

## Modeling CO<sub>2</sub> and water vapor turbulent flux distributions within a forest canopy

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**Abstract.** One-dimensional multilayer biosphere-atmosphere models (e.g., CANVEG) describe ecosystem carbon dioxide (CO<sub>2</sub>) and water vapor (H<sub>2</sub>O) fluxes well when cold temperatures or the hydrologic state of the ecosystem do not induce stomatal closure. To investigate the CANVEG model framework under such conditions, CO<sub>2</sub>, H<sub>2</sub>O, and sensible heat fluxes were measured with eddy-covariance methods together with xylem sap flux and leaf-level gas exchange in a 16-year-old (in 1999) southeastern loblolly pine forest. Leaf-level gas exchange measurements, collected over a 3-year period, provided all the necessary biochemical and physiological parameters for the CANVEG model. Using temperature-induced reductions of the biochemical kinetic rate constants, the CANVEG approach closely captures the diurnal patterns of the CO<sub>2</sub> and H<sub>2</sub>O fluxes for two different formulations of the maximum Rubisco catalytic capacity ( $V_{c\max}$ ) – temperature function, suggesting that the CANVEG approach is not sensitive to  $V_{c\max}$  variations for low temperatures. A soil moisture correction ( $w_r$ ) to the Ball-Berry leaf-conductance approach was also proposed and tested. The  $w_r$  magnitude is consistent with values predicted by a root-xylem hydraulic approach and with leaf-level measurements. The  $w_r$  correction significantly improves the model's ability to capture diurnal patterns of H<sub>2</sub>O fluxes for drought conditions. The modeled bulk canopy conductance ( $G_m$ ) for pine foliage estimated from the CANVEG-modeled multilevel resistance values agreed well with canopy conductance ( $G_c$ ) independently estimated from pine sap flux measurements. Detailed sensitivity analysis suggests that the leaf-level physiological parameters used in CANVEG are not static. The dynamic property of the conductance parameter, inferred from such sensitivity analysis, was further supported using 3 years of porometry measurements. The CANVEG model also reproduced basic biochemical processes as demonstrated by the agreement between modeled and leaf-level measured  $C_i/C_a$ , where  $C_i$  and  $C_a$  are the intercellular and atmospheric CO<sub>2</sub> concentration, respectively. The model estimated that vapor pressure deficit does not vary significantly within the canopy but that  $C_i/C_a$  varied by more than 15%. The broader implication of this variation is that “big-leaf” approaches that compress physiological and biochemical parameters into bulk canopy stomatal properties may be suitable for estimating water vapor flux but biased for CO<sub>2</sub> ecosystem fluxes.

### 1. Introduction

Coupling biophysical, physiological, and biochemical principles with detailed turbulent transport mechanics to estimate carbon dioxide (CO<sub>2</sub>) and water vapor (H<sub>2</sub>O) sources and sinks (hereinafter referred to as source) and flux distributions within a forest canopy offers a promising approach to model biosphere-atmosphere exchange from forested ecosystems. An example of such framework, termed CANVEG by *Baldocchi and Meyers* [1998], permits realistic accounting for the primary interdependencies between the vegetation and its microclimate. Models based on the CANVEG framework reproduced well measured scalar fluxes in several vegetation types [*Baldocchi and Harley*, 1995; *Baldocchi*, 1997; *Baldocchi et al.*, 1997a; *Baldocchi and Meyers*, 1998].

In current CANVEG models, velocity statistics, particularly the standard deviation of vertical velocity ( $\sigma_w$ ) and Lagrangian integral timescales ( $T_L$ ) within the canopy are assumed or heuristically specified [*Raupach*, 1988; *Baldocchi*, 1992; *Baldocchi and Meyers*, 1998]. In addition to being variable from stand to stand, the flow statistics also evolve with leaf area dynamics. Thus this approach prohibits using CANVEG for long-term flux estimation because the effects of variable leaf area density on the required flow statistics cannot be explicitly resolved. To circumvent these limitations, *Lai et al.* [2000] developed a CANVEG approach that includes a one-dimensional second-order Eulerian closure model to compute the velocity statistics within the canopy volume which are needed for estimating sources and fluxes. The CANVEG approach of *Lai et al.* [2000] has the added advantage of combining leaf area density distribution with mean momentum and Reynolds stress equations inside the canopy to infer first and second moments of the flow field. Thus the effects of variation in leaf area density on the flow statistics required for CO<sub>2</sub> and H<sub>2</sub>O transport can be explicitly treated.

Over the past decade, many field experiments highlighted

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Paper number 2000JD900468.  
0148-0227/00/2000JD900468\$09.00

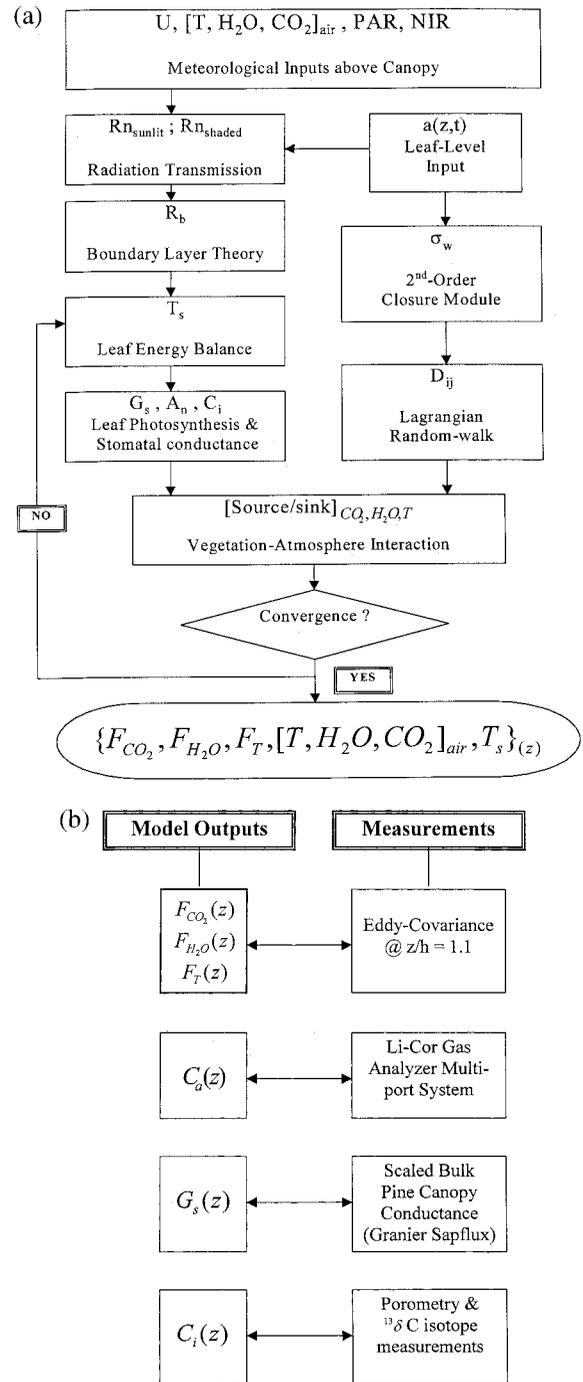
other limitations to the CANVEG approach. In particular, when soil moisture content ( $\theta$ ) or mean air temperature ( $T_a$ ) are low enough to restrict stomatal opening [Hinckley et al., 1978; Gollan et al., 1986; Schulze, 1986; Kelliher et al., 1993; Cornic, 1994; Kramer and Boyer, 1995; Baldocchi et al., 1997b; Oren et al., 1998a; Pataki et al., 1998], existing CANVEG models poorly reproduce measured CO<sub>2</sub> and H<sub>2</sub>O fluxes [Baldocchi, 1997]. In the case of low  $T_a$ , current CANVEG models reduce the biochemical kinetic constants and other physiological parameters by a semiempirical temperature response function. It is now recognized that the form of such temperature response functions is sufficiently general but that the coefficients can vary among species [Harley and Baldocchi, 1995]. Hence it is not clear how accurate the temperature response functions must be described in CANVEG models to reproduce CO<sub>2</sub> and H<sub>2</sub>O fluxes for low  $T_a$ . In the case of low  $\theta$ , typical leaf-conductance models in CANVEG (e.g., a Ball-Berry-type model) do not consider the reduction in conductance induced by drought effects. It is these hydrologic and climatic conditions that motivated the present study.

Our objective is twofold: (1) to develop stomatal closure corrections that consider the effect of soil moisture deficit on stomatal conductance and to evaluate the performance of the CANVEG model when “generic” biochemical temperature response functions are replaced by species-specific measured functions between the canopy and its microclimate can be collapsed to a single effective layer as in “big-leaf” models. Toward this end, these corrections and formulations are integrated into the Lai et al. [2000] version of the CANVEG model with the aim of evaluating the model performance for a range of hydrologic and climatic conditions.

In particular, we evaluated the revised CANVEG model calculations against eddy-covariance measurements of CO<sub>2</sub> and H<sub>2</sub>O fluxes above the canopy. Scaled sap flux measurements are used to estimate bulk canopy conductance for the dominant species in the ecosystem, which in turn, are compared to modeled bulk canopy conductance derived from the CANVEG calculations. A unique feature about the CANVEG approach is its ability to fully resolve the interaction between vegetation and its microclimate, thereby producing realistic solutions that satisfy both the physiological properties and their corresponding microclimate. Hence as an additional line of model evaluations, we will compare predicted and measured mean CO<sub>2</sub> concentration profiles to independently assess the combined source and turbulent dispersion calculations. At its finest scale, the CANVEG model reproduces physiological and biochemical properties of the forest that can be evaluated against measurements made at scales of a whole tree and leaf level with sap flux and porometry. If the model performs well against measurements at ecosystem, tree, and leaf scales, it serves to increase confidence in its ability to correctly describe CO<sub>2</sub> and H<sub>2</sub>O exchange processes between the biosphere and the atmosphere. Four experimental periods (each between 7 and 12 days, leading to a total of 1648 half-hour runs) were chosen to contrast periods in which plant stress was caused by drought or low mean air temperatures with predominantly “stress-free” periods.

## 2. Theory

The CANVEG approach of Baldocchi and Meyers [1998] couples conservation equations for mean scalar mass and heat,



**Figure 1.** Schematic display of CANVEG framework: (top) Model inputs and operation, (bottom) model outputs and validation.

a Lagrangian turbulent dispersion algorithm, energy and radiation conservation, and biophysical and biochemical mechanisms responsible for stomatal opening and carbon assimilation. Lai et al. [2000] modified the CANVEG approach by using a second-order closure model for momentum and Reynolds stress equations to solve for  $\sigma_w(z)$  given a foliage distribution profile. For clarity, we provide a schematic linkage between these conservation equations and submodels as well as the model outputs in Figure 1. In all calculations the canopy height ( $h$ ) is divided into  $N$  layers, each of thickness  $dz$ , and all

the schemes listed in Figure 1 are solved iteratively for each discrete layer. Next we provide a brief review of these models.

### 2.1. Scalar Mass Balance

In a uniform and rigid canopy, the one-dimensional scalar flux budget for a planar homogeneous turbulent flow can be described (after proper time and horizontal averaging) by the scalar conservation equation

$$\frac{\partial \bar{C}}{\partial t} + \frac{\partial F_c}{\partial z} = S_c, \quad (1)$$

where  $\bar{C}$  is the mean scalar concentration or temperature (i.e., H<sub>2</sub>O, CO<sub>2</sub>, and temperature  $T$ ),  $F_c$  is the mean vertical flux of a scalar entity  $C$  (e.g.,  $F_{\text{CO}_2}$ ,  $F_{\text{H}_2\text{O}}$ , and  $F_T$  are CO<sub>2</sub>, H<sub>2</sub>O, and sensible heat turbulent fluxes at height  $z$ , respectively), and  $S_c$  is the mean vegetation source strength at time  $t$  and height  $z$  above the forest floor. All mean quantities are subject to both time and horizontal averaging as described by *Raupach and Shaw* [1982]. The scalar continuity equation in (1) requires two additional prognostic equations to solve for the three unknowns ( $\bar{C}$ ,  $F_c$ , and  $S_c$ ).

