

Modelling assimilation and intercellular CO₂ from measured conductance: a synthesis of approaches

G. G. KATUL,¹ D. S. ELLSWORTH^{1,2} & C.-T. LAI¹

¹School of the Environment, Box 90328, Duke University, Durham, NC 27708–0328, USA and ²Environmental Sciences Department, Brookhaven National Laboratory, Upton, NY 11973–5000, USA

ABSTRACT

A spectrum of models that estimate assimilation rate A from intercellular carbon dioxide concentration (C_i) and measured stomatal conductance to CO₂ (g_c) were investigated using leaf-level gas exchange measurements. The gas exchange measurements were performed in a uniform loblolly pine stand (*Pinus taeda* L.) using the Free Air CO₂ Enrichment (FACE) facility under ambient and elevated atmospheric CO₂ for 3 years. These measurements were also used to test a newly proposed framework that combines basic properties of the $A-C_i$ curve with a Fickian diffusion transport model to predict the relationship between C_i/C_a and g_c , where C_a is atmospheric carbon dioxide concentration. The widely used Ball–Berry model and five other models as well as the biochemical model proposed by Farquhar *et al.* (1980) were also reformulated to express variations in C_i/C_a as a function of their corresponding driving mechanisms. To assess the predictive capabilities of these approaches, their respective parameters were estimated from independent measurements of long-term stable carbon isotope determinations ($\delta^{13}C$), meteorological variables, and ensemble $A-C_i$ curves. All eight approaches reproduced the measured A reasonably well, in an ensemble sense, from measured water vapour conductance and modeled C_i/C_a . However, the scatter in the instantaneous A estimates was sufficiently large for both ambient and elevated C_a to suggest that other transient processes were not explicitly resolved by all eight parameterizations. An important finding from our analysis is that added physiological complexity in modeling C_i/C_a (when g_c is known) need not always translate to increased accuracy in predicting A . Finally, the broader utility of these approaches to estimate assimilation and net ecosystem exchange is discussed in relation to elevated atmospheric CO₂.

Key-words: carbon isotope; conductance; CO₂ assimilation; elevated CO₂; Free Air CO₂ Enrichment; intercellular CO₂; pine forest.

Correspondence: Gabriel Katul. Fax: 919 6848741; e-mail: Gaby@duke.edu

INTRODUCTION

Considerable research effort is devoted to measuring annual carbon balance of vegetation either by enumeration of carbon storage in biomass components and soils, or by monitoring ecosystem–atmosphere carbon dioxide (CO₂) exchange. Knowledge of long-term ecosystem CO₂ fluxes or net ecosystem exchange (NEE), may be attained using the eddy-covariance (EC) technique, which is now being applied at a number of sites world-wide (Hollinger *et al.* 1994; Amthor *et al.* 1994; Fan *et al.* 1995; Waring *et al.* 1995; Greco & Baldocchi 1996; Baldocchi & Vogel 1996; Baldocchi *et al.* 1996; Baldocchi, Vogel & Hall 1997a,b; Frohling *et al.* 1996; Goulden *et al.* 1996a,b, 1998; Katul *et al.* 1997a,b; Baldocchi & Meyers 1998; Kaiser 1998; Lai *et al.* 2000a). Despite the wide usage of EC methods, quantifying NEE from estimates of gross primary productivity (GPP) and ecosystem respiration (R_E) remains a critical research thrust in quantifying annual carbon balance because such a separation (i.e. $NEE = GPP - R_E$) resolves the effects of environmental perturbations and transient ecosystem properties on carbon sources from the effects on sinks. This study focuses on practical methods to estimate net assimilation rate A , the primary variable needed to compute GPP.

One approach to estimating net assimilation is to relate CO₂ uptake to conductance derived from water vapour. Establishing such a relationship is practical for two reasons:

- 1 Water vapour flux measurements are readily available for estimating conductance. Water vapour fluxes can be measured by a wide range of techniques other than EC such as sapflux (Granier 1987; Phillips & Oren 1998; Pataki, Oren & Tissue 1998; Oren *et al.* 1998a), heat balance (Cermak *et al.* 1995; Katul *et al.* 1997c), energy balance–Bowen ratio methods (Andre *et al.* 1988) which were used in FIFE and HAPEX-MOBILHY, aerodynamic methods (Brutsaert, Parlange & Gash 1989), and long-term hydrologic budget approaches (Jarvis & McNaughton 1986; Gourtorbe *et al.* 1989; Oren *et al.* 1998b). Much of the historical long-term water vapour fluxes have been monitored by such techniques.
- 2 Recent developments in Free Air CO₂ Enrichment (FACE) experiments presently in Arizona (Pinter *et al.* 1996), Switzerland, North Carolina (Ellsworth *et al.* 1995; Hendrey *et al.* 1999), Nevada (Jordan *et al.* 1999) and elsewhere do not allow for routine monitoring of CO₂ fluxes

by EC because of the large CO₂ source produced by the FACE system (Hendrey *et al.* 1999). In such experiments, estimating ecosystem CO₂ flux is achieved by a hybrid combination of model development and carbon storage measurements in all the ecosystem carbon pools. Such budget calculations require carbon measurements collected at a wide range of spatial and temporal scales to represent the mean for plots > 20 m in diameter, many of which are not invariant to aggregation and scaling uncertainties.

A practical solution to these problems is estimating or measuring water vapour fluxes and subsequent conductance at the desired spatial scale and inferring CO₂ fluxes from such conductance measurements. This approach exploits the well-known coupling of photosynthesis and stomatal conductance as CO₂ and water vapour exchange between leaves and the atmosphere occur through the stomatal aperture (Cowan & Farquhar 1977; Wong, Cowan & Farquhar 1979; Nikolov, Massman & Schoettle 1995; Jarvis, Mansfield & Davies 1999). However, the approach is complicated by the need to estimate intercellular CO₂ concentration (C_i), which itself depends on ambient CO₂ concentration (C_a), the leaf conductance to CO₂ (g_c) and its CO₂ exchange rate. Hence, the objective of this study is to explore practical formulations for C_i with the aim of predicting A from available g_c . Extensive gas exchange measurements, collected in the Free Air CO₂ Enrichment (FACE) facility at Duke Forest over a 3 year period, are used in our investigation.

We consider a class of methods spanning from a simple constant C_i/C_a hypothesis proposed by Wong *et al.* (1979) and Norman (1982) to a detailed biochemical model of photosynthesis of Farquhar (Farquhar, von Caemmerer & Berry 1980; Farquhar & von Caemmerer 1982) which is widely employed in both leaf and canopy-scale gas exchange studies (Collatz *et al.* 1991; Harley *et al.* 1992; Lloyd *et al.* 1995; Sellers *et al.* 1996; Baldocchi & Meyers 1998; Arneth *et al.* 1999). To successfully predict A at multiple scales, we sought models that would be independently parameterized from available physiological measurements and would well-reproduce leaf gas exchange measurements. Hence, this study differs from previously reported comparisons (e.g. Leuning 1995; Baldocchi & Meyers 1998; Jarvis *et al.* 1999) in that (1) g_c is directly measured and used in the A estimation; (2) independent experiments are conducted to estimate all model parameters to avoid the circularity of using a subset of the gas exchange measurements in both the model calibration and its evaluation; and (3) the comparison among models is performed using the same gas exchange measurement technique with data collected for ambient and elevated atmospheric CO₂. Thus rather than assessing how well the models describe the measurements, our aim is to investigate the predictive capacity of these models for estimating A from independent measurements and in situations where CO₂ fluxes are difficult to measure at the canopy scale. The broader implications of these find-

ings to estimating carbon fluxes in elevated CO₂ experiments such as those employing the FACE technique are also discussed.

THEORY

The relationship between CO₂ assimilation (A) and conductance (g_c) is given by a system of equations based on Fick's law

$$A = -g_c(C_i - C_a);$$

$$g_c = \frac{D_{CO_2}}{D_q} \frac{E}{q^* - q} \quad (1)$$

where D_{CO_2} and D_q are the molecular diffusivities of CO₂ and water vapour, respectively, E is the evaporation rate (in molar units), q^* and q are the saturation and actual water vapour mole fractions within the leaf corresponding to surface T_s and bulk air T_a temperatures, respectively. The variables g_c and g_w (conductance to water vapour) can be equated by the ratio of the diffusivities of CO₂ and water vapour in air (= 1.6) if the diffusion pathways are assumed identical. With estimates of g_c from transpiration measurements, and with measured C_a , Fick's law equations in (1) can not predict A because C_i is unknown. Additional equations relating C_i to other known quantities is required to mathematically 'close' this system in (1). Next, we consider eight 'closure' formulations representing a wide spectrum of biochemical approaches used as principal models or hypotheses employed in canopy-atmosphere carbon exchange (Sellers *et al.* 1996; Wang & Leuning 1998; Arneth *et al.* 1999).

The Norman model

Wong *et al.* (1979) and Norman (1982) were among the first to conjecture that C_i/C_a in plant leaves may be nearly constant for a wide range of environmental conditions, but that this constant varies from species to species. In a series of experiments Wong *et al.* (1979) found that perturbations in A resulted in parallel changes in g_c such that a nearly constant C_i/C_a (= R_c) was maintained for a wide range of environmental conditions. A constant R_c was also reported from a wide range of field experiments (Ehleringer 1993; Ellsworth 1999) as well as from detailed eco-physiological model simulations (Baldocchi 1994). Sage (1994) and Drake, Gonzalez-Meler & Long (1997) summarized results from many elevated CO₂ studies and also found that despite a large increase in C_a , the C_i/C_a of leaves grown in elevated CO₂ was generally not significantly different from that of ambient leaves. This lends support to the use of a single R_c for a given species as a first order approximation.

With a constant R_c and measured g_c Eqn 1 reduces to:

$$A = -g_c C_a (R_c - 1) \quad (2)$$

Hence, with a known R_c , which may be measured from stable carbon isotope $\delta^{13}C$ (Farquhar, Ehleringer & Hubick 1989), A can be readily computed.

The Cowan–Farquhar (1977) model

In Cowan and Farquhar (1977), optimal stomatal behaviour was defined as the state that maintains $\partial E/\partial A$ constant ($= \lambda_{cf}$) provided $\partial^2 E/\partial A^2 > 0$. Upon defining water use efficiency (WUE) as $(\partial E/\partial A)^{-1}$, and approximating $(\partial E/\partial A)^{-1}$ by A/E leads to

$$\frac{C_i}{C_a} = 1 - \frac{D}{C_a} WUE \quad (3a)$$

where D is the vapour pressure deficit, and WUE is a constant. Hence, the WUE approximation leads to a linear dependence of C_i/C_a on D . In Farquhar *et al.* (1993) and Lloyd & Farquhar (1994), it was suggested that coupling the Cowan–Farquhar approximation of constant $\partial E/\partial A$ with a linearized relationship between carboxylation efficiency and C_i leads to

$$\frac{C_i}{C_a} = 1 - \sqrt{\frac{1.6D(C_a - \Gamma)}{\lambda_{cf} C_a^2}} \quad (3b)$$

which leads to $C_i/C_a \propto \sqrt{D}$ rather than linear, and Γ is the leaf CO₂ compensation point.

