. The construction cost of stems and branches of all species is similar (Wullschlegel *et al.*, 1997; Hamilton *et al.*, 2002), and is not affected by atmospheric CO<sub>2</sub> concentration (Carey *et al.*, 1996). Thus, the construction cost for these organs was taken as 1.50 g glucose g<sup>-1</sup> dry weight of constructed tissue (Carey *et al.* 1996). Construction respiration of coarse roots was estimated using 1.47 g glucose g<sup>-1</sup> dry weight (Maier, unpublished results), assuming no difference among species and CO<sub>2</sub> treatments. The construction cost of *P. taeda* needles was estimated using 1.45 g glucose g<sup>-1</sup> dry weight for both CO<sub>2</sub> treatments (Griffin *et al.*, 1993, 1996; Hamilton *et al.*, 2001). However, there is evidence that construction respiration for the hardwood leaves increased under CO<sub>2</sub> from 1.41 g glucose g<sup>-1</sup> dry weight under CO<sub>2</sub> to 1.46 g glucose g<sup>-1</sup> dry weight for leaves produced under CO<sub>2</sub> (Wullschlegel *et al.*, 1997).

Unless otherwise stated, data were analysed based on a paired *t*-test (*n* = 3) with plot paired according to sapwood area per unit of ground area (Schäfer *et al.*, 2002).

## Results

### Model evaluation

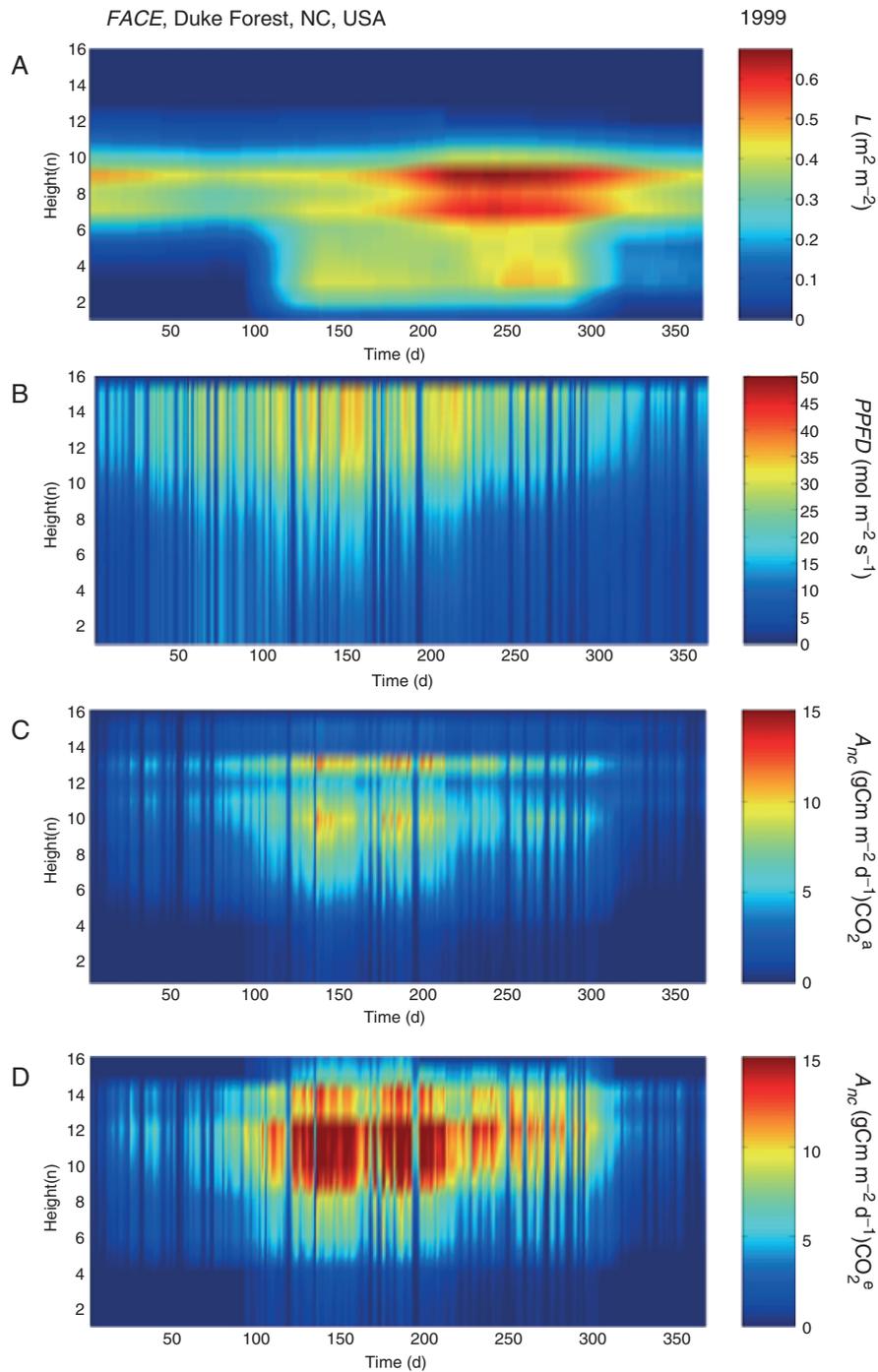
The  $c_i/c_a$  as a function of varying *PPFD* alone or together with  $g_{CO_2}$  is shown for sun- and shade-type foliage of the two main species (Fig. 1c,d), along with their  $g_s$  (Fig. 1a,b) and estimated leaf level  $A_{net}$  (Fig. 1e,f). The 4C-A model reproduced the expected pattern of responses of  $c_i/c_a$  and  $A_{net}$  to light, and a number of additional responses to  $g_s$ ,  $D$ , and  $\theta$  (data not shown). The canopy-level 4C-A model reproduced the expected corresponding patterns in  $A_{nC}$  (Fig. 1g,h). As shown for 1999, the model produced a spatio-temporal light pattern (Fig. 2b) that captured both the dynamics in *L* (Fig. 2a) and in incoming light, influenced by the sun angle and clouds, and especially by the ephemeral pattern of the broadleaf foliage (Fig. 2a). The seasonal and vertical patterns in  $A_{nC}$  (Fig. 2c) reflect the dynamics in incoming light and *L*, and the effect of CO<sub>2</sub> is discernible (Fig. 2d). Day-to-day variations in light due to clouds are clearly reflected in the vertical pattern of  $A_{nC}$ . The vertical pattern of  $A_{nC}$  shows the relative little contribution of the broadleaf



**Fig. 1** Modelled responses of stomatal conductance ( $g_s$ , a and b), ratio of leaf internal to external atmospheric CO<sub>2</sub> concentration ( $c_i/c_a$ , c and d), leaf net assimilation ( $A_{net}$ , e and f), and canopy net assimilation ( $A_{nC}$ , g and h) vs. light (*PPFD*) for the canopy dominant species *P. taeda* (a, c, e, and g) and the most abundant broadleaf species *L. styraciflua* (b, d, f, and h) at the Duke Forest site.

species to the total canopy photosynthesis, and the high contribution of *P. taeda*, especially during the period in which the sun angle is steepest.

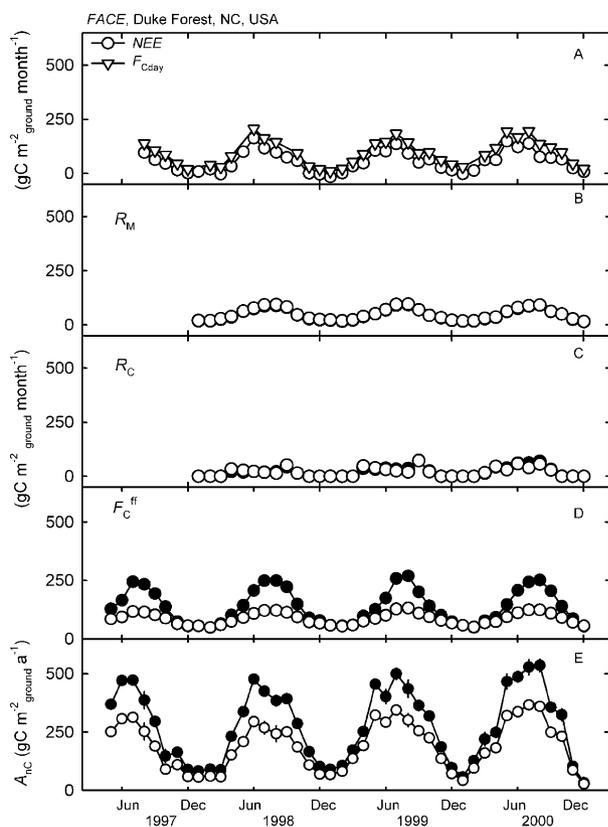
The ecosystem net assimilation estimate was first evaluated under ambient conditions by comparing it with: (1) with daytime net ecosystem exchange ( $F_e^D$ ) measured *via* eddy covariance over the entire canopy of an ambient plot, augmented with daytime forest floor CO<sub>2</sub> flux ( $F_C^{ff}$ ) and above-ground construction and maintenance respiration ( $R_M$  and  $R_C$ ), with construction respiration assumed to be one half the daily estimate, and with the change in CO<sub>2</sub> storage in the forest air



**Fig. 2** Daily values for 1999 of vertical distribution in the canopy for (a) mean leaf area index ( $L$ ), (b) integrated light ( $PPFD$ ), (c) integrated canopy net assimilation ( $A_{nC}$ ) averaged for ambient plots ( $CO_2^a$ ), and (d) integrated  $A_{nC}$  averaged for elevated plots ( $CO_2^e$ ).

volume ( $\Delta S_C^a$ ) (Lai *et al.* 2000); (2)  $NPP$  estimates derived from allometric relationships augmented with whole plant maintenance ( $R_M$ ) and construction respiration ( $R_C$ ); and (3) instantaneous measurements of  $A_{net}$  at the upper third of the canopy *via* leaf gas exchange measurements under both  $CO_2^a$  and  $CO_2^e$ .

