

Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. II. Model testing and application

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ABSTRACT

The scaling of CO₂ and water vapour transfer from leaf to canopy dimensions was achieved by integrating mechanistic models for physiological (photosynthesis, stomatal conductance and soil/root and bole respiration) and micrometeorological (radiative transfer, turbulent transfer and surface energy exchanges) processes. The main objectives of this paper are to describe a canopy photosynthesis and evaporation model for a temperate broadleaf forest and to test it against field measurements. The other goal of this paper is to use the validated model to address some contemporary ecological and physiological questions concerning the transfer of carbon and water between forest canopies and the atmosphere. In particular, we examine the role of simple versus complex radiative transfer models and the effect of environmental (solar radiation and CO₂) and ecophysiological (photosynthetic capacity) variables on canopy-scale carbon and water vapour fluxes.

Key-words: carbon balance; ecophysiology; eddy-covariance measurements; micrometeorology; net ecosystem carbon exchange; photosynthesis; transpiration.

INTRODUCTION

A major focus of contemporary ecological research is on understanding how carbon, water and nutrient cycles of forest ecosystems respond to environmental and climatic perturbations (Dixon *et al.* 1990; Agren *et al.* 1991; Running & Hunt 1993; McMurtrie & Wang 1993). An integral component of this ecosystem research involves the development of mathematical models. The rationale for this approach stems from the adeptness of models at synthesizing and integrating the complex and non-linear forcing of environmental variables on biological systems.

Mechanistic models of carbon and water exchange exist and have been verified at the leaf scale (Farquhar & von Caemmerer 1982; Collatz *et al.* 1991; Harley *et al.* 1985, 1992). Ecosystem and biogeochemical cycling models, on

the other hand, require carbon and water flux densities at the canopy scale. Frameworks exist for integrating water and carbon fluxes from leaf to forest dimensions (e.g. Miller 1971; Jarvis *et al.* 1985; Baldocchi 1989, 1993, Hollinger 1992; Caldwell *et al.* 1986; Grace *et al.* 1987; Wang & Jarvis 1990; McMurtrie & Wang 1993). What is lacking is a definitive test of leaf-to-canopy integration and scaling schemes; either micrometeorological flux measurements have been unavailable to test the integration and scaling schemes (Hollinger 1992; Miller 1971; Caldwell *et al.* 1986; McMurtrie *et al.* 1992; Running & Hunt 1993; Grace *et al.* 1987) or insufficient *in situ* measurements of leaf physiological processes were obtained to parametrize model calculations (Baldocchi 1989, 1993; Jarvis *et al.* 1985).

During the summer of 1992, we conducted a comprehensive physiological and micrometeorological study on the carbon and water vapour exchange of a temperate, broadleaf forest to fill this identified knowledge gap. Leaf-scale physiological measurements were made to derive the photosynthesis and stomatal conductance model parameters. Micrometeorological measurements of canopy CO₂ and energy flux densities were made to test an integration model (CANOAK) for calculating canopy CO₂, water vapour and energy flux densities.

The key objectives of this paper are to describe a canopy photosynthesis and evaporation integration and scaling model and to test it against field data. An additional objective is to use the model to address contemporary ecological and physiological questions concerning the transfer of carbon and water between forest canopies and the atmosphere. One important issue involves the level of detail that should be incorporated into an ecosystem or biogeochemical cycling model (see Raupach & Finnigan 1988; Bonan 1993). Other ecological and physiological questions that we address include: (1) the biochemical and physical constraints that define the response of canopy photosynthesis to solar energy; (2) the impact of optimizing photosynthetic capacity on the canopy flux density of CO₂; (3) the effect of future CO₂ scenarios on mass and energy exchange rates; (4) the role of photosynthetic capacity (stemming from soil nutrient status) on the partitioning of solar energy into sensible and latent heat transfer, and (5) the environmental controls on canopy water use efficiency.

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MATERIALS AND METHODS

Site

Physiological and micrometeorological measurements were made in a mixed deciduous forest, representative of the Eastern deciduous biome, between 15 July and 10 August 1992. The field site was located on the United States Department of Energy reservation near Oak Ridge, TN (lat. 35° 57' 30"; long. 84° 17' 15"; 365 m above mean sea level). The mean annual temperature at this site is 13.9 °C and the mean annual rainfall is 1350 mm. During July and August, the mean air temperature ranges between 24 and 30°C and the mean monthly rainfall ranges between 95 and 137 mm.

The surrounding area was vegetated within uneven stands of oak (*Quercus*), maple (*Acer*), hickory (*Carya*) and loblolly pine (*Pinus taeda*). The mean canopy height was 24 m and the leaf area index was of the order of 4.9 (Hutchison *et al.* 1986). The vertical distribution of foliage of this temperate broadleaf forest differs from that of other forest types. About 75% of the leaf area is concentrated in the upper 25% of the canopy, leaves are clumped and the leaf inclination angle varies with canopy height (Baldocchi *et al.* 1985). The field site was adjacent to the Walker Branch Watershed, which has been the subject of numerous ecological, meteorological and biogeochemical studies over the past 20 years. Additional information on the site, vegetation and climate are provided by Hutchison *et al.* (1986) and Johnson & van Hook (1989).

Soil moisture was measured daily by gravimetric means. The vegetation was supplied with adequate moisture throughout the duration of the experiment as soil moisture content ranged between 0.2 and 0.4 cm³ cm⁻³.

Stand-scale flux measurements

The eddy covariance technique was employed to measure flux densities of sensible heat, water vapour and CO₂ between the forest stand and the atmosphere and at the forest floor (see Baldocchi *et al.* 1988; Baldocchi & Meyers 1991 for details). Positive flux densities represent mass and energy transfer away from the surface and negative values denote the reverse. Vertical flux densities of CO₂ (F_c), and latent (LE) and sensible (H) heat between the forest and the atmosphere are proportional to the mean covariance between vertical velocity (w') and scalar (c') fluctuations. Turbulent fluctuations were computed as the difference between instantaneous and mean scalar quantities.

Over a tall forest canopy, the CO₂ flux density measured by the eddy covariance system does not always equal the net biotic CO₂ exchange during the period of integration. A bias error can occur when CO₂ is stored in the layer of air below the eddy flux system (Wofsy *et al.* 1993; Hollinger *et al.* 1994). This storage is most likely to be significant during the night when the atmosphere is stably stratified and winds are weak. The CO₂ storage term equals the integration with respect to height of the time rate of change of the CO₂ concentration profile,

$$\int_0^{z_r} \frac{\partial c(z)}{\partial t} dz.$$

We approximated this storage term as

$$z_r \frac{\Delta c(z_r)}{\Delta t}$$

(z_r is the reference measurement height) and added it to our eddy covariance measurements. Recent measurements by Hollinger *et al.* (1994) indicate that errors associated with this simple approximation are relatively small; they reported that the approximated storage term equalled the actual storage term over an evergreen broadleaf forest. Furthermore, the CO₂ storage term over a 24 h period sums to zero, on average (D. Baldocchi & C. Vogel, unpublished results).

A 44 m walk-up tower in the forest canopy allowed access and support for micrometeorological instrumentation. One set of micrometeorological instruments was placed on a boom which extended 3 m in front of the tower 35 m above the ground. Another eddy flux system was operated 2 m above the forest floor. Wind velocity and virtual temperature fluctuations were measured with three-dimensional sonic anemometers (Applied Technology, Boulder, CO; model SWS-211/3K). The pathlength between transducers was 0.15 m. The sensor software corrected for transducer shadowing effects. Virtual temperature heat flux was converted to sensible heat flux. Measurement of the three wind vectors allowed numerical coordinate rotations to align the vertical velocity measurement normal to the mean wind streamlines.

CO₂ and water vapour fluctuations were measured with an open-path, infrared absorption gas analyser, developed at NOAA/ATDD (Auble & Meyers 1992). The sensor responds to frequencies up to 15 Hz, and has low noise and high sensitivity (20 mg m⁻³ volt⁻¹). The sensor is rugged and experiences little drift.

Micrometeorological data were digitized, processed and stored using a microcomputer-controlled system and in-house software. Digitization of analogue sensor signals was performed at 10 Hz with hardware on the sonic anemometer. Mean scalar values, for covariance calculations, were determined in real time, using a digital recursive filter with a 400 s time constant; this method yields results identical to those computed via conventional Reynold's averaging. Individual flux covariance calculations were performed on 30 min averaging periods. Previous computations of power spectra and co-spectra indicated that these sampling rates and durations are adequate for measuring fluxes above and below this tall and aerodynamically rough forest canopy (Anderson *et al.* 1986; Baldocchi & Meyers 1991). Data were rejected when winds blew through the tower and when sensors were wet or off-scale. Despite rigorous data acceptance criteria, we obtained almost 200 flux measurements, which represent one of the largest bodies of data yet available for canopy carbon model testing.

Proper interpretation of experimental results and model

evaluation require measurements of environmental variables and energy balance components. Three soil heat flux plates (Radiation Energy Balance Systems (REBS), Seattle, WA; model HFT-3) were buried 0.08 m below the surface. Soil heat flux measurements were corrected for soil heat storage in the upper layer by measuring the time rate of change of the mean soil temperature (T_s) profile and the heat capacity of the soil [$C(z)$]. Soil temperature was measured with multi-level thermocouple probes, spaced logarithmically at 0.02, 0.04, 0.08 and 0.16 m below the surface. Shortwave radiation, photosynthetically active photon flux density and the net radiation balance were measured above the forest with a pyranometer (Eppley, Newport, RI; model 0-48), a quantum sensor (LICOR, Lincoln, NE; model LI-190S) and a net radiometer (REBS model 6, Seattle, WA), respectively. Air temperature and relative humidity were measured above the canopy and near the forest floor with appropriate sensors (Campbell Scientific Inc., Logan, UT; model 207). Wind speed and direction were measured with a propeller wind speed/direction monitor (RM Young, Traverse City, MI; model 05701). Canopy heat storage was calculated by measuring the time rate of change in bole temperature; three thermocouple probes were placed at 1 cm depth at several locations on the trunk of a tree. Ancillary environmental data were acquired and logged on Campbell CR-7 and CR-21x data loggers.

The solar radiation field below a forest canopy is highly variable. To account for this variability, measurements of solar radiation components were made using an instrument package that traversed at 1 cm s⁻¹ along a 30 m transect on a tram system (see Baldocchi *et al.* 1985).

Physiological measurements

Leaf-level physiological measurements are described and presented in the companion paper (Harley & Baldocchi, 1995, this issue). A brief description of these measurements follows. Leaf photosynthesis and transpiration were measured using a commercially available gas exchange system (Campbell Scientific, Logan, UT; model MPH-1000). The system included a temperature-controlled, fan-stirred cuvette tethered to a measurement and control system. Air of specified water vapour and CO₂ concentrations was generated by mass flow controllers and passed through the cuvette. Water vapour concentrations were measured with a dew-point hygrometer (General Eastern) and CO₂ concentrations were measured with an infrared gas analyser (model LI-6251, LICOR, Lincoln, NE). Light was provided using a portable system, consisting of a quartz halogen bulb (ELH, 120v-300W, General Electric, Cleveland, OH). The bulb was mounted in a slide projector lamp holder and was directed with a Tempax cold mirror (Optical Coating Labs, Santa Rosa, CA). Neutral density filters (blackened window screen) were inserted in the light path to vary the photon flux density on the leaf. Calculations of net photosynthesis, transpiration, internal CO₂ concentration and stomatal conductance were derived

from the cuvette measurements using equations described by von Caemmerer & Farquhar (1981).