### 2.2. Turbulent Dispersion Mechanics

One approach to establish an additional prognostic equation is to consider the interdependency between  $S_c(z)$  and  $\bar{C}(z)$  via Lagrangian dispersion theory. *Raupach* [1988, 1989] introduced a dispersion matrix ( $D_{ij}$ ) that relates concentration difference between a given height  $\bar{C}_z$  and a reference level above canopy ( $\bar{C}_r$ ) to the scalar source strength by

$$\bar{C}_z - \bar{C}_r = \sum_{j=1}^N S_{cj} D_{ij} \Delta z_j, \quad (2)$$

where  $i$  and  $j$  are the indices for concentration and source strength location, respectively,  $\Delta z_j$  is the discrete layer thickness within the canopy, and  $N$  is, as before, the number of layers within the canopy volume. The  $D_{ij}$  matrix is calculated from the velocity statistics by following the trajectory of an ensemble of fluid parcels released uniformly from a unit source placed at each  $j$ th layer. The parcel trajectories and velocities are computed using the random walk algorithm of *Thomson* [1987]. We use the finite difference form of such vertical velocity model in our numerical calculation, as described by *Luhar and Britter* [1989], where

$$w_{i+1} = w_i + \left[ -\frac{w_i}{T_L} + \frac{1}{2} \left( 1 + \frac{w_i^2}{\sigma_w^2} \right) \frac{\partial \sigma_w^2}{\partial z} \right] \Delta t + \left( \frac{2\sigma_w^2}{T_L} \Delta \right)^{1/2} d\Omega, \quad (3)$$

and  $w_i$  is the parcel vertical velocity at time  $t_i$ ,  $\Delta t$  is the time step increment, and  $d\Omega$  is a Gaussian random increment with zero mean and unit variance, and  $T_L$  is assumed constant within the canopy as suggested by *Raupach* [1988]. To estimate  $\sigma_w$  and  $\partial \sigma_w^2 / \partial z$  in (3), the Eulerian second-order closure model of *Wilson and Shaw* [1977] is adopted. Although third-order closure models have been developed for canopy flows [e.g., *Meyers and Paw U*, 1986; *Meyers and Baldocchi*, 1991], a recent study demonstrated that the model of *Wilson and Shaw* [1977] performs as well as third-order closure models [*Katul and Albertson*, 1998]. The model of *Wilson and Shaw* [1977] assumes steady state adiabatic flow with all triple-velocity

products closed by a gradient-diffusion approximation [*Donaldson*, 1973; *Mellor*, 1973; *Mellor and Yamada*, 1974; *Wilson and Shaw*, 1977; *Shaw*, 1977; *Wilson*, 1988, 1989; *Andren*, 1990; *Canuto et al.*, 1994; *Abdella and McFarlane*, 1997]. The closure model computes vertical variation in mean horizontal velocity, mean momentum flux, and longitudinal, lateral, and vertical velocity standard deviations based on a specified leaf area density and foliage drag coefficient ( $C_d$ ). The determination of  $C_d$ , the specification of boundary conditions, and the numerical implementation of the closure model are described by *Katul and Albertson* [1998] and *Katul and Chang* [1999].

### 2.3. Physiological Functions

After combining (1) and (2), one additional equation is still required to solve for  $\bar{C}$ ,  $F_c$ , and  $S_c$ . This equation is derived from physiological controls on  $S_c$  via

$$S_c(z) = -\rho_a a(z) \frac{\bar{C}(z) - \bar{C}_{ic}(z)}{r_b(z) + r_s(z)}, \quad (4)$$

where  $\rho_a$  is the mean air density,  $a(z)$  is the plant area density,  $\bar{C}_{ic}$  is the mean intercellular scalar concentration,  $r_b(z)$  is the boundary layer resistance, and  $r_s(z)$  is the stomatal resistance. Equations (1), (2), and (4) permit a complete mathematical description of  $\bar{C}$ ,  $F_c$ , and  $S_c$  if  $\bar{C}_{ic}$ ,  $r_s$ , and  $r_b$  are known or parameterized. The parameterization of these variables is described next.

The estimation of  $r_b$  is based on flat plate theory [*Schuepp*, 1993; *Baldocchi and Meyers*, 1998] and is given by

$$r_b = \frac{l_d}{d_m Sh}, \quad (5)$$

where  $l_d$  is the characteristic leaf length scale,  $d_m$  is the molecular diffusivity of a scalar entity, and  $Sh$  is the Sherwood number, which can be determined from the mean longitudinal velocity inside the canopy. While a cylinder flow approximation (vis-à-vis flat plate) is also plausible, the difference between the two formulations of  $r_b$  is minor, as demonstrated by *Campbell and Norman* [1998] for Reynolds numbers not exceeding 100,000. Again, the second-order closure model of *Wilson and Shaw* [1977] provides the necessary flow statistics (i.e., mean wind field  $u$ ) for estimating  $r_b$ .

The stomatal conductance  $G_s$  ( $= r_s^{-1}$ ) is computed by linking  $G_s$  to leaf photosynthesis ( $A_n$ ), relative humidity ( $rh$ ), and CO<sub>2</sub> concentration at the leaf surface ( $C_s$ ), as described by *Ball et al.* [1987] and *Collatz et al.* [1991], and is given by

$$G_s = m \frac{A_n rh}{C_s} + b, \quad (6)$$

where  $m$  and  $b$  are empirical parameters that vary with vegetation type (but can be independently determined from porometry measurements). The relationship between  $G_s$  and  $A_n$  in (6) is now widely used in coupling the biochemical model proposed by *Farquhar et al.* [1980] with  $G_s$  [*Harley et al.*, 1992; *Baldocchi and Meyers*, 1998]. According to *Farquhar et al.* [1980],  $A_n$  is given by

$$A_n \approx \min \left\{ \begin{matrix} J_E \\ J_C \\ J_S \end{matrix} \right\} - R_d, \quad (7)$$

where  $J_E$ ,  $J_C$ , and  $J_S$  are the assimilation rates restricted by either electron transport through the photosystem, ribulose

**Table 1.** Physiological Parameters Used in CANVEG Calculations

Variable	Value	Unit	Source
Characteristic leaf length, $l_d$	0.001	m	measurement
Spherical leaf distribution, $x_e$	1		<i>Campbell and Norman</i> [1998]
$V_{c \max}$ at 25°C	59	$\mu\text{mol m}^{-2} \text{s}^{-1}$	<i>Ellsworth</i> [1999, 2000]
Stomatal slope factor, $m$	5.9 (4–9)		measurement (see Figure 3b)
Stomatal intercept factor, $b$	0.015	$\mu\text{mol m}^{-2} \text{s}^{-1}$	measurement
Clumping factor, $\Pi$	0.8		<i>Baldocchi and Meyers</i> [1998]
Max. quantum efficiency, $e_m$	0.08		<i>Collatz et al.</i> [1991]
Michaelis constant for CO <sub>2</sub> , $K_c$	404	$\mu\text{mol mol}^{-1}$	<i>De Pury and Farquhar</i> [1997]
Inhibition constant for O <sub>2</sub> , $K_o$	240	$\text{mmol mol}^{-1}$	<i>De Pury and Farquhar</i> [1997]
Leaf absorptivity for PAR, $\alpha_p$	0.83		measurement
CO <sub>2</sub> /O <sub>2</sub> specificity ratio, $\tau$	2.6	$\text{mmol } \mu\text{mol}^{-1}$	<i>Collatz et al.</i> [1991]

bisphosphate carboxylase (or Rubisco), and the export rate of synthesized sucrose, respectively, and  $R_d$  is the respiration rate during daytime but in the absence of photorespiration. The details of the formulation and parameterization of  $J_E$ ,  $J_C$ ,  $J_S$ , and  $R_d$  as a function of photosynthetically active radiation (PAR), the intercellular CO<sub>2</sub> concentration ( $C_i$ ), and surface temperature ( $T_s$ ) are described in Appendix A. The physiological coefficients used in these calculations are determined from porometry measurements and summarized in Table 1. We note that (6) and (7) require  $A_n$ ,  $rh$ , and  $T_s$  within the canopy; hence all three scalars (H<sub>2</sub>O, CO<sub>2</sub>, and  $T_a$ ) must be simultaneously considered in (1), (2), and (4) (i.e., nine equations).

#### 2.4. Leaf Energy Balance and Radiative Transfer

An energy budget is employed at the leaf surface for each level within the canopy to compute both mean leaf temperature ( $T_s$ ) and absorbed radiation. These parameters are necessary to calculate  $C_i$  for the  $A - C_i$  model of *Farquhar et al.* [1980]. The determination of  $T_s$  is critical to modeling photosynthesis because the leaf biochemical reactions inside the chloroplast nonlinearly depend on  $T_s$ .

The extraterrestrial radiation was decomposed into solar radiation and thermal radiation. The solar radiation was further divided into direct beam and diffuse radiation [*Campbell and Norman*, 1998]. After subtracting the reflected quantities for PAR and near-infrared radiation (NIR) by the canopy surface, the remaining radiation is transmitted through canopy volume. The light transmission through the canopy is computed for sunlit and shaded portions separately to estimate PAR and NIR irradiance absorbed at each canopy level. This waveband decomposition is necessary because leaf absorptivity is different for these two spectral bands [*Monteith and Unsworth*, 1990; *Campbell and Norman*, 1998]. The light transmission model of *Campbell and Norman* [1998] was used in these calculations and is briefly described below.

The fraction  $\tau_b(\psi)$  of incident beam radiation from a zenith angle  $\psi$  penetrating the canopy is given by

$$\tau_b(\psi) = \exp(-\sqrt{\alpha} K_{be}(\psi) a_l \Pi), \quad (8)$$

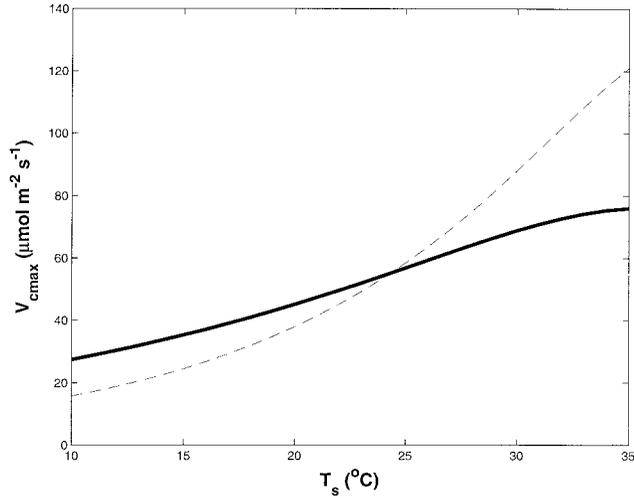
where  $\alpha$  is the leaf radiation absorptivity,  $K_{be}(\psi)$  is the extinction coefficient for an ellipsoidal leaf distribution [see *Campbell and Norman*, 1998],  $a_l$  is the cumulative leaf area density integrated from the canopy top, and  $\Pi$  is the clumping factor of leaf distribution ( $\Pi = 1$  when leaves are randomly distributed in space). The model in (8) is sufficiently accurate if  $a(z) < 0.5$  for a given layer [*Norman and Welles*, 1983] as is the case for our study.

#### 2.5. Stomatal Closure Induced by Low Temperatures and Droughts

Because assimilation is restricted by  $T_s$  [*Björkman et al.*, 1980; *Farquhar et al.*, 1980; *Harley and Tenhunen*, 1991; *Cornic*, 1994], many empirical temperature functions have been proposed to adjust the kinetic coefficients of the *Farquhar et al.* [1980] model [*Johnson and Thornley*, 1985; *Harley et al.*, 1985; *Harley and Tenhunen*, 1991; *Collatz et al.*, 1991; *Campbell and Norman*, 1998]. In our CANVEG framework, explicit accounting for variation in  $T_s$  is performed by adjusting the kinetic variables ( $K_c$ ,  $K_o$ ,  $\omega$ ,  $V_{c \max}$ , and  $R_d$ ; see Appendix A for definition) using the *Campbell and Norman* [1998] formulation. We also parameterize the same function for temperature corrections to  $V_{c \max}$  using porometry  $A - C_i$  curve measurements for loblolly pine (*Pinus taeda*) needles collected in February 1999 and August 1999. The  $A - C_i$  data consists of measurements of net CO<sub>2</sub> assimilation at light saturation made using a climate-controlled chamber (Li-6400 portable photosynthesis system, Li-Cor) for pine needles that were detached and rehydrated in pure water. Leaf net CO<sub>2</sub> assimilation was measured as a function of  $C_i$  for nine different CO<sub>2</sub> levels (ranging from 60 to 1000  $\mu\text{mol CO}_2 \text{ mol}^{-1}$ ) and three different temperatures (15°, 28°, and 35°C) for three replicate trees at each time of year. Figure 2 shows the comparison of the generic dependence of carboxylation enzyme kinetics  $V_{c \max}$  on leaf temperature  $T_s$  using the parameterization of *Campbell and Norman* [1998] and the empirical fit of the same function to  $A - C_i$  curve porometry measurements for loblolly pines. Our measurements show that for loblolly pine,  $V_{c \max}$  increases slightly with  $T_s$ , in contrast to the *Campbell and Norman's* [1998] formulation at high temperature. For low temperature conditions, needles in this pine stand remain at about the same  $V_{c \max}$  until  $T_a < 10^\circ\text{C}$ . We assess how sensitive the bulk canopy conductance is to the  $V_{c \max}$  parameterization by utilizing both *Campbell and Norman's* and the  $V_{c \max} - T_s$  curve derived from  $A - C_i$  (Figure 2).