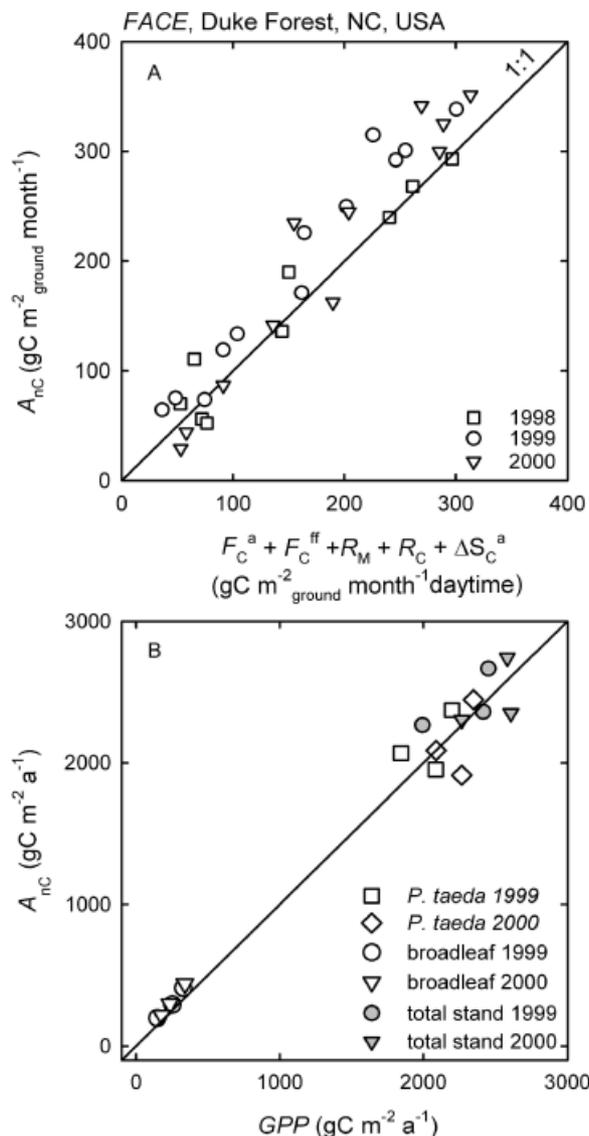
Reliable estimates of net ecosystem exchange (24 h,  $NEE$ ) were available for 37 of the months from August 1997 to December 2000 (Fig. 3a). For the same period we show the seasonal dynamics of the estimated values of  $R_M$  and  $R_C$ ,  $A_{nC}$ , combined for broadleaf and *P. taeda*, and  $F_C^{ff}$  (Fig. 3b–e). We note that the period in which  $A_{nC}$



**Fig. 3** Monthly fluxes throughout the study period of (a) net ecosystem exchange ( $F_C$ , open circles) and net ecosystem exchange for daytime only ( $F_{Cday}$ , open triangles) for ambient CO<sub>2</sub> only, (b) maintenance respiration ( $R_M$ ) summed for woody components, roots, leaves, and needles, (c) construction respiration ( $R_C$ ) summed for woody components, roots, leaves, and needles, (d) forest floor CO<sub>2</sub> efflux ( $F_C^{ff}$ ), and (e) canopy net assimilation ( $A_{nC}$ ) under ambient (open symbols) and elevated (filled symbols) conditions. Where filled symbols are not seen, they are obstructed by open symbols.

is highest occurs 2 months before  $L$  reaches its maximum late in the season (Phillips & Oren, 2001), and result in that maintenance and construction respiration reaching their highest values while  $A_{nC}$  is already decreasing (Fig. 3b,c and e). The most noticeable patterns are the relative invariance of the annual course of all respiration components, and the progressive increase in the maximum monthly value of  $A_{nC}$  during the experiment, reflecting mostly the increase in  $L$ .

We tested the 4C-A model skill by comparing  $A_{nC}$  against the balance of fluxes measured or calculated for the site. The monthly estimates of  $A_{nC}$  were higher than the sum of the contributing flux components (Fig. 4a). Modelled  $A_{nC}$  summed for each month showed a clear positive bias, averaging about 13% higher than the contributing components in the 3 years with sufficient data, with the worst annual agreement of 29% in 1999,



**Fig. 4** (a) Monthly flux comparison of net canopy assimilation ( $A_{nC}$ ) vs. the sum of contributing components during daytime: net ecosystem exchange ( $F_C^a$ ), forest floor CO<sub>2</sub> efflux ( $F_C^{ff}$ ), maintenance respiration of woody biomass during daytime ( $R_M$ ), construction respiration ( $R_C$ ), and change in CO<sub>2</sub> storage in the forest air volume ( $\Delta S_C^a$ ). (b) Comparison of  $A_{nC}$  vs. gross primary production (not including daytime leaf respiration) on an annual basis for 1999 and 2000 for individual plots for the *P. taeda* component, the broadleaf canopy component, and for the combined canopy. The 1:1 line is also shown for reference. Both comparisons made ambient CO<sub>2</sub>.

and a best of 4% in 2000 (Fig. 4a). We evaluated the effect of uncertainty in the least well-quantified parameters of the 4C-A model, the mean annual value of maximum light saturated  $CE_{max}$  and the light levels at which  $CE_{max}$  is set to zero or to the maximum, by changing each parameter  $\pm 10\%$ . Changing the mean annual  $CE_{max} \pm 10\%$  causes a corresponding change of

**Table 3** Components of the annual carbon balance (in  $\text{g C m}^{-2} \text{a}^{-1}$ ) including net primary productivity, respiration, and estimates for canopy photosynthesis from the 4-CA model ( $A_{\text{nC}}$ ) and from the sum of components ( $GPP$ ). Bold type indicates differences significant at  $P \leq 0.09$ 

	1999			2000		
	$\text{CO}_2^{\text{a}}$	$\text{CO}_2^{\text{b}}$	<i>P</i> value	$\text{CO}_2^{\text{a}}$	$\text{CO}_2^{\text{b}}$	<i>P</i> value
<i>P. taeda</i>						
Total $R_{\text{M}}^*$	1014 (71)	1036 (206)	0.93	1022 (78)	1060 (209)	0.88
Total $R_{\text{C}}$	204 (14)	250 (23)	<b>0.07</b>	241 (12)	296 (38)	0.17
Total $NPP^{\dagger, \ddagger}$	825 (50)	1026 (101)	<b>0.09</b>	972 (37)	1207 (162)	0.19
<i>GPP</i>	2043 (105)	2312 (326)	0.45	2235 (77)	2563 (408)	0.47
$A_{\text{nC}}$	2131 (125)	2830 (278)	<b>0.04</b>	2148 (157)	2967 (299)	<b>0.03</b>
$\Delta = A_{\text{nC}} - GPP$	88 (122)	518 (66)		-86 (137)	404 (110)	
$\Delta > 0, P =$	0.57	<b>0.02</b>		0.52	<b>0.08</b>	
<i>Hardwoods</i>						
Total $R_{\text{M}}^*$	137 (32)	184 (50)	0.18	137 (32)	184 (51)	0.17
Total $R_{\text{C}}$	22 (5)	25 (7)	0.35	25 (3)	26 (7)	0.84
Total $NPP^{\dagger}$	84 (16)	101 (26)	0.23	89 (14)	106 (32)	0.44
<i>GPP</i>	244 (53)	310 (82)	0.19	252 (48)	316 (90)	0.27
$A_{\text{nC}}$	300 (60)	557 (241)	0.30	317 (65)	563 (239)	0.30
$\Delta = A_{\text{nC}} - GPP$	56 (11)	247 (164)		66 (18)	246 (150)	
$\Delta > 0, P =$	<b>0.05</b>	0.26		<b>0.05</b>	0.24	
<i>Stand</i>						
Total $R_{\text{M}}^*$	1152 (103)	1220 (89)	0.76	1160 (109)	1245 (190)	0.71
Total $R_{\text{C}}$	226 (15)	275 (19)	<b>0.05</b>	266 (10)	322 (33)	0.14
Total $NPP^{\dagger}$	909 (54)	1127 (88)	<b>0.06</b>	1060 (25)	1313 (141)	0.15
<i>NEP</i> Ia§	488 (172)	185 (219)	0.34	669 (141)	397 (281)	0.47
<i>NEP</i> II§	576 (37)	872 (55)	<b>0.02</b>	654 (4)	1030 (106)	<b>0.07</b>
<i>NEE</i>	661			792		
<i>GPP</i>	2287 (148)	2622 (292)	0.32	2486 (110)	2879 (364)	0.36
$A_{\text{nC}}$	2431 (120)	3387 (160)	<b>&lt;0.01</b>	2466 (139)	3530 (212)	<b>0.01</b>
$\Delta = A_{\text{nC}} - GPP$	144 (102)	765 (191)		-20 (123)	651 (240)	
$\Delta > 0, P =$	0.39	<b>0.05</b>		0.64	0.11	

The data are provided separately for *Pinus taeda* and for the broadleaf species, and summed to the stand level. Net ecosystem exchange (*NEE*) is given for the stand under  $\text{CO}_2^{\text{a}}$  only.

