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Modeling CO_2 and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales

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Abstract

Fluxes of carbon dioxide, water and energy between a temperate deciduous forest and the atmosphere were quantified across time scales of hours, days, seasons, years and decades. This exercise was performed using stand-level eddy covariance flux measurements and a biophysical model, CANOAK. The CANOAK model was tested with measurements of carbon dioxide, water vapor and energy flux densities we have been collecting since October 1994. Model calculations reproduced 80% of CO_2 and water vapor flux variance that are contained in a year-long time series, when the model was forced with hourly weather data and seasonal information on plant structure and physiological capacity. Spectral analysis of measured and computed time series revealed that peak time scales of flux variance have periods of a day, half-week, season and year. We examined questions relating to inter-annual variability of mass and energy exchange by forcing the validated model with a decade-long meteorological record. Theoretical estimates of year-to-year variability of net ecosystem CO_2 exchange were on the order of ± 200 gC m^{-2} year. We also deduced that significant variance of water vapor and CO_2 exchange occurs on the time scale of 5–6 years, the time scale associated with El Nino phenomena. Sensitivity tests performed with the model examined issues associated with model complex and parameterization issues. Of particular importance were the effects of leaf clumping and length of the growing season on canopy photosynthesis and net ecosystem CO_2 exchange. Ignoring the effects of leaf clumping caused an error as large as 50% in the estimation of annual biosphere–atmosphere net carbon exchange. Each incremental day change in the length of the growing season altered the net ecosystem CO_2 exchange by 5.9 gC m^{-2}. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Biophysical model; Biosphere–atmosphere interactions; Canopy photosynthesis; Carbon balance; Evaporation; Net ecosystem carbon exchange

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1. Introduction

The rates at which carbon dioxide and water vapor are transferred between the biosphere and atmosphere depend upon a complex and non-lin-

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ear interplay among physiological, ecological, biochemical, chemical and edaphic factors and meteorological conditions (Jarvis, 1995; Leuning et al., 1995). Time scales of processes that produce or regulate the transfer of carbon dioxide and water vapor between the biosphere and atmosphere span hours, days, seasons, years (Baldocchi et al., 2000a; Jarvis, 1995; Wofsy et al., 1993) and decades (Grant et al., 1999; Kinderman et al., 1996). The spatial scales that impose variation on carbon dioxide and water vapor fluxes span the scale of leaves (Schuepp, 1993), their position in a canopy (Kull and Kruijt, 1999), the dimension of plant crowns (Wang and Jarvis, 1990) and their placement across a landscape (Schmid and Lloyd, 1999). How to model the biotic and abiotic processes that govern carbon dioxide and water vapor fluxes across a spectrum of biologically relevant time and space scales remains a challenge to contemporary ecologists (Amthor, 1994; Rastetter et al., 1992; Rastetter, 1996; Law et al., 2000a,b), biometeorologists (Jarvis, 1995; Leuning et al., 1995; Su et al., 1996; Baldocchi and Harley, 1998) and biogeochemists (Running and Hunt, 1993; Woodward et al., 1995; Kinderman et al., 1996; Hurtt et al., 1998; Cramer et al., 1999).