Modelling canopy CO₂ and vapour exchange

Physiological processes (photosynthesis, respiration, stomatal conductance and transpiration) are regulated in a non-linear manner by a host of environmental variables (solar and terrestrial radiation, temperature, humidity, wind speed and soil moisture). Integration of leaf fluxes to the canopy scale requires the computation of controlling environmental variables as they vary with depth through the canopy and as they differ on sunlit and shaded leaf fractions (Baldocchi 1993; Norman 1993).

CANOAK is the one-dimensional, multi-layer canopy photosynthesis/evaporation model tested and evaluated in this paper. CANOAK consists of coupled micrometeorological and physiological modules. The micrometeorological model computes leaf and soil energy exchange, turbulent diffusion and radiative transfer within the canopy. These environmental variables, in turn, drive the physiological models, which compute leaf photosynthesis, stomatal conductance and leaf, bole and soil/root respiration. An outline of the CANOAK model is presented below.

- (1) Compute continuous vertical distribution of leaf area index.
- (2) Input environmental variables: day, time, PAR, air temperature, wind speed, CO₂ concentration, humidity, atmospheric stability and Lagrangian dispersion matrix.
- (3) Compute solar elevation angle.
- (4) Compute solar radiation profiles (PAR and NIR wavebands).
- (5) Compute sunlit and shaded leaf fractions.
- (6) Estimate stomatal conductances.
- (7) Compute infrared radiation profiles assuming leaf temperature equals air temperature.
- (8) Compute leaf energy balance (leaf temperatures, sensible heat flux and transpiration) on sunlit and shaded leaf fractions.
- (9) Compute leaf photosynthesis, respiration and stomatal conductance on sunlit and shaded leaf fractions.
- (10) Compute soil energy balance and soil/litter/root respiration.
- (11) Compute temperature, humidity and CO₂ profiles in the canopy and boundary layer airspace.
- (12) Iterate from step (7) to (11) until convergence.
- (13) Stop or Go to (2) and repeat.

Discussion of the major component submodels follows.

Micrometeorology

The conservation budget for a scalar provides the foundation for computing fluxes and concentration profiles of trace gases. This model assumes that the canopy is horizontally homogeneous and that environmental conditions

are temporally steady. This assumption allows the scalar conservation equation to be expressed as an equality between the partial derivative, with respect to height, of the vertical turbulent flux and the diffusive source/sink strength, $S(c, z)$:

$$\frac{\partial F(c, z)}{\partial z} = S(c, z). \quad (1)$$

The diffusive source/sink strength of a scalar in a unit volume of leaves is proportional to the concentration gradient normal to individual leaves, the surface area of individual leaves and the number of leaves in the volume (Finnigan 1985). The diffusive source strength can be expressed in the form of a resistance-analogue relationship (Meyers & PawU 1987):

$$S(c, z) = -\rho_a a(z) \frac{[c(z) - c_i]}{r_{bc}(z) + r_{sc}(z)}, \quad (2)$$

where $a(z)$ is the leaf area density, $[c(z) - c_i]$ is the concentration difference between air outside the laminar boundary layer of leaves and the air within the stomatal cavity, r_{bc} is the boundary layer resistance to molecular diffusion, r_{sc} is the stomatal resistance and ρ_a is the air density.

Turbulence and diffusion

The evaluation of Eqn 2 depends upon a turbulence and diffusion model that resolves the scalar concentration field above and within the forest canopy. A Lagrangian random walk model was used to perform this task because it is better able to resolve concentration fields within vegetation (Raupach 1988; Baldocchi 1992). Concentration differences between an arbitrary level (c_l) and a reference level (c_r) (located above a plant canopy) were computed by summing the contributions of material diffusing to or from layers in the canopy (denoted by the subscript j) (Raupach 1988):

$$c_l - c_r = \sum_{j=1}^N S_j(c_j) D_{l,j} \Delta z_j, \quad (3)$$

where $D_{l,j}$ is a dispersion matrix and has the same units as a resistance ($s \text{ m}^{-1}$). The dispersion matrix was calculated using a Lagrangian random walk model, based on the algorithm of Thomson (1987). Details of how the random walk model was implemented for this application are reported elsewhere (Raupach 1988; Baldocchi 1992, 1993).

Radiative transfer

The radiative transfer model was derived from probabilistic theory (Norman 1979; Myneni *et al.* 1989). Two model versions were used and tested. The simple radiative transfer model assumed that the canopy was a turbid medium and that the leaf inclination angle distribution was spherical. It used the Poisson distribution to calculate the probability of beam penetration:

$$P_o = \exp\left(-\frac{fG}{\sin \beta}\right), \quad (4)$$

where f is the leaf area index, β is the solar elevation angle and G is the foliage orientation function, which represents the cosine of the angle between the sun and the mean leaf normal (Lemur & Blad 1974; Myneni *et al.* 1989). For the ideal spherical case, G is constant and equals 0.5 (Norman 1979).

The alternative model assumed that the spatial distribution of foliage was clumped. It used a negative binomial probability function to compute the probability of beam penetration (Myneni *et al.* 1989; Baldocchi 1993):

$$P_{nb} = \exp\left\{-\frac{f}{g} \left[\ln\left(1 + \frac{Gg}{\sin \beta}\right)\right]\right\}, \quad (5)$$

where g is the index of foliage dispersion. Vertical variations in the G -function were computed using algorithms reported by Lemur and Blad (1974). Photon scattering was computed using algorithms published by Norman (1979). Both radiative transfer models have been tested against photon flux density measurements at this field site. Results of these tests, presented by Baldocchi *et al.* (1985) and Baldocchi (1993), indicate that the negative binomial model yields truer estimates of the within-canopy radiation field.

The radiative transfer models were also used to evaluate the probability of leaves being sunlit or shaded, as described in Eqn 1. Gutschick (1991) states that the sunfleck probability (P_{sun}) equals the product of the derivative of the probability of beam penetration, with respect to leaf area, and the ratio of the cosine of the solar zenith angle and the average cosine of the leaf-sun angle. For the random, spherical canopy, p_{sun} equals the Poisson probability function. For the clumped canopy,

$$p_{sun} = p_{nb} \left[\frac{\sin \beta \ln\left(1 + \frac{Gg}{\sin \beta}\right)}{gG} \right]. \quad (6)$$

In both cases, p_{shade} equals $1 - p_{sun}$.

Sources and sinks: photosynthesis, respiration, stomatal conductance and transpiration

Net leaf carbon exchange is a compromise between carbon gain, through photosynthetic carbon reduction, and carbon losses, through photorespiratory carbon oxidation and mitochondrial (dark) respiration (Farquhar & von Caemmerer 1982; Farquhar & Sharkey 1982). The rate of carbon assimilation depends on the abundance of substrates [CO_2 and ribulose biphosphate (RuBP)] and the degree to which carboxylation (photosynthetic carbon reduction) outcompetes oxygenation (photorespiratory carbon oxidation) for sites on the enzyme RuBP carboxylase-oxygenase. The supply of CO_2 to the chloroplast is regulated by diffusion through the leaf boundary layer and stomatal aperture (see Collatz *et al.* 1991). At low intercellular CO_2 levels, RuBP carboxylase-oxygenase is saturated with respect to the RuBP, so photosynthetic activity increases with additional CO_2 . When intercellular CO_2 is

ample, carbon assimilation becomes limited by the capacity of the leaf electron transport system — a light dependent process — to produce adenosine triphosphate (ATP) and NADPH, which are needed to regenerate RuBP (see Farquhar & Sharkey 1982).

Leaf photosynthetic rates (A) were computed with an analytical expression that simultaneously solves equations for the rates of carboxylation (V_c), oxygenation (V_o), and dark respiration (R_d), stomatal conductance (g_s), and internal (C_i) and surface (C_s) CO₂ concentrations. The analytical solution for the coupled leaf photosynthesis–stomatal conductance model is described in Baldocchi (1994a). The biochemical equations for the carbon exchange processes are taken from Farquhar & von Caemmerer (1982), Harley & Tenhunen (1991) and Harley *et al.* (1992). Stomatal conductance was computed as a function of leaf photosynthetic rate, relative humidity and the surface CO₂ concentration (Collatz *et al.* 1991).

Bole respiration is a significant component of a forest's carbon balance (Ryan 1991; Edwards & Hanson 1995). Bole respiration was computed using algorithms from Edwards & Hanson (1995) and biomass information from Johnson & Henderson (1989).

Leaf temperature was calculated to determine enzymatic rates associated with carboxylation, electron transport, and respiration. Leaf temperature is a function of transpiration and sensible heat fluxes. Transpiration and sensible heat exchange of leaves were computed using an iterative scheme described by Bristow (1987). These calculations depend on leaf surface, stomatal and boundary layer conductances, and the amount of short- and long-wave energy absorbed by the leaf.

Soil

Soil constitutes the lowest boundary of a canopy CO₂ and water exchange model. Soil/root respiration rates were computed using algorithms derived by Hanson *et al.* (1993) at the Walker Branch field site. Flux densities of heat and water at the soil/litter boundary were computed using a 10-layer numerical heat transfer model (Campbell 1985). A simple resistance model was used to evaluate soil evaporation. The surface resistance to soil evaporation was assigned a value of 1500 s m⁻¹, based on prior measurements at this site (Baldocchi & Meyers 1991).

Model parametrizations

Physiological variables

The maximum carboxylation rate (V_{cmax}), the maximum rate of electron transport (J_{max}), and the dark respiration rate (R_d) at a reference temperature are needed to compute leaf photosynthesis and stomatal conductance (Collatz *et al.* 1991; Harley & Tenhunen 1991; Harley *et al.* 1992). Parameter values used by the photosynthesis and stomatal conductance models are listed in Table 1. These were derived from sunlit leaves of oak (*Quercus alba*). Additional information on leaf photosynthesis measure-

Table 1. Summary of CO₂ exchange and stomatal conductance model parameters on sunlit leaves of *Quercus alba* (*Q. alba*). V_{cmax} is the maximum carboxylation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), J_{max} is the maximum rate of electron transport [$\mu\text{mol (e}^-) \text{m}^{-2} \text{s}^{-1}$], R_d is the dark respiration rate and R_{bole} is the bole respiration rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$). The number in parenthesis denotes the temperature ($^{\circ}\text{C}$) at which the parameter is valid. E_a is the activation energy value. k is the slope of the stomatal conductance algorithm and g_o is the zero intercept

Variable	Units	<i>Q. alba</i>
V_{cmax} (38 $^{\circ}\text{C}$)	$\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$	73
J_{max} (38 $^{\circ}\text{C}$)	$\mu\text{mol (e}^-) \text{m}^{-2} \text{s}^{-1}$	170
R_d (25 $^{\circ}\text{C}$)	$\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$	0.34
$E_a: V_{cmax}$	J mol^{-1}	55000
$E_a: J_{max}$	J mol^{-1}	55000
$E_a: R_d$	J mol^{-1}	38000
α	$\text{mol e}^- (\text{mol quanta})^{-1}$	0.20
R_{bole} (10 $^{\circ}\text{C}$)	$\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$	1.86
k		9.5
g_o	$\text{mol m}^{-2} \text{s}^{-1}$	0.0175

ments made at this site is presented by Harley & Baldocchi (1995), in the companion paper.