\*Augmented with fine root respiration (Matamala & Schlesinger, 2000).

†Augmented with fine root increment (Matamala & Schlesinger, 2000).

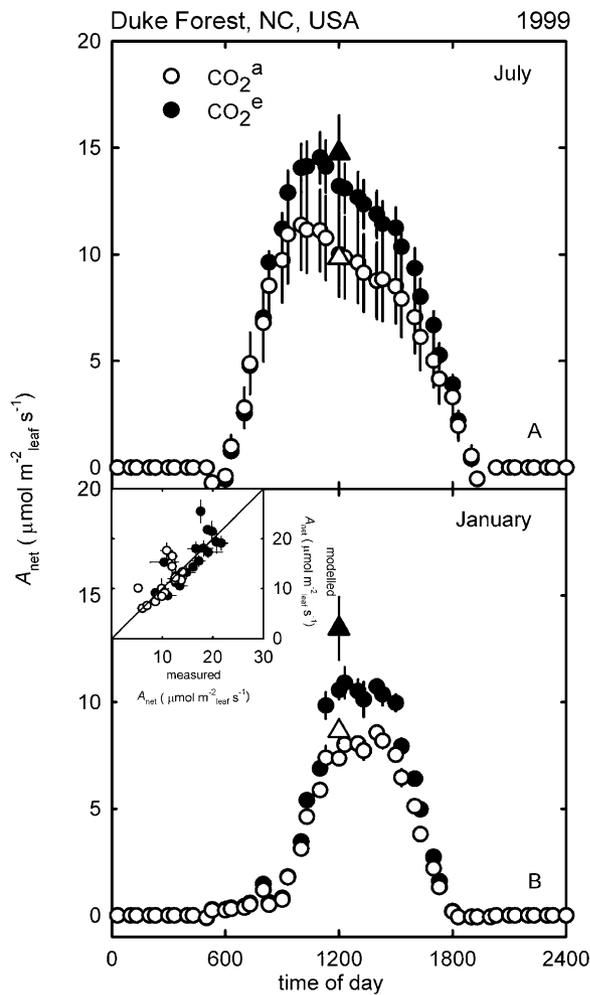
‡Augmented with litter fall data (Finzi *et al.*, 2001).

§*NEPI* based on flux components ( $NPP - R_{\text{F}}$ ), and *NEP* II based on C pools; see text for details.

$\sim \pm 5\%$  in  $A_{\text{nC}}$  ( $\pm 120 \text{ g m}^{-2} \text{ a}^{-1}$ ). Increasing and decreasing the light level at which  $CE_{\text{max}} = 0$  caused a  $-6\%$  and  $+1\%$  change in  $A_{\text{nC}}$ , respectively, while these changes in the light level at which  $CE_{\text{max}}$  reaches its maximum value caused a  $-9\%$  and  $+4\%$  change in  $A_{\text{nC}}$ . Thus, the likely errors in parameter values used in the 4C-A model runs would not reduce  $A_{\text{nC}}$  sufficiently to match the estimates based on the sum of flux components (Fig. 4a).

On an annual basis,  $A_{\text{nC}}$  under  $\text{CO}_2^{\text{a}}$  balanced well with the sum of  $NPP$ ,  $R_{\text{C}}$  and  $R_{\text{M}}$  (i.e.  $GPP$ , not including daytime leaf respiration) for both *P. taeda* and the broadleaf species, and for their sum (Fig. 4b; Table 3).

Averaged for the 2 years,  $A_{\text{nC}}$  in  $\text{CO}_2^{\text{a}}$  was 3% more than  $GPP$ . Using a constant  $C_i/C_a$  for each foliage type (after Norman 1982) but keeping the conductance as in the 4C-A model resulted in  $\sim 20\%$  higher  $A_{\text{nC}}$  than that estimated with 4C-A, while a big-leaf calculation with no vertical pattern in  $g_s$  and a constant  $C_i/C_a$  resulted in  $\sim 16\%$  lower  $A_{\text{nC}}$ , an underestimation found in other single-layer models (DePury & Farqhar, 1997; Lai *et al.*, 2000; Friend, 2001). Thus, the complexity added by using a multilayered model with variable  $c_i/c_a$  and  $g_{\text{CO}_2}$  was necessary to attain closure of the C balance under  $\text{CO}_2^{\text{a}}$  conditions, and the good agreement between  $A_{\text{nC}}$  and  $GPP$  (Fig. 4b) suggests that the



**Fig. 5** Comparison of ensemble mean canopy net assimilation ( $A_{\text{net}}$ ) for the upper canopy third (corresponding to mostly sunlit leaves) with midday measurements of  $A_{\text{net}}$  via leaf gas exchange measurements (shown as triangles) for a warm (July) and a cold (January) month in 1999 ( $n = 3$  treatment plots; bars represent 1 standard error). The inset shows are upper canopy midday modelled  $A_{\text{net}}$  vs. midday  $A_{\text{net}}$  measured via leaf gas exchange measurements for both months with the 1:1 line for reference.

estimate based on the sum of flux components is a little low.

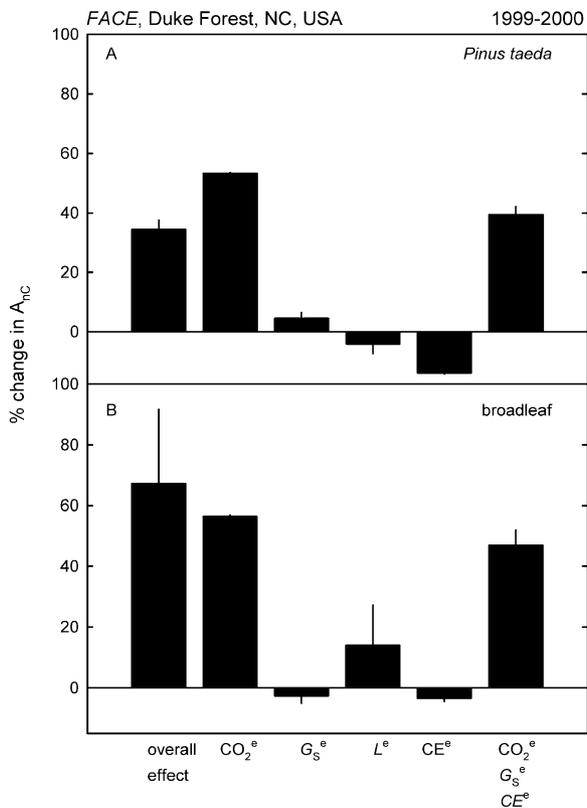
As a final test of our multilayered model, we compared  $A_{\text{net}}$  estimates of sun foliage in the upper *P. taeda* canopy with gas exchange measured midday values (Ellsworth, 2000). The diurnal  $A_{\text{net}}$  pattern in the upper one-third of the canopy obtained through a monthly ensemble average of estimates from the 4C-A model is shown along with the leaf gas exchange measured values for a midsummer and a midwinter month, with favourable and unfavourable conditions for photosynthesis, respectively (Fig. 5). This analysis was repeated throughout the year for every month in

which leaf gas exchange measurements were available, showing a good agreement between the 4C-A and leaf gas exchange values (inset in Fig. 5: each datum represents a different month); the few points clearly above unity reflect a higher stomatal conductance calculated for the whole canopy relative to that measured with leaf gas exchange measurements on a small section of fascicles. In (Fig. 5), we also show the only test available of the model performance under CO<sub>2</sub><sup>e</sup>, demonstrating that the model is able to reproduce direct measurements of  $A_{\text{net}}$  under CO<sub>2</sub><sup>e</sup>. Schäfer *et al.* (2002) observed that the elevated CO<sub>2</sub> did not affect transpiration at the stand. Using their transpiration data and the 4C-A estimate of  $A_{\text{net}}$ , stand level water use efficiency was 4.7 g C kg<sup>-1</sup> H<sub>2</sub>O under CO<sub>2</sub><sup>a</sup> and 7.0 g C kg<sup>-1</sup> H<sub>2</sub>O under CO<sub>2</sub><sup>e</sup>, similar to leaf-level values for the *P. taeda* at this stand (Ellsworth, 1999).