A third variant on this model is that proposed by Wong and Dunin (1987) in which C_i/C_a was fitted by a quadratic function to D and is given by:

$$\frac{C_i}{C_a} = 0.96 - 0.0194D + 3.282 \times 10^{-4} D^2 \quad (4)$$

where D is in units of mbars (see their Fig. 8). The above relationship was derived for *Eucalyptus maculata* and is assumed to be similar for *Pinus* here.

The Ball–Berry model

One widely used g_c model is the Ball–Berry model (see Collatz *et al.* 1991), given by:

$$g_c = m \frac{ARH}{C_s} + b' \quad (5)$$

where m and b' are empirical parameters, C_s and RH are the CO₂ concentration and relative humidity at the leaf surface, respectively. Using Eqn 1 to quantify A while neglecting the leaf boundary layer resistance relative to g_c^{-1} (i.e. $C_a \approx C_s$), a closure model for C_i/C_a , given by

$$\frac{C_i}{C_a} = 1 - \frac{1}{m} \frac{1}{RH} \quad (6)$$

can be derived if b' is neglected (Baldocchi & Harley 1995). The combination of Eqn 1 and Eqn 6 permit direct estimation of A if g_c and RH are measured. The above relation constrains $m RH > 1$ or $m > RH^{-1}$. With a maximum $RH = 1$, m must exceed unity for all plants. In fact, m ranges from 3 to 10 for a wide range of species (Leuning 1995; Baldocchi *et al.* 1997a).

A variant on this approach is the Leuning (1990, 1995) approach in which RH in Eqn 5 is replaced by a vapour pressure deficit correction function $f_L(D)$ to reflect a more

appropriate driving mechanism for stomatal response (Aphalo & Jarvis 1991; Monteith 1995; Oren *et al.* 1999). Using similar approximation, the Leuning (1995) model reduces to:

$$\frac{C_i}{C_a} \approx 1 - \frac{1 - \Gamma}{m_L f_L(D)}; f_L(D) = \frac{1}{1 - \frac{D}{D_o}} \quad (7)$$

where m_L is a constant analogous (but not identical) to m in the Ball–Berry formulation and D_o is an empirical constant describing the species sensitivity to D . We note that $f_L(D)$ shown above is not unique and may vary in formulation. The $f_L(D)$ above was suggested by Leuning (1995) after detailed analysis on 20 species.

The Farquhar model

For C₃ plants, the well-defined relationship between A and C_i (hereafter referred to as the A – C_i curve), can be used to provide the additional equations to close (1). The A – C_i curves are used to parameterize the biochemical model of C₃ photosynthesis as described by Farquhar *et al.* (1980) and Farquhar & von Caemmerer (1982) with recent modifications (see Harley *et al.* 1992; Medlyn *et al.* 1999). According to the model which we refer to hereafter as the Farquhar model, light-saturated leaf CO₂ assimilation rate (A) is limited either by regeneration of ribulose 1,5-bisphosphate (RuBP) in the photosynthetic carbon reduction cycle or by the catalytic activity of Rubisco when the chloroplast RuBP concentration is saturating. Thus the initial slope of the relationship between A and C_i (here for $C_i < 250 \mu\text{mol mol}^{-1}$) is considered to be the region of limitation by Rubisco activity under light saturation. Under these conditions, A is given by

$$A = V_{c\max} \frac{C_i - \Gamma^*}{C_i + k_c \left(1 + \frac{O_i}{k_o}\right)} - R_d \quad (8)$$

where $V_{c\max}$ is the maximum catalytic activity of Rubisco with saturating RuBP, Γ^* is the compensation point, but in the absence of photorespiration, R_d is the dark respiration rate, O_i is the intercellular O₂ concentrations, and k_c and k_o are the Michaelis coefficients of Rubisco for CO₂ and O₂, respectively. The temperature dependencies of the kinetic parameters k_c , k_o , and R_d are calculated as described in De Pury & Farquhar (1997) and Medlyn *et al.* (1999). When C_i is close to saturation for photosynthesis such that RuBP regeneration limits photosynthesis, A is given by

$$A = J \frac{C_i - \Gamma^*}{4.5C_i + 10.5\Gamma^*} - R_d \quad (9)$$

where J is the rate of electron transport. Both Eqn 8 and Eqn 9 provide the necessary closure equations to link A to C_i thus permitting the estimation of A if the above Farquhar model parameters are known. The above application of the

Farquhar model differs from other comparisons because g_c is directly measured and not modelled. Previous approaches commonly combine Eqns 8 and 9 from the Farquhar model with Eqns 1 and 5 from the Ball–Berry model to solve for g_c , A , and C_i (Sellers *et al.* 1996; Baldocchi & Meyers 1998; Arneth *et al.* 1999; Lai *et al.* 2000a).

Hybrid approach

Hybrid modelling approaches have the parsimonious advantages of requiring few parameters, yet retaining the mechanistic form of the A – C_i curve. Approaches such as the Ball–Berry, Leuning, and Norman have such parsimony yet ignore well-established characteristics of the A – C_i relationship. In contrast, Farquhar’s model considers the full A – C_i curve at the expense of requiring a larger number of physiological parameters that are not trivial to determine for a wide variety of species and sites. Hence, there is a need for intermediate approaches that are simple enough to be parameterized robustly, but retain mechanistic attributes. One such approach was described by Jarvis *et al.* (1999), and we propose a similar formulation below. A principal distinction between the proposed approach and the Jarvis *et al.* (1999) approach is in the definition of the relationship between g_c and A , and how the model is parameterized.

Typical A – C_i curves exhibit three well-defined regimes: a flat regime in which A becomes nearly independent of C_i so that $\partial A/\partial C_i \approx 0$ and which is often referred to as RuBP regeneration-limited A (Farquhar & von Caemmerer 1982); a curvilinear regime in which $\partial A/\partial C_i$ is nonlinearly related to C_i ; and a linear regime in which $\partial A/\partial C_i$ is a constant independent of C_i and which is often referred to as the carboxylation-limited portion of the curve as specified by the Farquhar & von Caemmerer (1982) model. The ‘flat-regime’ is associated with large C_i values rarely encountered in field conditions (including many FACE experiments). The linear portion of the A – C_i curve represents the common state under field conditions for many C_3 canopies in sun. Hence, the proposed hybrid model explicitly considers the linear portion of the A – C_i curve, parameterizes the nonlinear portion following a simplistic assumption, and neglects the CO_2 -saturated portion. We first consider the hybrid model with reference to the curvilinear portion of the A – C_i curve.

The curvilinear regime of the A – C_i curve

In such a regime, the A – C_i curve is influenced by a wide range of environmental conditions. However, if plants are operating at a high g_c such that C_i is sufficiently high as to approach CO_2 saturation, then any changes in g_c will have minimal effects on A . Thus to simplify, we assume that plants operating in this region of the A – C_i curve tend to buffer the effects of environmental perturbations on A such that $\delta A/\delta g_c \approx 0$. In combination with (1), this assumption naturally leads to a constant C_i/C_a . In essence, our proposed hybrid approach adopts Norman’s (1982) hypothesis for the curvilinear portion of the A – C_i curve only (vis-à-vis the full

A – C_i). Model simulations by Baldocchi (1994) demonstrate that for large g_c , C_i/C_a approaches a constant (hereafter referred to as R_c for consistency with Norman’s model). For clarity, we refer to the conductance associated with such a large C_i as g_{opt} .

The approximately linear portion of the A – C_i curve

When $g_c < g_{\text{opt}}$, the A – C_i curve is no longer in the curvilinear portion but can be described by its linear component, given by

$$A = (aC_i - b) \quad (10)$$

where the slope a and the intercept $b > 0$. Following the Farquhar photosynthesis model formalism (Farquhar & von Caemmerer 1982; Harley, Tenhunen & Lange 1986), a can be equated to carboxylation efficiency which is a function of $V_{c \text{ max}}$ for the Rubisco enzyme, and b can be derived from the CO_2 compensation point Γ^* ($\approx b/a$). Hence, upon eliminating A by equating Eqn 1 to Eqn 10, we obtain an explicit relationship for C_i as a function of a and b given by

$$\frac{C_i}{C_a} = \frac{g_c + \frac{b}{C_a}}{g_c + a} \quad (11)$$

The above relationship constitutes the hybrid model closure approximation for a linear A – C_i . Equation 11 predicts the correct limits of C_i/C_a for a wide range of environmental conditions and reduced g_c (i.e. $g_c < g_{\text{opt}}$) if the following arguments are considered.

Case (1): $g_c \leq b/C_a$. This condition typically occurs when quantum flux density (Q) limits g_c . For such a condition, the slope of the A – C_i curve rapidly decays so that $a \gg 0$. With $a \sim 0$ and $g_c > 0$ Eqn 11 correctly predicts a $C_i/C_a > 1$ consistent with model simulation results in Baldocchi (1994) and Farquhar & Wong (1984). Based on this limit, it is expected that C_i/C_a exceed unity as evening conditions are approached. This condition will not be considered in great detail since the magnitude of A is likely to be small at these times, but with $a = f(Q)$, the hybrid model can predict light-limited A . As an illustration, we compare the relationship between C_i/C_a and Q computed by the hybrid model with the idealized relationship reported in Farquhar & Wong (1984; their Fig. 1). Both models showed a constant C_i/C_a for most of the range in Q (e.g. $Q > 100 \text{ mmol m}^{-2} \text{ s}^{-1}$, Fig. 1) and also show increasing C_i/C_a with very low Q ($Q < 30 \text{ mmol m}^{-2} \text{ s}^{-1}$). However, the hybrid model further accounts for the reduction in C_i/C_a with decreasing g_c when Q is sufficiently large ($Q \sim 150 \text{ mmol m}^{-2} \text{ s}^{-1}$) and so resolves well changes in C_i/C_a for a wide range of light levels.

Case 2: When $g_c \gg b/C_a$. This condition typically occurs if sufficient Q is available to maintain partially open stomates but still $g_c < g_{\text{opt}}$. For this condition Eqn 11 reduces to:

$$f(g_c) = \frac{C_i}{C_a} \approx \frac{1}{1 + \frac{a}{g_c}} \quad (12)$$

such that:

$$\frac{\partial f(g_c)}{\partial g_c} = \frac{1}{a + g_c} - \frac{g_c}{(a + g_c)^2} = \frac{a}{(a + g_c)^2} \quad (13)$$

which is **positive** ($a, g_c > 0$) suggesting that C_i/C_a **decreases with decreasing** g_c . Such conditions are common when soil moisture (θ) or water vapour pressure deficit (D) limits stomatal opening.