Scaling photosynthetic parameters as a function of specific leaf weight is a surrogate for the impact that the vertical variation of leaf nitrogen has on photosynthetic capacity (see Field & Mooney 1986; Gutschick & Weigel 1988; Field 1991). The model was run by scaling V_{cmax} , J_{max} and R_d according to the vertical variation of specific leaf weight; justification for this parametrization is provided by Harley & Baldocchi (1995). The vertical variation of specific leaf weight is based on data from Hutchison *et al.* (1986), and was corroborated by independent measurements reported by Harley & Baldocchi (1995).

Enzyme kinetic rates — associated with carboxylation, electron transport, and respiration — were corrected for their non-linear dependence on leaf temperature. Functional distributions discussed by Harley *et al.* (1992) and Harley & Tenhunen (1991) were used.

The reference bole respiration rate is a function of the maintenance and growth components and bole temperature (Ryan 1991). Model parameters were derived from biomass data presented in Hanson (1995) and Johnson & Henderson (1989) and were measured on trees growing nearby the flux measurement site. The reference bole respiration rate at 10 $^{\circ}\text{C}$ was assumed to equal 1.86 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (on a ground area basis).

Micrometeorology

Turbulence parameters for the random walk model were derived from prior turbulence studies made at this forest site (Baldocchi & Meyers 1988). A double exponential function was fitted to field data to compute vertical variations in σ_w , which drive the Lagrangian random walk model. Above the canopy, σ_w equals 1.25 times friction velocity (u^*) under near-neutral conditions. For unstable

conditions, σ_w was assumed to vary according to the 1/3 power law on z/L , where L is the Monin-Obukhov scale length (Stull 1988).

The Lagrangian random walk model of Thomson (1987) was employed to calculate the dispersion matrix, presented in Eqn 3. Calculations of D_{ij} were performed by following the trajectories of 5000 fluid parcels for 2000 s within a domain 3 times the canopy height. To economize on computer time, instead of re-running the Lagrangian model for individual simulation runs, dispersion matrices were parametrized as a function of friction velocity and z/L .

Radiation transfer

The foliage clumping index (g) was derived from a radiation transfer study at this field site (Chason *et al.* 1991). Calculations of the probability of beam penetration were performed using an index of foliage dispersion (g) equalling 1.6. Optical properties of leaves were measured in previous work and are reported in Hutchison & Baldocchi (1989).

RESULTS AND DISCUSSION

Field data

Before testing a model it is imperative to demonstrate that the test data are reliable. In micrometeorology, one tests

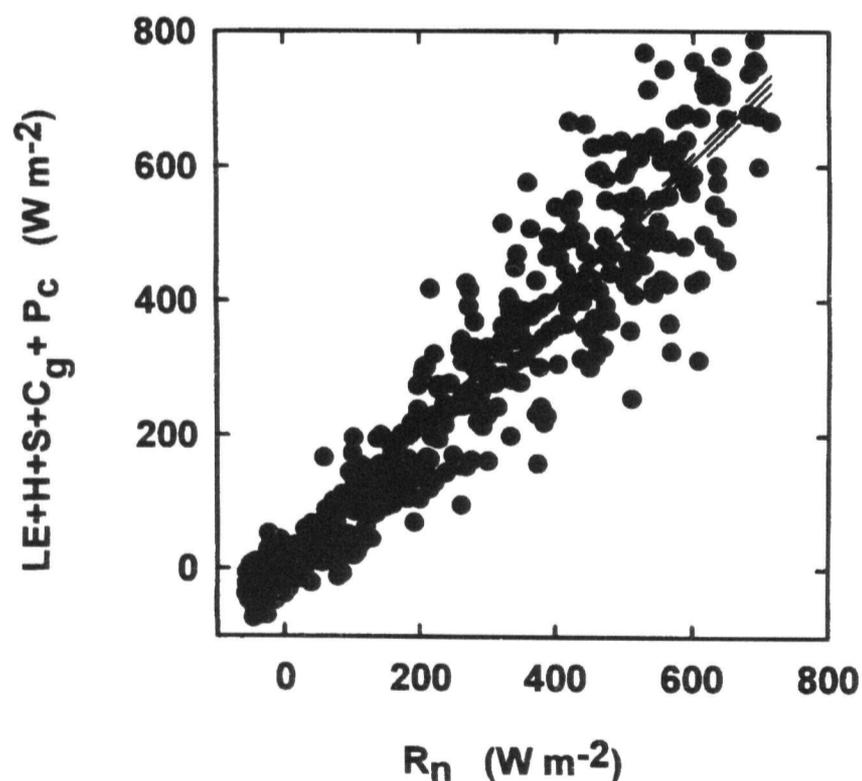


Fig. 1. A test for closure of the surface energy balance measured over a deciduous forest using flux covariances averaged over 30 min. Student's paired t -test reveals that there is no significant difference between net radiation (R_n) measurements and its partitioning into the sum among latent (LE), sensible (H), canopy heat storage (C_g), soil (S) and photosynthetic (P) energy flux densities at the 0.05 probability level ($t = -1.72$). The slope between measured net radiation and its components [latent (LE) and sensible (H) heat exchange, soil heat transfer, canopy heat storage and canopy photosynthesis] was 1.00, the zero intercept was 3.47 W m^{-2} and the coefficient of determination (r^2) was 0.923.

the reliability of eddy flux measurements by demonstrating whether or not there is closure of the surface energy balance. Figure 1 compares measurements of net radiation flux density against its partitioned components, namely the sum of latent, sensible and soil heat flux densities, plus canopy heat storage and photosynthetic energy fixation. The slope of the relationship between measured net radiation and its partitioned components was 1.00. Furthermore, there was no significant difference between the population means of these variables at the 5% probability level. This favourable closure of the surface energy balance indicates that measurement errors associated with the eddy flux measurements were relatively small and unbiased over this non-uniform site. Furthermore, this degree of the surface energy balance closure agrees with previous measurements made over this forest (Verma *et al.* 1986).

Model testing: the influence of radiative transfer models on leaf to canopy scaling of scalar flux densities

At the canopy scale, both simple, lumped-parameter and complex, multi-layer models exist (Dixon *et al.* 1990; Agren *et al.* 1991). For some ecological applications, simple, lumped-parameter models are preferred. Such cases often involve yearly to decadal time integrations and landscape to global spatial integration (see Agren *et al.* 1991; Aber & Federer 1992; Running & Hunt 1993). On the other hand, detailed, mechanistic models mimic reality better and are thus more appropriate to evaluate the impact of an environmental perturbation than simple, lumped-parameter models (see Bonan 1993).

One solution to the conundrum of whether to use simple or complex models is to use mechanistic models as theoretical guides for developing lumped-parameter models. One question we address involves examining how much detail is needed to simulate radiative transfer through a forest canopy; radiative transfer schemes are ubiquitous in ecosystem models because they are required to calculate photosynthesis, stomatal conductance and leaf and soil energy balances. Simple radiative transfer models assume that leaves are distributed randomly in space and that they have a spherical leaf inclination angle distribution (Norman 1979). This assumption is valid for crops and yields accurate calculations of canopy CO_2 flux density (Baldocchi 1994b) and latent and sensible heat flux densities (Norman 1979; Meyers & Paw U 1987; Baldocchi 1992). The validity of representing a deciduous forest canopy as a turbid medium, however, is questionable. Foliage of a broadleaf, deciduous forest is clumped and mean leaf inclination angles vary with height (Baldocchi *et al.* 1985; Hutchison *et al.* 1986). Such clumping enhances the probability of beam penetration over what would otherwise occur through a canopy with randomly distributed and spherically oriented leaves (Baldocchi *et al.* 1985). Under these conditions, there is potential for simple radiative transfer models to yield significant errors in the assessment of non-linear, energy-dependent processes. We there-

fore propose and test the following hypothesis.

Can simple radiative transfer models be used to integrate carbon and water flux of a broadleaf forest from the leaf to the canopy scale?

In the following sections, mass and energy flux densities are computed using two radiative transfer schemes. One scheme assumes that the spatial leaf distribution is random and its leaf angle orientation is spherical (we designate this the 'spherical' model). The other scheme accounts for the clumping of foliage and vertical variations in leaf inclination angles (we call this the 'clumped' model).

Net radiation balance

The net radiation balance of the canopy (R_n) must be simulated accurately if we are to compute latent and sensible heat and CO₂ flux densities correctly. To model R_n correctly it is necessary to compute the net transfer between incoming and outgoing short- and long-wave radiation throughout the foliage space. A comparison between measured and calculated net radiation flux densities (R_n) is presented in Fig. 2. Regression analysis reveals that both models account for a very high percentage of variance in

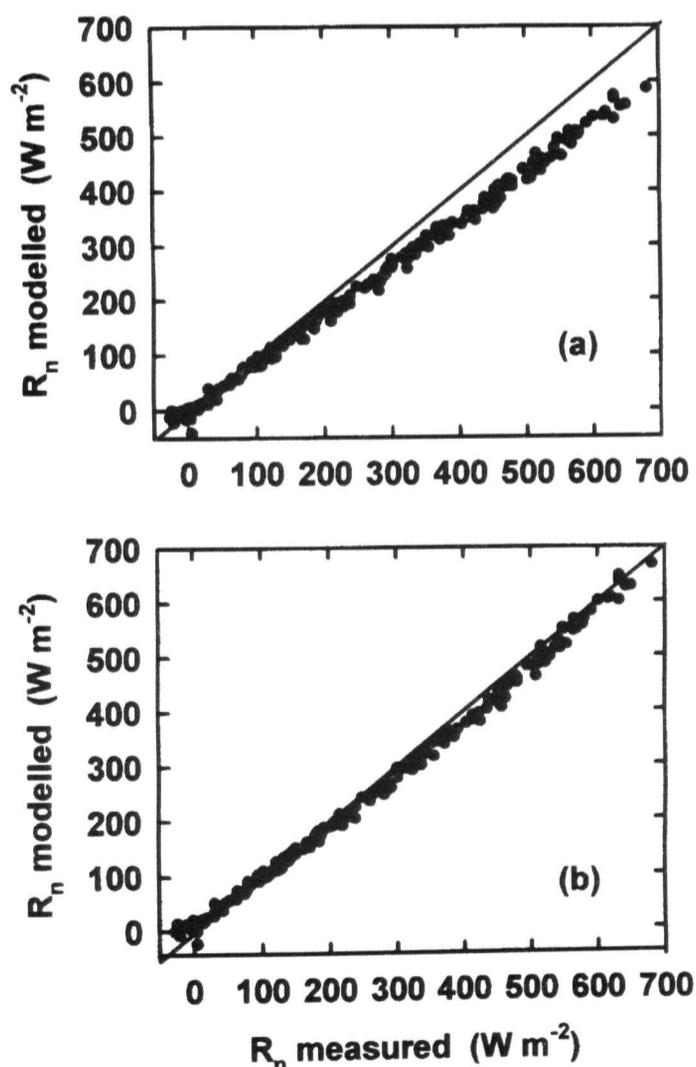


Fig. 2. A comparison between measurements and calculations of the net radiation balance over a deciduous forest. (a) Calculations were derived from the version of CANOAK that used a random and spherical radiative transfer model. (b) Calculations were derived from the version of CANOAK that used a negative binomial radiative transfer model, which accounts for clumping of leaves.