#### Effects of elevated CO<sub>2</sub>

The seasonal pattern of monthly  $A_{\text{net}}$ , and associated  $R_{\text{C}}$ ,  $R_{\text{M}}$  and  $F_{\text{C}}^{\text{ff}}$  under CO<sub>2</sub><sup>e</sup> is shown in (Fig. 3b–e). The pattern is similar, although not identical to that under CO<sub>2</sub><sup>a</sup>, but with greater amplitude.  $A_{\text{net}}$  on a monthly basis under CO<sub>2</sub><sup>e</sup> was linearly correlated with that under CO<sub>2</sub><sup>a</sup>, for both *P. taeda* (slope 1.34) and the broadleaf species (slope 1.67), and for the entire canopy (slope 1.41, minimum  $r^2 = 0.98$ ;  $P < 0.0001$ ).

The effect of CO<sub>2</sub><sup>e</sup> on modelled  $A_{\text{net}}$  (expressed as  $A_{\text{net}}$  under CO<sub>2</sub><sup>e</sup> divided by that under CO<sub>2</sub><sup>a</sup>) was slightly greater for *P. taeda* in 2000 than in 1999, with the opposite occurring for the broadleaf species. However, the difference between years was not significant ( $P > 0.35$ ) and the response in both years was not significant for presentation (Fig. 6). Modelled  $A_{\text{net}}$  was 34% higher in CO<sub>2</sub><sup>e</sup> plots in *P. taeda* and 67% higher in broadleaf species than in CO<sub>2</sub><sup>a</sup> plots (see overall effect, Fig. 6). Several factors can contribute to the enhancement of modelled  $A_{\text{net}}$  based on the 4C-A model: (1) elevated atmospheric CO<sub>2</sub> concentration; (2) effect of CO<sub>2</sub><sup>e</sup> on stomatal conductance; (3) effect of CO<sub>2</sub><sup>e</sup> on  $CE_{\text{max}}$ ; and (4) effect of CO<sub>2</sub><sup>e</sup> on  $L$  and, in the Duke Forest FACE, pretreatment differences in  $L$  even though plots were paired prior to the onset of enrichment to minimized differences. The contribution of each factor to the overall effect was evaluated by running the model with only one factor at a time representing the conditions of the plots under CO<sub>2</sub><sup>e</sup>. Our results show that the potential enhancement solely due to CO<sub>2</sub><sup>e</sup> is ~55% for both species types (Fig. 6). Higher *P. taeda* stomatal conductance due to increased water availability in CO<sub>2</sub><sup>e</sup> plots could potentially increase  $A_{\text{net}}$  under otherwise CO<sub>2</sub><sup>a</sup> conditions by 5%. The broadleaf species showed a reduction of 3% in  $A_{\text{net}}$  due to



**Fig. 6** Effect of different components on canopy net assimilation ( $A_{nC}$ ) for *P. taeda* (a) and the broadleaf canopy (b) as a % change of effect vs. ambient conditions (see text). First a comparison was made between elevated and ambient plots with the model parameterized best to represent each set of plots ('overall effect'). Then, components were altered in ambient plots to represent differences in a single parameter, or a combination of parameters, with elevated  $CO_2$  plots. The resulting model runs altered the  $CO_2$  concentration itself ( $CO_2^e$ ), canopy stomatal conductance ( $G_s^e$ ), leaf area index ( $L^e$ ), carboxylation efficiency ( $CE^e$ ), and a combination of all but  $L^e$ .

stomatal response to  $CO_2^e$ . Leaf area index did not respond to  $CO_2^e$  in this experiment; thus, using  $L$  from  $CO_2^e$  plots to estimate  $A_{nC}$  under otherwise  $CO_2^e$  conditions reflects mostly differences in initial conditions in which  $L$  of *P. taeda* was slightly lower under  $CO_2^e$  and that of the broadleaf was slightly higher. For both species the potential change in  $A_{nC}$  due to the inherent initial difference in  $L$  was not significant ( $P > 0.29$ ), but influenced the overall effect. Down-regulation of  $CE_{max}$  by different needle age classes reduced  $A_{nC}$  of *P. taeda* by 14% and that of the broadleaf species by 4%. Thus, we estimated  $A_{nC}$  exclusive of inherent, pretreatment differences among plots by using the values of  $L$  found for different species in the  $CO_2^e$  plots with all other factors as in the  $CO_2^e$  plots. The estimated  $CO_2$  effect in this forest is 39% and 47% for *P.*

*taeda* and the broadleaf species, respectively, or 41% for the entire canopy.

Based on paired *t*-test comparisons of *NPP* and respiration estimates between treatments, only  $R_C$  and *NPP* for *P. taeda* and the entire stand in 1999 showed a significant difference between treatments (Table 3). We average the components of the autotrophic C balance for the two years (shown in Table 3) and present them together with the additional ecosystem C balance components to facilitate a comparison between treatments (Table 4). The major components of the autotrophic and whole ecosystem C balance (taken from Table 4) are presented in Fig. 7. We also calculated certain ratios amongst C balance components (Table 5) to compare under ambient conditions with commonly published ratios, and under elevated  $CO_2$  conditions with ratios available from studies using different approaches at this site.

Monthly estimates of  $A_{nC}$  were related to stand level transpiration ( $E_C$ ; Schäfer *et al.* 2002).  $A_{nC}$  was linearly related to  $E_C$  under both  $CO_2^a$  and  $CO_2^e$  (minimum  $r^2 = 0.87$ ;  $P < 0.0001$ ) without observable differences among years (minimum  $P = 0.14$ ), and with 50% higher water use efficiency under  $CO_2^e$  ( $P < 0.0001$ ). This enhancement in water use efficiency is greater than the 13% calculated based on *GPP* due to the 20% lack of closure in the C balance under  $CO_2^e$ , as opposed to the closure obtained under  $CO_2^a$  (Table 4; Fig. 7).

## Discussion

During the third and fourth years of this experiment, the uptake of  $CO_2$  by the plant canopy under  $CO_2^e$  was significantly greater ( $1010 \text{ g C m}^{-2} \text{ a}^{-1}$  or 41% enhancement) than under  $CO_2^a$  (Figs 2 and 3; Table 3). The additional C that was assimilated under  $CO_2^e$  was allocated to tree growth ( $243 \text{ g C m}^{-2} \text{ a}^{-1}$  during the 1999 and 2000 growing seasons) and respiration ( $129 \text{ g C m}^{-2} \text{ a}^{-1}$ ). Most of the remaining extra C is unaccounted for by the measured or modelled fluxes of C in this study (Table 4; Fig. 7). The lack of closure in our C budgets under  $CO_2^e$  is in sharp contrast to the near-complete closure under  $CO_2^a$ . This, coupled with the observation that modelled gas exchange agreed with measured leaf-level values equally well under both  $CO_2$  conditions (Fig. 5), suggests that one or more C budget components is underestimated following fixation under  $CO_2^e$ . In what follows, we analyse and discuss the pools and fluxes that may account for this 'missing' C.

### Assessment of C balance under ambient $CO_2$

Estimating  $CO_2$  uptake using process-based ('bottom-up') or empirical ('top-down') approaches has been an