The critical (and usually variable) conductance (g_{critical}) responsible for the transition from constant to variable C_i/C_a can be estimated by equating Eqn 11 to R_c , which after some algebraic manipulation, results in:

$$g_{\text{critical}} = \frac{aR_c - \frac{b}{C_a}}{1 - R_c} \quad (14)$$

The result in Eqn 14 sets a lower conductance limit to the onset of Norman's (1982) constant C_i/C_a approximation for the hybrid scheme. In summary, C_i/C_a for the two regimes of the $A-C_i$ curve, when Q is not limiting, are given by:

$$\frac{C_i}{C_a} = \begin{cases} R_c & \text{if } g_c > g_{\text{critical}} \\ g_c + \frac{b}{C_a} & \text{if } 0 < g_c < g_{\text{critical}} \end{cases} \quad (15)$$

The predictions in Eqn 15 are well supported by a wide range of C_3 vegetation experiments shown in Fig. 2. Particularly, leaf-level measurements by Brodribb (1996) demonstrated the strong coupling between C_i/C_a and g_c in a soil drying experiment. Their measurements (Fig. 2, tri-

angle) showed a decrease in C_i/C_a with decreasing g_c resulting from a decrease in θ . The predictions using Eqn 15 (Fig. 2, thick solid line) is in good agreement with their measured C_i/C_a . The result in Eqn 15 and the measurements in Fig. 2 may appear to contradict model simulation findings in Baldocchi (1994 – his Fig. 6) for which C_i/C_a increased with decreasing g_c . However, the model calculations in Baldocchi (1994) are based on Q -limited g_c with $a \sim 0$ and $g_c > 0$. Table 1 summarizes all models discussed above along with a list of required parameters to estimate A from measured g_c and C_a .

EXPERIMENT

General site description

The gas exchange measurements were collected at the Blackwood Division of the Duke Forest near Durham, North Carolina (35°98'N, 79°8'W, elevation = 163 m). The site is a uniformly aged managed loblolly pine (*Pinus taeda* L.) forest that extends at least 1000 m in the north–south direction and 300 m to 600 m in the east–west direction (Katul *et al.* 1999). The stand was originally grown from *P. taeda* seedlings planted at 2.0 m × 2.4 m spacing in 1983 following clear cutting and burning. The mean canopy height was 13.0 m (± 0.5 m) in 1998.

Leaf level gas exchange measurements

The leaf-level measurements of A and g_c described in Ellsworth (1999) and Ellsworth (2000) were performed using a portable infra-red gas analyser system for CO₂ and water vapour (CIRAS-1, PP-Systems, Hitchin, Herts, UK). The system was operated in open flow mode with a 5.5 cm

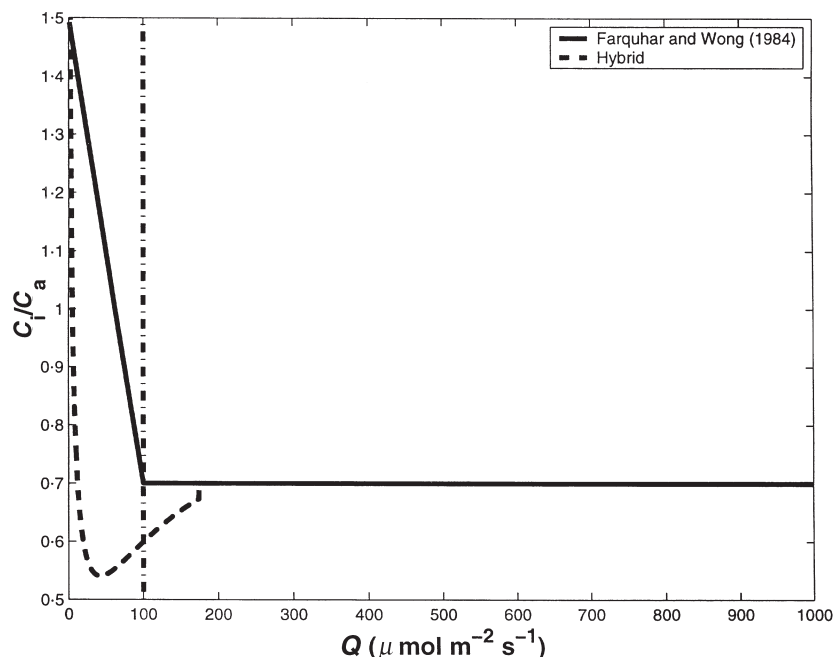


Figure 1. An illustration of the modelled variations in C_i/C_a with quantum flux density Q for *Eucalytus* by the hybrid scheme using parameters from Farquhar & Wong (1984). The hybrid scheme modelled C_i/C_a are contrasted with the Farquhar *et al.* (1980) photosynthesis approach. For the hybrid scheme, the conductance (g_c) – Q relationship was digitized by us from Farquhar & Wong's (1984) Fig. 1.

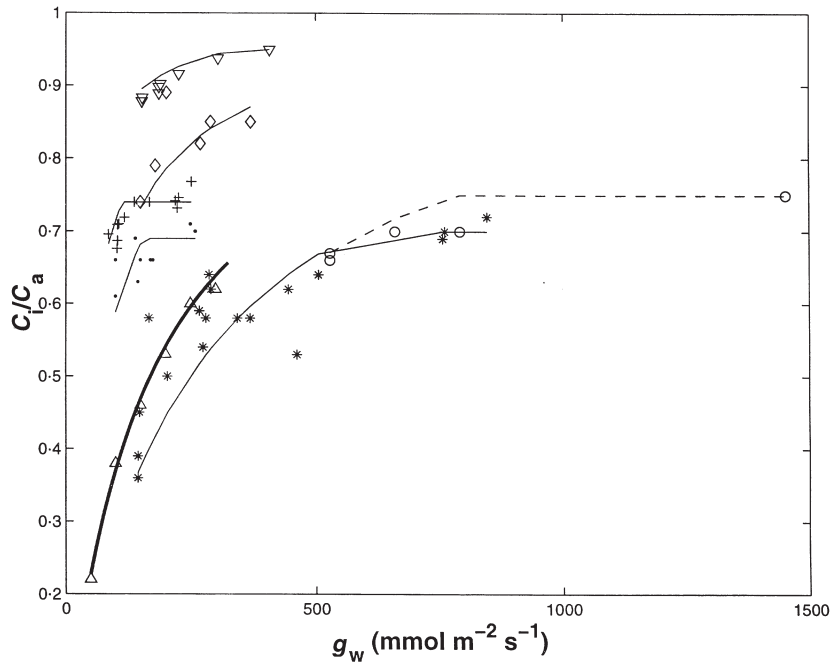


Figure 2. Comparison between measured (symbols) and predicted C_i/C_a (lines) as a function of leaf level conductance (g_w) for a wide range of C_3 species. The symbols are: triangle up for *Podocarpus lawrencii* (Brodrribb 1996) in a soil drying experiment, plus for *Quercus rubra* (Weber & Gates 1990), dots for *Vitis vinifera* (Downton, Grant & Loveys 1987), open circle for *Mavastrum rotundifolium* (Forseth & Ehleringer 1983), diamond for *Encelia frutescens* in the field (Ehleringer 1988), star for glasshouse-grown *Encelia frutescens* (Comstock & Ehleringer 1984), and down triangle for *Eucalyptus grandis* (Leuning 1995). For these studies, the parameters used in the hybrid scheme are: $a = 170, 40, 70, 260, 55, 180,$ and $18 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively; $R_c = 0.70, 0.74, 0.69, 0.75, 0.90, 0.70,$ and 0.95 (unitless), respectively; $g_{\text{crit}} = 400, 115, 155, 780, 495, 420,$ and $340 \text{ mmol m}^{-2} \text{ s}^{-1}$.

long leaf chamber and an integrated gas CO_2 supply system. The chamber was modified with an attached Peltier cooling system to maintain chamber temperature near ambient atmospheric temperature. The data were collected for upper canopy foliage at 11–12 m height, accessed with a system of towers and mobile vertically telescoping lifts. All measured gas exchange rates are reported on a unit projected area basis in this article so as to be more consistent with planar fluxes, although they were originally calculated using a geometric approximation to calculate all-sided fluxes for the needle surface (Ellsworth 1999). For the modelling here, we use measurements collected over a broad range of environmental conditions spanning 70 sampling days over a 3 year period (May 1996 to October 1999), excluding severe winter periods. Year-to-year and seasonal variation in leaf CO_2 and water vapour exchange have been analysed elsewhere (Ellsworth 2000).

The Free Air CO_2 Enrichment (FACE) setup

Measurements on elevated CO_2 -grown foliage are from the FACE facility at the Duke Forest site and were made in parallel with the measurements in ambient atmospheric CO_2 (Ellsworth 1999). In 30 m diameter circular plots, an array of vertical pipes was used to emit air with enhanced CO_2 concentration into the stand in a controlled manner (Hendrey *et al.* 1999). The data used here are from measurements made in 1997–99, the first to third full years of CO_2 exposure. The measurements in elevated CO_2 are described in Ellsworth (1999). The target for the FACE system exposure is $200 \mu\text{mol mol}^{-1}$ above the ambient CO_2 level monitored outside of the FACE rings, yielding a long-term average CO_2 of $569 \mu\text{mol mol}^{-1}$. For the measurements within the leaf chamber, the CO_2 delivery system

enabled measurement at a controlled CO_2 concentration of $560 \mu\text{mol mol}^{-1}$, near the mid-day average CO_2 concentration within the FACE array (Ellsworth 1999).

Model parameter estimation

Because our objective is to contrast the eight models (Table 1) in terms of their ability to predict A (vis-à-vis describe A), it is desirable to estimate the model parameters independently from the gas exchange measurements described in the experimental set-up. Separate experiments were conducted to estimate these model parameters, which are derived for ambient and elevated CO_2 measurements pooled together. For predictive purposes, we assume that elevated CO_2 itself has no direct effect on any of the parameters, which is generally consistent with Ellsworth (1999) and Myers, Thomas & DeLucia (1999). The model parameters were determined as follows:

Norman's (1982) model

The parameter R_c (see Table 1) was estimated from long-term stable carbon isotope determinations ($\delta^{13}\text{C}$). Farquhar *et al.* (1989) describe the approach for calculating C_i/C_a on the basis of leaf $\delta^{13}\text{C}$. Upper crown foliage samples (2 mg) were collected in September of 1997 in parallel with the leaf-level gas exchange measurements, and analyzed for $\delta^{13}\text{C}$ content relative to a pee-dee belemnite standard at the Duke University Phytotron Stable Carbon Ratio facility. The C_i/C_a was estimated for the foliage samples according to calculations in Farquhar *et al.* (1989), assuming a source air $\delta^{13}\text{C}$ as given in Ellsworth (1999) and ignoring internal conductances to CO_2 transfer from the cell surfaces to the sites of carboxylation. The estimated assimilation-weighted

Table 1. Summary of model formulation and closure approximations for predicting A from g_c and C_a for different models. The g_c from water vapour flux measurements is an assumed input for all the models