For low soil moisture condition, several investigators heuristically reduced the slope coefficient  $m$  in the Ball-Berry model (equation (6)) [*Tenhunen et al.*, 1990; *Williams et al.*, 1996; *Baldocchi*, 1997]. Here we depart from the descriptive approach of *Tenhunen et al.* [1990], water balance approach of *Williams et al.* [1996], or scaling  $m$  by a water stress index derived from a precipitation/evaporation ratio [*Baldocchi*, 1997], by proposing a normalized reduction function to modify  $G_s$  via soil moisture as

$$G_s = w_r \left[ m \frac{A_r rh}{C_s} \right] + b, \quad (9)$$



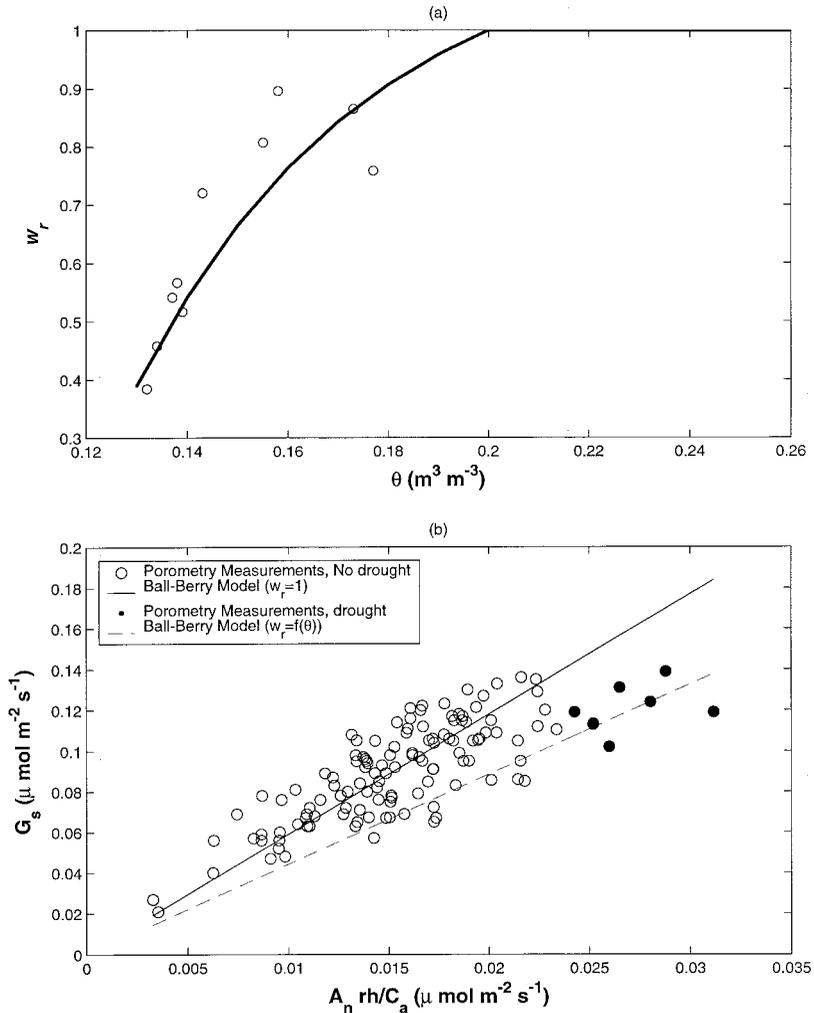
**Figure 2.** Comparison of the generic dependence of carboxylation enzyme kinetics  $V_{cmax}$  on leaf temperature  $T_s$  between the parameterization of Campbell and Norman [1998] (dashed line) and the empirical fit of the same function to  $A - C_i$  curve data from loblolly pine measured in both winter and summer months (solid line).

where

$$w_r = \begin{cases} 1 & ; \frac{\bar{\theta}}{\bar{\theta}_R} \geq 1 \\ \frac{f(\bar{\theta})}{f(\bar{\theta}_R)} & ; \frac{\bar{\theta}}{\bar{\theta}_R} < 1 \end{cases} \quad (10a)$$

$$f(\bar{\theta}) = a_m[1 - \exp(-b_m\bar{\theta})] + c_m, \quad (10b)$$

where  $\bar{\theta}$  is the mean surface (0–30 cm) soil moisture content, and  $\bar{\theta}_R$  is the threshold at which soil moisture content begins to limit stomatal aperture. The determination of  $\bar{\theta}_R$  is described in section 3.2.1. The function  $w_r$ , applied to every layer in the canopy, is shown in Figure 3a (with  $a_m = 83.46$ ,  $b_m = 21.68$ , and  $c_m = -75.99$ ) and  $f(\bar{\theta})$  is derived from maximum mean canopy stomatal conductance measurements presented by Oren *et al.* [1998a]. Notice in Figure 3a that  $G_s$  can decrease by 30% for a  $\bar{\theta}$  reduction from 0.2 to 0.15. In (10), when  $\bar{\theta} > \bar{\theta}_R$ , carbon assimilation and canopy microclimate regulate  $G_s$ . However, if  $\bar{\theta} < \bar{\theta}_R$ , these processes are modulated by hydraulic constraints resulting in nonlinear dependence of  $m$  on  $\bar{\theta}$ .



**Figure 3.** (a) Normalized reduction curve  $w_r$  for the slope parameter  $m$  in the Ball-Berry stomatal conductance model (solid line). (b) Comparison between  $G_s$  from porometry measurements and the Ball-Berry model for drought and nondrought conditions. The open circles represent  $G_s$  estimated from daily sap flux measurements reported by Oren *et al.* [1998a].

While  $w_r$  in (10) is derived from sap flux measurements, such stomatal decline with decreasing soil moisture content is consistent with the hydraulic limitation approach of *Sperry et al.* [1998]. In their mechanistic approach, hydraulic conductivity in the soil ( $K_s$ ) and xylem ( $K_{\text{xylem}}$ ) declines with declining water potential (which is related to  $\theta$  by the soil-water characteristic curve) resulting in a maximum rate of steady state transpiration ( $E_{\text{crit}}$ ) and corresponding minimum leaf water potential at values above which hydraulic failure occurs. Recently, *Ewers et al.* [2000] and *Hacke et al.* [2000] derived the above  $w_r - \theta$  relation using this hydraulic limitation approach of *Sperry et al.* [1998] with good agreement reported between model calculations and sap flux measurements. It is not our intent to repeat this derivation or comparison but rather to emphasize that  $w_r$  can independently be derived from the hydraulic-cavitation model of *Sperry et al.* [1998].

Our estimate of  $w_r$  from sap flux measurements (or hydraulic-cavitation theory) assumes that the same reduction applies at both leaf and canopy scales. In short, (9), (10a), and (10b) assume that  $w_r$  is scale independent. We use 3 years of porometry measurements (123 runs) collected for sunlit foliage at the same pine stand [*Ellsworth, 2000*] to further investigate whether signatures of a  $w_r$  reduction is present at the leaf scale.

The relationship between measured leaf-level  $G_s$  and  $A_n rh/\bar{C}_a$  is presented in Figure 3b for drought (solid circles) and nondrought (open circles) conditions. The slope of this relationship is, by definition, the empirical Ball-Berry  $m$  (also shown as solid line), which we determined as 5.9 for nondrought conditions. Clearly, the porometry measurements collected during drought events are lower than this nondrought value. Many nondrought data show  $m$  values similar to the identified drought data. These are probably caused by seasonal variation in  $m$ , as demonstrated by *Tenhunen et al.* [1990], and will be discussed later. To investigate whether leaf-level measurements experience conductance reduction comparable to the pine canopy scale, the product  $w_r m$  was computed from (10a) and (10b) for the drought conditions as a modified slope of the  $G_s$  to  $A_n rh/\bar{C}_a$  relationship. It is evident that the revised Ball-Berry model calculations (dashed line, Figure 3b) reproduced the porometry measurements (solid circles) collected during drought conditions better than the mean  $m$ . This agreement is consistent with the measured reduction in bulk canopy conductance for low soil moisture content. Such agreement also suggests that the application of (9), (10a), and (10b) with the parameters determined from *Oren et al.* [1998] or the hydraulic-cavitation approach of *Sperry et al.* [1998] is a reasonable approximation of the effect of  $\theta$  on  $G_s$  at the leaf scale in this study site. We compare the computed canopy fluxes with scalar flux measurements above the canopy for both  $w_r = 1$  and  $w_r$  as a function of the measured  $\bar{\theta}$  time series to assess whether the proposed  $w_r$  formulation corrects for the effect of drought.

## 2.6. Model Parameterization, Input, and Output

The model inputs are 30-min mean meteorological conditions at a reference height above the canopy ( $T_a$ , H<sub>2</sub>O, and CO<sub>2</sub> concentrations, mean longitudinal velocity, and PAR), mean soil moisture content within the root zone, and all radiative, physiological, biochemical, and drag properties of the canopy (particularly  $a(z)$ ,  $l_d$ ,  $\Pi$ ,  $\alpha$ ,  $C_d$ , and the kinetic constants listed in Table 1). All kinetic constants are temperature dependent but assumed to be independent of soil moisture content [*Weber and Gates, 1990; Tenhunen et al., 1990; Sala and*

*Tenhunen, 1996; Williams et al., 1996; Baldocchi, 1997*], which implies no drought effect on the mesophyll capacity for photosynthesis. The model calculates mean scalar concentrations, sources, and fluxes within and above the canopy for heat, CO<sub>2</sub>, and H<sub>2</sub>O. Additionally,  $C_i$ ,  $T_s$ , absorbed radiation, and first and second moments of the flow statistics at all levels within the canopy are computed. The lower boundary conditions are soil respiration and evaporation rates. We use the flow statistics from the closure model of *Wilson and Shaw* [1977], and a gradient-diffusion approach just above the forest floor, to estimate the scalar ground fluxes from the mean measured CO<sub>2</sub> and H<sub>2</sub>O concentration [see *Lai et al., 2000*] at  $z = 0.1$  and 0.75 m. The forest floor is treated as a rough-wall boundary layer in which flux-gradient relationships for CO<sub>2</sub> and H<sub>2</sub>O follow similarity theory arguments [*Monin and Yaglom, 1971*].

## 2.7. Assessment of the Model Performance

The performance of the CANVEG model, modified to incorporate the effects of soil moisture deficit and low air temperature, is assessed by comparing predicted CO<sub>2</sub> and H<sub>2</sub>O fluxes above the canopy against eddy-covariance  $F_{\text{CO}_2}$  and  $F_{\text{H}_2\text{O}}$  measurements, and sap flux scaled stand transpiration ( $E_c$ ). The calculations of radiation/energy balance are indirectly evaluated by comparing predicted and eddy-covariance measured  $F_T$  above the canopy. Additionally, at the canopy scale, the modeled CO<sub>2</sub> concentration inside the canopy is compared with measured mean CO<sub>2</sub> concentration to assess the adequacy of the source/dispersion calculations.

At a finer scale, the model is assessed for its ability to reproduce the essential biophysical and biochemical controls on CO<sub>2</sub> and H<sub>2</sub>O sources and fluxes. This is done by comparing the bulk canopy conductance ( $G_m$ ) derived from the modeled  $r_s(z)$  for pine foliage only with the scaled conductance ( $G_c$ ) estimated from  $E_c$  measurements collected within pine trees. For the scaled canopy conductance comparisons, we choose the sap flux measurements as our reference because they are not influenced by soil evaporation, and they uniquely define the pine transpiration and bulk conductance. This latter point is critical because the CANVEG model assumes uniform pine physiology over the entire leaf area while eddy-covariance measurements are influenced by nonpine understory flux contribution. Sap flux measurements isolate the flux contribution of the pine trees in the stand from the ecosystem flux and hence are better suited to assess the overall CANVEG conductance calculations.

As a final line of testing the model, we used  $C_i/C_a$  estimates representing long-term average from <sup>13</sup>δC isotope analysis [*Ellsworth, 1999*] and instantaneous values from leaf-level gas exchange measurements to evaluate whether the model reasonably reproduces the biochemical mechanisms of CO<sub>2</sub> assimilation. The measurements used to evaluate the model outputs are shown in Figure 1.

## 3. Experiment

### 3.1. Study Site

Measurements were made at the Blackwood Division of the Duke Forest near Durham, North Carolina (36°2'N, 79°8'W, elevation = 163 m). The site is a uniformly planted loblolly pine (*Pinus taeda* L.) forest that extends 300–600 m in the east-west direction and 1000 m in the north-south direction. The mean canopy height ( $h$ ) was 14 m ( $\pm 0.5$  m) at the time of the experiment. The topographic variations are small (terrain

**Table 2.** Plant Area Index (PAI) and Hydrological and Environmental Conditions for Four Study Periods

Period	PAI	$P_r$ , mm	$T_a$ , °C		$\bar{\theta}$ , cm <sup>3</sup> cm <sup>-3</sup>		$R_n$ , <sup>b</sup> W m <sup>-2</sup>		
			Mean	s.d.	Mean	s.d.	Mean	Max	
07/16/98 / 07/28/98 04/02/99 / 04/11/99 11/17/98 / 11/24/98 01/26/99 / 01/31/99	1	2.69/4.89 <sup>a</sup>	0	27.4	4.0	0.15	0.002	429.2	745.8
	2	2.02	35.2	18.6	5.2	0.36	0.02	332.2	710.0
	3	2.89	3.9	11.7	5.7	0.30	0.01	115.9	345.6
	4	2.00	0	9.5	5.7	0.24	0.01	212.8	471.8

s.d., standard deviation; max, maximum.

<sup>a</sup>PAI for the whole stand, including pine and understory foliage; other PAIs are for pine component of the stand only.

<sup>b</sup>Daytime (0900–1500) average.

slope changes <5%) so that the influence of topography on the turbulence transport can be neglected [Kaimal and Finnigan, 1994].

### 3.2. Measurement Periods

Four experimental periods (each between 7 and 12 days) were chosen to investigate potential plant stress due to drought and low mean air temperature. These periods were in July 1998, November 1998, January 1999, and April 1999 and are described below.