**Table 4** Plant and ecosystem components in g C m<sup>-2</sup> a<sup>-1</sup> averaged for 1999 and 2000

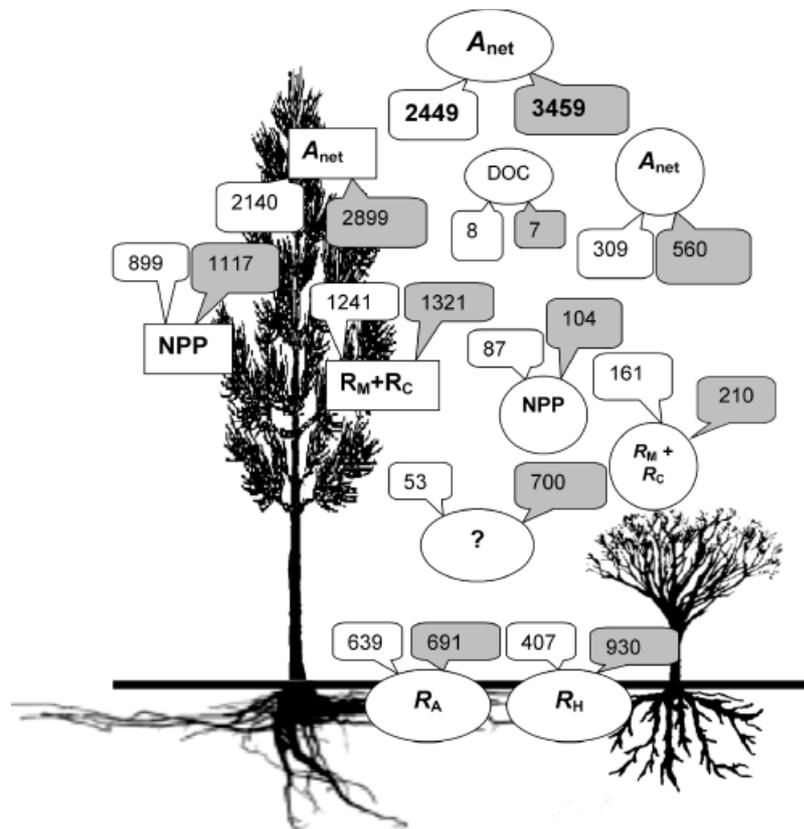
Scale	CO <sub>2</sub> <sup>a</sup>	CO <sub>2</sub> <sup>b</sup>
<i>Daytime ecosystem C balance</i>		
A <sub>nC</sub>	2449	
F <sub>C</sub> <sup>a</sup>	-1175	
F <sub>C</sub> <sup>ff</sup> daytime	-540	
ΔS <sub>C</sub> <sup>a</sup>	-22	
R <sub>MA</sub> daytime	-280	
R <sub>CA</sub> daytime	-116	
LOC	316	
<i>Plant C balance</i>		
A <sub>nC</sub>	2449	3459
GPP	2396	2759
R <sub>A</sub>	1402	1531
R <sub>M</sub>	1155	1233
R <sub>MA</sub>	532	561
R <sub>MB</sub>	623	672
R <sub>C</sub>	246	298
R <sub>CA</sub>	230	278
R <sub>CB</sub>	16	20
NPP	994	1228
growth	750	960
Δlitter	222	241
Δroots	14	20
DOC	8	7
LOC	53	700
<i>Heterotrophic C balance</i>		
R <sub>H</sub>	407	930
F <sub>C</sub> <sup>ff</sup>	1046	1621
R <sub>AB</sub> *	639	691
INPUT	342	404
litter	320	377
DOC	8	7
root turnover	14	20
Δstorage	-15	80
Δforest floor	42	50
Δroot	4	6
Δsoil C	-61	24
Input - Δstorage	357	324
LOC	50	606
<i>Ecosystem (24 h)</i>		
NEE	721	
NEP Ia	585	301
NPP	986	1221
R <sub>Hg</sub> I	407	930
R <sub>HI</sub> I	7	10
LOC I	136	
NEP Ib	636	907
NPP	986	1221
R <sub>Hg</sub> II	357	324
R <sub>HI</sub> II	7	10
LOC II	91	
NEP II	613	885
ΔB <sub>s</sub>	633	811
Δforest floor	42	50
Δsoil C	-61	24
LOC III	114	

\*DIC is not considered. DIC was 16 g C m<sup>-2</sup> a<sup>-1</sup> under CO<sub>2</sub><sup>a</sup> and 22 g C m<sup>-2</sup> a<sup>-1</sup> under CO<sub>2</sub><sup>b</sup>; subscript g and l in the *Ecosystem* R<sub>H</sub> component refers to CO<sub>2</sub> losses in gas and liquid form, respectively.

active field of research for more than four decades (Duncan *et al.*, 1967; Monteith, 1977, see Jarvis *et al.*, 1985). Balancing the C budget to account for A<sub>nC</sub> by independent measurements of biomass production and estimates of respiration of individual branches, trees, and canopies builds confidence in the skills of models to estimate A<sub>nC</sub> and respiration. These skills are especially important when productivity might not be accurately measured, as is often the case in below-ground measurements, and is estimated as the residual of the C balance between A<sub>nC</sub> and the sum of respiration and above-ground productivity (Schulze *et al.*, 1977; Matyssek & Schuize, 1988; Oren & Zimmermann, 1989; Law *et al.*, 2000). Recently, C balances have been cross-validated by comparing modelled A<sub>nC</sub> with ecosystem scale CO<sub>2</sub> fluxes measured with eddy covariance, or with NPP and plant respiration (Wofsy *et al.*, 1993; Baldocchi *et al.* 1996, Arneth *et al.* 1998, Granier *et al.* 2000, Lai *et al.* 2002). When modelled fluxes of C are in simultaneous agreement with independently measured fluxes of C from both plant and ecosystem pools, it is possible to conclude that the modelled estimate of A<sub>nC</sub> has a high degree of accuracy. We are aware of only a few studies that have utilized such an approach (e.g. Granier *et al.*, 2000; Law *et al.*, 2000).

In this study, monthly A<sub>nC</sub> under CO<sub>2</sub><sup>a</sup> was higher (~13%) than estimated based on eddy covariance measurements (Fig. 4a), but very similar to (within 3% of) the annual GPP estimate based on growth and respiration (Fig. 4b). The discrepancy with the estimate based on eddy covariance is within the spatial variability in fluxes measured over this stand (Katul *et al.*, 1999). The 4C-A estimate of A<sub>nC</sub> under CO<sub>2</sub><sup>a</sup> is twice that estimated with MAESTRA (Luo *et al.*, 2001) and one-third higher than that estimated with a light response curve and a constrained source-optimization model that neglects above-ground daytime respiration (CSO; Lai *et al.*, 2002; Table 6). Our estimate of GPP in 1999 and 2000 is ~100 g m<sup>-2</sup> a<sup>-1</sup> greater and smaller, respectively, than the estimate of GPP presented by Hamilton *et al.* (2002) for the 1998 calendar year. The difference between our study and that of Hamilton *et al.* (2002) reflects methodological differences (e.g. Hamilton *et al.* (2002) include daytime photorespiration, which is not included in our model), and annual variation in growing conditions superimposed on the dynamics of this rapidly aggrading forest ecosystem.

In addition to working at the stand level, we compared the modelled estimates of A<sub>nC</sub> with NPP plus autotrophic construction and maintenance respiration (= GPP) for *P. taeda* and the broadleaf species separately. Averaged over 1999 and 2000, the A<sub>nC</sub> of the broadleaf component was 20% higher than that present-



**Fig. 7** Components of the forest carbon balance averaged for 1999 and 2000. Components identified in ellipsoid boxes are for the entire ecosystem, in squares are for *Pinus taeda* (terms on the left-hand side), and in circles are for the broadleaf canopy (terms on the right-hand side). Shown are canopy net assimilation,  $a_{\text{nc}}$ , net primary productivity,  $NPP$ , construction respiration,  $R_C$ , combined with maintenance respiration,  $R_M$ , and the amount of  $\text{CO}_2$  efflux from the forest floor attributed to autotrophic and heterotrophic respiration,  $R_A$  and  $R_H$ , respectively. The lack of closure in the autotrophic carbon balance is shown as '?'.

ted in Hamilton *et al.* (2002) (Fig. 7). In contrast, there was very strong agreement between studies in  $GPP$  for the *P. taeda* component of this ecosystem (Table 3).

We evaluated our C balance under ambient conditions by comparing commonly calculated ratios between balance components (Table 5) with published values. Our  $NPP/GPP$  ratio was slightly lower (Table 5) than a general ratio estimated for a large number of stands (0.47) by Landsberg & Waring (1997). Our  $R_A/GPP$  ratio ( $= 1 - NPP/GPP$ , similar to  $R_A/A_{\text{nc}}$ ) is within the range calculated based on the amount of standing biomass or tree height (Ryan *et al.*, 1994; Mäkelä & Valentine, 2001; Table 5), higher than the 0.42 estimated for 1999 by Lai *et al.* (2002) and lower than the 0.7 estimated for 1998 by Hamilton *et al.* (2002). Notably, Hamilton *et al.* (2002) include estimates of daytime foliage respiration in their estimate while Lai *et al.* (2002) neglected daytime above-ground respiration.

The  $F_C^{\text{ff}}/NPP$  ratio was lower in this study than the 'global' average ratio of 1.24 (Raich & Schlesinger 1992) and the 1.65 estimated in a young *Pinus ponderosa* L.

stand (Law *et al.*, 1999). It is likely that our stand is at a different stage of development in which much of the assimilated C is invested in slow turnover woody biomass. Subtracting  $R_A$  (both construction and maintenance) of roots from total  $F_C^{\text{ff}}$  (Table 4), we estimated that  $\sim 38\%$  ( $407 \text{ g C m}^{-2} \text{ a}^{-1}$ ) of this flux was due to heterotrophic respiration. This proportion is in agreement with values obtained with a similar methodology in similar stands (Maier & Kress 2000), but lower than the 45% that was estimated by Andrews *et al.* (1999) in the plots under  $\text{CO}_2^s$  using isotopic mixing ratios. This may reflect lower rates of rhizodeposition under  $\text{CO}_2^s$  (Table 4).  $R_H$  estimated by Hamilton *et al.* (2002) as the difference between  $F_C^{\text{ff}}$  and  $R_A$  was 22% of  $F_C^{\text{ff}}$  (Table 6), allowing only  $216 \text{ g C m}^{-2} \text{ a}^{-1}$  on average to balance C turnover in the forest floor–soil subsystem – significantly lower than the estimate in this study. Assuming, as a lower boundary, that the forest floor C is at steady state under  $\text{CO}_2^s$ , the sum of C in (1) litterfall (Finzi *et al.* 2001, 2002), (2) the turnover of fine roots (Matamala & Schlesinger, 2000), (3) dissolved in organic forms in

**Table 5** Ratios of respiration components (autotrophic  $R_A$ , heterotrophic  $R_H$ , construction  $R_C$ , maintenance  $R_M$  and soil CO<sub>2</sub> efflux  $F_C^{ff}$ ) under ambient (CO<sub>2</sub><sup>a</sup>) and elevated (CO<sub>2</sub><sup>e</sup>) atmospheric CO<sub>2</sub> concentrations with gross primary productivity ( $GPP$ ) and modelled canopy net assimilation ( $A_{nC}$ ). Bold type indicates differences significant at  $P \leq 0.009$

Ratio	CO <sub>2</sub> <sup>a</sup>	CO <sub>2</sub> <sup>e</sup>	<i>P</i> value
$R_A/A_{nC}$	0.58 (0.028)	0.44 (0.027)	<b>0.03</b>
$R_A/GPP$	0.58 (0.012)	0.55 (0.009)	<b>0.05</b>
	0.55–0.60*		
	0.57–0.59†		
$R_C/A_{nC}$	0.10 (0.004)	0.09 (0.004)	<b>0.01</b>
$R_C/GPP$	0.10 (0.004)	0.10 (0.003)	0.22
$R_M/A_{nC}$	0.48 (0.028)	0.36 (0.024)	<b>0.04</b>
$R_M/GPP$	0.48 (0.016)	0.44 (0.012)	<b>0.07</b>
$R_H/F_C^{ff}$	0.38 (0.090)	0.57 (0.050)	0.13
$F_C^{ff}/NPP$	1.07 (0.060)	1.36 (0.084)	< <b>0.01</b>

$R_H$  was calculated as the difference between  $F_C^{ff}$  and root respiration (construction and maintenance). All ratios are averages for 1999 and 2000.