We, as a scientific community, possess a hierarchy and rapidly growing number of biophysical models that assess mass and energy exchange between vegetation and the atmosphere by coupling the fluxes of carbon dioxide and water vapor (Jarvis et al., 1985; Caldwell et al., 1986; Norman and Polley, 1989; Baldocchi, 1992; McMurtrie et al., 1992; Running and Hunt, 1993; Amthor, 1994; Amthor et al., 1994; Baldocchi and Harley, 1995; Bonan, 1995; Leuning et al., 1995; Waring et al., 1995; Aber et al., 1996; Denning et al., 1996; Sellers et al., 1996, 1997a; Su et al., 1996; Williams et al., 1996; De Pury and Farquhar, 1997; Landsberg and Waring, 1997; Hanan et al., 1998; Wang and Leuning, 1998; Grant et al., 1999; Anderson et al., 2000; Kellomäki and Wang, 2000; Law et al., 2000a,b; Verhoef and Allen, 2000; Wohlfahrt et al., 2000). The cited models vary in conceptual complexity, by how they treat the spatial and temporal variability of the canopy microclimate, the plant and community structure and the functionality of the ecosystem. With regards to the spatial domain, biophysical trace gas flux models treat the canopy as: (1) a big-leaf; (2) a big-leaf with dual sources; (3) two layers (one for plants and the other for soil); (4) multiple layers; and (5) a three-dimensional array of plants and canopy elements (e.g. Sinclair et al., 1976; Wang and Jarvis, 1990; Amthor, 1994; Baldocchi and Harley, 1995; Leuning et al., 1995; De Pury and Farquhar, 1997; Sellers et al., 1997a; Beyschlag and Ryel, 1999). With respect to temporal variability, carbon–water flux models with micrometeorological origins focus on radiative and turbulence transfer within and above the vegetative canopy and how stomata respond to environmental and physiological forcings. These models are capable of simulating the response of canopy-scale carbon and water fluxes to short-term weather variations over the diurnal course of fine summer days (Jarvis et al., 1985; Caldwell et al., 1986; Norman and Polley, 1989; Baldocchi, 1992; Leuning et al., 1995; Su et al., 1996; Williams et al., 1996; De Pury and Farquhar, 1997; Wang and Leuning, 1998). Models based on ecological and biogeochemical principles focus on how carbon and water fluxes may vary on daily, monthly and annual time scales (McMurtrie et al., 1992; Running and Hunt, 1993; Wang and Polglase, 1995; Waring et al., 1995; Aber et al., 1996; Kinderman et al., 1996; Landsberg and Waring, 1997; Hanan et al., 1998; Cramer et al., 1999; Law et al., 2000a,b). These models account for changes in plant, soil and root carbon pools by understanding their respective sizes and turnover times, but tend to oversimplify or ignore the effects of microclimate variability within a plant canopy. Biogeochemical models that extend to longer time scales need to consider disturbance by fire and land use change, nitrogen balance of plants and the soil and changes in stand composition, hydrological balance and climate (Hurtt et al., 1998).

The development, application and popularity of coupled carbon–water flux models have evolved rapidly over the past 3 decades in correspondence with a growing body of micrometeorological field data and physiological cuvette measurements. Prior to 1980, the majority of papers on this topic were mathematical exercises that used light dependent models for photosynthesis, stomatal conductance and transpiration (e.g. Miller, 1971; Sinclair et al., 1976; Goudriaan, 1977; Norman, 1979). The biochemically-based photosynthesis model by Farquhar and Caemmerer (1982) and its linkage to a photosynthetically dependent stomatal conductance algorithm (Collatz et al., 1991) revolutionized the topic of modeling carbon dioxide and water vapor fluxes by providing a theoretical framework for integrating leaf-level fluxes to the stand level. A special appeal of using coupled carbon–water flux models stems from their ability to constrain attributes of the system (Sellers et al., 1996, 1997a; Baldocchi and Meyers, 1998). The self-constrained nature of coupled carbon and water flux models enables contemporary scientists to extend these ideas to continental and global scale models that are addressing biogeochemical, meteorological, climatological problems (Woodward et al., 1995; Sellers et al., 1996, 1997a).

The earliest stand-level models that coupled carbon–water fluxes appeared in the literature during the mid 1980s and early 1990s (e.g. Jarvis et al., 1985; Norman and Polley, 1989; Kim and Verma, 1991; Baldocchi, 1992). Often these models were parameterized with data from the literature, rather than with data from the plants under investigation. Model tests were rare and when conducted were often based on less than 30 h of data that were attained during the peak of the growing season. Consequently, the accuracy of carbon and water flux density calculations was uncertain.