**3.2.1. Drought period.** In July 1998 the measured precipitation was well below the long-term average for the month. We computed the long-term mean precipitation ( $= 121.4 \pm 60.5$  mm) for July by averaging 67 years of monthly precipitation collected from a nearby weather station. The measured monthly precipitation in July 1998 was 24.4 mm, which is less than 30% of the long-term average. At this site, more than 90% of the water uptake by pine roots occurs in the top 30-cm soil layer [Oren *et al.*, 1998a]. Thus drought effects are related to the near-surface (30 cm) horizontally averaged volumetric soil moisture content ( $\bar{\theta}$ ), which was shown to exert a strong control over canopy stomatal conductance for  $\bar{\theta} < 0.2$  ( $= \bar{\theta}_R$ ). The time variation of  $\bar{\theta}$  was measured by averaging 24 30-cm vertical reflectometer rods (CS615, Campbell Scientific, Logan, Utah) distributed throughout the study site.

The  $\bar{\theta}$  measurements in July 1998 confirmed that the low precipitation resulted in soil drought ( $\bar{\theta} \cong 0.15$  cm<sup>3</sup> cm<sup>-3</sup>,  $< \bar{\theta}_R$ ). To investigate the effect of drought on CO<sub>2</sub> and H<sub>2</sub>O fluxes, we selected a 12-day experimental duration (period 1, July 16–28, 1998) in which eddy-covariance  $F_{CO_2}$  and  $F_{H_2O}$ , sap flux, and  $\theta$  measurements were simultaneously available with few interruptions and gaps within the record. A “reference” period for assessing the performance of the CANVEG model under well-watered condition was also selected. This period (period 2, April 2–11, 1999) was characterized by  $\bar{\theta} > 0.27$  over the entire duration (i.e.,  $\bar{\theta} > \bar{\theta}_R$ ).

**3.2.2. Low air temperature.** The reduction in CO<sub>2</sub> assimilation and transpiration rate caused by low mean air temperature was investigated using two periods (period 3, November 17–24, 1998, and period 4; January 26–31, 1999). The mean  $T_a$  for these two periods were  $11.7 \pm 5.7^\circ\text{C}$  and  $9.5 \pm 5.7^\circ\text{C}$ , respectively. Stomata of loblolly pine close in response to low

temperature when  $T_a < 10^\circ\text{C}$  [Ellsworth, 2000]. On the basis of these findings, period 3 represents mild winter conditions when stomata should not appreciably respond to low  $T_a$ , while during period 4, low  $T_a$  should reduce stomatal conductance and exchanges of H<sub>2</sub>O and CO<sub>2</sub>. We note that both soil moisture and temperature regulation are unlikely to be threshold phenomena, so while periods are selected in which the current data would suggest strong regulation by these factors, there may be interactions between  $\bar{\theta}$  and  $T_a$  and other environmental factors not explicitly considered here. Table 2 summarizes the climatic and hydrologic conditions along with the measured plant area index (PAI) for these four experimental periods.

### 3.3. Eddy Covariance Measurements

The  $F_{CO_2}$ ,  $F_{H_2O}$ , and  $F_T$  turbulent fluxes were measured by an eddy-covariance system composed of a CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer (Licor-6262, LI-COR, Lincoln, Nebraska), a tri-axial sonic anemometer (CSAT3, Campbell Scientific, Logan, Utah), and a krypton hygrometer (KH<sub>2</sub>O, Campbell Scientific). The anemometer and hygrometer were positioned 15 m above the ground surface and anchored on a horizontal bar extending 1.5 m away from the walk-up tower. The hygrometer was used to assess and correct tube attenuation effects and lagged maximum cross correlation between the vertical velocity and the measured scalar concentration as discussed by Katul *et al.* [1997a, 1997b]. Analog signals from these instruments were sampled at 10 Hz using a Campbell Scientific 21X data logger. All the digitized signals were transferred to a portable computer via an optically isolated RS232 interface for future processing. Raw 10 Hz measurements were processed using the procedures described by Katul *et al.* [1997a, 1997b].

It must be emphasized that these flux measurements were conducted in the canopy sublayer but not the atmospheric surface layer; hence the spatial variability in scalar fluxes is larger due to the influence of “near-field” source variability. In fact, a recent spatial variability experiment, conducted at this site, suggests that the scalar fluxes near the canopy-atmosphere interface vary by about 20% [Katul *et al.*, 1999]. Hence for practical purposes, we use the term “close agreement” when the CANVEG model reproduces the measured fluxes to within 20%. This estimate is consistent with a recent estimate by Moncrieff *et al.* [1996] which also showed eddy-covariance mea-

measurements possess  $\pm 20\%$  combined random and systematic errors.

### 3.4. Other Meteorological Variables

In addition to the flux measurements, a Ta/RH probe (HMP35C, Campbell Scientific) was positioned at 15.5 m to measure the mean  $T_a$  and relative humidity. A Fritchen-type net radiometer and a quantum sensor (Q7 and LI-190SA, respectively, LI-COR) were installed to measure net radiation ( $R_n$ ) and PAR, respectively. All the meteorological variables were sampled at 1 s and averaged every 30 min using a 21X Campbell Scientific data logger.

### 3.5. CO<sub>2</sub>/H<sub>2</sub>O Profiles Within the Canopy

A multiport system was installed to measure the CO<sub>2</sub>/H<sub>2</sub>O concentrations inside the canopy at 10 levels (0.1, 0.75, 1.5, 3.5, 5.5, 7.5, 9.5, 11.5, 13.5, and 15.5 m). Each level was sampled for 1 min (45 s sampling and 15 s purging) at the beginning, the middle, and the end for each 30-min sampling period. The flow rate within the tube (internal diameter = 0.423 cm) was 0.9 L min<sup>-1</sup> to dampen all turbulent fluctuations.

### 3.6. Xylem Sap Fluxes

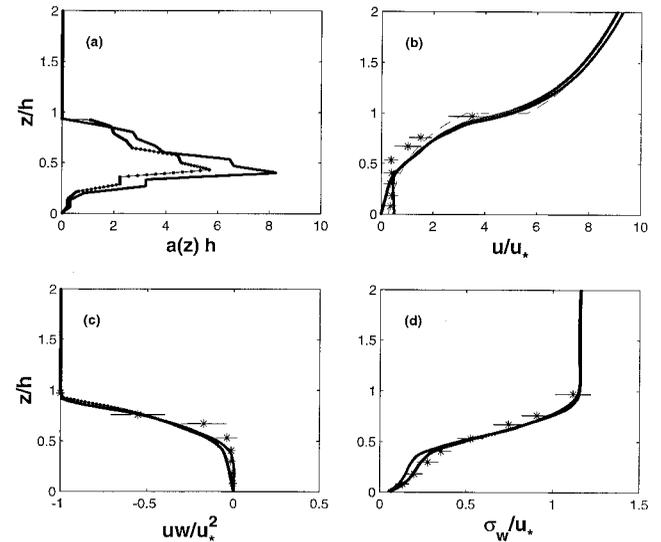
Sap flow (in g H<sub>2</sub>O m<sup>-2</sup> sapwood s<sup>-1</sup>) within eight individual pine trees was measured with constant-heat probes [Granier, 1987]. Sap flux densities of individual trees were scaled to attain a plot-level values using the respective sapwood area per unit ground area in the stand [Phillips and Oren, 1998; Oren et al., 1998b].

### 3.7. Leaf-Level Physiological Parameters

The leaf-level measurements presented in Table 1 are described by Ellsworth [1999, 2000] and are briefly repeated here for completeness. The leaf-level physiological parameters ( $m$  and  $b$ ) were determined from gas exchange measurements (see Figure 3b) by a portable infrared gas analyzer system for CO<sub>2</sub> and H<sub>2</sub>O (CIRAS-1, PP-Systems) operated in open flow mode with a 5.5-cm-long leaf chamber and an integrated CO<sub>2</sub> gas 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 reported here are on a unit-projected area basis. These measurements were collected over a broad range of environmental and hydrologic conditions spanning a period of nearly 3 years (May 1997 to March 2000).

### 3.8. Leaf Area Density

The vertical variation of the leaf area plus branches was measured by gap fraction techniques following theory presented by Norman and Welles [1983]. A pair of optical sensors with hemispherical lenses (LAI-2000, Li-Cor, Lincoln, Nebraska) was used for canopy light transmittance measurements from which gap fraction and plant area densities were calculated. The measurements were made at 1-m intervals from the top of the canopy to 1 m above the ground to produce the vertical profile in plant area index (PAI). PAI measurements were made within 2 weeks of each of the measurement periods, from the same tower used for measuring flow statistics, CO<sub>2</sub> concentration, and  $F_{\text{CO}_2}$  and  $F_{\text{H}_2\text{O}}$ .



**Figure 4.** Effect of leaf area density dynamics on modeled velocity statistics. Modeled flow statistics inside the canopy are conducted for two different plant area index (PAI) values, one collected during the summer (maximum PAI) and the other collected during winter (minimum PAI) are discussed. The modeled statistics for maximum and minimum PAI are shown in solid line and open circle line, respectively. Triaxial sonic anemometry measurements (star) collected in August 1999 are also shown for reference. (a) Maximum and minimum measured plant area density  $a(z)$ . (b) Comparison between modeled  $\bar{u}$  using the commonly assumed exponential profiles inside the canopy (dashed line), and the closure model calculations for the two PAI profiles in Figure 4a. (c) The maximum effect of variable PAI on modeled  $\overline{uw}$ . (d) The maximum effect of variable PAI on modeled  $\sigma_w$ .

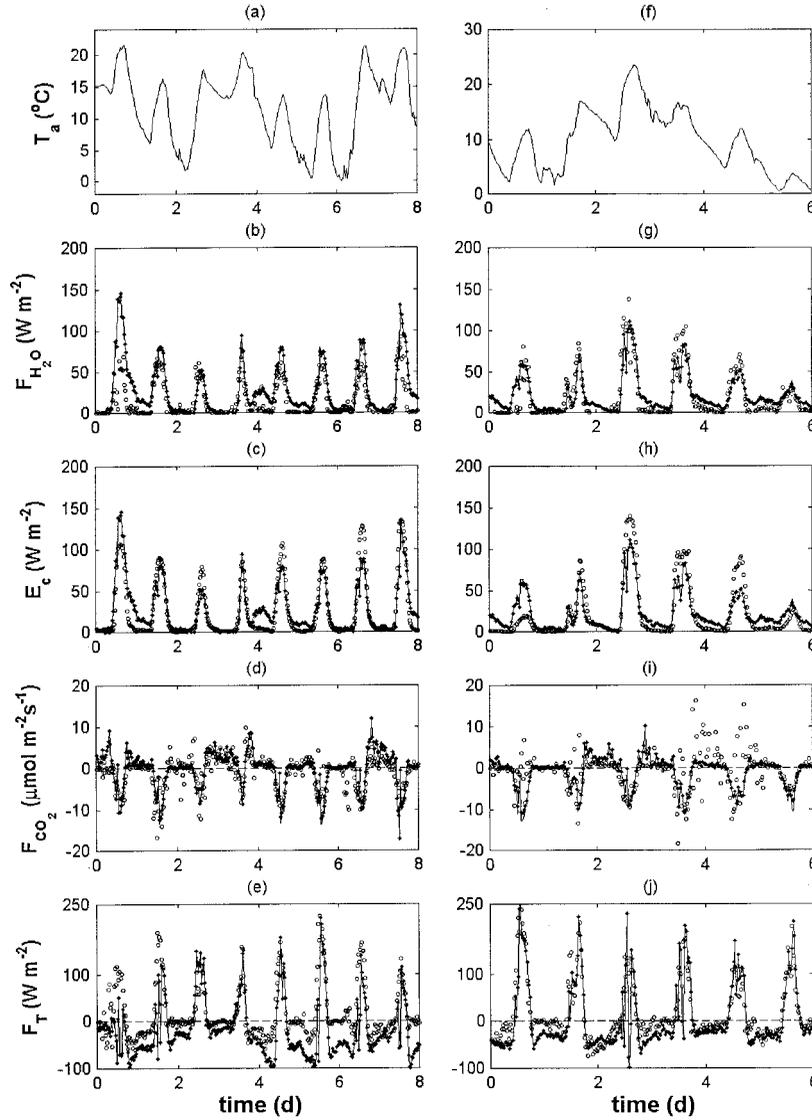
## 4. Results and Discussion

### 4.1. Flow Statistics

Before investigating the scalar transport, we briefly describe the flow statistics within the canopy. Figure 4 shows the velocity statistics inside the canopy predicted by the second-order closure model [Wilson and Shaw, 1977], based on the measured plant area density for two cases: highest foliage density in July and lowest in January. To demonstrate the differences in the flow statistics resulting from these two PAI extremes, we compared the mean longitudinal wind velocity ( $\bar{u}$ ), shear stress ( $\overline{uw}$ ), and standard deviation of vertical velocity ( $\sigma_w$ ) for the two plant area density profiles ( $a(z)$ ). In this comparison the velocity scales are normalized by  $u_*$  at  $z/h = 1.1$  and the length scales are normalized by  $h$ . As shown in Figure 4, the modeled flow statistics (particularly  $\sigma_w$ ) are fairly robust to variations in plant area density. However, the  $d\sigma_w/dz$ , which is crucial to the Lagrangian random walk calculation as in (3), is sensitive to variations in PAI. Such variations in  $d\sigma_w/dz$  can affect  $D_{ij}$  and the scalar concentration as demonstrated by the detailed sensitivity analysis of Lai et al. [2000].