Model	Closure	A calculation	Needed parameters
Norman (1982)	$\frac{C_i}{C_a} = R_c = \text{constant}$	$A = -g_c C_a (R_c - 1)$	R_c
Cowan–Farquhar (1977) with constant WUE	$\frac{C_i}{C_a} = 1 - \frac{WUE}{C_a} D$	$A = g_c (WUE D)$	WUE and measured D
Farquhar <i>et al.</i> (1993)	$\frac{C_i}{C_a} = 1 - \sqrt{\frac{1.6D(C_a - \Gamma)}{\lambda_{cf} C_a^2}}$	$A = -g_c (C_i - C_a)$	λ_{cf} , Γ and measured D
Wong–Dunin (1987)	$\frac{C_i}{C_a} = 0.96 - 0.0194D + 3.282 \times 10^{-4} D^2$	$A = -g_c (C_i - C_a)$	measured D
Ball–Berry (1991)	$\frac{C_i}{C_a} = 1 - \frac{1}{m} \frac{1}{RH}$	$A = \frac{g_c C_a}{m RH}$	m and measured RH
Leuning (1995)	$\frac{C_i}{C_a} = 1 - \frac{1 - \frac{\Gamma}{C_a}}{m_L} \left(1 + \frac{D}{D_o}\right)$	$A = \frac{g_c C_a}{m_L} \left(1 - \frac{\Gamma}{C_u}\right) \left(1 + \frac{D}{D_o}\right)$	m_L , D_o , Γ and measured D
Farquhar <i>et al.</i> (1980)	$A = f(C_i)$, where $f(\cdot)$ is computed from Eqns 8 and 9	$A = -g_c (C_i - C_a)$	$V_{c \max}$, J , Γ^* , and measured PAR and T_s
Hybrid model	$\frac{C_i}{C_a} = \begin{cases} R_c & \text{if } g_c > g_{\text{critical}} \\ g_c + \frac{b}{C_a} & \text{if } 0 < g_c < g_{\text{critical}} \\ \frac{a + g_c}{a} & \end{cases}$	$A = -g_c (C_i - C_a)$	a , b and R_c

C_i/C_a (hereafter referred to as $\overline{C_i/C_a}$) from the $\delta^{13}C$ measurements of upper crown *Pinus taeda* foliage was 0.66 ± 0.02 for eight trees in the stand (Ellsworth 1999). Accounting for source air $\delta^{13}C$ from the constant-label used in the Duke Forest FACE study, Ellsworth (1999) found no significant difference in $\overline{C_i/C_a}$ between foliage grown in ambient and elevated CO₂ during the first full summer of CO₂ exposure. Leaf $\delta^{13}C$ content was assayed on foliage at different points during the growing season to confirm the constant $\overline{C_i/C_a}$ in the elevated CO₂ experiment (data not shown). We repeated analyses for samples from 1998 and 1999 and found that $\overline{C_i/C_a}$ is within ± 0.03 of the 1997 value for both ambient and elevated CO₂ foliage. Hence, we used $\overline{C_i/C_a} = 0.66$ as our best estimate of R_c .

Cowan–Farquhar model

The Cowan–Farquhar model (with constant WUE) requires an estimate of the species-specific WUE in the calculation of A as in Table 1. Upon averaging the model formulation for $\overline{C_i/C_a}$, we obtain:

$$\frac{\overline{C_i}}{\overline{C_a}} = 1 - \frac{\overline{D}}{\overline{C_a}} \overline{WUE}$$

A consequence of the constant WUE is that the interaction between D and WUE is no longer relevant in the averaging. Using the $\delta^{13}C$ measured $\overline{C_i/C_a}$ ($= 0.66$) and the long-term daytime \overline{D} ($= 2.1$ kPa), the $\overline{WUE} = 6.0 \times 10^{-3}$ mol CO₂ [mol H₂O]⁻¹. This estimate of WUE is very consistent with values for *Pinus taeda* in Ellsworth *et al.* (1995), Fites & Teskey (1998), and Ellsworth (1999). For elevated atmos-

pheric CO₂, $\overline{C_a} = 560$ p.p.m. leading to $\overline{WUE} = 9.0 \times 10^{-3}$ mol CO₂ [mol H₂O]⁻¹.

For the Farquhar *et al.* (1993) version of the model, λ_{cf} can also be estimated from $\delta^{13}C$ measured $\overline{C_i/C_a}$ and \overline{D} using

$$\lambda_{cf} \approx \frac{1.6\overline{D}(C_a - \Gamma)}{C_a^2 \left(1 - \frac{\overline{C_i}}{C_a}\right)^2}$$

Using $\overline{D} = 2.1$ kPa and $\overline{C_i/C_a} = 0.66$ we obtain $\lambda_{cf} = 708$ mol mol⁻¹ for $C_a = 360$ μ mol mol⁻¹

This estimate is similar to the generic λ_{cf} for warm mixed evergreen forests in Lloyd & Farquhar (1994).

Wong–Dunin model

If their proposed empirical quadratic function is used without alteration, then the Wong–Dunin model does not require any parameter estimation. Fortunately, with $\overline{D} = 2.1$ kPa from the leaf-level measurements used here, the estimated $\overline{C_i/C_a} = 0.7$, sufficiently close to our $\delta^{13}C$ measured $\overline{C_i/C_a}$.

Ball–Berry model

We estimated m from $\overline{C_i/C_a}$ derived from the $\delta^{13}C$ measurements using

$$m = \frac{1}{\overline{RH} \left(1 - \frac{\overline{C_i}}{C_a}\right)}$$

where \overline{RH} is the assimilation-weighted relative humidity. The latter quantity was calculated for 1996–99 using 30 min RH measurements conditionally averaged for Q exceeding $200 \mu\text{mol m}^{-2} \text{s}^{-1}$. The instruments and setup used for the RH and Q measurements is reported in Oren *et al.* (1998b). This weighted averaging scheme yielded an $\overline{RH} = 0.49$, which, when combined with $\overline{C_i/C_a} = 0.66$ resulted in $m = 6.0$ (unitless).

Leuning's model

In a first-order analysis of parameter estimation and assuming Γ/C_a is known, the parameters m_L and D_o of the Leuning (1995) model are related to C_i/C_a and D via:

$$\frac{C_i}{C_a} \approx \left(1 - \frac{1 - \Gamma}{C_a} \right) - \left(1 - \frac{1 - \Gamma}{C_a} \right) D$$

If measurements of C_i/C_a and D are available, then regressing C_i/C_a on D directly permits estimating m_L from the regression intercept, and subsequently D_o from the regression slope. We used this method on the C_i/C_a versus D in measurements reported for *P. taeda* in Fites & Teskey (1988) and found $D_o = 17.84$ and $m_L = 6.84$. The resulting model runs for these parameters showed very poor fits to measured A for the dataset from Ellsworth (1999; 2000). Given that the Leuning model does not permit independent estimates of m_L and D_o as in all other approaches, we determined m_L and D_o using a subset of the gas exchange measurements (specifically, measurements collected in 1996, less than 20% of the entire data set). With this subset, the estimated $D_o = 30$ and $m_L = 4.0$. These parameters were used in subsequent model inter-comparisons.

The Farquhar model

Steady-state $A-C_i$ curve measurements were conducted during the growing season using a temperature-controlled photosynthesis system (PP-Systems CIRAS-1, Hitchin, Herts, UK or Li-Cor 6400, Lincoln, NE, USA). Measurements were performed at saturating quantum flux density Q and leaf temperatures of 28 or 30 °C and at leaf-air vapour pressure differences < 1.7 kPa. A projector bulb emitting white light (PP-Systems) or light-emitting diodes (Li-Cor) was used to achieve $Q > 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. These $A-C_i$ gas exchange measurements began at the ambient CO_2 concentration and stepped through eight to ten different CO_2 concentrations from the CO_2 compensation point to CO_2 saturation ($C_i > 1000 \mu\text{mol mol}^{-1}$). The $V_{c \text{ max}}$ and R_d were determined by least-squares regression fits to the data for $C_i < 250 \mu\text{mol mol}^{-1}$ for curves measured on four to six separate trees at three different points in the growing season. The above equations were then solved for the values of J_{max} , the potential rate of electron transport in photosystem II, that provided the best fit for the entire

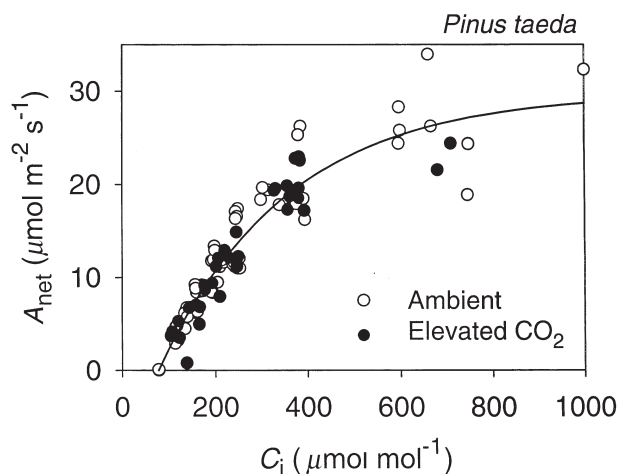


Figure 3. Measured ensemble $A-C_i$ curves from ambient (open symbols) and elevated (closed symbols) atmospheric CO_2 used in the estimation of the parameter a for the hybrid scheme. The data are generated from 18 $A-C_i$ curves collected from *Pinus taeda* at six locations in the forest, three each from ambient and elevated CO_2 , at three different times of year. Measurements were made at saturating Q and leaf temperatures of 28–30 °C. a is estimated as the initial slope of these ensemble curves ($C_i < 270 \mu\text{mol mol}^{-1}$). Data are expressed on a projected leaf area basis.

$A-C_i$ curve for each tree. In the calculations, Γ^* is determined from the polynomial function in Jordan & Ogren (1984). $V_{c \text{ max}}$ and J_{max} parameters were adjusted for temperature using the Arrhenius function and activation energy parameters $E_{V_{c \text{ max}}} = 68\,000 \text{ J mol}^{-1}$ and $E_{J_{\text{max}}} = 199\,000 \text{ J mol}^{-1}$ (see De Pury & Farquhar 1997; Medlyn *et al.* 1999). Other parameters in the model were used as described in De Pury & Farquhar (1997).

The hybrid model

The hybrid model parameter a was estimated from the $A-C_i$ curve data shown in Fig. 3. The current analysis assumes that the concentration of CO_2 at the chloroplast surface (C_{chl}) is near that in the intercellular air space. The parameter b was estimated from Γ^* , described above, and R_c is identical to Norman's model (see Table 2).

RESULTS

We compared measured and modelled A for ambient and elevated atmospheric CO_2 . The sensitivity of A in a subset of the models to their respective primary variables for ambient and enriched atmospheric CO_2 conditions is discussed in the Appendix. The sample models are chosen to reflect different classes of closure approximations (see Appendix), and the sensitivity analysis indicates that the models were all well-parameterized from the independent measurements or formulations.