Mean of 2 years and three plots and 1 standard error from the mean in parentheses.

\*Based on Mäkelä & Valentine (2001).

†Generated after equation  $R_A/GPP = 0.6191 (1 - e^{0.0004Bs})$  derived from Ryan *et al.* (1994).

precipitation (DOC), (4) and depleted from the mineral soil (1.43–1.31% over 3 years; see Schlesinger & Lichter, 2001) would release  $357 \text{ g C m}^{-2} \text{ a}^{-1}$  (cf. Table 4). This C release accounts for 88% of our estimate of  $R_H$ , leaving us with the need to account for  $\sim 50 \text{ g m}^{-2} \text{ a}^{-1}$ . Richter *et al.* (1999) estimated that root exudation in young *P. taeda* stands is  $\sim 50 \text{ g m}^{-2} \text{ a}^{-1}$  and can account for the remaining flux of C from the top of the forest floor (Table 3, 4; Fig. 7).

In summary, the budget for C in autotrophic and whole-ecosystem components is balanced under CO<sub>2</sub><sup>a</sup>. The pools and fluxes of the measured components are reasonable in absolute terms, relative to each other, and are similar to values published in the literature. Based on this, we applied the same set of analyses to the balances of C in the forest plots under CO<sub>2</sub><sup>e</sup>.

#### Assessment of C balance under elevated CO<sub>2</sub>

Applying the 4C-A model to CO<sub>2</sub><sup>e</sup> conditions produced an enhancement of  $A_{nC}$  by 41% relative to that under CO<sub>2</sub><sup>a</sup> (a 35% and 67% stimulation for the *P. taeda* and broadleaf components, respectively; Fig. 6). This enhancement is reduced to 39% when we factor out the pre treatment difference in leaf area index (L) between the plots under CO<sub>2</sub><sup>a</sup> and CO<sub>2</sub><sup>e</sup>. Both enhancement ratios are similar to that modelled for the 1998 calendar year

(43%) by Luo *et al.* (2001). The 4C-A model estimated an enhancement of 55% in  $A_{nC}$  due to elevated CO<sub>2</sub>, and in addition a 5% enhancement due to increase in  $G_S$  of *P. taeda* (Fig. 6). Canopy stomatal conductance of *P. taeda* increased with increasing water availability under CO<sub>2</sub><sup>e</sup> (Schäfer *et al.*, 2002, in review). The model also estimated a decline of 3% in  $A_{nC}$  due to a decrease in  $G_S$  of the broadleaf species, and 14% due to a progressive decline in  $CE_{max}$ , mostly in previous-year foliage of *P. taeda* (Rogers & Ellsworth, 2002) that assimilates 70% of annual  $A_{nC}$  (Fig. 6). In absolute terms, the enhancement in  $A_{nC}$  attributable to the effect of CO<sub>2</sub><sup>e</sup> was  $963 \text{ g C m}^{-2} \text{ a}^{-1}$ . This value is lower than the  $1010 \text{ g C m}^{-2} \text{ a}^{-1}$  value (Fig. 7), reflecting the effect of pretreatment differences in  $L$  (Fig. 6).

$GPP$  – based on production and respiration – was only enhanced by 13% under CO<sub>2</sub><sup>e</sup>. This enhancement is lower than the 18% that was estimated for the 1998 calendar year (Hamilton *et al.* 2002), and less than half that estimated for  $A_{nC}$  by the 4C-A model. The enhancement in  $GPP$  is attributable to a 23% increase in  $NPP$ , a slight reduction over that observed in the second year of CO<sub>2</sub> enrichment (26%, DeLucia *et al.*, 1999; Hamilton *et al.*, 2002). Averaging across years, *P. taeda* wood production was enhanced by 29% under CO<sub>2</sub><sup>e</sup> and broadleaf wood production by 34% (Table 3). This resulted in a 29% enhancement of C storage in woody biomass, a moderately long-term storage pool of C. The other component of  $GPP$ , autotrophic respiration ( $R_A$ ), was enhanced by 13% under CO<sub>2</sub><sup>e</sup>, in contrast to Hamilton *et al.* (2002) who reported a 6% decline in this flux. Their reduction in  $R_A$  was due to a decrease in the rate of root  $R_M$  under CO<sub>2</sub><sup>e</sup>. Estimates of specific respiration rates obtained from excised and intact roots are subject to methodological artefact (Clinton & Vose, 1999; McDowell *et al.*, 1999; Matamala & Schlesinger, 2000). The reduction in  $R_M$  reported by Hamilton *et al.* (2002) contrasts with the increase reported by Matamala & Schlesinger (2000) for this FACE site and on which we based our calculations.

In contrast to the similarity in  $F_C^{ff}$  under CO<sub>2</sub><sup>a</sup>, we estimated much higher  $F_C^{ff}$  under CO<sub>2</sub><sup>e</sup> than did Hamilton *et al.* (2002) at  $602$  and  $248 \text{ g C m}^{-2} \text{ a}^{-1}$ , respectively. The 54% enhancement under CO<sub>2</sub><sup>e</sup> is well within the range of reported values from the prototype FACE plot at this site (Andrews *et al.*, 1999). It is also similar to that found for *P. ponderosa* under CO<sub>2</sub><sup>e</sup> (Johnson *et al.*, 1994). At the Duke Forest FACE site, the CO<sub>2</sub> enhancement in mean annual midday  $F_C^{ff}$  increased from 24% in 1997 to 43% in 1998 (Andrews *et al.*, 1999), suggesting that  $F_C^{ff}$  was still responding to the step increase in atmospheric CO<sub>2</sub> commencing in August 1996.

In this study,  $R_A$  contributed  $691 \text{ g C m}^{-2} \text{ a}^{-1}$  to  $F_C^{ff}$  under CO<sub>2</sub><sup>e</sup>, leaving  $930 \text{ g C m}^{-2} \text{ a}^{-1}$  for  $R_H$  (Table 4).

**Table 6** Comparison of estimates of different components of C balance

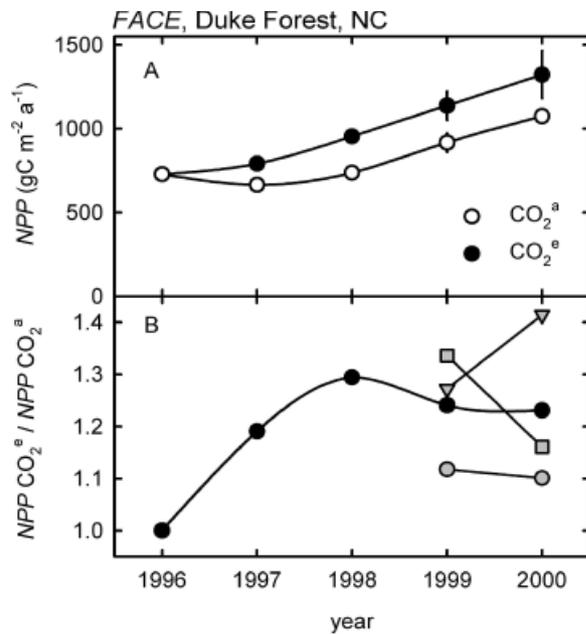
g C m <sup>-2</sup> a <sup>-1</sup>		DeLucia <i>et al.</i> (1999)		Luo <i>et al.</i> (2001)		Lai <i>et al.</i> (2002)	Hamilton <i>et al.</i> (2002)		This study	
		CO <sub>2</sub> <sup>a</sup>	CO <sub>2</sub> <sup>e</sup>	CO <sub>2</sub> <sup>a</sup>	CO <sub>2</sub> <sup>e</sup>	CO <sub>2</sub> <sup>a</sup>	CO <sub>2</sub> <sup>a</sup>	CO <sub>2</sub> <sup>e</sup>	CO <sub>2</sub> <sup>a</sup>	CO <sub>2</sub> <sup>e</sup>
GPP	1997			1224	1695					
	1998			1250	1786		2371	2805		
	1999					1808			2287	2622
	2000								2486	2879
NPP	1997	633	744							
	1998						705	897		
	1999								909	1127
	2000								1060	1313
NEP	1997									
	1998						428	602		
	1999					605			576	872
	2000								654	1030
R <sub>e</sub>	1997									
	1998						1932			
	1999					1203				
	2000									
R <sub>A</sub>	1997									
	1998						1704	1604		
	1999					214			1378	1495
	2000								1426	1567
R <sub>H</sub>	1997									
	1998						216	574		
	1999								464	753
	2000								457	749
F <sub>C</sub> <sup>ff</sup>	1997									
	1998						928	1176		
	1999					989			1051	1620
	2000								1039	1619