### 4.2. Comparisons of CO<sub>2</sub> and H<sub>2</sub>O Fluxes

To compute  $F_{\text{CO}_2}(h)$ ,  $F_{\text{H}_2\text{O}}(h)$ , and  $F_T(h)$ , steady state conditions are first assumed. Over tall forests such an approximation may produce a bias if the CO<sub>2</sub> storage flux is significant [Wofsy et al., 1993; Hollinger et al., 1994; Fan et al., 1995; Grace et al., 1995; Baldocchi et al., 1997; Lee, 1998]. Earlier estimates



**Figure 5.** Effect of different  $V_{c \max} - T_s$  formulations shown in Figure 2 on CANVEG-modeled  $F_{\text{H}_2\text{O}}$ ,  $F_{\text{CO}_2}$ , and  $F_T$  for moderately low temperature period 3 (left column) and low temperature period 4 (right column). Solid line is the CANVEG fluxes using the pine-specific  $V_{c \max} - T_s$ , dots represent the CANVEG fluxes using the generic form of  $V_{c \max} - T_s$  [Campbell and Norman, 1998], and open circles are for eddy-covariance or sap flux ( $E_c$ ) measurements. The eddy-covariance measurements were conducted at  $z/h = 1.1$ .

of mean CO<sub>2</sub> concentration from measurements within this stand demonstrated that the CO<sub>2</sub> storage flux is much smaller than the CO<sub>2</sub> flux above the canopy, except in early morning and late afternoon hours [Lai et al., 2000]. Therefore the CO<sub>2</sub> storage flux is assumed negligible relative to  $F_{\text{CO}_2}(h)$  in all four periods.

**4.2.1. Temperature effects on fluxes.** To evaluate the dependency of the kinetic constants on temperature as in the work of Campbell and Norman [1998] (Appendix A), we compared the modeled  $F_{\text{CO}_2}(h)$  and  $F_{\text{H}_2\text{O}}(h)$  with eddy-covariance measurements using the two  $V_{c \max} - T_s$  relationships shown in Figure 2. For period 3 (the “stress-free” period) the model estimates closely follow the measured diurnal patterns of  $F_{\text{CO}_2}(h)$  and  $F_{\text{H}_2\text{O}}(h)$  for both  $V_{c \max} - T_s$  functions (Figure 5). To verify the model performance using another independent measure, we also show the sap flux scaled  $E_c$  time

series in Figures 5c and 5h. While the regression statistics in Table 3 suggest some biases between measured and modeled fluxes (see regression slopes), the root-mean-square errors are relatively small ( $<30 \text{ W m}^{-2}$  for water vapor). The reason for such a bias will be discussed later in the sensitivity analysis. Regardless of the bias, it is important to note that the difference between the resulting H<sub>2</sub>O and the CO<sub>2</sub> fluxes is small when either  $V_{c \max} - T_s$  relationship is used, suggesting that the CANVEG flux calculations are not very sensitive to the  $V_{c \max}$  formulation.

**4.2.2. Soil moisture effects on fluxes.** During the drought (period 1), soil moisture content was well below  $\bar{\theta}_R (= 0.2)$ , the threshold below which  $\bar{\theta}$  begins to exert control over stomata, while during the reference period (period 2),  $\bar{\theta}$  was consistently  $>\bar{\theta}_R$  (see Figures 6a and 6f). The modeled  $F_{\text{H}_2\text{O}}(h)$ ,  $F_{\text{CO}_2}(h)$ , and  $F_T(h)$  are compared with the eddy-

**Table 3.** Regression Statistics for Comparisons Between Measurement and Model Estimation

Variable	Measurement/Model Type	$N_r$	$A$	$B$	$R^2$	RMSE
Period 1, July 1998						
$[F_{\text{H}_2\text{O}} (\text{W m}^{-2})]$	eddy covariance at $z/h = 1.1$	544	0.99	-10.68	0.83	35.05
$F_{\text{H}_2\text{O}} (\text{W m}^{-2})$	eddy covariance at $z/h = 1.1$	544	0.84	-6.78	0.86	38.17
$[F_{\text{H}_2\text{O}} (\text{W m}^{-2})]$	xylem sap flux	544	0.91	-3.85	0.94	15.47
$F_{\text{H}_2\text{O}} (\text{W m}^{-2})$	xylem sap flux	544	0.75	-1.47	0.95	24.28
$[F_{\text{CO}_2} (\mu\text{mol m}^{-2} \text{s}^{-1})]$	eddy covariance at $z/h = 1.1$	544	1.09	-1.59	0.53	6.17
$F_{\text{CO}_2} (\mu\text{mol m}^{-2} \text{s}^{-1})$	eddy covariance at $z/h = 1.1$	544	1.02	-1.40	0.54	0.49
$[F_T (\text{W m}^{-2})]$	eddy covariance at $z/h = 1.1$	544	0.73	45.86	0.83	73.12
$F_T (\text{W m}^{-2})$	eddy covariance at $z/h = 1.1$	544	0.95	59.26	0.75	73.12
$[G_m/G_c (\text{mm s}^{-1})]$	loblolly pine measurement	478	0.84	-0.22	0.79	0.64
$G_m/G_c (\text{mm s}^{-1})$	loblolly pine measurement	478	0.58	-0.008	0.79	1.03
Period 2, April 1999						
$F_{\text{H}_2\text{O}} (\text{W m}^{-2})$	eddy covariance at $z/h = 1.1$	421	1.20	-2.26	0.86	29.36
$F_{\text{H}_2\text{O}} (\text{W m}^{-2})$	xylem sap flux	421	0.87	2.25	0.76	29.39
$F_{\text{CO}_2} (\mu\text{mol m}^{-2} \text{s}^{-1})$	eddy covariance at $z/h = 1.1$	421	0.85	-0.16	0.56	4.64
$F_T (\text{W m}^{-2})$	eddy covariance at $z/h = 1.1$	421	0.80	-3.92	0.87	40.48
$G_m/G_c (\text{mm s}^{-1})$	loblolly pine measurement	242	0.81	0.25	0.70	1.19
Period 3 <sup>a</sup> , Nov. 1998						
$F_{\text{H}_2\text{O}} (\text{W m}^{-2})$	eddy covariance at $z/h = 1.1$	384	0.55	-1.09	0.61	23.78
$F_{\text{H}_2\text{O}} (\text{W m}^{-2})$	xylem sap flux	384	1.05	-2.45	0.83	14.98
$F_{\text{CO}_2} (\mu\text{mol m}^{-2} \text{s}^{-1})$	eddy covariance at $z/h = 1.1$	384	0.60	-0.95	0.50	3.35
$F_T (\text{W m}^{-2})$	eddy covariance at $z/h = 1.1$	384	0.71	30.25	0.52	56.85
$G_m/G_c (\text{mm s}^{-1})$	loblolly pine measurement	132	1.22	-0.65	0.71	1.04
Period 4 <sup>b</sup> , Jan. 1999						
$F_{\text{H}_2\text{O}} (\text{W m}^{-2})$	eddy covariance at $z/h = 1.1$	288	1.09	-6.79	0.75	15.42
$F_{\text{H}_2\text{O}} (\text{W m}^{-2})$	xylem sap flux	288	1.29	-7.63	0.79	16.88
$F_{\text{CO}_2} (\mu\text{mol m}^{-2} \text{s}^{-1})$	eddy covariance at $z/h = 1.1$	288	0.48	-0.11	0.20	4.37
$F_T (\text{W m}^{-2})$	eddy covariance at $z/h = 1.1$	288	0.79	13.85	0.69	41.63
$G_m/G_c (\text{mm s}^{-1})$	loblolly pine measurement	56	0.83	1.84	0.52	1.60
$G_m/G_c (\text{mm s}^{-1})$	<i>Campbell and Norman</i> [1998]	56	0.85	1.81	0.51	1.63
Other variables						
$C_a^b$ , ppm	gas analyzer at 6 levels	9822	1.07	-26.50	0.87	10.53
$F_{\text{CO}_2} (\mu\text{mol m}^{-2} \text{s}^{-1})$	big-leaf model (period 2)	421	0.68	2.14	0.54	6.66
$F_{\text{CO}_2} (\mu\text{mol m}^{-2} \text{s}^{-1})$	big-leaf model (period 3)	384	0.46	1.19	0.48	5.77
$F_{\text{CO}_2} (\mu\text{mol m}^{-2} \text{s}^{-1})$	big leaf/CANVEG (period 2)	421	0.89	2.75	0.94	3.88
$F_{\text{CO}_2} (\mu\text{mol m}^{-2} \text{s}^{-1})$	big leaf/CANVEG (period 3)	384	0.71	3.27	0.83	5.38
$D/D_a$ (kPa)	CANVEG model	1415	0.96	0.05	0.99	0.08

The regression slope ( $A$ ), the intercept ( $B$ ), the coefficient of determination ( $R^2$ ), and the root-mean-square error (RMSE) are presented for the regression model  $y = Ax + B$ , where  $y$  and  $x$  are measured and modeled variables, respectively. Modeled H<sub>2</sub>O fluxes are compared with measurements conducted by eddy-covariance and sap-flux techniques.  $G_c$  and  $G_m$  are the bulk canopy conductance computed by equations (11) and (13), respectively.  $C_a$  is the mean CO<sub>2</sub> concentration inside the canopy and  $N_r$  is the number of points in the regression analysis. For  $G_m/G_c$  comparison,  $x$  is  $G_m$ . For period 1, variables in brackets are regression results after implementing soil moisture correction for the drought effect in the modeled  $G_s$ . For period 4,  $G_m/G_c$  comparison was shown for the temperature dependency of  $V_{c \text{ max}}$  derived from *Campbell and Norman* [1998] and measurement performed on the loblolly pine. For the comparison between big-leaf and CANVEG models,  $x$  is the value of big-leaf calculation.

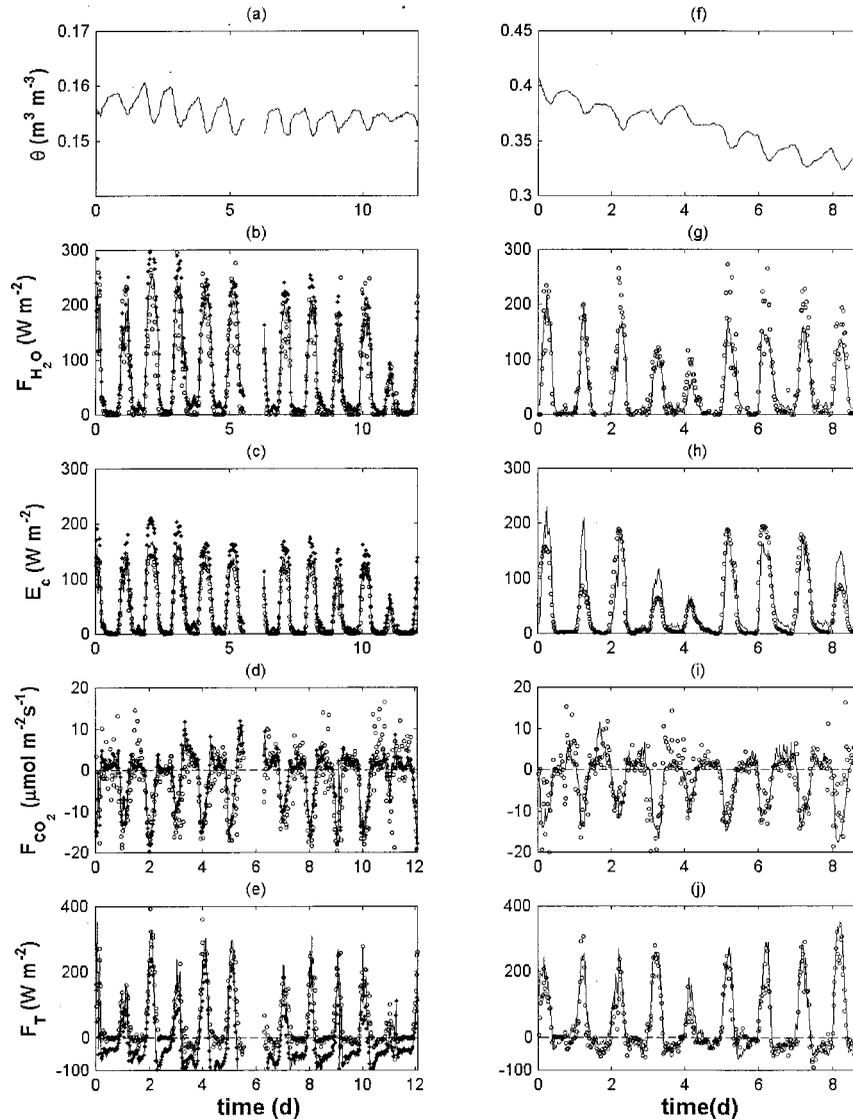
<sup>a</sup>Comparisons are for the measured  $V_{c \text{ max}} - T_s$  relationship of Figure 2. Similar statistics were found for the *Campbell and Norman* [1998] formulation and hence are not displayed.