Table 2. Estimated or measured model parameter for each closure scheme. These parameters are unaltered for enriched atmospheric CO₂ model predictions. For the Farquhar and Hybrid schemes, the unit area of the parameter is based on the projected leaf area

Model	Parameter	Method of estimation
Norman	$R_c = 0.66$	Long-term leaf $\delta^{13}\text{C}$
Cowan–Farquhar with constant WUE	$\text{WUE} = 6 \times 10^{-3} \frac{C_a}{360}$, C_a in ppm.	Long-term leaf $\delta^{13}\text{C}$ and measured \bar{D}
Farquhar <i>et al.</i> (1993)	$\lambda_{\text{cf}} = 708 \left(\frac{360}{C_a} \right)$, mol mol ⁻¹	Long-term leaf $\delta^{13}\text{C}$ and measured \bar{D}
Wong–Dunin	No parameters are required	
Ball–Berry	$m = 5.9$	Regression analysis on $A = \frac{C_a}{mRH} g_c$ for leaf gas exchange data, and independently for $R_c = 0.66$ along with measured $\frac{RH}{RH} = 0.49$.
Leuning	$D_o = 30$ and $m_L = 4$.	Estimated from 1996 subset of gas exchange measurements
Farquhar <i>et al.</i> (1980)	$V_{c \text{ max}} = 98.98$ ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) $J_{\text{max}} = 2.46 V_{c \text{ max}}$ $\Gamma^* = 3.69 + 0.188(T_s - 25) + 0.0036(T_s - 25)^2$	Ensemble-averaging $A-C_i$ curves for upper crown foliage
Hybrid model	$a = 0.076 \mu\text{mol m}^{-2} \text{ s}^{-1}$ $b = 6.70 \mu\text{mol m}^{-1}$ $R_c = 0.66$	Ensemble-averaging $A-C_i$ curves for upper crown foliage (Fig. 3), and leaf $\delta^{13}\text{C}$

Model assessment with independent parameters

The modelled A for all closure schemes generally compared well with leaf-level measured A for ambient and elevated atmospheric CO₂ conditions (Fig. 4) in an ensemble sense. The scatter in the instantaneous runs is large suggesting that not all the processes affecting short-term C_i dynamics are well resolved by all these models. An important consideration here is that the model parameters used for the ambient and elevated atmospheric CO₂ calculations are assumed to be identical, except for the Wong–Dunin model, and are derived from independent measurements. Despite fundamental differences in the closure schemes, six out of the eight models recovered measured A with comparable root-mean squared error ($RMSE$). Table 3 reports the statistical details of the comparisons between modelled and measured A . All the models underestimated the measured A when A was larger than $15 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for ambient atmospheric CO₂ conditions as evidenced by the significant departure from unity for the regression slopes. All models, except the Ball–Berry and the Cowan–Farquhar (constant WUE), explained more than 60% of the measured A variability in ambient CO₂ conditions. Interestingly, Norman's constant C_i/C_a model, the hybrid approach, and the Leuning models all yielded the lowest $RMSE$ in this case despite differences in the closure assumptions (Table 1). Additionally, the Farquhar *et al.* (1993) version of the Cowan–Farquhar model is a major improvement over the constant water use efficiency approximation. This improvement, in part, is due to the fact that $C_i/C_a \propto D$ in the constant WUE approach whereas the Farquhar *et al.* (1993)

version leads to $C_i/C_a \propto \sqrt{D}$ thereby reducing the sensitivity of modelled A on D , analogous to Norman's model.

For elevated atmospheric CO₂ conditions, the Farquhar, Wong–Dunin, Cowan–Farquhar (both constant WUE and the Farquhar *et al.* 1993 version), and Leuning model predictions were statistically similar to the measurements. All the models, except the Ball–Berry explained more than 50% of the variations in measured A . The hybrid, Leuning, and Farquhar models as well as the Farquhar *et al.* (1993) version of the Cowan–Farquhar model had the lowest $RMSE$ when contrasted with the other models.

It is important to note that the Farquhar model requires the largest number of independent parameters (Table 1); hence, errors in any of these parameter measurements or estimates tend to amplify errors in modelled C_i and A . A basic difference between the ambient and elevated data is the increase in C_i leading to an increased likelihood of J regulating A . This may explain why the hybrid model did not have a 1 : 1 regression slope when compared to the Farquhar model performance. The uncertainty in estimating A when Eqn 9 limits the assimilation rate is typically larger than Eqn 8. We found that 18% of our data points at elevated atmospheric CO₂ were limited by J for C_a of 560 p.p.m. For these time points, the $RMSE$ was four times higher when compared with the $V_{c \text{ max}}$ -limited A for elevated atmospheric CO₂, since additional parameters for the light response of leaves are used to characterize the J -limited part of the $A-C_i$ curve.

To further investigate the closure approximations, a comparison between measured and modelled C_i/C_a is shown in Fig. 5. Seasonal droughts resulted in declines in measured C_i/C_a with g_c , consistent with Brodrigg's (1996) measure-

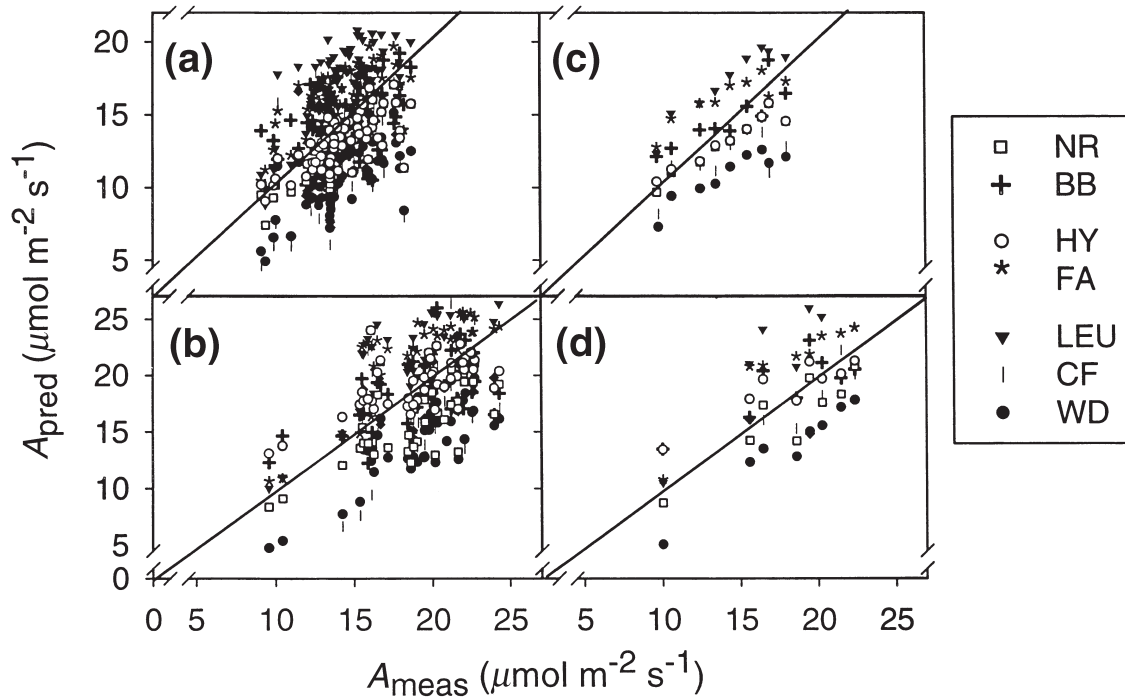


Figure 4. Comparison between measured (A_{meas}) and predicted (A_{pred}) leaf net CO_2 assimilation for *Pinus taeda* in ambient (top panels, a and c) and elevated atmospheric CO_2 (bottom panels, b and d) using seven models with contrasting closure criteria. Each point in panels a, b represents the mean of a series of measurements in the upper crown of *Pinus taeda* at mid-day on a given sunny day over a 3 year period. The right panels (c, d) are bin-averaged by measured A to demonstrate model trends in a and b. The symbols are: \square for Norman (NR); + for Ball-Berry (BB); \circ for the Hybrid approach (HY); * for Farquhar *et al.* (FA) biochemical model; \blacktriangledown for Leuning (LEU); | for Cowan-Farquhar with constant WUE (CF); and \bullet for Wong-Dunin (WD). The 1 : 1 line (solid-thick) is also shown.

ments shown in Fig. 2 and were partially reproduced by a variety of models, including the hybrid model in both ambient and elevated CO_2 (Fig. 5). Such summer droughts are common in the region (Oren *et al.* 1998a, Ellsworth 1999). Again, the instantaneous scatter in modelled C_i/C_a was sufficiently large and indicated that processes affecting

the dynamics of C_i/C_a were not resolved by all closure models, at least with their static parameters. We restate again that these measurements were all conducted for $Q > 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$; hence, the reduction in g_c shown in Fig. 5 is due to environmental and hydrologic conditions, but not Q .

Independent variable	Model	R	Slope/Intercept	RMSE
A (Ambient)	NR	0.70	0.62*/4.11	1.98
	BB	0.42	0.45*/7.98	2.43
	HY	0.69	0.55*/5.35	1.92
	FA	0.62	0.55*/7.95	2.38
	CF	0.42	0.66*/2.71	3.82
	LF	0.60	0.70 */3.17	2.40
	LEU	0.66	0.66*/3.92	1.99
	WD	0.65	0.62*/ 1.97	3.78
A (elevated)	NR	0.58	0.75*/2.97	3.79
	BB	0.27	0.41*/11.69	5.05
	HY	0.56	0.45*/10.92	2.78
	FA	0.78	0.86/4.75	3.03
	CF	0.66	1.07/-3.67	4.51
	LF	0.76	1.00 /-1.30	3.03
	LEU	0.71	0.92/ 1.15	2.95
	WD	0.80	0.87/-2.07	5.07

Table 3. Comparison between modelled and measured mid-day A of *Pinus taeda* for all closure schemes. The closure schemes are based on the approaches of Norman (NR), Ball-Berry (BB), the proposed hybrid scheme (HY), Farquhar (FA), Leuning (LEU), Cowan-Farquhar (CF) with constant WUE, Lloyd-Farquhar (LF), and Wong-Dunin (WD) models as parameterized for *Pinus taeda* according to Table 2. The root-mean squared error (RMSE) and the regression statistics (slope, intercept, and correlation coefficient R) with measured A as the independent variable are shown. The regression slopes that are statistically different from unity at the 95% level are indicated by *, and the best R , slope and RMSE among the eight models are shown in bold

Model assessment with optimized parameters

It is conceivable that the scatter in modelled A (Fig. 4a & b, Table 3) is due to our method of parameter estimation. Matching long-term modelled C_i/C_a to the $\delta^{13}\text{C}$ measurements may inject biases and degrade the predictive capacity of the closure models, in part because of inconsistencies between the integration period of the $\delta^{13}\text{C}$ and the instantaneous gas exchange and meteorological measurements. To minimize such inconsistencies and investigate the model performance for their optimal parameters, we fit the model closure approximations (Table 2) to the instantaneous gas exchange measured C_i/C_a with time-synchronized meteorological drivers (D , RH , etc.) for the full data record. The outcome summarized in Table 4 revealed that for ambient CO₂ conditions, most parameters were comparable to those determined from the independent measurements (see Table 2) though not identical. The Leuning model parameters were most sensitive to the parameterization approach (Table 2, Table 4). The parameters fitted to measured C_i/C_a for ambient CO₂ resulted in slopes not statistically different from unity at the 95% confidence level (Table 4). Although the optimized parameters of the Norman, Ball–Berry, hybrid and Cowan–Farquhar models for elevated CO₂ were similar to those for ambient CO₂, the Farquhar *et al.* (1993), Leuning and Wong–Dunin parameters were different. The regression slopes in Table 4 for the Leuning, Wong–Dunin and Norman models were also significantly different from unity in elevated CO₂. For each CO₂ level, the different models were generally comparable in terms of $RMSE$, suggesting comparable scatter around

measured A . In short, this analysis suggests that by fitting the closure models to measured C_i/C_a , the biases in modelled A were reduced and most of the regression slopes reached unity but this did not generate any significant improvements in $RMSE$. The consistency in $RMSE$ demonstrates that the refined parameters do not reduce the scatter around measured A (Fig. 4) perhaps indicating that assuming static parameters in these physiological models may not be appropriate for such a long time course (3 years). Unavoidable sampling error and spatial inhomogeneity within branches and age classes of needles may also contribute to variability in the data and parameters, along with the knowledge that parameters such as $V_{c\text{max}}$, WUE and m have been shown to be dynamic with time (Myers *et al.* 1999; Ellsworth 2000; Lai *et al.* 2000b). Thus to highlight the overall model trends with minimal distortion from this intrinsic variability, Figs 4 and 5 also include the ensemble trends for model calculations and measurements.