Mass balance calculations – assuming that the efflux of C from the forest floor is in a short-term steady state – imply the addition of C to the soil from an unmeasured source. The data presented in Schlesinger & Lichter (2001) suggest that the pool of C in the forest floor and mineral soil horizons under CO<sub>2</sub><sup>e</sup> is increasing by 80 g C m<sup>-2</sup> a<sup>-1</sup>. The components that turn over annually – above-ground litterfall, root mortality, and DOC – contribute an additional 404 g C m<sup>-2</sup> a<sup>-1</sup> to the forest floor (Table 4). Thus, the difference between R<sub>H</sub> plus the increment of C in soil pools (1010 g C m<sup>-2</sup> a<sup>-1</sup>) and inputs *via* turnover components (404 g C m<sup>-2</sup> a<sup>-1</sup>) implies a source for C of 606 g C m<sup>-2</sup> a<sup>-1</sup> (Fig. 7). This quantity is in very close agreement with the 700 g C m<sup>-2</sup> a<sup>-1</sup> of A<sub>nC</sub> predicted by the 4C-A model and not accounted for by the estimate of GPP from NPP and R<sub>A</sub> under CO<sub>2</sub><sup>e</sup>. Rhizodeposition can account for 20% of net CO<sub>2</sub> assimilation, most of which is immediately respired by microbes (Merbach *et al.*, 1999). Thus, the higher R<sub>H</sub>/F<sub>C</sub><sup>ff</sup> obtained under CO<sub>2</sub><sup>e</sup> than under CO<sub>2</sub><sup>a</sup>

(Table 5) reflects the allocation of C to rhizodeposition and subsequent metabolism by the microbial community (Table 4). The remaining C (700 – 606 = 94 g C m<sup>-2</sup> a<sup>-1</sup>) is 3% of A<sub>nC</sub>. This remainder may be explained by measurement error. Alternatively, it may reflect an increase in the allocation of C to fine root and mycorrhizal production in response to increasing nutrient limitation under CO<sub>2</sub><sup>e</sup> (Norby *et al.*, 1992; Zak *et al.*, 2000; Finzi *et al.*, 2001; Oren *et al.*, 2001; Constable *et al.*, 2001).

#### *Effects of elevated CO<sub>2</sub> on C sequestration*

Hamilton *et al.* (2002) estimated that NEP in 1998 (measured as the difference between NPP and R<sub>H</sub>) was lower under CO<sub>2</sub><sup>e</sup> than under CO<sub>2</sub><sup>a</sup>, and we found the same pattern in this study for 1999 and 2000 (Tables 3 and 4, NEP 1a). The 94 g C m<sup>-2</sup> a<sup>-1</sup> modelled by A<sub>nC</sub>, but unaccounted for by the component C balance method under CO<sub>2</sub><sup>e</sup>, may represent an underestimate of



**Fig. 8** (a) Net primary productivity (*NPP*) for the first 5 years of CO<sub>2</sub> fumigation in the Duke FACE experiment since commencement in 1996. Data from 1996 and 1997 are taken from DeLucia *et al.* (1999) and in 1998 from Hamilton *et al.* (2002) scaled to the plots in this study (see Discussion). CO<sub>2</sub><sup>e</sup> denotes elevated and CO<sub>2</sub><sup>a</sup> denotes ambient CO<sub>2</sub> conditions. (b) Enhancement ratio of *NPP* under CO<sub>2</sub><sup>e</sup> relative to that under CO<sub>2</sub><sup>a</sup> since commencement of fumigation in 1996. The temporal and spatial variation in the response to CO<sub>2</sub><sup>e</sup> within each plot pair is shown for 1999 and 2000 (grey symbols, different symbol types represent different plots).

*NPP* of approximately 7%. Adding this quantity to *NPP* would not make *NEP* Ia under CO<sub>2</sub><sup>e</sup> higher than under CO<sub>2</sub><sup>a</sup>. To minimize error, we also estimated *NEP* based on two additional methods: *NEP* Ib that relied on estimates of heterotrophic respiration from changes in C pools, but was otherwise calculated as *NEP* Ia (see Table 4), and *NEP* II calculated as the difference between C pools at the end of successive years (Tables 3 and 4, *NEP* II). Both approaches estimated values of *NEP* that were much closer to *NEE* under CO<sub>2</sub><sup>e</sup>, providing us with confidence in our estimate. Furthermore, *NEP* calculated based on both approaches was ~270 g C m<sup>-2</sup> a<sup>-1</sup> higher under CO<sub>2</sub><sup>e</sup>. This additional C is partitioned into the following pools: 235 g C m<sup>-2</sup> a<sup>-1</sup> are sequestered in woody biomass and 36 g C m<sup>-2</sup> a<sup>-1</sup> are sequestered in soils. The remainder of the extra C taken up by photosynthesis is used in fast turnover pools (e.g. root exudates) at the forest floor–soil subsystem.

We note that not all enhancements in C cycle components were significantly higher under CO<sub>2</sub><sup>e</sup> either for *P. taeda*, the broadleaf component, or the stand as a

whole. Notably, there was a large variation in component fluxes in 2000, leading to few statistically significant differences between treatments (Table 3). The reason for the increase in variation is clear when evaluating *NPP* (Table 3; Fig. 8). During the first 2 years of CO<sub>2</sub> fumigation, there was a linear increase in the rate of *NPP* under CO<sub>2</sub><sup>e</sup> relative to CO<sub>2</sub><sup>a</sup> (Fig. 8b). However, in 1999 and 2000, the ratio remained relatively constant. While the variation in *NPP* under CO<sub>2</sub><sup>a</sup> is relatively small, the variation under CO<sub>2</sub><sup>e</sup> increased through time (note the size of the standard error bars in Fig. 8a). The variability increased because of increasing differences in CO<sub>2</sub> response of *NPP* among the plot pairs, including a drastic increase in the enhancement ratio of *NPP* for one pair from 1999 to 2000 and a decrease for another (Fig. 8b). Although speculative, the drastic decrease in one of the pairs in the fourth full year of enrichment resembles that observed at the FACE prototype where the decrease was shown to reflect a decline in nutrient availability (Oren *et al.*, 2001).

## Conclusion

A combination of methods has demonstrated that the concentration of atmospheric CO<sub>2</sub> predicted for 2060 may increase the rate of C sequestration in woody biomass and soil. These pools represent moderate- to long-term storage of C in the terrestrial biosphere. However, the variation in the response of *NPP* among plots and years indicates that C storage is sensitive to other growth-limiting factors. Soil nutrient availability is a key candidate for this limitation (Eamus & Jarvis, 1989; Körner, 1995), as suggested by the results from a nutrient amendment study at the prototype FACE plot at this site (Oren *et al.*, 2001). If nutrient limitation imposes a constraint on future productivity, it is likely that C allocation to the production of wood will decrease in favour of the allocation to fine root production, rhizodeposition, and mycorrhizal symbionts (Norby *et al.*, 1992, 2001). Allocation of C to these pools will likely result in a rapid return of fixed C to the atmosphere (Merbach *et al.*, 1999). Thus, if nutrient limitations to growth increase at this site (Finzi *et al.*, 2001, 2002), it is possible that high rates of C fixation under elevated CO<sub>2</sub> will result in an acceleration of the C cycle through the forest ecosystem with little of the C remaining in long-term storage pools.

## Acknowledgements

The senior author would like to thank J.M. Rivin for insightful discussions and the creation of Fig. 7 and M. Hempel for financial support. The authors would like to thank Y. Para-

shenkov for data assistance, J. Nagy, K. Lewin and G. Hendrey for operating the FACTS-1 site. This study was supported by the US Department of Energy (DOE) through both the Office of Biological and Environmental Research and the National Institute of Global Environmental Change (NIGEC) Southeastern Regional Center at the University of Alabama. This work contributes to the Global Change and Terrestrial Ecosystem (GCTE) core project of the International Geosphere–Biosphere Program (IGBP).