<sup>b</sup>Combined regression statistics are shown for all four periods and the six selected levels.

covariance measurements for these two periods in Figure 6. When  $\bar{\theta} > \bar{\theta}_R$ , modeled fluxes are close to measured fluxes (see Figures 6g, 6h, and 6i), consistent with findings in other studies [*Amthor et al.*, 1994; *Baldocchi and Harley*, 1995; *Leuning et al.*, 1995; *Aber et al.*, 1996; *Williams et al.*, 1996; *Baldocchi and Meyers*, 1998; *Gu et al.*, 1999]. When  $\bar{\theta} < \bar{\theta}_R$ , the modeled H<sub>2</sub>O fluxes departed from the measured fluxes when  $w_r$  was not applied in CANVEG calculation (see regression slopes in Table 3). These calculations overestimated measured  $F_{\text{H}_2\text{O}}(h)$  by 16%. With the  $w_r$  modification the CANVEG overestimated measured  $F_{\text{H}_2\text{O}}(h)$  by only 1% (see regression slope in Table 3) which is not significantly different from unity ( $P > 0.05$ ). However, we found that the  $w_r$  improvements in modeling  $F_{\text{H}_2\text{O}}(h)$  degraded the comparison with the measured  $F_{\text{CO}_2}(h)$  ( $P < 0.05$ , Table 3). We attribute the effect of the  $w_r$  correction to the significant proportion of understory foliage (45% of total PAI) during the summer period, which contributes more to  $F_{\text{CO}_2}(h)$  than to  $F_{\text{H}_2\text{O}}(h)$ . We evaluated

this hypothesis by repeating the CANVEG calculation on the pine foliage only with and without the  $w_r$  adjustment and comparing these two calculations with the  $E_c$  estimated from sap flux measurements (Figures 6c and 6h). Consistent with eddy-covariance comparisons, the  $w_r$  correction resulted in better agreement between  $E_c$  and modeled pine latent heat flux, suggesting that the CANVEG model correctly reduced the pine transpiration for drought conditions. Because pine transpiration, unlike pine photosynthesis, comprises most of the total mass flux (e.g.,  $F_{\text{H}_2\text{O}}(h)$ ), the  $w_r$  correction was important in improving the model agreement with eddy-covariance-measured  $F_{\text{H}_2\text{O}}(h)$ . We hypothesize that the understory species contribute relatively more to total stand  $F_{\text{CO}_2}(h)$  than to  $F_{\text{H}_2\text{O}}(h)$  under drought conditions. We explore this hypothesis using detailed sensitivity analysis discussed next.

**4.2.3. Sensitivity analysis on fluxes.** The inconsistency in model performance led us to conduct a detailed sensitivity



**Figure 6.** Effect of drought on CANVEG modeled  $F_{\text{H}_2\text{O}}$ ,  $F_{\text{CO}_2}$ , and  $F_T$  for the drought period 1 (left column) and the stress-free period 2 (right column). Solid line is the CANVEG fluxes using  $w_r \neq 1$ , dots represent CANVEG fluxes for  $w_r = 1$ , and open circles are for eddy-covariance or sap flux ( $E_c$ ) measurements. For the  $E_c$  comparisons (Figures 6c and 6h), the PAI for pine only is used in the CANVEG calculations. A short (<1 day) data gap exists in period 1. For period 2,  $w_r = 1$  is used throughout. The eddy-covariance measurements were conducted at  $z/h = 1.1$ .

analysis on how modeled water vapor and CO<sub>2</sub> flux errors vary with  $m$  for all four periods. We varied  $m$  from 3.0 to 9.0 and computed the root-mean-square error (RMSE) and the regression slope of fluxes measured with eddy covariance versus modeled fluxes (Table 4). These two statistics were chosen to assess the magnitude of the scatter (RMSE) and model bias (the regression slope). We found that modeled  $F_{\text{H}_2\text{O}}(h)$  (without any  $w_r$  adjustments) is much more sensitive to variations in  $m$  than  $F_{\text{CO}_2}(h)$  except in period 1, the drought period. In all other periods the RMSE and regression slopes appear robust to variations in  $m$  for  $F_{\text{CO}_2}(h)$  estimates. This is not surprising given that many factors influence  $F_{\text{CO}_2}(h)$  (such as soil respiration); however, variations in  $F_{\text{H}_2\text{O}}(h)$  are intimately linked with  $G_s$ , thereby increasing their sensitivity to  $m$ .

In the drought period (period 1),  $m$  optimized by water vapor was reduced by about 30% when compared to its well-

watered state, consistent with the  $w_r$  reduction derived from Figure 3. However,  $m$  optimized by CO<sub>2</sub> for period 1 is 1.6 times larger than its counterpart for  $F_{\text{H}_2\text{O}}(h)$ , suggesting that an effective  $m$  (and subsequent drought reductions) solely derived from pine physiological measurements does not represent the entire ecosystem  $F_{\text{CO}_2}(h)$  during summer droughts. Consequently, we conclude that the understory physiological attributes and their separate response to drought must be considered when estimating  $F_{\text{CO}_2}(h)$ .

An interesting finding from Table 4 is that the optimum  $m$  required to minimize the RMSE and recover a unit regression slope varied among periods for  $F_{\text{H}_2\text{O}}(h)$ . Whether the variations in  $m$  among periods is an artifact of the sensitivity, measurement errors, or a real physiological signature requires further investigation. Using the 3-year porometry record shown in Figure 3b, we estimated the leaf-level  $m$  for each porometry

**Table 4.** Sensitivity Analysis of CO<sub>2</sub> and Water Vapor Fluxes Above the Canopy on the Ball-Berry Stomatal Conductance Parameter  $m$ 

$m$	Period 1		Period 2		Period 3		Period 4	
	H <sub>2</sub> O	CO <sub>2</sub>						
RMSE								
3.0	37.46	6.31			(20.09)	(3.27)	17.72	(4.29)
3.5	36.09	6.25			20.51	3.30	17.10	4.31
4.0	35.26	6.19	32.77	(4.70)	21.03	3.31	16.56	4.32
4.5	(35.06)	6.14	30.10	4.71	21.65	3.32	16.12	4.34
5.0	35.54	6.10	27.96	4.79	22.34	3.34	15.77	4.35
5.5	36.73	6.06	26.48	4.85	23.11	3.33	15.53	4.36
6.0	38.60	6.03	(25.80)	4.87	23.95	3.34	15.41	4.37
6.5	41.06	6.01	26.00	4.87	24.85	3.35	(15.40)	4.37
7.0	44.04	5.99	27.04	4.91	25.80	3.36	15.50	4.38
7.5	47.46	(5.97)	28.83	4.97	26.79	3.36	15.72	4.39
8.0			31.24	4.99	27.82	3.36	16.04	4.39
8.5			34.14	5.01	28.90	3.37	16.46	4.40
9.0			37.39	5.06	30.00	3.36	16.97	4.40
Slope								
$A$								
3.0	1.08	1.16			(0.65)	(0.63)	1.47	(0.50)
3.5	1.04	1.13			0.63	0.62	1.40	0.50
4.0	(1.00)	1.10	1.31	(0.81)	0.61	0.61	1.33	0.49
4.5	0.96	1.08	1.23	0.80	0.59	0.61	1.26	0.49
5.0	0.91	1.05	1.15	0.78	0.58	0.60	1.20	0.49
5.5	0.87	1.03	1.08	0.77	0.56	0.60	1.14	0.48
6.0	0.83	1.02	(1.01)	0.76	0.54	0.60	1.08	0.48
6.5	0.80	(1.00)	0.95	0.75	0.53	0.60	1.04	0.48
7.0	0.76	0.98	0.90	0.75	0.51	0.60	(0.99)	0.48
7.5	0.73	0.97	0.86	0.74	0.50	0.60	0.95	0.48
8.0			0.81	0.73	0.48	0.60	0.91	0.48
8.5			0.77	0.73	0.47	0.59	0.87	0.47
9.0			0.74	0.72	0.45	0.59	0.84	0.47

Both root-mean-square error (RMSE) and regression slope  $A$  of the regression model  $y = Ax + B$  ( $y$  = measured flux,  $x$  = CANVEG modeled flux) are shown. Numbers in parentheses indicate optimum values.

measurement. These  $m$  values are shown as a function of time (Figure 7a) to investigate potential seasonal variations in leaf physiological properties as reported by *Tenhunen et al.* [1990]. It is clear that the scatter in leaf-level  $m$  is large, but the signature of a seasonal pattern is discernible. When combined with the sensitivity analysis of Table 4, Figure 7a suggests that  $m$  is lowest in the middle of the growing season, with a rise later in the season concurrent with maturation of new pine needles. In fact, the trends in the optimized  $m$  are consistent with the leaf-level ensemble-averaged  $m$  (Figure 7b). Thus it is not surprising that the CANVEG model, with static vegetation parameters such as  $m$  (= 5.9), shows inconsistent performance among periods. We also point out that seasonal variations in leaf-level  $m$  (Figure 7a) are larger than the maximum drought correction encountered in this experiment, suggesting that using CANVEG for estimating annual carbon uptake requires estimates of the seasonal variability in its physiological parameters (e.g.,  $m$ ).

#### 4.3. Comparisons of Sensible Heat Flux

An indirect assessment of the radiation transmission and energy distribution of the CANVEG model is performed by comparing the modeled  $F_T(h)$  with values from eddy-covariance measurements shown in Figures 5 and 6 for all four periods. Despite the underestimation in period 3, and some discrepancy during evening runs, the daytime diurnal patterns of  $F_T(h)$  are closely captured in all four periods. *Baldocchi and Meyers* [1998] and *Gu et al.* [1999] also found their model calculations to overestimate  $|F_T(h)|$  in the evening. Such a

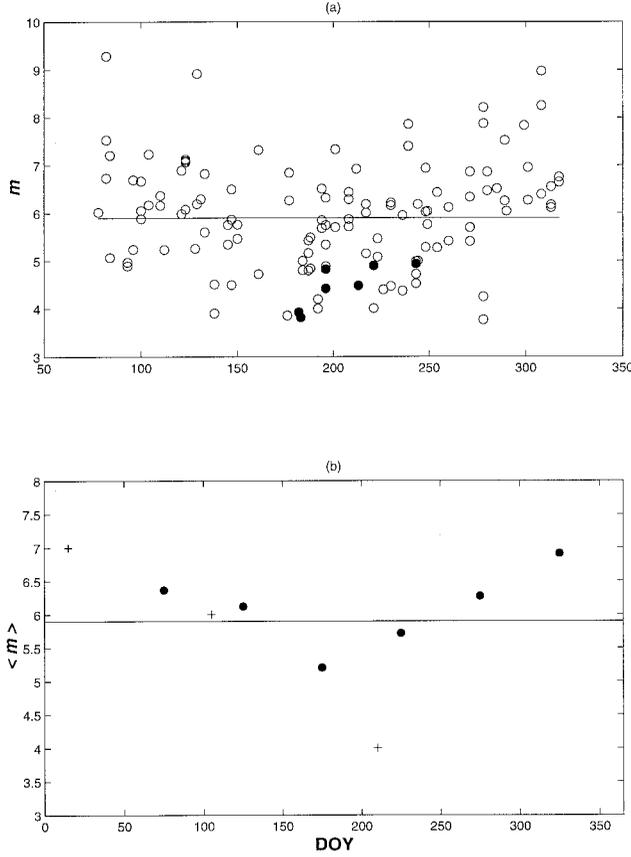
bias is attributed to the idealization in the terrestrial thermal radiation parameterization and its primitive emissivity formulation.

#### 4.4. Comparison Between Measured and Modeled Mean CO<sub>2</sub> Concentration

In addition to estimating fluxes above the canopy, estimates of CO<sub>2</sub> concentration profiles within the canopy are compared to measurements from the multiport system (Figure 8). Such a comparison permits a unique assessment of the CANVEG model performance to reproduce both spatial and temporal patterns of the mean concentration field, a state variable influenced by the combined source variation and turbulent transport mechanics. In Figure 8 the modeled and measured  $C_a$  are contrasted in time (left panels) and in space (right panels) in the canopy for all four periods. The close agreement (see Table 3) between modeled and measured values indicates that the model captures the variation in canopy microclimate temporally and vertically and further supports using the coupled source-dispersion algorithm in the CANVEG model framework.

#### 4.5. Comparison Between Sap Flux Measured and Modeled Bulk Conductance

While eddy covariance flux measurements permit bulk canopy conductance estimates, they are less than optimum for assessing how well leaf-level measurements are integrated to canopy scale by the CANVEG approach. An alternative method is to quantify the pine conductance from sap flux and



**Figure 7.** (a) Slope parameter  $m$  in the Ball-Berry formulation estimated from porometry measurements over a 3-year period. The  $m$  values collected during drought periods are in solid circles. (b) Ensemble means of  $m$  values (solid circles) as a function of day of year (DOY) for the 3-year measurement period. The plus symbols are  $m$  values determined from the sensitivity analysis for periods 1, 2, and 4, as shown in Table 4. For both panels, the solid line represents the long-term-averaged  $m$  ( $= 5.9$ ) determined from the regression analysis in Figure 3.

to contrast these estimates with the pine canopy conductance modeled by the CANVEG based on the pine leaf area and physiological properties.

To compute the bulk canopy conductance ( $G_c$ ) from the measured  $E_c$ , the formulation described by Monteith and Unsworth [1990] and Phillips and Oren [1998] is used and is given by

$$G_c = \frac{\gamma(T_a) \cdot \lambda(T_a) \cdot E_c}{C_p \cdot \rho(T_a) \cdot D_a}, \quad (11)$$

where  $\gamma$  is the psychrometric constant ( $\text{kPa K}^{-1}$ ),  $\lambda$  is the latent heat of vaporization of water,  $C_p$  is the specific heat of water, and  $D_a$  is the vapor pressure deficit defined as  $e_a^*(T_a) - e(T_a)$ , where  $e_a^*$  and  $e$  are the saturation and actual vapor pressure at  $T_a$ . Ewers and Oren [2000] demonstrated that for small  $D_a$ ,  $G_c$  estimates from (11) may contain large measurement errors. They suggested a threshold  $D_a \geq 0.6$  kPa when computing  $G_c$  to keep conductance errors to  $<10\%$ ; their recommended threshold for  $D_a$  is used when estimating  $G_c$ .