DISCUSSION AND CONCLUSIONS

This study is the first to compare the performance of eight widely used models employed to estimate net CO₂ assimilation from conductance measurements for current and elevated CO₂ conditions. The elevated atmospheric CO₂ comparison was performed in the Duke Forest free-air CO₂ enrichment facility but using parameters derived from independent experiments in ambient CO₂ conditions. The models ranged in conceptual approximations and parsimony in number of physiological parameters from a simple

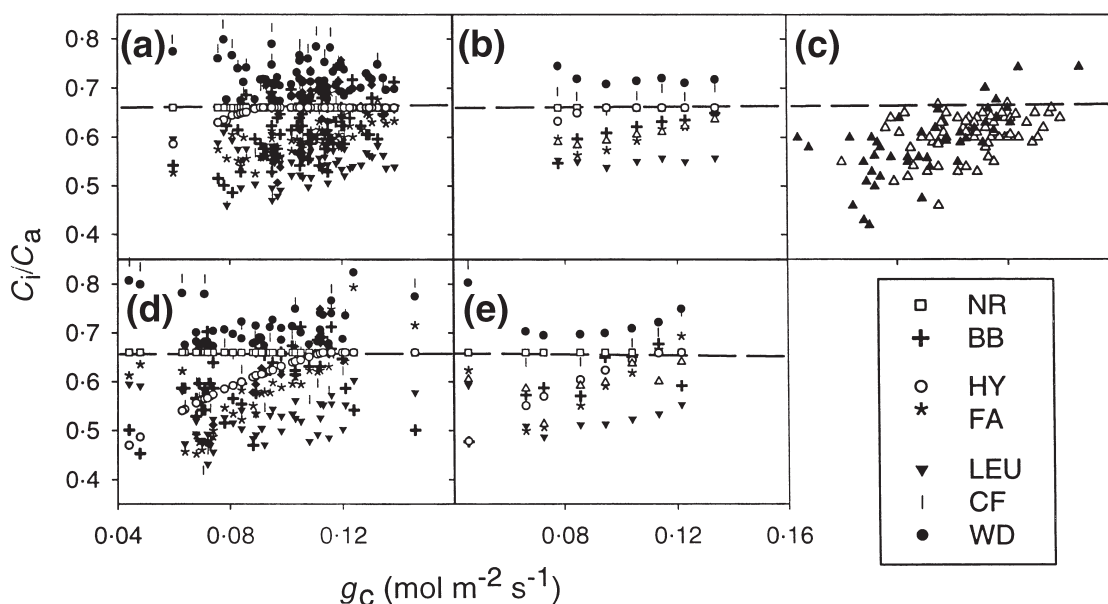


Figure 5. Comparison of modelled C_i/C_a as a function of measured g_c for *Pinus taeda* measured at mid-day on sunny days for ambient (top panels, a, b) and elevated CO₂ (bottom panels, d, e). Scatter plots of the data (left panels, a, d) and their ensemble-averaged runs (right panels, b, e) are shown. The modelled C_i/C_a follows the same symbols as the models shown in Fig. 4, with the measured C_i/C_a (panel c) indicated by Δ (open symbols for ambient and closed symbols for elevated CO₂). The horizontal dashed line is the $C_i/C_a = 0.66$ determined from $\delta^{13}\text{C}$ measurements (1997–99).

Table 4. A reassessment of modelled versus measured mid-day A of *Pinus taeda* for the parsimonious closure schemes, using model parameters directly calculated from the 3 years of gas exchange measured C_i/C_a . The closure schemes are as indicated in **Table 3** with the exception of FA, because not all terms in this model could be fully parameterized from the measurements. The parameters shown were optimized for measured C_i/C_a for ambient and elevated atmospheric CO_2 . The root-mean squared error ($RMSE$) and the regression statistics (slope, intercept, and correlation coefficient R) with measured A as the independent variable are shown. The regression slopes that are statistically different from unity at the 95% level are indicated by *

Assimilation	Model	Parameters	R	Slope/Intercept	$RMSE$
Ambient	NR	$R_c = 0.58$	0.83	1.04/0.45	2.2
	BB	$m = 5.5$	0.70	0.84*/2.9	2.6
	HY	$R_c = 0.58$, Same a, b	0.83	1.0/0.93	2.2
	CF	$WUE = 7.1$	0.57	0.79*/3.0	3.3
	LF	$\lambda_{cf} = 708 \text{ mol mol}^{-1}$	0.60	0.70*/3.2	2.4
	LEU	$m_L = 2.24, D = 99.5$	0.83	0.99/1.06	2.2
	WD	$C_i/C_a = 0.565 + 0.0052D - 0.0002D^2$	0.83	0.99/1.18	2.1
Elevated	NR	$R_c = 0.58$	0.81	1.41*/-5.37	5.1
	BB	$m = 5.5$	0.64	1.05/1.03	5.6
	HY	$R_c = 0.58$, Same a, b	0.79	1.20/-1.3	5.1
	CF	$WUE = 6.9$	0.75	1.26/-3.55	4.9
	LF	$\lambda_{cf} = 452 \text{ mol mol}^{-1}$	0.76	1.00/-1.3	3.0
	LEU	$m_L = 3.54, D = 29.7$	0.86	1.36*/-4.6	4.4
	WD	$C_i/C_a = 0.72 - 0.0047D - 0.00008D^2$	0.85	1.36*/-4.34	4.5

constant C_i/C_a (Norman 1982) to a detailed biochemical model of photosynthesis (Farquhar *et al.* 1980). Our use of independent model parameters derived from separate measurements (Table 2) permitted an unbiased comparison of the predictive A performance of these models from measured g_c . Many previous studies did not independently measure these parameters but derived them from a subset of the same data set also used to evaluate the model performance, as in Table 4.

The constant C_i/C_a approximation, which is the most parsimonious in number of input parameters, yielded results that are comparable or better than more elaborate models for predicting short-term A . This finding is consistent with the framework presented by Jarvis *et al.* (1999). However, this simple closure approximation clearly does not reflect measured variation in C_i/C_a , with environmental conditions underlying reduced g_c such as drought. If seasonal droughts are short in persistence, then this simplification permits robust estimation of long-term A while sacrificing the mechanistically appropriate short-term A estimation during the drought duration. The constant C_i/C_a model does not permit much interpretation of the sources of variability in A other than due to variation in g_c . The success of this approach implies that control over leaf gas exchange (particularly A) by g_c in *Pinus taeda* is strong (Ellsworth 2000). However, variability in other environmental conditions (e.g. Q) over the day can influence C_i and are not explicitly treated in the Norman model. From a practical modelling perspective, the use of classes of models that employ a simple C_i/C_a closure approximation may well be justified for species whose assimilation is much more sensitive to g_c than C_i/C_a . As an example for *Pinus taeda*, g_c can decrease by two orders of magnitude for low light whereas C_i/C_a may increase by only 20%. In short, C_i/C_a is a useful

parameter to be evaluated in the context of elevated CO_2 experiments such as FACE.

The widely used Ball–Berry formulation yielded the poorest A estimates when compared to the other closure schemes. However, the Leuning corrections to the Ball–Berry formulation produced among the best A estimates. Hence, when employing coupled photosynthesis conductance models, revisions to the Ball–Berry model along the several closure model frameworks investigated here will improve the capacity to estimate A as the main determinant of ecosystem GPP without the added complexity of increased number of parameters.

The detailed biochemical photosynthesis model of Farquhar *et al.* (1980) was also contrasted with simpler models. In terms of minimizing the deviation of predicted and measured A ($RMSE$), we found no clear statistical advantage to utilizing the Farquhar *et al.* model for predicting assimilation. It is important to note that the leaf level measurements were made under sunny, mid-day conditions (high Q) and hence represent a narrower range of C_i/C_a conditions than may occur diurnally, so the advantages of the $A-C_i$ curve description for longer-term prediction of A is not completely apparent. Nonetheless, for low Q an accurate C_i/C_a description as is given by the Farquhar model is masked by large reductions in g_c from sunlit to shaded conditions.

We also developed and tested a hybrid scheme that adopts the parsimony of Norman's empirical model but retains the mechanistic advantages of the Farquhar model. Unlike Farquhar's model, this new approach is computationally simpler to implement and requires only the ensemble-averaged slope of the $A-C_i$ curve. Because of its novelty, we tested the approach for a wide range of species, including the Duke pine forest for ambient and elevated atmospheric CO_2 , and found that the hybrid approach reproduces well the

decrease in C_i/C_a with decreasing g_c (Fig. 2) following drought or high vapour pressure deficit (i.e. not light-limited g_c reduction). The agreement between measured and predicted A by the proposed hybrid scheme is no worse than the Farquhar model (Fig. 4). The hybrid approach (and the closely related version presented in Jarvis *et al.* 1999) is not proposed as a replacement of the Farquhar model or other closure schemes but a complementary approach that is sensitive to specific mechanisms in the $A-C_i$ relationship absent in the simpler closure schemes.

Despite the fact that $RMSE$ of A was larger for elevated atmospheric CO₂, all the closure approximations resulted in better goodness of fit (see regression slopes in Tables 3 and 4) when compared to ambient CO₂ data with the exception of the Ball-Berry approach. A combination of higher A and reduced sensitivity to absolute errors in C_i (Ellsworth 1999) probably contributed to the better fits in Table 3. Although the Farquhar model best describes the underlying physiological mechanisms affecting A , the added number of physiological parameters required to describe these additional interactions also introduces additional uncertainty in parameterization. Caution is needed when applying this approach to understanding variation in A in ambient and elevated atmospheric CO₂ in species or environments where few of the kinetic parameters are available or can be inferred. Also, the implication of good ensemble performance (Figs 4 & 5) of the simpler models is that added physiological complexity need not always translate to increased model accuracy.

The comparison here fundamentally differs from the widely used approach of combining the Ball-Berry type conductance or other conductance formulations with Fickian diffusion principles and the $A-C_i$ curve description (Collatz *et al.* 1991; Baldocchi 1994; Leuning 1995; Baldocchi *et al.* 1997a) in that the degrees of freedom in all model parameterizations have been reduced because g_c is specified from measurements. A direct consequence of such reduced degrees of freedom is that modelled A becomes very sensitive to the physiological parameterizations (e.g. C_i/C_a) adopted in all closure schemes thus permitting explicit assessment of such approximations. Each of the modelling approaches that have been summarized (Table 2) can be used with leaf and stand-level g_c measurements made with a variety of techniques (porometry, sapflux by heat-pulse or Granier sensors, micrometeorology, Bowen ratio/energy balance methods, etc.) along with appropriate physiological parameterizations such as the ones considered here.