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## Appendix: Estimating the vertical profile of PPFD

### Leaf area density dynamics

The vertical profile of leaf area index ( $L$  in  $\text{m}^2 \text{m}^{-2}$ ) and its seasonal variation for *P. taeda* were obtained by measuring plant area index (Lai *et al.* 2000, LiCor, Lincoln, NE, USA) during winter when the broadleaf species were leafless and *P. taeda* was at minimum  $L$ . This profile was expressed on a relative basis, and employed with  $L$  obtained based on allometric relationships and  $L$  dynamics to estimate the dynamics of the profile (Kinerson *et al.*, 1974; Pataki *et al.*, 1998; Schäfer *et al.*, 2002).  $L$  of broadleaf species was estimated as in Schäfer *et al.* (in review) and distributed vertically based on allometric relationships derived from individuals at this site. Seasonal  $L$  dynamics of deciduous broadleaf species was assumed to correspond to the time series of the increase in the maximum sap-flux density, obtained from boundary line analysis on data

collected between the time in which bud break was observed and the time of full leaf expansion; a similar dynamics was employed between the onset of chlorosis and full senescence (Oren & Pataki, 2001).

The vertical distribution of current- and previous-year foliage was accounted for by 'growing' the canopy in relation to needle elongation measured for 5 years without a noticeable CO<sub>2</sub> effect (Rogers & Ellsworth, 2002). The observations made at three vertical positions in the canopy demonstrated that needle elongation, expressed cumulatively for all flushes, was nearly linear with time since bud break until full expansion, but was completed 20 days earlier at the bottom of the canopy than at the middle, and 40 days earlier than at the top. Thus, from bud break until day-of-year 210 in which needle elongation at the bottom of the canopy was complete, the increase in leaf area was partitioned vertically in proportion to the leaf area density profile observed at bud break. Thereafter, during the following 40 days before needle elongation ceased at the top of the canopy, leaf area increases were restricted to progressively higher levels in the canopy, removing 1/40th of the total canopy length per day before distributing the daily increase in leaf area in proportion to the leaf area density profile of the remaining actively growing canopy. The decrease in *P. taeda* leaf area index with senescence at the end of the growing season was partitioned vertically in proportion to the amount of previous-year foliage.

*Partitioning of incoming radiation*

Incoming PPF<sub>D</sub> was partitioned into direct and diffuse components according to Erbs *et al.* (1982):

$$K_T = \frac{I_o}{I_{ex}}, \tag{A1}$$

where  $K_T$  is the clearness index,  $I_o$  is total incoming radiation and  $I_{ex}$  is total extraterrestrial radiation.  $K_T$  is related to the fraction of the diffuse component by the following:

$$\begin{aligned} \text{if } K_T \leq 0.22 \text{ then } I_d/I_o &= 1.0 - 0.09 \times K_T \\ \text{if } 0.22 < K_T < 0.80 \text{ then } I_d/I_o &= 0.95 - 0.16 \times K_T \\ &+ 4.38 \times K_T^2 - 16.63 \times K_T^3 + 12.33 \times K_T^4 \\ \text{if } K_T \geq 0.80 \text{ then } I_d/I_o &= 0.16, \end{aligned} \tag{A2}$$

where  $I_d$  is diffuse radiation.

*Vertical distribution of PPF<sub>D</sub>*

*Direct beam radiation*

The extinction coefficient for the direct beam radiation  $K_{be}$  is calculated according to Campbell & Norman (1998) as

$$K_{be}(\kappa) = \frac{\sqrt{x^2 + \tan^2 \kappa}}{x + 1.744(x + 1.182)^{-0.733}}, \tag{A3}$$

where  $K_{be}$  is the light extinction coefficient for ellipsoidal distributed leaves in the canopy,  $\kappa$  is zenith angle (which depends on time of year and time of day), and  $x$  is the ratio of average projected leaf area of canopy elements on the horizontal and vertical surfaces (e.g. for a spherical leaf distribution  $x = 1$ , chosen for this canopy composed mostly of conifers based on Campbell & Norman, 1998). From  $K_{be}$  the transmission coefficient ( $\tau_b$ ) is computed, which determines light attenuation of the direct beam through the canopy:

$$\tau_b(\kappa) = e^{(-K_{be}(\kappa) \times L_{ti} \times \Pi)}, \tag{A4}$$

where  $L_{ti}$  is cumulative leaf area density in layer  $i$ ,  $\Pi$  is the clumping factor (Campbell & Norman, 1998; Stenberg, 1998). The coefficients for the broadleaf species were assumed to be similar to the values of the more prevailing, canopy dominant *P. taeda* (see Table 2, Schäfer *et al.*, 2002). The direct beam radiation enjoyed by the leaf in each layer ( $I_{bi}$ ) can be computed as follows:

$$\text{for } P. \text{ taeda, } I_{bi} = K_{be} \times I_b \times c^k \tag{A5a}$$

$$\text{for broadleaf, } I_{bi} = K_{be} \times I_b, \tag{A5b}$$

where  $I_b$  is the direct beam radiation above the canopy,  $c$  is a coniferous shoot specific transmission coefficient and  $k$  is the number of shoots obstructing the light beam in each light category ( $k = 0, 1, 2, \dots, 9$ ).

*Diffuse radiation*

The light extinction coefficient for diffuse radiation ( $K_d$ ) is a function of  $L_{ti}$  and thus changes throughout the canopy. After obtaining  $K_d$  from the  $K_d$ - $L_{ti}$  relationship shown in Campbell & Norman (1998), the transmission coefficient for diffuse light ( $\tau_d$ ) is computed as

$$\tau_d = e^{(-\sqrt{\alpha_p} \times K_d(L_{ti}) \times L_{ti})}, \tag{A6}$$

where parameters are as in Eqn (A4) and where  $\alpha_p$  is leaf absorptivity of PPF<sub>D</sub> (see Table 2). The diffuse radiation in the  $i$ th canopy layer ( $I_{di}$ ) is computed as for *P. taeda* and the broadleaf canopy by:

$$I_{di} = I_d \times \tau_d, \tag{A7}$$

where  $I_d$  is diffuse radiation above the canopy (see also Eqn (A2)).

*Scattered radiation*

Scattered radiation is created by reflection of radiation from the leaves. The transmission coefficient for scattered radiation ( $\tau_s$ ) is computed by using the

extinction coefficient of the direct beam  $K_{be}$  (Eqn (A3)),

$$\tau_s(\kappa) = e^{(-\sqrt{\alpha_p} \times K_{be}(\kappa) \times L_i \times \Pi)}, \quad (\text{A8})$$

and the scattered radiation in the  $i$ th canopy layer ( $I_{sc}$ ) can be computed as

$$I_{sc} = (\tau_s - \tau_b) \times I_b. \quad (\text{A9})$$

The three radiation types were combined at each canopy level to calculate the light intensity incident on the leaf surface in each of the 10 light categories.

#### Proportion of foliage in each PPFD category

For estimating stomatal conductance and  $C_i/C_a$  broadleaf foliage was assigned to two categories (sunlit vs. shaded) and *P. taeda* foliage was assigned to 10 categories of varying PPFD ranges. For broadleaf species, the amount of sunlit and shaded foliage was estimated throughout the canopy as the fraction that receives sunlight at each canopy depth, according to Campbell & Norman (1998):

$$f_{sl}(\kappa) = e^{(-K_{be}(\kappa) \times L_i)} \quad (\text{A10a})$$

where  $f_{sl}$  is the fraction of sunlit leaves at depth  $i$  as a function of the zenith angle  $\kappa$  which depends on time of year and time of day (Campbell & Norman, 1998). Shaded foliage was illuminated with diffuse and scattered light, while sunlit foliage enjoyed direct light in addition. For *P. taeda*, a penumbral effect resulting from coniferous shoot structure distributes direct light into intensity regimes below that of the unobstructed light (Stenberg, 1998); thus, the probability of light

category  $f_{sl}$  in the  $i$ th canopy layer is

$$f_{sl}(k) = \frac{(K_{be} \times L_i \times \Pi)^k}{k!(1-c)^k} \times e^{\left[\frac{-K_{be} \times L_i \times \Pi}{(1-c)}\right]}. \quad (\text{A10b})$$

Canopy conductance was distributed vertically separately in the broadleaf and *P. taeda* canopy. In the broadleaf canopy the fraction of conductance of each foliage category in each layer relative to the total was used as weights to rescale the mean canopy stomatal conductance ( $G_C$ ) obtained from sap-flux, such that the total water uptake would be preserved, as

$$G_C = G_S \times L = \sum_{i=1}^n (g_{sli} \times L_i \times f_{sli} + g_{shi} \times L_i \times (1 - f_{sli})), \quad (\text{A11})$$

where  $G_S$  is mean stomatal conductance for hardwoods,  $L$  is leaf area index,  $i$  is canopy layer,  $n$  is number of canopy layers (here  $n = 16$ ),  $g_{sl}$  and  $g_{sh}$  is stomatal conductance of sunlit and shaded foliage, respectively, and  $f_{sl}$  is sunlit fraction of the foliage. In the *P. taeda* canopy a penumbral effect on the PPFD distribution within the canopy of *P. taeda* was incorporated according to Stenberg (1998). Accounting for this effect, the foliage in each canopy layer was divided into 10 light categories. Using a similar weighting methodology to that described above for the broadleaf canopy,  $G_C$  of *P. taeda* was repartitioned such that

$$G_S \times L = \sum_{i=1}^n (g_{ij} \times L_{ij} \times k_j), \quad (\text{A12})$$

where  $j$  represents the light class, and  $k_j$  is the probability of light category  $j$  (Stenberg 1998).