Table 2. Statistics for comparison between measurements and model calculations of micrometeorological flux densities. In this case, the model assumed that the foliage was randomly distributed with a spherical leaf inclination distribution. 197 samples were compared. Energy flux densities (R_n , LE , H and S) have units of $W m^{-2}$. Canopy CO₂ flux density has units of $\mu mol m^{-2} s^{-1}$

Variable	Intercept	Slope	r^2	Mean difference
R_n	-3.14	0.87	0.99	38
LE	11.2	0.69	0.86	47
H	25.7	1.09	0.80	-31
S	8.18	0.89	0.71	-7.8
F_c	-4.0	0.65	0.76	-8.38

measurements of R_n ($r^2 > 0.99$). On the other hand, the two models performed differently. Calculations of R_n from the radiation model that considered clumping and leaf angle variations agreed more closely with measurements than did calculations from the model that assumed that leaves were arranged spherically (Tables 2 and 3). Statistically, both radiative transfer models yielded estimates of R_n that were significantly different from their paired measured values. Nevertheless, the $12 W m^{-2}$ mean difference between calculations of R_n from the 'clumped' model and measured values is small and approaches the accuracy typical of the field measurements (Halldin & Lindroth 1992). Hence, we conclude that the 'clumped' radiative transfer model is better able to predict the canopy net radiation balance of a broadleaf deciduous forest.

Latent, sensible and soil heat exchange

The net radiation balance over a forest provides the energy that drives the transfer of sensible and latent heat and warms the soil. How well the models simulate these components is examined next.

Figure 3 compares measurements of latent heat flux density (LE) against calculations derived from the spherical and clumped radiative transfer models. The models accounted for more than 86% per cent of the variance in LE measurements (Tables 2 and 3), but the model calculations tended to

Table 3. Statistics for comparison between measurements and model calculations of micrometeorological flux densities. In this case, the model assumed that the foliage was clumped. 197 samples were compared. Energy flux densities (R_n , LE , H and S) have units of $W m^{-2}$. Canopy CO₂ flux density has units of $\mu mol m^{-2} s^{-1}$

Variable	Intercept	Slope	r^2	Mean difference
R_n	1.41	0.95	0.99	11.7
LE	8.96	0.82	0.86	25.9
H	0.98	1.31	0.78	-17.0
S	11.8	1.28	0.50	-16.1
F_c	-0.82	0.80	0.73	-1.65

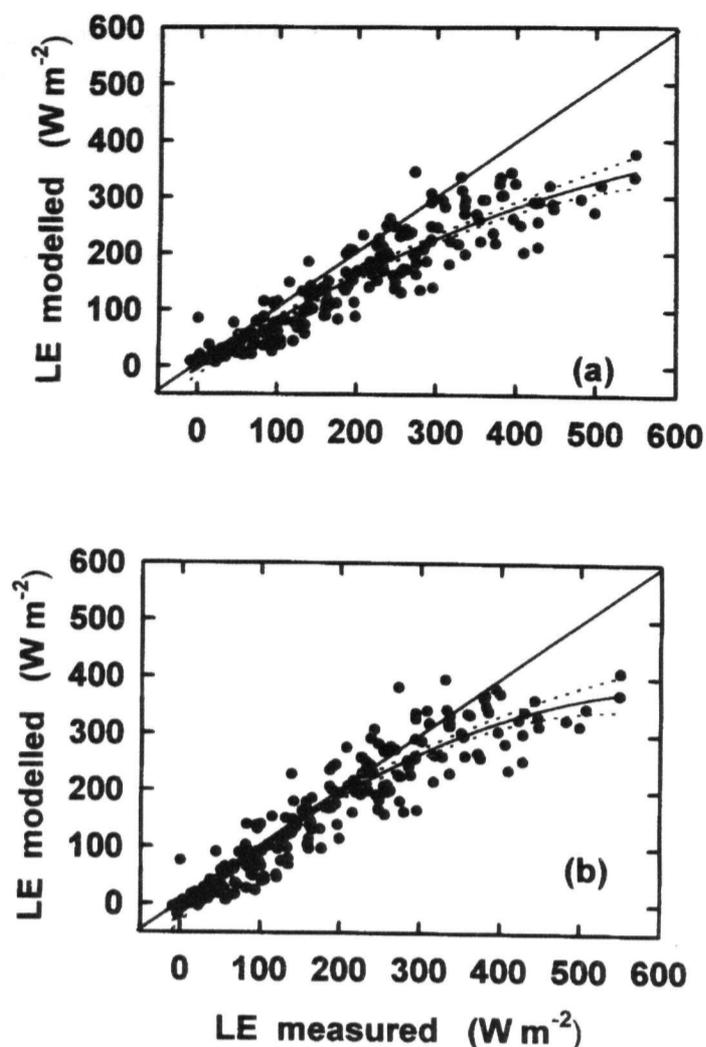


Fig. 3. A comparison between measurements and calculations of the latent heat flux densities over a deciduous forest.

- (a) Calculations were derived from the version of CANOAK that used a random and spherical radiative transfer model.
 (b) Calculations were derived from the version of CANOAK that used negative binomial radiative transfer model, which accounts for clumping of leaves.

underestimate measured latent heat flux densities. On average, the 'spherical' model underestimated LE by 47 W m^{-2} , while the 'clumped' model underestimated LE by 26 W m^{-2} (Tables 2 and 3). These differences were, respectively, 25 and 14% of the mean measured latent heat flux density.

Closer inspection of Fig. 3 reveals that the agreement between measurements and LE calculated with the 'clumped' model was non-linear. When the magnitude of LE was below 200 W m^{-2} , there was little difference between measured and simulated values, while at greater LE the model underestimated measurements.

Our ability to model latent heat exchange of a forest canopy relatively well with the 'clumped' model stems, in part, from the demonstrated ability to simulate the net radiation balance (Fig. 2) — net radiation is the primary variable driving LE of a deciduous forest (Verma *et al.* 1986) and accounts for about 70% of its variation. Additional sources of variation are attributed to leaf temperature, atmospheric humidity and stomatal conductance (g_s). We were unable to evaluate our ability to simulate leaf temperatures and humidity profiles directly. However, an underestimation of leaf temperature or atmospheric humidity would reduce the leaf-to-air vapour pressure gradient and cause latent heat flux densities to be underestimated, as observed. With respect to stomatal conductance, we have reasonable confidence in our

ability to compute this variable. We show in the companion paper (Harley & Baldocchi 1995) that the simple algorithm for computing stomatal conductance (Collatz *et al.* 1991) is robust and accounted for much variation in g_s .

Our recent adoption of the Collatz *et al.* (1991) stomatal conductance model into this canopy integration scheme merits additional comment. While this stomatal model is semi-empirical, it has several notable advantages over other semi-empirical models we have used (e.g. Jarvis 1976). One positive feature of the Collatz *et al.* model is its requirement of fewer tuning factors: once we know the photosynthetic variable, V_{cmax} , we have excellent guesses of the other variables, J_{max} and the base respiration rate, R_d , because they scale with one another (Collatz *et al.* 1991; Wullschlegel 1993). Another advantage stems from the linkage of g_s to photosynthetic capacity, which in turn scales with the nutrient status of leaves or the ecosystem (Schulze *et al.* 1994). We favour this linkage because it enables one to assign model parameters systematically. A weakness of the Collatz *et al.* algorithm involves its dependence on relative humidity instead of the vapour pressure deficit at the leaf's surface (Alphalo & Jarvis 1993).

Our ability to simulate sensible heat flux densities (H) is examined in Fig. 4 and Tables 2 and 3. This comparison

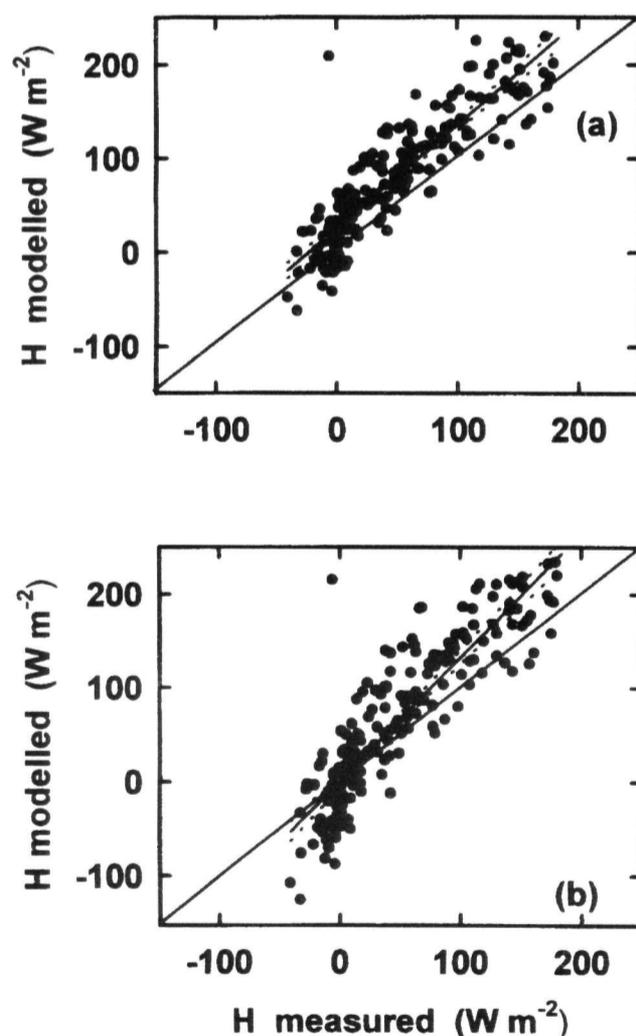


Fig. 4. A comparison between measurements and calculations of the sensible heat flux densities over a deciduous forest.

- (a) Calculations were derived from the version of CANOAK that used a random and spherical radiative transfer model.
 (b) Calculations were derived from the version of CANOAK that used a negative binomial radiative transfer model, which accounts for clumping of leaves.

between measured and calculated sensible heat flux densities shows that calculations of sensible heat flux densities (H) were highly correlated with measurements (r^2 exceeded 0.78), but tended to overestimate them. On average, the 'spherical' model overestimated measured sensible heat flux densities by 31 W m^{-2} , while the 'clumped' model overestimated measurements by 17 W m^{-2} . To give these discrepancies perspective, they constitute a bias within 11% of the mean net energy input into the forest (271 W m^{-2} ; Fig. 2).

Errors in simulating H can be partly attributed to the sensitivity of H to deviations in its driving potential (air minus leaf temperature). From Fig. 4b, for example, it can be inferred that we overestimated leaf temperature when H was greater than zero and underestimated leaf temperature when H was less than zero. Calculations of sensible heat flux density are very sensitive to its driving potential because its sensitivity ($\frac{\partial H}{\partial T}$) is inversely dependent on only one resistance, the canopy boundary layer resistance. In contrast, LE is less sensitive to changes in its driving potential because it is inversely dependent on the sum of the leaf and atmosphere boundary layer resistances and the stomatal resistances; the stomatal resistance of the leaf is typically greater than its boundary layer resistances.