A continuing area of research focuses on the question of whether the fundamental CO₂ response of leaves and the Farquhar parameterization of this response is affected by elevated CO₂ (Sage 1994; Drake *et al.* 1997; Medlyn *et al.* 1999). Our analysis uses the same parameters for trees grown in ambient and elevated CO₂ for 3 years, which reflects the analyses that have been conducted for *Pinus taeda* (Ellsworth 1999; Myers *et al.* 1999). However, the analysis may apply for any species and environment so long as the physiological parameters in elevated CO₂ are known.

At the canopy scale, effects of elevated CO₂ on A of forests cannot be quantified by direct eddy-covariance measurements, but the approaches summarized here can place upper bounds on the enhancement of canopy A . For example, using the simplest approach (Norman's model), the enhancement of A with elevated CO₂ ($= \partial A / \partial C_a$) is directly proportional to the enhancement in C_a assuming $\partial g_c / \partial C_a$ is small for the leaf (Ellsworth *et al.* 1995) and canopy scale (Pataki *et al.* 1998). However, the approach we have described need not assume that $\partial g_c / \partial C_a$ is zero for all species, but only that C_i/C_a is measured. In the Duke Forest FACE experiment with ambient + 200 p.p.m. CO₂, the concentration enhancement is 1.55 and the computed enhancement of A from Norman's model is also 1.55. This is in agreement with direct measurements of A enhancement for upper crown *P. taeda* foliage during the summer (1.56; Ellsworth 1999), since C_i at elevated atmospheric CO₂ largely remains in the linear region of the $A-C_i$ curve. In short, when water vapour fluxes are available in conjunction with vapour pressure deficit, A can be estimated with reasonable accuracy if first-order physiological information is available from elevated CO₂ experiments.

ACKNOWLEDGMENTS

The authors would like to thank Greg Burkland, Andrew Palmiotti, and Galen Hon for their assistance at the Duke Forest, Ram Oren and Graham Farquhar for the numerous helpful discussions and comments on the manuscript, and George Hendrey for his support. This project was funded, in part, by the Department of Energy (DOE) through the FACE-FACTS project under cooperative agreement (ED-AC02-98CH10886 and DE-FG05-95ER62083) and the National Institute of Global Climate Change (NIGEC) through the South-East Regional Center at the University of Alabama, Tuscaloosa (cooperative agreement DE-FC03-90ER61010), and through the National Science Foundation (NSF-BIR-95-12333 and EAR-99-03471).

REFERENCES

- Amthor J.S., Goulden M.L., Munger J.W. & Wofsy S.C. (1994) Testing a mechanistic model of forest-canopy mass and energy exchange using eddy correlation: carbon dioxide and ozone uptake by a mixed oak-maple stand. *Australian Journal of Plant Physiology* **21**, 623–651.
- Andre J.C., Goutorbe J.P., Perrier A., *et al.* (1988) Evaporation over land-surfaces: First results from HAPEX-MOBILHY special observation period. *Annales Geophysicae* **6**, 477–492.
- Aphalo P.J. & Jarvis P.G. (1991) Do stomata respond to relative humidity? *Plant, Cell and Environment* **14**, 127–132.
- Arneeth A., Kelliher F.M., McSeveny T.M. & Byers J.N. (1999) Assessment of annual carbon exchange in a water-stressed *Pinus radiata* plantation: an analysis based on eddy-covariance measurements and an integrated biophysical model. *Global Change Biology* **5**, 531–545.
- Baldocchi D. (1994) An analytical solution for coupled leaf photosynthesis and stomatal conductance models. *Tree Physiology* **14**, 1069–1079.
- Baldocchi D. & Harley P.C. (1995) Scaling carbon-dioxide and

- water-vapor exchange from leaf to canopy in a deciduous forest. 2. Model testing and application. *Plant, Cell and Environment* **18**, 1157–1173.
- Baldocchi D. & Meyers T. (1998) On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective. *Agricultural and Forest Meteorology* **90**, 1–25.
- Baldocchi D. & Vogel C.A. (1996) Energy and CO₂ flux densities above and below a temperate broad-leaved forest and a boreal pine forest. *Tree Physiology* **16**, 5–16.
- Baldocchi D., Valentini R., Running S., Oechel W. & Dahlman R. (1996) Strategies for measuring and modelling carbon dioxide and water vapor fluxes over terrestrial ecosystems. *Global Change Biology* **2**, 159–168.
- Baldocchi D., Vogel C.A. & Hall B. (1997a) Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. *Agricultural and Forest Meteorology* **83**, 147–170.
- Baldocchi D., Vogel C.A. & Hall B. (1997b) Seasonal variation of energy and water vapor exchange rates above and below a boreal jack pine forest canopy. *Journal of Geophysical Research* **102**, 28939–28951.
- Brodribb T. (1996) Dynamics of changing intercellular CO₂ concentration during drought and determination of minimum functional C_i. *Plant Physiology* **111**, 179–185.
- Brutsaert W., Parlange M.B. & Gash J.H. (1989) Neutral humidity profiles in the boundary layer and regional evaporation from sparse pine forest. *Annales Geophysicae* **7**, 623–630.
- Cermak J., Cienciel E., Kucera J., Lindroth A. & Bednarova E. (1995) Individual variation of sap flow rate in a large pine and spruce trees and stand transpiration: a pilot study at the central NOPEX site. *Journal of Hydrology* **168**, 17–27.
- Collatz C.J., Ball J.T., Griwet C. & Berry J.A. (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis, and transpiration: a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology* **54**, 107–136.
- Comstock J. & Ehleringer J.R. (1984) Photosynthetic responses to slowly decreasing leaf water potentials in *Encelia frutescens*. *Oecologia* **61**, 241–248.
- Cowan I.R. (1977) Stomatal behaviour and environment. *Advances in Botany Research* **4**, 117–228.
- Cowan I.R. & Farquhar G.D. (1977) Stomatal function in relation to leaf metabolism and environment: Stomatal function in the regulation of gas exchange. In *Symposium of the Society for Experimental Botany*, (ed. D.H. Jennings), Vol. 31, pp. 471–505. Cambridge University Press, Cambridge.
- De Pury D.G.G. & Farquhar G.D. (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell, and Environment* **20**, 537–557.
- Downton W.J.S., Grant W.J.R. & Loveys B.R. (1987) Diurnal changes in the photosynthesis of field-grown grapevines. *New Phytologist* **105**, 71–80.
- Drake B.G., Gonzalez-Meler M. & Long S.P. (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology* **48**, 609–639.
- Ehleringer J.R. (1988) Comparative ecophysiology of *Encelia farinosa* and *Encelia frutescens*. I. Energy balance considerations. *Oecologia* **76**, 553–561.
- Ehleringer J.R. (1993) Carbon and water relations in desert plants: an isotopic perspective. In *Stable Isotopes and Plant Carbon-Water Relations* (eds J.R. Ehleringer, A.E. Hall & G.D. Farquhar), pp. 155–172. Academic Press, San Diego, CA.
- Ellsworth D.S. (1999) CO₂ enrichment in a maturing pine forest: are CO₂ exchange and water status in the canopy affected? *Plant, Cell, and Environment* **22**, 461–472.
- Ellsworth D.S. (2000) Seasonal CO₂ assimilation and stomatal limitations in a *Pinus taeda* canopy with varying climate. *Tree Physiology* **20**, 435–445.
- Ellsworth D.S., Oren R., Huang C., Phillips N. & Hendrey G.R. (1995) Leaf and canopy responses to elevated CO₂ in a pine forest under free-air CO₂ enrichment. *Oecologia* **104**, 139–146.
- Fan A.S.-M., Goulden M.L., Munger J.W., Daube B.C., Bakwin P.S., Wofsy S.C., Amthor J.S., Fitzjarrald D.R., Moore K.E. & Moore T.R. (1995) Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy correlation. *Oecologia* **102**, 443–452.
- Farquhar G.D. & von Caemmerer S. (1982) Modeling of photosynthetic response to environmental conditions. In *Encyclopedia of Plant Physiology*, New Series, Vol 12B (eds O.L. Lange, P.S. Nobel & C.B. Osmond), pp. 549–587. Springer-Verlag, Berlin.
- Farquhar G.D. & Wong S.C. (1984) An empirical model of stomatal conductance. *Australian Journal of Plant Physiology* **11**, 191–210.
- Farquhar G.D., von Caemmerer S. & Berry J.A. (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* **149**, 78–90.
- Farquhar G.D., Ehleringer J.R. & Hubick K.T. (1989) Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**, 503–537.
- Farquhar G.D., Lloyd J., Taylor J.A., Flanagan L.B., Syvertsen J.P., Hubick K.T., Wong S.C. & Ehleringer J.R. (1993) Vegetation effects on the isotope composition of oxygen in atmospheric CO₂. *Nature* **363**, 439–443.
- Fites J.A. & Teskey R.O. (1998) CO₂ and water vapor exchange of *Pinus taeda* in relation to stomatal behavior: test of an optimization hypothesis. *Canadian Journal of Forest Research* **18**, 150–157.
- Forseth I. & Ehleringer J.R. (1983) Ecophysiology of two solar tracking desert winter annuals. III. Gas exchange responses to light, CO₂ and VPD in relation to long-term drought. *Oecologia* **57**, 344–351.
- Frolking S., Goulden M.L., Wofsy S.C., et al. (1996) Temporal variability in the carbon balance of a spruce/moss boreal forest. *Global Change Biology* **2**, 343–366.
- Goulden M.L., Munger J.W., Fan S.M., Daube B.C. & Wofsy S.C. (1996a) Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* **271**, 1576–1578.
- Goulden M.L., Munger J.W., Fan S.M., Daube B.C. & Wofsy S.C. (1996b) Measurements of carbon storage by long-term eddy correlation: methods and a critical evaluation of accuracy. *Global Change Biology* **2**, 169–182.
- Goulden M.L., Wofsy S.C., Harden J.W., et al. (1998) Sensitivity of boreal forest carbon balance to soil thaw. *Science* **279**, 214–217.
- Gourtorbe J.P., Noilhan J., Valancogne C. & Cuenca R.H. (1989) Soil moisture variations during HAPEX-MOBILHY. *Annales Geophysicae* **7**, 415–426.
- Granier A. (1987) Evaluation of transpiration in a douglas fir stand by means of sap flow measurements. *Tree Physiology* **3**, 309–320.
- Greco S. & Baldocchi D. (1996) Seasonal variations of CO₂ and water vapour exchange rates over a temperate deciduous forest. *Global Change Biology* **2**, 183–197.
- Harley P.C., Thomas R.B., Reynolds J.F. & Strain B.R. (1992) Modeling photosynthesis of cotton grown in elevated CO₂. *Plant, Cell and Environment* **15**, 271–282.
- Harley P.C., Tenhunen J.D. & Lange O.L. (1986) Use of analytical model to study limitations on net photosynthesis in *Arbutus unedo* under field conditions. *Oecologia* **70**, 393–401.
- Hendrey G.R., Ellsworth D.S., Lewin K.F. & Nagy J. (1999) A free-