The CANVEG model does not compute bulk canopy conductance directly and hence must be inferred from modeled

conductance at each canopy layer. In the absence of a storage flux, these individual conductance calculations are related to the bulk canopy conductance, after integrating (1), by

$$\begin{aligned} F_{\text{H}_2\text{O}}(h) - F_{\text{H}_2\text{O}}(0) &= G_m D = \int_0^h S_{\text{H}_2\text{O}} dz \\ &= \int_0^h a(z) \frac{e^*(z) - e(z)}{r_s(z) + r_b(z)} dz, \end{aligned} \quad (12)$$

where  $G_m$  is the modeled bulk canopy conductance to water vapor,  $e^*$  is the saturation vapor pressure at  $T_s$ , and  $D$  is the vapor pressure deficit calculated by  $e^*(T_s) - e(T_a)$ . If  $D \approx D_a$  and  $dD/dz \approx 0$ , and assuming that  $r_b \ll r_s$ , a parallel resistor analogy can then be derived for  $G_m$ :

$$G_m \approx \sum_{i=1}^N \frac{a(z_i)}{r_s(z_i)} \cdot \Delta z, \quad (13)$$

where

$$z_{i+1} = z_i + \Delta z, \quad i=1, \dots, N-1. \quad (14)$$

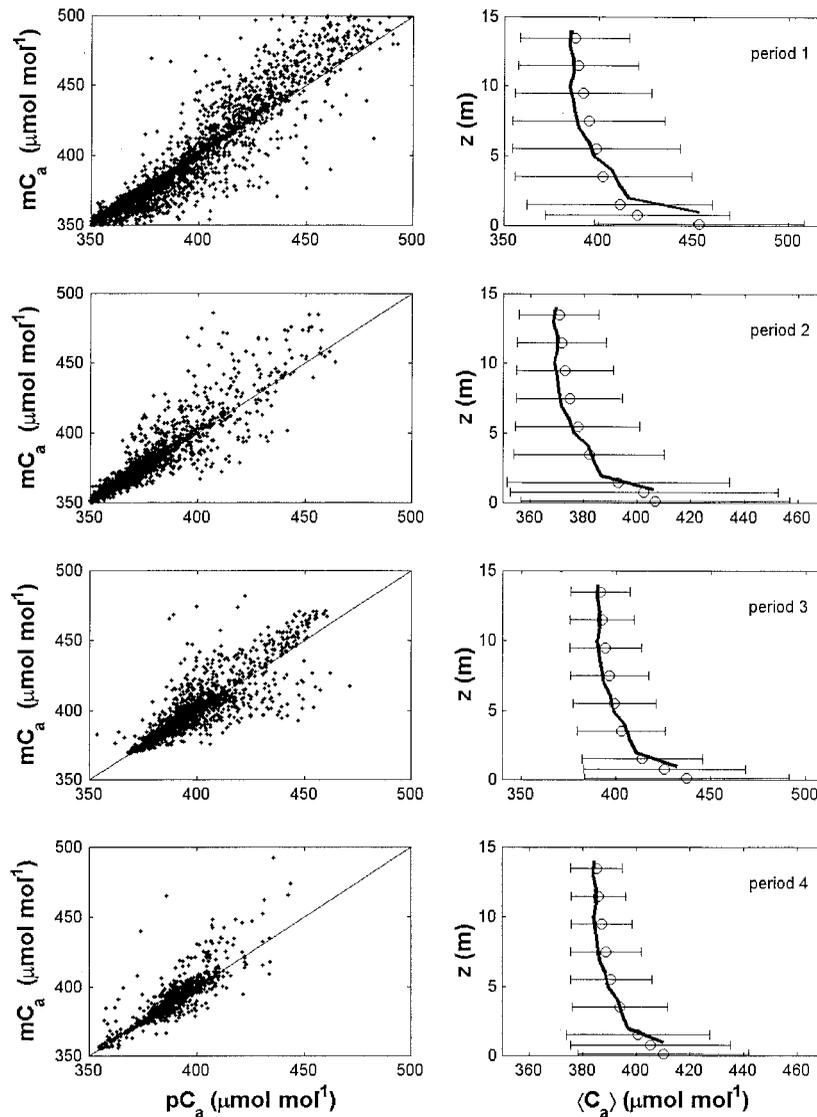
For using the parallel resistor analogy, we selected runs in which  $D$  modeled with CANVEG did not vary vertically by more than 5%. In fact, for the majority of daytime runs, the modeled vertical variation of  $D$  within the canopy rarely exceeded 5%, as was shown in another loblolly pine plantation of a similar total PAI [Ewers and Oren, 2000].

We note that  $G_m$  and  $G_c$  are computed with  $D$  and  $D_a$ , respectively, as a driving force for transpiration. We regressed  $D$  with  $D_a$  and found that for conductance calculations the approximation  $D \approx D_a$  is reasonable (see Table 3). This simplification has also been verified from measurements made in another loblolly pine stand of a similar PAI [Ewers and Oren, 2000]. Figure 9 shows the comparison between  $G_m$  and  $G_c$  for all four periods. In period 1 (drought condition),  $G_c$  was compared with  $G_m$  adjusting for  $w_r$ , which improved the comparison by  $\sim 26\%$  over a comparison that does not correct  $G_m$  by  $w_r$  for low soil moisture (see Table 3). For the two nonstress periods, modeled  $G_m$  was reasonably close to  $G_c$ , with period 4 as a notable exception. The scatter in these conductance comparisons may be related to the difficulty in estimating bulk canopy conductance of a forest from sap flux measurements conducted at the base of individual trees [Phillips et al., 1997; Oren et al., 1998b].

Despite the uncertainty in model calculations and sap flux measurements, the overall agreement between measured and modeled bulk canopy conductance is reasonable. Such agreement suggests that the parallel resistor analogy in (13) is appropriate to derive bulk canopy conductance from leaf-level conductance for water vapor if the vapor pressure deficit is nearly uniform within the canopy volume. Whether such an analogy exists for CO<sub>2</sub> is discussed in the following section, particularly with regard to the vertical variation in  $C_a - C_i$  or  $C_i/C_a$ .

#### 4.6. Comparison of Modeled and Measured Intercellular CO<sub>2</sub> Concentration

After testing the capability of this version of the CANVEG model to reproduce mass and momentum fluxes and scalar concentrations above and within the canopy, we calculated



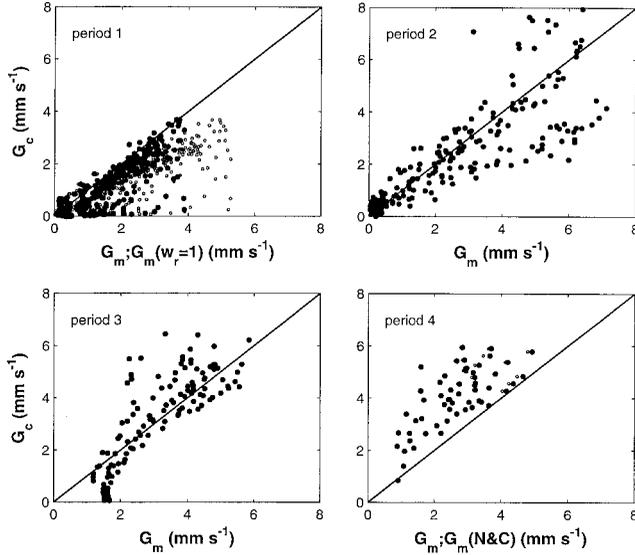
**Figure 8.** Temporal (left column) and spatial (right column) comparisons between measured ( $mC_a$ ) and CANVEG-predicted ( $pC_a$ ) CO<sub>2</sub> concentration variation. For the spatial comparison the ensemble modeled  $\langle C_a \rangle$  for each period is the solid line, while the ensemble measurements are plotted as open circles with one standard deviation.

$C_i/C_a$  profiles and compared these estimations with long-term isotope carbon measurements collected on sunlit and shaded foliage, the two expected end members of the range in  $C_i/C_a$ . Figure 10 shows the ensemble average of modeled  $C_i/C_a$  profiles at three selected layers (5.5, 7.5, and 13.5 m) for the four periods. Also shown is the  $C_i/C_a$  value obtained from carbon isotope measurements representing the  $C_i/C_a$  integral over the life of leaves, along with porometry measurements on sunlit foliage only averaged for each of the respective months [Ellsworth, 1999, 2000].

The carbon isotope measurements showed that  $C_i/C_a$  varied between 0.66 to 0.75 from the top of the canopy to its bottom, while the porometry measurement of sunlit foliage suggested a lower value (as low as 0.56). The modeled  $C_i/C_a$  at the canopy top agrees with the  $^{13}\delta C$  measurements for midday hours (Figure 10). The modeled  $C_i/C_a$  at the lower layers are higher but also consistent with the  $^{13}\delta C$  measurements ( $\approx 0.75$ ) of shaded foliage values. The best agreement occurred in period

2, when temperature and soil moisture did not limit stomatal conductance. The porometry measurements set the lowest  $C_i/C_a$  limit for the upper canopy layers. As expected, the modeled  $C_i/C_a$  values are marginally higher because they represent integrated sunlit and shaded fractions within each canopy layer. The observed vertical variations in  $C_i/C_a$  are consistent with findings in other forests [Weber and Gates, 1990; Yoder *et al.*, 1994; Williams *et al.*, 1996].

The broader implication of vertical variability in  $C_i/C_a$ , and its dependence on environmental conditions, is that an “effective”  $C_i/C_a$  in “big-leaf” models is ambiguously defined. Therefore compressing photosynthesis parameters in bulk canopy models is likely to increase the uncertainty in CO<sub>2</sub> flux predictions, or worse, inject a systematic bias. We next investigated the impact on the modeled fluxes if big-leaf (or single layer) formulations are adopted. We focused on periods 2 and 3 that reflected the weakest and strongest degree of vertical variation in  $C_i/C_a$  with depth.



**Figure 9.** Comparison between modeled conductance ( $G_m$ ) and sap flux scaled conductance ( $G_c$ ) of the bulk pine canopy for all four periods. For period 1 (drought), dots and open circles represent the modeled  $G_m$  with and without  $w_r$  correction, respectively. For period 4 (low temperature) the open circles and dots represent the modeled  $G_m$  with  $V_{c \max} - T_s$  curve derived from *Campbell and Norman* [1998] and measured on loblolly pine, respectively. The 1:1 line (solid line) is also shown.

For a single layer (or big leaf) whose conductance is identical to the bulk canopy conductance  $G_m$  derived in section 4.5, the net assimilation is given by

$$A_n = G_m \overline{(C_a - C_i)} = G_m \overline{C_a} \left( 1 - \frac{\overline{C_i}}{\overline{C_a}} \right),$$

where the overbar represents depth averaging. The canopy CO<sub>2</sub> flux from this single layer can be estimated from

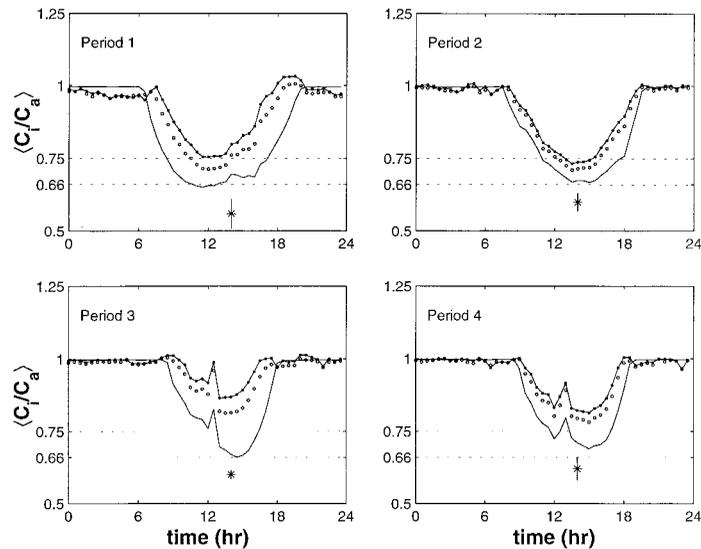
$$F_{\text{CO}_2} = A_n - R_d - F_g$$

if  $R_d$  and  $F_g$  are known, where  $\overline{C_a - C_i}$  is the effective  $C_a - C_i$  of the big leaf,  $R_d$  is the plant respiration and  $F_g$  is the soil CO<sub>2</sub> efflux. One approach to estimating  $\overline{C_a - C_i}$  is to rearrange the Ball-Berry model as