The third component of the surface energy balance is the transfer of heat into the soil (S). Calculations of soil heat

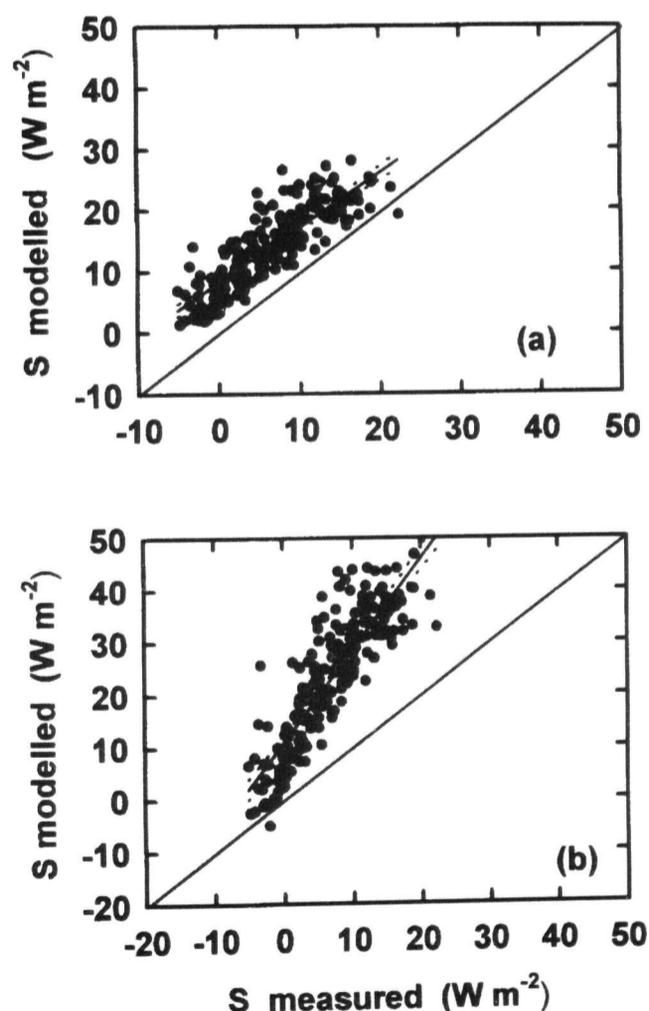


Fig. 5. A comparison between measurements and calculations of the soil heat flux densities over a deciduous forest. (a) Calculations were derived from the version of CANOAK that used a random and spherical radiative transfer model. (b) Calculations were derived from the version of CANOAK that used a negative binomial radiative transfer model, which accounts for clumping of leaves.

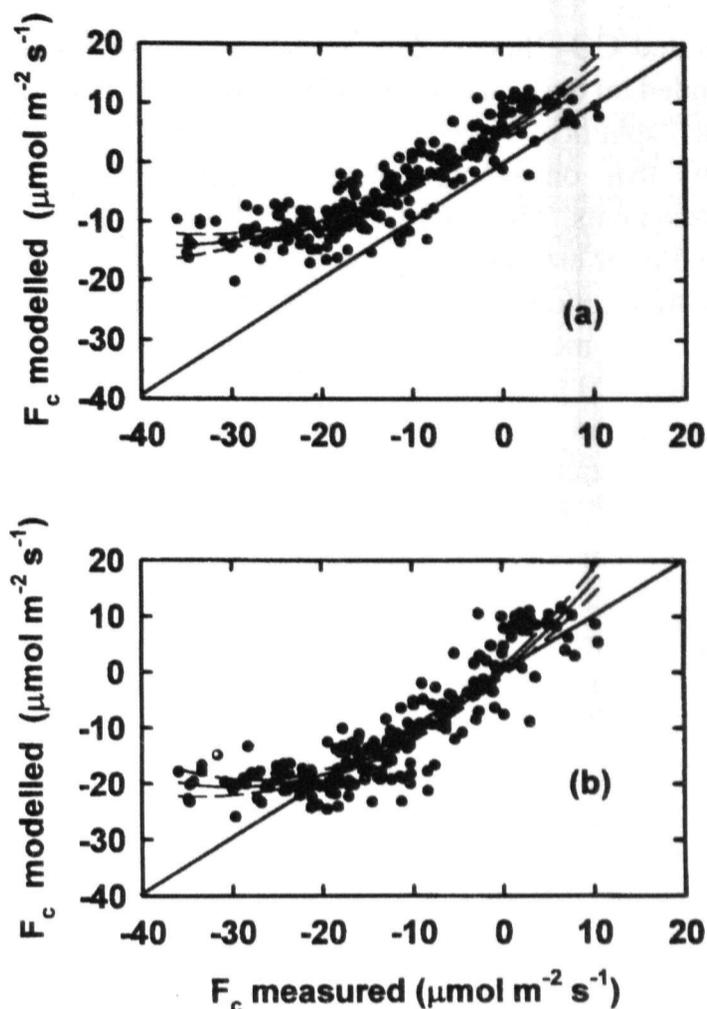


Fig. 6. A comparison between measurements and calculations of the CO₂ flux densities over a deciduous forest. (a) Calculations were derived from the version of CANOAK that used a random and spherical radiative transfer model. (b) Calculations were derived from the version of CANOAK that used a negative binomial radiative transfer model, which accounts for clumping of leaves.

conduction overestimated measurements constantly (Fig. 5; Tables 2 and 3). From a practical standpoint, the mean bias was small (within 16 W m^{-2}) considering the magnitude of the energy flowing into the system.

In the field, the residual energy not consumed as LE or H is consumed as S and heat stored in the biomass (C_s). We neglected canopy heat storage (whose magnitude can reach 50 to 100 W m^{-2}) since this model does not account for the transience of temperature and other environmental variables. Consequently, this residual storage term is effectively distributed among LE , H and S to attain energy balance closure. Additional sources of error attributed to the calculation of S arise from the simple parametrization of the soil resistance to evaporation, errors in the calculations of the net radiation balance at the soil surface and errors associated with assigning heat conduction coefficients to the litter and soil layers.

CO₂ flux densities

Calculations of canopy CO₂ flux densities involve estimates of leaf photosynthesis and leaf, bole and soil-litter respiration. Despite the integration of a plethora of complex and disparate processes, calculated canopy CO₂ flux densities accounted for over 73% of the variance in the measurements (Fig. 6; Tables 2 and 3). How well a canopy

integrated CO₂ flux model-simulated field measurements depended on the radiative transfer model that was used.

The 'spherical' model yielded estimates of CO₂ flux density that, on average, underestimated the direct field measurements. The 'clumped' model, on the other hand, yielded truer estimates of canopy CO₂ flux, but the agreement was conditional. In general, the 'clumped' model agreed with measured F_c values during the day until they exceeded $-20 \mu\text{mol m}^{-2} \text{s}^{-1}$. At this point, the 'clumped' canopy model saturated, while measurements show that the canopy could fix carbon dioxide at a rate as high as $-40 \mu\text{mol m}^{-2} \text{s}^{-1}$. At night, the 'clumped' model yielded calculations of canopy CO₂ flux densities that overestimated nocturnal measurements of canopy respiration.

The favourable agreement between the 'clumped' model and measurements indicates that model calculations of canopy CO₂ exchange are sensitive to how well radiative transfer and radiation-dependent driving variables (e.g. temperature and humidity deficits) are calculated. This latter observation is also consistent with our past work which indicated that the 'clumped' radiative transfer model yields truer estimates of photon flux densities throughout the canopy of this forest (Baldocchi *et al.* 1985).

From a broad perspective, one may consider that the 'clumped' models performed satisfactorily in view of the complexity of the system being modelled. For instance, the integrated sink strength is proportional to leaf area index and varies spatially by 20% (Chason *et al.* 1991). Furthermore, the model calculations for this multi-species forest were based on photosynthetic parameters of a single species, a sunlit *Quercus alba* leaf. In our companion paper (Harley & Baldocchi 1995) we report that significant spatial variability was observed among photosynthetic rates of leaves of similar and different species (e.g. *Acer rubrum*). On the other hand, the criterion for satisfactory model performance depends on the intended use of the model. If one's goal is to use the CANOAK model to compute daily and seasonal sums of net ecosystem carbon uptake, the $1.65 \mu\text{mol m}^{-2} \text{s}^{-1}$ bias error, noted in Table 3, adds up to $1.71 \text{ g C m}^{-2} \text{ d}^{-1}$ or 307 g C m^{-2} over a 180 d growing season.

Environmental control of canopy CO₂ transfer

Solar radiation

It is necessary to understand how CO₂ flux densities respond to key driving variables to develop simpler models. Both measured and calculated CO₂ flux densities were curvilinear functions of incoming photosynthetic photon flux density (PPFD) (Fig. 7). This response differs from observations made over crops, which show a highly linear response of F_c to PPFD (Denmead 1976; Baldocchi 1994b). For example, in Fig. 7, the r^2 value for the linear regression of F_c on PPFD was 0.75, while over wheat the linear regression between F_c and PPFD yielded an r^2 of 0.90 (Baldocchi 1993).

Why is the response of net canopy CO₂ uptake rates to PPFD curvilinear over a broadleaf forest? In a closed forest

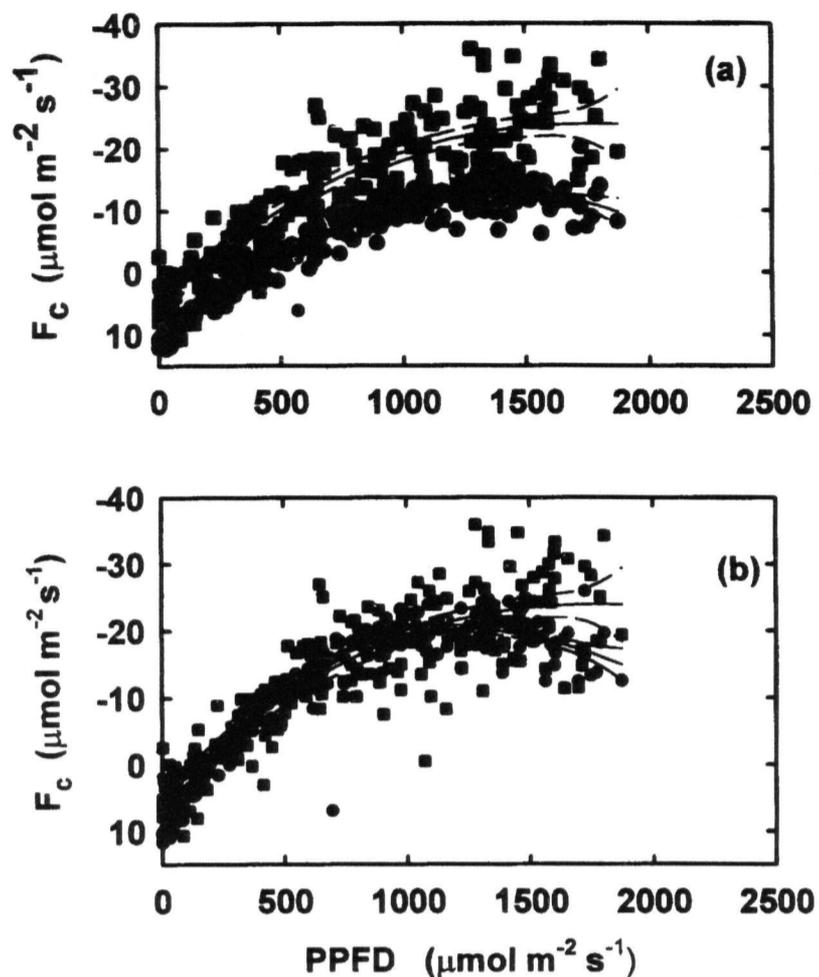


Fig. 7. The dependence of canopy CO₂ flux densities on incoming photosynthetic photon flux density. (a) Calculations were derived from the version of CANOAK that used a random and spherical radiative transfer model. (b) Calculations were derived from the version of CANOAK that used a negative binomial radiative transfer model, which accounts for clumping of leaves. Circles: measured; squares: calculated.