- air enrichment system for exposing tall forest vegetation to elevated atmospheric CO₂. *Global Change Biology* **5**, 293–309.
- Hollinger D.Y., Kelliher F.M., Byers J.N., Hunt J.E., McSeveny T.M. & Weir P.L. (1994) Carbon dioxide exchange between an undisturbed old growth temperate forest and the atmosphere. *Ecology* **75**, 134–150.
- Jarvis P.G. & McNaughton K.G. (1986) Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research* **15**, 1–49.
- Jarvis A.J., Mansfield T.A. & Davies W.J. (1999) Stomatal behaviour, photosynthesis and transpiration under rising CO₂. *Plant, Cell and Environment* **22**, 639–648.
- Jordan D.B. & Ogren W.L. (1984) The CO₂/O₂ specificity of ribulose 1,5-bisphosphate carboxylase/oxygenase. Dependence on ribulose bisphosphate concentration, pH and temperature. *Planta* **161**, 308–313.
- Jordan D.F., Zitzer S.F., Hendrey G.R., Lewin K.F., Nagy J., Nowak R.S., Smith S.D., Coleman J.S. & Seemann J.R. (1999) Biotic, abiotic and performance aspects of the Nevada desert Free Air CO₂ Enrichment (FACE) facility. *Global Change Biology* **5**, 659–688.
- Kaiser J. (1998) Climate change – new network aims to take the world's CO₂ pulse source. *Science* **281**, 506–507.
- Katul G.G., Hsieh C.I., Bowling D., *et al.* (1999) Spatial variability of turbulent fluxes in the roughness sublayer of an even-aged pine forest. *Bound Layer Meteorology* **93**, 1–28.
- Katul G.G., Oren R., Ellsworth D., Hsieh C.I., Phillips N. & Lewin K. (1997a) A Lagrangian dispersion model for predicting CO₂ sources, sinks, and fluxes in a uniform Loblolly pine (*Pinus taeda* L.) stand. *Journal of Geophysical Research* **102**, 9309–9321.
- Katul G.G., Hsieh C.I., Kuhn G., Ellsworth D. & Nie D. (1997b) The turbulent eddy motion at the forest–atmosphere interface. *Journal of Geophysical Research* **102**, 13409–13421.
- Katul G.G., Todd P., Pataki D., Kabala Z. & Oren R. (1997c) Soil water depletion by oak trees and the influence of root water uptake on the soil moisture content spatial statistics. *Water Resource Research* **33**, 611–623.
- Lai C.T., Katul G.G., Ellsworth D. & Oren R. (2000a) Modelling vegetation-atmosphere CO₂ exchange by a coupled Eulerian-Lagrangian approach. *Boundary Layer Meteorology* **95**, 91–122.
- Lai C.T., Katul G.G., Oren R., Ellsworth D. & Schäfer K. (2000b) Modelling CO₂ and water vapour turbulent flux distributions within a forest canopy. *Journal of Geophysical Research*, in press.
- Leuning R. (1990) Modeling stomatal behaviour and photosynthesis of *Eucalyptus grandis*. *Australian Journal of Plant Physiology* **17**, 159–175.
- Leuning R. (1995) A critical appraisal of a combined stomatal-photosynthesis model for C₃ plants. *Plant, Cell and Environment* **18**, 339–355.
- Lloyd J. & Farquhar J.D. (1994) ¹³C discrimination during CO₂ assimilation by the terrestrial biosphere. *Oecologia* **99**, 201–215.
- Lloyd J., Grace J., Miranda A.C., Meir P., Wong S.C., Miranda H.S., Wright I.R., Gash J.H.C. & McIntyre J. (1995) A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. *Plant, Cell and Environment* **18**, 1129–1146.
- Medlyn B.E., Badeck F.-W., de Pury D.G.G., *et al.* (1999) Effects of elevated [CO₂] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant, Cell and Environment* **23**, 1475–1496.
- Monteith J.L. (1995) A reinterpretation of stomatal responses to humidity: theoretical paper. *Plant, Cell and Environment* **18**, 357–364.
- Myers D.A., Thomas R.B. & DeLucia E.H. (1999) Photosynthetic capacity of loblolly pine (*Pinus taeda* L.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. *Plant Cell and Environment* **22**, 473–482.
- Nikolov N.T., Massman W.J. & Schoettle A.W. (1995) Coupling biochemical and biophysical processes at the leaf level: an equilibrium photosynthesis model for leaves of C₃ plants. *Ecological Modelling* **80**, 205–235.
- Norman J.M. (1982) Simulation of Microclimates. In *Biometeorology and Integrated Pest Management* (eds J.L. Hatfield & I. Thompson), pp. 65–99. Academic Press, New York.
- Oren R., Phillips N., Katul G., Ewers B. & Pataki D. (1998a) Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests. *Annales Des Sciences Forestieres* **55**, 191–216.
- Oren R., Ewers B., Todd P., Phillips N. & Katul G.G. (1998b) Water balance delineates the soil layer in which moisture affects canopy conductance. *Ecological Applications* **8**, 990–1002.
- Oren R., Sperry J.S., Katul G.G., Pataki D.E., Ewers B.E., Phillips N. & Schafer K.V.R. (1999) Survey and synthesis of intra and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell, and Environment* **22**, 1515–1526.
- Pataki D.E., Oren R. & Tissue D. (1998) Elevated carbon dioxide does not affect canopy stomatal conductance of *Pinus taeda* L. *Oecologia* **117**, 47–52.
- Phillips N. & Oren R. (1998) A comparison of two daily representations of canopy conductance based on two conditional time-averaging methods and the dependence of daily conductance on environmental factors. *Annales Des Sciences Forestieres* **55**, 217–235.
- Pinter P.J., Kimball B.A., Garcia R.L., Wall G.W., Hunsaker D.J. & LaMorte R.L. (1996) Free air CO₂ enrichment. In *Responses of Cotton and Wheat Crops, in Carbon Dioxide and Terrestrial Ecosystems* (eds G.W. Koch & H. Mooney), pp. 215–249. Academic Press, San Diego, CA.
- Sage R.F. (1994) Acclimation of photosynthesis to increasing atmospheric CO₂: the gas exchange perspective. *Photosynthesis Research* **39**, 351–368.
- Sellers P.J., Dickinson R.E., Randall D.A., *et al.* (1996) Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science* **275**, 502–509.
- Wang Y.P. & Leuning R. (1998) A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I: Model description and comparison with a multi-layered model. *Agricultural Forest Meteorology* **91**, 89–111.
- Waring R.H., Law B.E., Goulden M.L., Bassow S.L., McCreight R.W., Wofsy S.C. & Bazzaz F.A. (1995) Scaling net photosynthesis at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. *Plant, Cell and Environment* **18**, 1201–1213.
- Weber J.A. & Gates D.M. (1990) Gas exchange of *Quercus rubra* (northern red oak) during a drought: analysis of relations among photosynthesis, transpiration and leaf conductance. *Tree Physiology* **7**, 215–225.
- Wong S.C. & Dunin F.X. (1987) Photosynthesis and transpiration of trees in a Eucalypt forest stand: CO₂, light and humidity responses. *Australian Journal of Plant Physiology* **14**, 619–632.
- Wong S.C., Cowan I.R. & Farquhar G.D. (1979) Stomatal conductance correlates with photosynthetic capacity. *Nature* **282**, 424–426.

Received 24 October 1999; received in revised form 1 June 2000; accepted for publication 11 July 2000

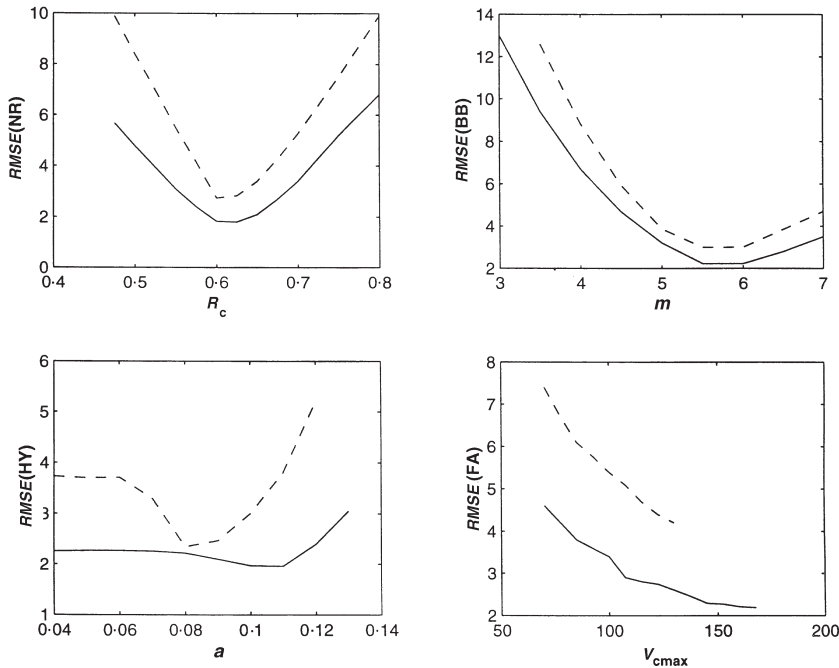


Figure 6. Sensitivity of the root-mean square error (*RMSE*) to primary model parameters (Table 1) for ambient (solid line) and elevated (dotted line) atmospheric CO₂ for four sample closure models (NR, BB, HY and FA models, see Fig. 4) is evaluated. Sensitivity of the Farquhar biochemical model was not evaluated if more than 40% of the data was lost due to lack of convergence with the closure criterion.

APPENDIX

Sensitivity analysis

A sensitivity analysis to assess how uncertainties in model parameters alter the *RMSE* is shown in Fig. 6. The models assessed include the simplest closure approach of Norman, the widely used Ball–Berry, the multiple parameter Farquhar, and the proposed hybrid approach. Hence, the full spectrum of closure model complexity is resolved in this sensitivity.

It is evident that the main parameters in the Norman, Ball–Berry, and the hybrid models are robust to perturbations around their optimal states. That is, for initial estimates of model parameters close to optimum, a 10% perturbation in the parameter increases the *RMSE* by less

than 10%. These *RMSE* findings are consistent for ambient and elevated atmospheric CO₂ conditions. It is interesting to note that the independently determined parameters (e.g. R_c from the $\delta^{13}\text{C}$ measurements) are near their optimum state for minimizing *RMSE*. Figure 6 suggests that increasing $V_{c\text{max}}$ in the Farquhar model tend to monotonically improve the *RMSE*. However, we found that for a $V_{c\text{max}} > 140$, the number of points for which a positive C_i solution exists to the quadratic equation formed by combining Eqn 8 or Eqn 9 with Eqn 1 diminished by more than 30%. Hence, such large $V_{c\text{max}}$ are not compatible with the independently measured g_c for at least 30% of the data, and thus much of the reduction in *RMSE* is attributed to rejecting points for which such convergence is not attained.