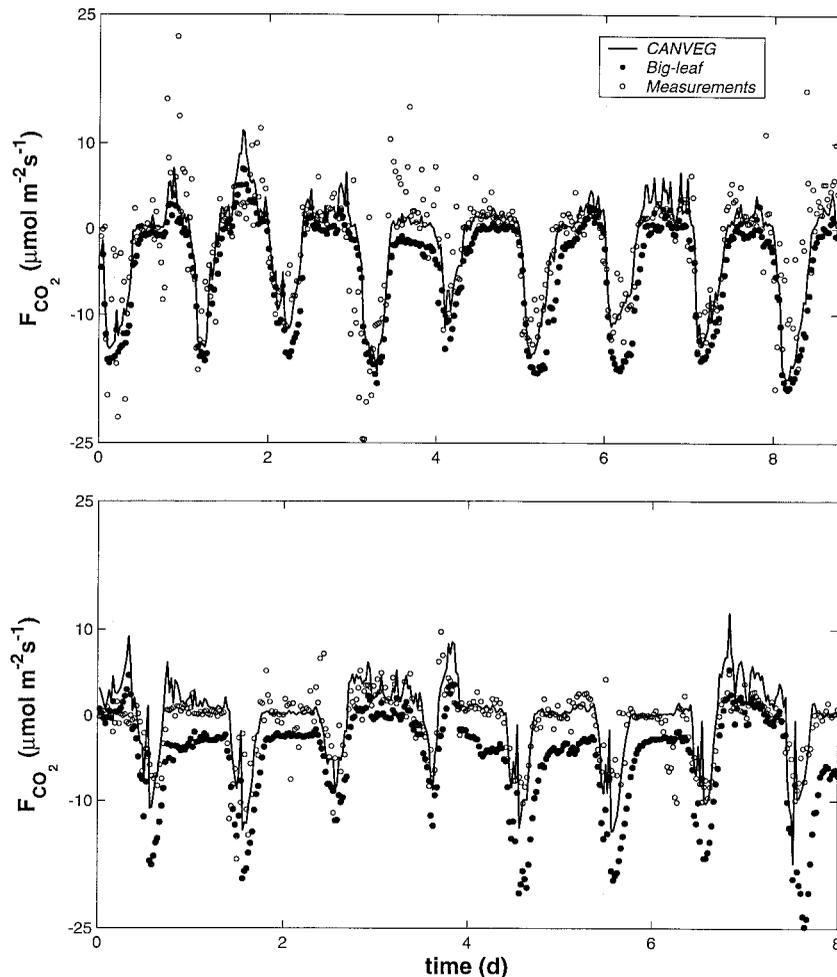
$$\frac{\overline{C_i}}{\overline{C_a}} \approx 1 - \frac{1}{mrh}.$$

This approximation naturally leads to a constant  $C_i/C_a$  with depth within the canopy volume but not with time. Using  $G_m$ ,  $R_d$ , and  $F_g$  modeled with CANVEG, we estimated  $F_{\text{CO}_2}$  for periods 2 and 3 and contrast these calculations with both measurements and calculations with the full CANVEG model. We restate that the only difference in calculating  $F_{\text{CO}_2}$  between the big-leaf and the detailed multilevel CANVEG model is the vertical variation in  $C_i/C_a$  as the driving force for the bulk canopy assimilation. The comparison between modeled  $F_{\text{CO}_2}$  based on the big-leaf approach and the multilayer CANVEG model, along with measured  $F_{\text{CO}_2}$  from eddy covariance is shown in Figure 11 for both periods.

The  $F_{\text{CO}_2}$  computed by the big-leaf approach continuously overestimated the values predicted by the full CANVEG model (Figure 11) with larger divergence between the two approaches in period 3 (regression slopes differed by 10% for period 2 and 30% for period 3). Predictably, when the gradients in  $C_i/C_a$  are large, a consistent divergence between CANVEG and big-leaf flux estimates is produced. However, if the root-mean-square error is used as the benchmark for comparisons, then the big-leaf approach is comparable to the CANVEG model calculations. This, in part, is due to the fact that temporal patterns of  $G_s$  vary by an order of magnitude, while the vertical variation in  $C_i/C_a$  is of the order of 15–25%,



**Figure 10.** Modeled diurnal  $C_i/C_a$  variation at three selected canopy layers ( $z = 5.5, 7.5,$  and  $13.5$  m, represented by dotted line, open circles, and solid line, respectively) for the four periods. The horizontal dashed lines are the long-term carbon isotope measurement at the top ( $\approx 0.66$ ) and bottom ( $\approx 0.75$ ) of the canopy [Ellsworth, 1999]. The ensemble leaf-level measurements [Ellsworth, 2000], collected around noon for sunlit foliage only, is shown by a star with one standard deviation.



**Figure 11.** Comparison between  $F_{CO_2}$  values estimated based on big leaf (dots) versus CANVEG (solid line) in period 2 (top) and period 3 (bottom), representing small and large vertical variations in modeled  $C_i/C_a$  with CANVEG, respectively. The measured  $F_{CO_2}$  is also shown by open circles.

meaning that accurate modeling of conductance in time is much more critical to predicting canopy  $F_{CO_2}$  than resolving the detailed vertical variation in  $C_i/C_a$ .

## 5. Conclusion

We presented an Eulerian-Lagrangian CANVEG framework that combines micrometeorological, biophysical, and biochemical principles with canopy turbulent transport theory for a wide range of temperature and soil moisture conditions. Modeled CO<sub>2</sub>, H<sub>2</sub>O, and sensible heat fluxes above the canopy, and CO<sub>2</sub> concentration within the canopy were reasonably close to measurements. In addition, modeled bulk canopy conductance compared well with the canopy conductance derived from scaled sap flux measurements for pine trees. On the basis of these results we conclude the following:

1. The generic temperature correction of the kinetic coefficients reported by *Campbell and Norman* [1998] is different from the locally derived correction for pine foliage. However, the overall CANVEG performance is not sensitive to such difference.
2. The CANVEG framework overestimates H<sub>2</sub>O fluxes and bulk canopy conductance without soil moisture adjustment when low soil moisture regulates stomatal conductance.
3. While our proposed reduction function significantly im-

proved the water vapor flux and canopy conductance, the CO<sub>2</sub> flux was not improved. Sensitivity analysis, in conjunction with leaf-level measurements, demonstrated that assuming static physiological parameters is overly simplistic and can inject systematic biases in modeling CO<sub>2</sub> fluxes.

4. Close agreement between the modeled bulk canopy conductance and the sap flux-scaled canopy conductance demonstrates that the parallel resistor analogy is an appropriate scheme to scale leaf conductance to the canopy scale for water vapor, when the vapor pressure deficit is nearly constant inside the canopy. The “big-leaf” canopy conductance is therefore appropriate for estimating stand transpiration.

5. The equivalent “big-leaf” approach for CO<sub>2</sub> was also investigated by showing that vertical variation in  $C_i/C_a$ , a parameter driving photosynthesis, is large within the canopy (at least when compared to vapor pressure deficit). Compressing vertical variation of physiological responses to canopy microclimate into “effective canopy” properties can induce systematic biases in CO<sub>2</sub> flux estimates. However, the estimated CO<sub>2</sub> fluxes did not differ between the multilayer CANVEG and the single-layer approximation (in terms of RMSE), because variations in  $G_s$  are an order of magnitude larger than the vertical variations in  $C_i/C_a$ .

## Appendix A: Model of *Farquhar et al.* [1980] and Temperature Adjustments

Using the models of *Farquhar et al.* [1980] and *Collatz et al.* [1991], the net photosynthetic rate at the leaf scale depends on light, CO<sub>2</sub>, and leaf temperature and can be described as

$$A_n \approx \min \left\{ \begin{array}{l} J_E \\ J_C \\ J_S \end{array} \right\} - R_d, \quad (\text{A1})$$

where  $J_E$ ,  $J_C$ , and  $J_S$  are the assimilation rate restricted by light, ribulose biphosphate ( $R_u$ BP) carboxylase (or Rubisco), and the export rate of synthesized sucrose, respectively, and  $R_d$  is the respiration rate during the day but in the absence of photorespiration. Photorespiration is treated separately in the model parameterization. The gross assimilation rate ( $= A_n + R_d$ ) is determined by the lowest of the three capacities since no photosynthesis can occur if the supply of any component is insufficient. In (A1),  $J_E$  describes the dependence of photosynthesis on light using

$$J_E = \alpha_p \times e_m \times Q_p \frac{\bar{C}_i - \Gamma_*}{\bar{C}_i + 2\Gamma_*}, \quad (\text{A2})$$

where  $\alpha_p$  is the leaf absorptivity for PAR,  $e_m$  is the maximum quantum efficiency for CO<sub>2</sub> uptake,  $Q_p$  is the PAR irradiance on the leaf,  $\bar{C}$  represents mean CO<sub>2</sub> concentration, and  $\Gamma_*$ , the CO<sub>2</sub> compensation point, is the CO<sub>2</sub> concentration at which  $A_n = 0$  in the absence of photorespiration and is given by

$$\Gamma_* = \frac{[\text{O}_2]}{2\omega}, \quad (\text{A3})$$

where  $[\text{O}_2]$  is the oxygen concentration in air ( $\approx 210$  mmol mol<sup>-1</sup>), and  $\omega$  is a ratio of kinetic parameters describing the partitioning of  $R_u$ BP to the carboxylase or oxygenase reactions of Rubisco. In other words,  $\omega$  is a measure of the competition between CO<sub>2</sub> and O<sub>2</sub> for  $R_u$ BP that is intrinsic to the Rubisco enzyme in C<sub>3</sub> species.

$J_C$  is the Rubisco-limited rate and is estimated from

$$J_C = \frac{V_{c \max}(\bar{C}_i - \Gamma_*)}{\bar{C}_i + K_c(1 + [\text{O}_2]/K_o)}, \quad (\text{A4})$$

where  $V_{c \max}$  is the maximum catalytic capacity of Rubisco per unit leaf area ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $K_c$  and  $K_o$  are the Michaelis constants for CO<sub>2</sub> fixation and O<sub>2</sub> inhibition with respect to CO<sub>2</sub>, respectively. Equation (A4) shows that  $J_C$  increases linearly with increasing  $\bar{C}_i$  but approaches a maximum value at  $V_{c \max}$  under high CO<sub>2</sub> concentration conditions that are generally not encountered under natural conditions.

$J_S$  is the capacity for the export or utilization of photosynthesis products, and sucrose synthesis is most probably the rate-limiting step [see *Collatz et al.*, 1991].  $J_S$  is estimated by

$$J_S = V_{c \max}/2. \quad (\text{A5})$$

The rapid cutoff transition implied in (A1) can be made more realistic if the mathematical scheme is made to account for gradual transition from one limitation to another and to allow for some colimitation among  $J_E$ ,  $J_C$ , and  $J_S$ . We used the quadratic functions described by *Collatz et al.* [1991] to circumvent these limitations (not shown here).

We assume that the respiration rate  $R_d$  in (A1) is linearly related to  $V_{c \max}$  [*Collatz et al.*, 1991] by

$$R_d = 0.015V_{c \max}. \quad (\text{A6})$$

The parameterization of model kinetic variables in terms of temperature dependence follows the procedure of *Campbell and Norman* [1998], in which five parameters are adjusted for temperature:  $K_c$ ,  $K_o$ ,  $\omega$ ,  $V_{c \max}$ , and  $R_d$ . For the first three parameters, a modified  $Q_{10}$  temperature function is employed:

$$k = k_{25} \exp [y(T_s - 25)], \quad (\text{A7})$$

where  $k$  is defined at leaf surface temperature  $T_s$ ,  $k_{25}$  is the value of the parameter at 25°C, and  $y$  is the temperature coefficient for that parameter from *Campbell and Norman* [1998]. In addition,  $V_{c \max}$  and  $R_d$  are adjusted by a more complex function incorporating deactivation effects at extremely high temperatures:

$$V_{c \max} = \frac{V_{c \max,25} \exp [a_1(T_s - 25)]}{1 + \exp [a_2(T_s - 41)]}, \quad (\text{A8})$$

$$R_d = \frac{R_{d,25} \exp [0.069(T_s - 25)]}{1 + \exp [1.3(T_s - 55)]}, \quad (\text{A9})$$

where  $V_{c \max,25}$  and  $R_{d,25}$  are the values of  $V_{c \max}$  and  $R_d$  at 25°C, respectively. For (A8), *Campbell and Norman* [1998] reported  $a_1 = 0.088$  and  $a_2 = 0.29$ . Our measured values specifically for pine are  $a_1 = 0.051$  and  $a_2 = 0.205$ .

Finally,  $\bar{C}_s$ ,  $\bar{C}_i$ , and  $\bar{C}_a$  are related by

$$\bar{C}_i = \bar{C}_s - \frac{A_n}{g_s}, \quad (\text{A10})$$

$$\bar{C}_s = \bar{C}_a - \frac{A_n}{g_b}, \quad (\text{A11})$$

where  $g_s$  ( $= r_s^{-1}$ ) is the stomatal conductance, and  $g_b$  ( $= r_b^{-1}$ ) is the leaf boundary layer conductance.

**Acknowledgments.** The authors thank Yavor Parashkevov and Andrew Palmiotti, for their help during the experiment, and Keith Lewin and John Nagy for their assistance in the CO<sub>2</sub>/H<sub>2</sub>O multipoint design and setup. This project was funded, in part, by the National Science Foundation (NSF-BIR 12333), and the U.S. Department of Energy (DOE) through the FACE-FACTS project, and through the Southeast Regional Center at the University of Alabama, Tuscaloosa (DOE cooperative agreement DE-FC030-90ER61010), and the National Institute for Global Environmental Change (NIGEC).

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(Received December 31, 1999; revised June 8, 2000; accepted July 26, 2000.)