stand, the majority of leaves are shaded. One might expect photosynthetic rates of a forest canopy to increase linearly with additional light energy because photosynthetic rates of shade leaves can respond linearly to additional quanta. To address this question, we examined vertical profiles of W_c (the carboxylation rate when RuBP is saturating), W_j (the carboxylation rate when RuBP regeneration is limited by electron transport) and net photosynthesis rates and leaf temperatures on sunlit and shaded leaf fractions. Sunlit leaves, by definition, receive direct radiation regardless of depth in the canopy. Photosynthetic saturation, consequently, occurred over a wide range of irradiances on sunlit leaves (Fig. 8) because W_j exceeded W_c (data not shown). Under high irradiance ($\text{PPFD} > 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$), photosynthetic rates of sunlit leaves diminished because large radiation loads increased leaf temperature and respiratory carbon losses (the mean leaf temperature on sunlit leaves theoretically increased from 24.5 to 31.2 °C as PPFD increased from 500 to $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$). Photosynthetic rates of shade leaves were limited by W_j . Consequently, photosynthetic rates of shade leaves were linear functions of PPFD because additional PPFD incident on the canopy increased electron transport rates.

An examination of vertical profiles of beam and diffuse PPFD and leaf photosynthetic rates illustrates why the 'clumped' model delivered larger flux densities of CO₂

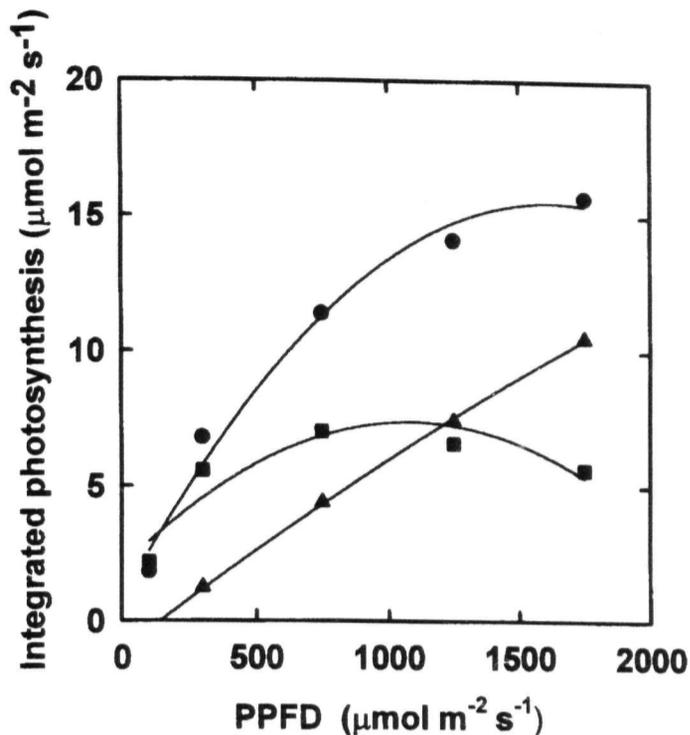


Fig. 8. Integrated photosynthetic flux densities for the canopy, and sunlit and shaded leaf area fractions. These calculations were based on environmental conditions for a clear day (direct radiation is 90% of incoming), with moderate temperatures (25°C) and moderate winds (3.0 m s⁻¹). Symbols: ●, total; ■, sunlit leaves; ▲, shaded leaves.

uptake than the 'spherical' model (Fig. 9). Higher flux densities of beam and diffuse PPFD were achieved deep inside a canopy with clumped leaves than within a canopy with random and spherically oriented leaves. Since the photosynthetic rates of shade leaves deep in a plant canopy do not saturate with respect to PPFD (Harley & Baldocchi 1995), they were able to respond to this additional solar radiation.

Soil

The computation of canopy CO₂ flux densities involves the parametrization of soil–root respiration. Independent measurements of CO₂ flux densities at the forest floor allowed us to inspect the validity of the soil–root respiration algorithm (Hanson *et al.* 1993). Figure 10a shows an average diurnal pattern of measured and calculated CO₂ efflux densities at the soil surface. Calculated CO₂ efflux densities approached 4 μmol m⁻² s⁻¹, while eddy flux measurements ranged between 2 and 4 μmol m⁻² s⁻¹. The measured values are modulated by variations in soil temperature (Fig. 10b) and an index of turbulent mixing, the standard deviation vertical velocity (Fig. 10c).

We discourage the reader from using these data to indict the soil CO₂ efflux algorithm. Both chamber and eddy correlation measurements at the forest floor are subject to sampling and measurement errors (Baldocchi & Meyers 1991; Hutchinson & Livingston 1992). Chamber-based measurements suffer from poor spatial replication and site modification effects. Understory eddy correlation fluxes, on the other hand, suffer from sampling errors resulting from intermittent turbulence and advection (see Baldocchi & Meyers 1991).

Carbon dioxide

Numerous experimental studies have demonstrated that rising atmospheric CO₂ concentrations will increase leaf photosynthesis and decrease stomatal conductance (Eamus & Jarvis 1989; Gifford 1992; Harley *et al.* 1992). There are fewer papers on how these leaf-scale physiological processes may scale to the canopy dimension (Long 1991; Reynolds *et al.* 1992; McMurtrie & Wang 1993). Even rarer are studies on how these physiological changes combine with environmental feedbacks to influence canopy carbon dioxide, evaporation and energy exchange (e.g. Jacob & deBruin 1992).

We attempt to remedy this deficiency by using the CANOAK model to examine how short-term energy and CO₂ flux densities of a deciduous forest may respond to a prescribed change of CO₂. Figure 11 shows calculations of canopy stomatal conductance (G_c), canopy photosynthesis (A_c) and latent heat flux density (LE) at CO₂ concentrations of 350 and 600 μmol mol⁻¹. Under high solar radiation loads (PPFD equalling 1800 μmol m⁻² s⁻¹), this prescribed change in CO₂ forces G_c to decrease by 16% and A_c to increase by 45%.

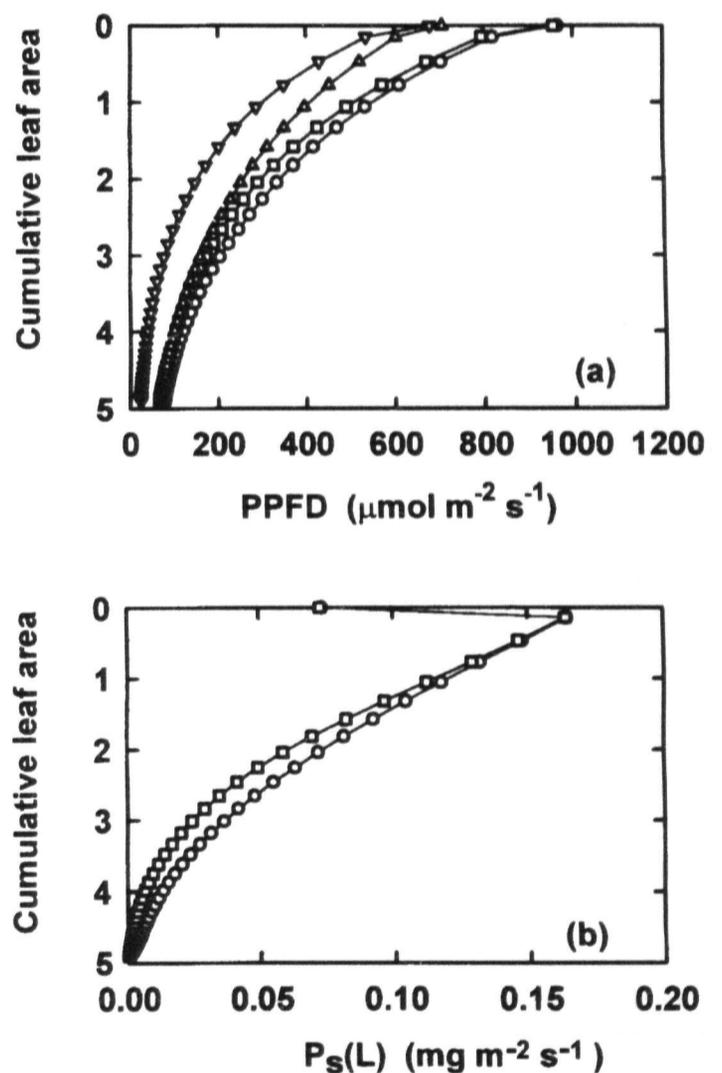


Fig. 9. (a) Vertical profiles of the flux densities of PPFD on the sunlit and shaded fractions of horizontal planes for a deciduous forest (day 210, 1100 h). Data were computed using the random and spherical and the clumped radiative transfer models. ○, P_{beam} clumped; □, P_{beam} spherical; △, P_{sh} clumped; ▽, P_{sh} spherical. (b) Vertical profiles of photosynthesis computed using the random and spherical and clumped radiative transfer models. ○, clumped model; □, spherical model. These computations are for a typical clear midday period.

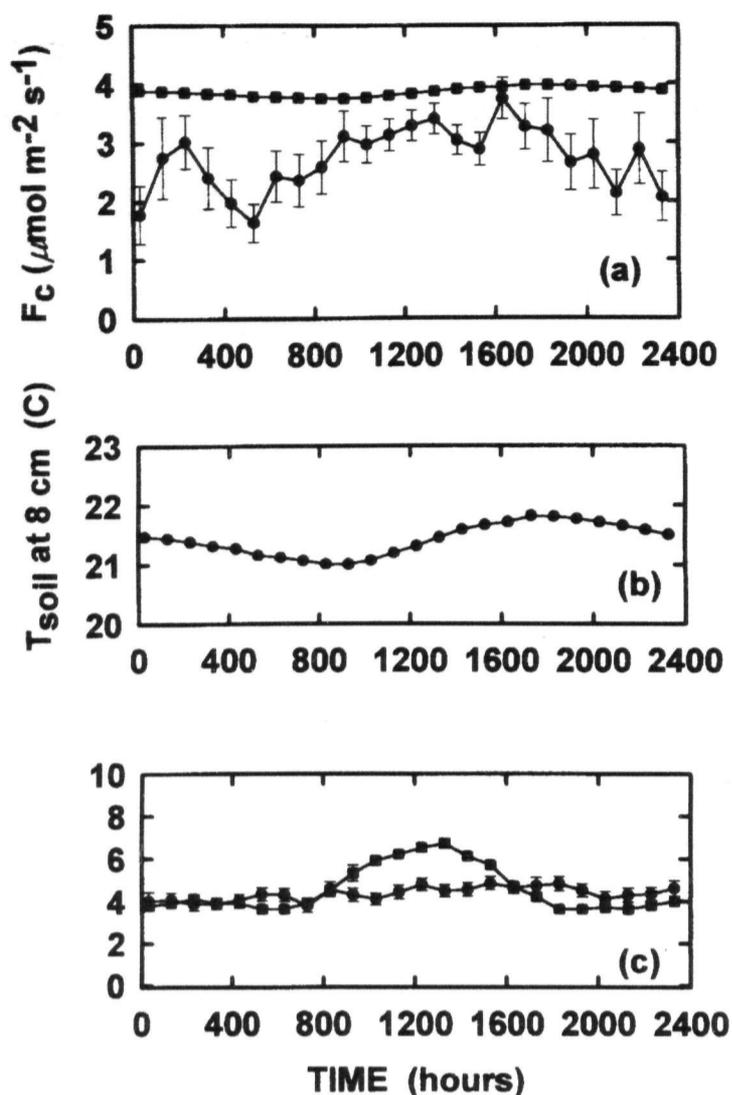


Fig. 10. (a) Mean daily trend of measured (—●—) and calculated (—■—) efflux densities of CO_2 on the floor of a deciduous forest. (b) Mean daily trend of soil temperature at 4 cm. (c) Mean daily trend of the standard deviations of vertical velocity (σ_w ; ■, cm s^{-1}) and static pressure (σ_p ; ●, Pa).

While leaf transpiration is proportional to stomatal conductance, the dependence of canopy evaporation on stomatal conductance is weaker. For example, the 16% decrease in G_c (from the prescribed change in CO_2) theoretically causes LE to decrease by only 4% and H to increase by 12% (data not shown). These calculations suggest that CO_2 -induced stomatal closure will have a small impact on the partitioning of energy under future global change scenarios.

Negative feedbacks involving the surface energy balance and humidification of the canopy airspace desensitize LE to variations in G_c (McNaughton & Jarvis 1991; Jacob & deBruin 1992). Consequently, partial stomatal closure does not cause a proportional decrease in transpiration at the canopy scale. Instead, a reduction in transpiration increases mean surface temperature and the vapour pressure deficit of air. This sequence of events re-establishes the vapour pressure gradient that drives transpiration and forces it to proceed near its original rate. This weakened sensitivity of LE to canopy stomatal conductance is consistent with field measurements over this forest (Verma *et al.* 1986).

On one hand, the results of this simulation should be viewed with caution. Omitted from these calculations are feedbacks concerning nutrient cycling and decomposition, which impact on photosynthetic capacity, soil-root respi-

ration, litter quality and canopy structure (Pastor & Pos 1988). Nor did these calculations consider the impact of CO_2 concentration on quantum yield, photosynthetic acclimation to high CO_2 (see McMurtrie & Wang 1993) and atmospheric feedbacks between the convective boundary layer and surface fluxes (Jacob & de Bruin 1992). On the other hand, one can argue that the simulations presented are plausible since they are derived from a validated and mechanistic model. Furthermore, the photosynthetic calculations are consistent with data from a CO_2 exposure study at a nearby site. Gunderson *et al.* (1994) reported that photosynthetic rates of *Quercus alba* seedlings growing under ambient plus $300 \mu\text{mol mol}^{-1}$ CO_2 were between 44 and 144% greater than those of seedlings growing under ambient Tennessee conditions. In addition, Gunderson *et al.* (1994) did not find any down-regulation of photosynthesis in treatments exposed to enhanced CO_2 and in the absence of irrigation and fertilization. The magnitude of the changes of canopy CO_2 uptake rates and stomatal conductance to CO_2 perturbations is also consistent with prior calculations by Long (1991), McMurtrie & Wang (1993) and Reynolds *et al.* (1992) for hypothetical crops and forests.

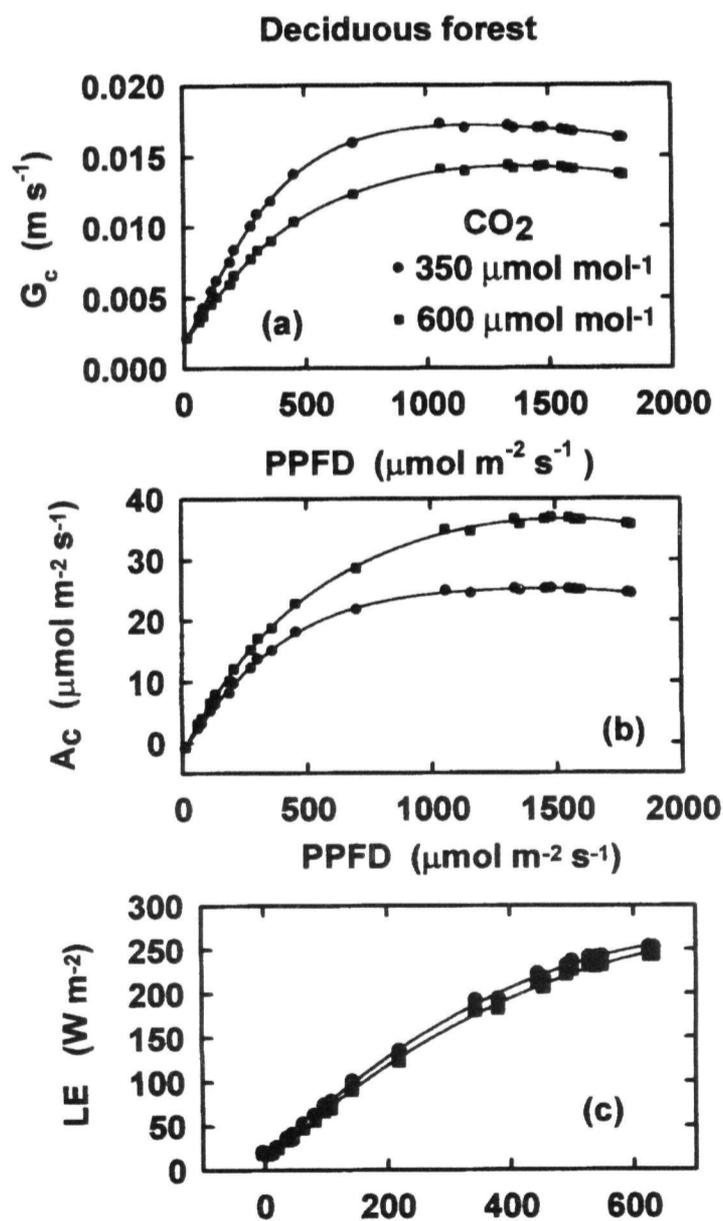


Fig. 11. The effect of changing CO_2 on canopy stomatal conductance (a), CO_2 flux density (b) and latent heat flux density (c). These calculations were based on environmental conditions having high PPFD ($1800 \mu\text{mol m}^{-2} \text{s}^{-1}$), moderate temperatures (25°C) and moderate winds (3.0m s^{-1}).

Physiological controls on canopy CO₂ transfer: photosynthetic capacity

Optimizing the allocation of resource

Leaf nitrogen is distributed with depth in a plant canopy to optimize (Gutschick & Wiegel 1988; Field 1991) or coordinate (Chen *et al.* 1993) canopy photosynthetic capacity. But what is the quantitative cost of optimizing photosynthetic capacity in deciduous forest?

Figure 12 shows simulations of canopy photosynthesis (A_c), as a function of PPFD, based on similar amounts of photosynthetic substrate distributed within the canopy in two different ways. One case assumes that the maximum carboxylation velocity ($V_{c\max}$) was constant with height, and the other case assumes that $V_{c\max}$ decreased linearly with depth into the canopy. Given the same amount of photosynthetic enzyme, we observe that PPFD-saturated canopy photosynthesis was 14% greater if photosynthetic capacity varied with depth instead of being held constant. From these simulations, and those of others (Gutschick & Wiegel 1988; Reynolds *et al.* 1992; Chen *et al.* 1993), the

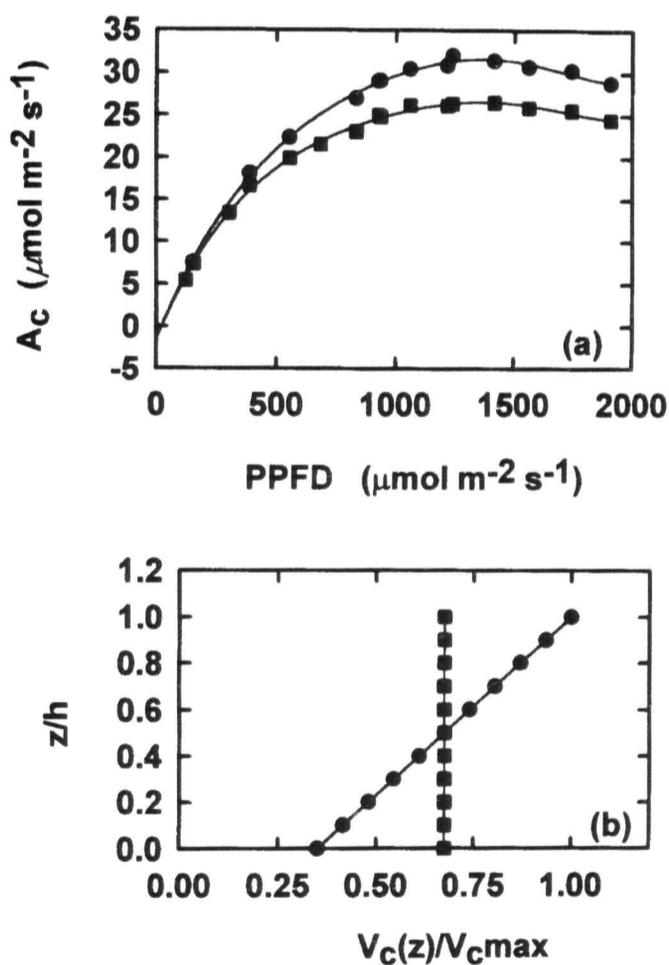


Fig. 12. (a) Impact of vertical variations of photosynthetic capacity (V_c) on canopy photosynthesis. Case one (●) assumes that V_c is a function of height. Case two (■) assumes that the V_c is constant with height. Integration of the area under each curve yields mean photosynthetic flux densities of 24.6 and 21.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively for cases one and two. Other environmental variables were held constant (temperature equalled 25°C, $[\text{CO}_2]$ equalled 350 $\mu\text{mol mol}^{-1}$ and wind speed equalled 3 m s^{-1}). (b) The variation of photosynthetic capacity (V_c) with depth in the canopy. The two curves allocate identical amounts of substrate to the computation of canopy photosynthesis.

conclusion can be drawn that it is advantageous for a plant stand to distribute nitrogen-containing enzymes systematically throughout the canopy in relation to the absorption of photons.

The influence of photosynthetic capacity on energy partitioning

The carbon, nitrogen and water cycles of a forest are tightly linked. Nitrogen availability moderates photosynthetic capacity (Field 1991), photosynthesis drives stomatal conductance (Collatz *et al.* 1990), and stomatal conductance regulates the partitioning of solar energy into sensible and latent heat transfer. Northern broadleaf forests, such as aspen, have lower photosynthetic capacity than forests in temperate regions (see Wullschleger 1993). This difference is a result, in part, of cooler soils in northern broadleaf forests which have lower rates of mineralization and less available nitrogen (Pastor & Post 1988; Bonan & Shugart 1989). The consequences that differences in N availability and photosynthetic capacity on the transfer of sensible and latent heat transfer, through consequential modifications of stomatal conductance have not been investigated.

Figure 13 shows the impact of different photosynthetic parameters on the sensible and latent heat exchange of a broadleaf deciduous forest growing in a temperate and a boreal region. One case uses parameters derived from this study and the other case draws on data from a boreal aspen forest (see Wullschleger 1993). A 2.5-fold decrease of J_{\max} was prescribed, to simulate the change in photosynthetic capacity as a broadleaf forest theoretically migrates from a temperate to a boreal region. This change in photosynthetic capacity led to a 30% increase in H and a 22% decrease in LE (when R_n equals 500 W m^{-2}). Such ecologically induced changes in surface energy partitioning are worth noting, for they may have an impact on weather and climate. For example, changes in H influence the growth of the planetary boundary layer (Jacob & de Bruin 1992), the humidification of the planetary boundary layer and the generation of convective clouds.

Long-scale ecological forcings will cause the noted changes to be exaggerated in the field. Lower rates of carbon uptake by the aspen stand will cause the mature forest to have less leaf area than its temperate cousin and a lower canopy stomatal conductance. This feedback will cause sensible heat flux and the maximum height of the planetary boundary layer to be greater than simulated.

Environmental control on water use efficiency

Humidity deficits

A host of field studies have shown that indices of short-term water use efficiency are inversely related to the atmosphere humidity deficit (e.g. Tanner & Sinclair 1983). One index of water use efficiency is the ratio between the flux densities of CO₂ uptake (F_c) and canopy evaporation (E).

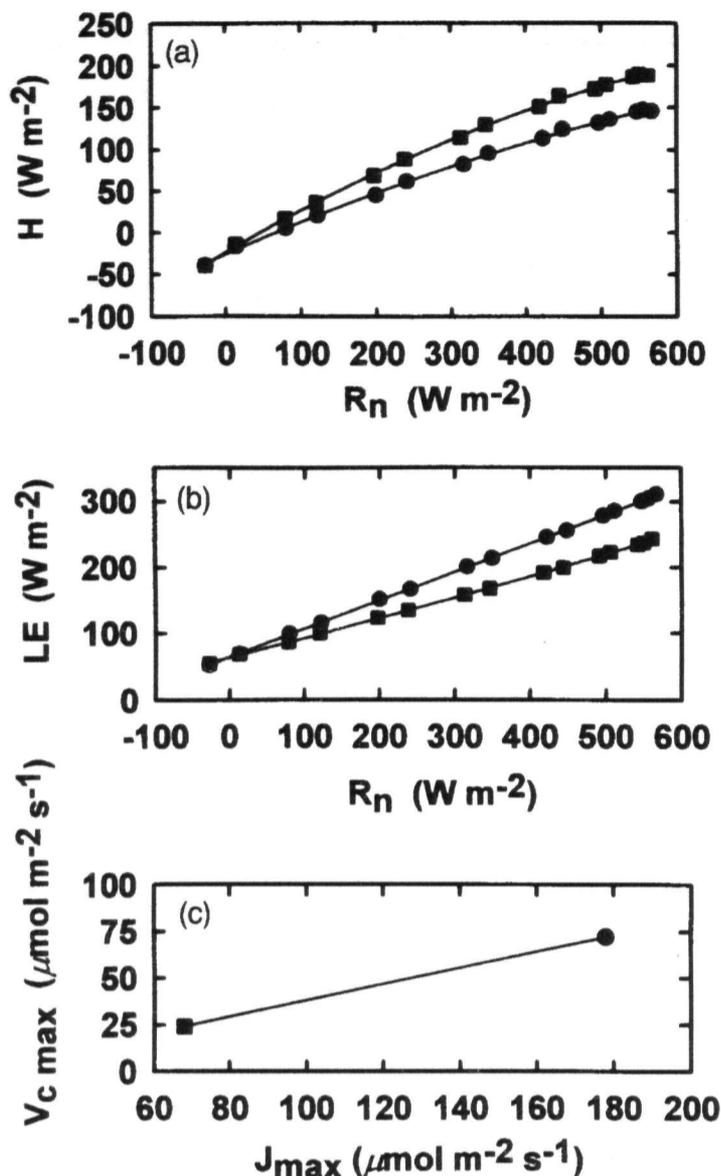


Fig. 13. The role of photosynthetic capacity in the calculation of (a) sensible heat transfer, (b) latent heat transfer, and (c) photosynthetic parameters for a typical temperate broadleaf forest (●) and a boreal aspen forest (■) (from Wullschleger 1993). For these calculations, structural features of the temperate and boreal forests were assumed to be identical. The following environmental variables were assumed: air temperature 20°C, wind speed 3 m s⁻¹ and relative humidity 75%.

Figure 14 presents measured and calculated values of water use efficiency, F_c/E . All estimates of water use efficiency were inversely dependent on humidity deficits. The fidelity of the model calculations, however, depended on which canopy radiative transfer model was used to generate these values. Calculations of F_c/E generated by the 'spherical' radiative transfer model fitted through the field data, while those generated by the 'clumped' model overestimated measurements. On the other hand, both models successfully mimicked the reciprocal dependence of F_c/E on humidity deficits.

SUMMARY AND CONCLUSIONS

We examined the ability to integrate fluxes of water and carbon from leaf to canopy dimensions of a mixed-species deciduous forest stand using contemporary micrometeorological and physiological models. Biases were observed between calculated and measured flux densities of net radi-

ation, latent and sensible heat and CO₂ flux densities. However, the size of the bias errors may be considered acceptable compared to the magnitude of available energy and the spatial variability of leaf area index (Chason *et al.* 1991) and leaf photosynthetic parameters (Harley & Baldocchi 1995).

Caution should be exercised when choosing a radiative transfer model to up-scale carbon fluxes from a leaf to a forest. Use of a simple radiative transfer model — one that assumes that the canopy is a turbid medium and its leaves have a spherical inclination angle distribution — causes calculations of net radiation and latent heat flux densities to underestimate field measurements. The simple radiative transfer model yields error-prone estimates of energy exchange because the clumped foliage of a deciduous forest enhances the probability of beam penetration. Scaling of energy flux densities improves if we use a radiative transfer model that accounts for the clumped architecture of a deciduous forest.

A validated and mechanistic carbon and water flux model has potential application to many ecological problems. Mooney *et al.* (1991), for example, argue that whole-ecosystem responses to elevated CO₂ concentrations

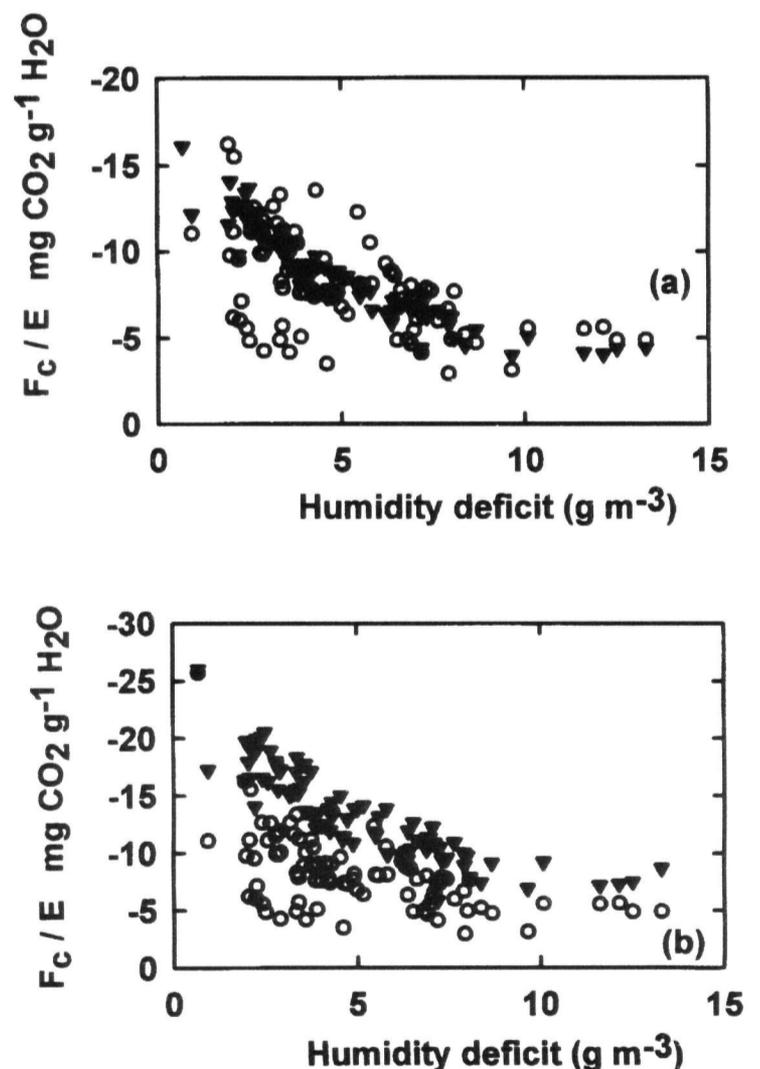


Fig. 14. (a) The dependence of the water use efficiency index (F_c/E) on the humidity deficit. Model calculations are based on the spherical radiative transfer model. Symbols: ▼, spherical model; ○, measured. (b) The dependence of the water use efficiency index (F_c/E) on the humidity deficit. Model calculations are based on the clumped radiative transfer model. Symbols: ▼, clumped model; ○, measured.

should be studied. From a practical standpoint it may be difficult to maintain enriched CO₂ concentrations around a forest ecosystem for a sustained period of time. Nor is it possible to make direct micrometeorological measurements of ecosystem carbon and water exchange over a small manipulated plot to measure the integrated forest response to elevated CO₂. An alternative approach is to treat a cohort of trees (e.g. to elevated CO₂), study their physiological and ecological responses to the treatment, and then use a model, such as CANOAK, to scale the responses to the whole canopy.

We made an initial attempt at this exercise by performing model simulations to investigate the role of changing CO₂ concentration and photosynthetic capacity on canopy mass and energy flux densities. Model calculations indicate that an increase of CO₂ concentrations from 350 to 600 $\mu\text{mol mol}^{-1}$ may increase canopy photosynthesis flux densities by 45% and reduce canopy stomatal conductance by 16%. Negative feedbacks involving humidity deficits and leaf energy balance, however, reduce the influence of stomata on canopy latent heat exchange. The prescribed change in CO₂ theoretically decreases *LE* by only 4%.

Finally, we used the model to evaluate the role of environmental and physiological variables on canopy-scale CO₂ exchange. Photon saturation of canopy CO₂ uptake rates occurs because photosynthetic rates of sunlit leaves are limited by the RuBP saturation and leaf temperature. This phenomenon contrasts with data from many crop studies, which reveal a linear relationship between CO₂ uptake rates and absorbed solar radiation (Baldocchi 1994b).

Optimization of the distribution of photosynthetic substrate provides a theoretical increase in canopy photosynthesis, as compared to allowing the same amount of substrate to be uniformly distributed throughout the canopy. Reductions in photosynthetic capacity (as one hypothetically migrates from a temperate to a boreal region) may also affect the partitioning of solar energy. Sensible heat transfer theoretically increased by 30% and latent heat transfer decreased by 16% as photosynthetic capacity decreased 2-fold. These data imply that linkages between ecological, physiological and climatic processes are important.

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