Limitations in the amount of physiological cuvette, which were needed to parameterize the models, and micrometeorological flux data, which were needed to test the models, began to diminish as the 1990s progressed. By this time, hundreds of papers on the functional behavior of leaf photosynthesis and stomatal conductance were becoming available in the literature. This growing body of data enabled Wullschleger (1993) and Schulze et al. (1994) to synthesize how photosynthetic and stomatal conductance model parameters varied with plant functional type and with such measures as leaf nitrogen content. Advances in the development of solid-state electronics enabled the design and fabrication of reliable meteorological flux instrumentation (e.g. Auble and Meyers, 1992). This feature enabled field experiments to be conducted for the duration of a month or more. Longer studies soon provided coupled carbon–water flux model developers with several hundred hours of data, a factor of ten increase, to test model performance, accuracy and scaling issues (Amthor et al., 1994; Baldocchi and Harley, 1995; Williams et al., 1996). At this stage the research community was able to address with statistical certainty a most fundamental question, whether we could integrate leaf-level flux information to the canopy scale during the peak of the growing season? The answer to this question was a qualified yes.

By the mid to late 1990's, the initiation of continuous and long-term carbon and water flux measurements (Wofsy et al., 1993; Grace et al., 1995; Black et al., 1996; Greco and Baldocchi, 1996; Valentini et al., 1996) and the execution of regional studies such as ABRACOS (Grace et al., 1995; Gash et al., 1996), HAPEX-Sahel (Goutorbe et al., 1997), BOREAS (Sellers et al., 1997b) and NOPEX (Halldin et al., 1999) provided the scientific community with another tenfold increase in data. Such data sets were used by Lloyd et al. (1995), Williams et al. (1996, 1998), Bonan et al. (1997), Baldocchi (1997), Hanan et al., (1998), Grant et al. (1999), Kimball et al., (1999); and Verhoef and Allen (2000), among others, for testing coupled carbon–water flux models over seasonal and annual time scales.

As we write this paper, at the start of the new millennium, the study at Harvard Forest has been ongoing for a decade and studies at Oak Ridge, TN, Prince Albert, Saskatchewan and Thompson Manitoba have over 5 years of data (Goulden et al., 1998; Chen et al. 1999; Wilson and Baldocchi, 2000) and a global network (FLUXNET) of over 120 long term eddy flux stations exists (Running et al., 1999). Consequently, data sets with over 50 000 h of flux measurements are now available to the modeling community. Tests of coupled carbon–water flux models on multi-year time scales plus are starting to be produced, yet the total number of papers that address and test models on this time scale is meager (Aber et al., 1996; Grant et al., 1999; Kimball et al., 1999; Law et al., 2000a,b).

With the availability of new and longer data sets new questions arise about the applicability and accuracy of coupled carbon–water flux models. The new applications of coupled carbon–water flux models needs to consider the seasonal dynamics of biology, as well as meteorology. This feature requires the dynamic adjustment of many model parameters that have been considered static in past applications, such as leaf area index (Greco and Baldocchi, 1996; Chen et al., 1999), photosynthetic capacity (Niinemets et al., 1999; Wilson et al., 2000a), basal rates of enzyme kinetics (Kull and Kruijt, 1999; Niinemets et al., 1999) and plant–water relations (Sala and Tenhunen, 1996; Williams et al., 1996; Baldocchi, 1997; Churkina et al., 1999).

Over a temperate broadleaved forest near Oak Ridge, TN, we have been monitoring meteorological variables since 1981 and we have been measuring fluxes of carbon dioxide, water vapor and energy across the canopy–atmosphere interface since October, 1994. The objectives of this paper are to quantify how CO_2, water vapor and energy exchange of a temperate deciduous forest vary across these multiple time scales and how weather, plant structure and physiological capacity impact these fluxes. To conduct this work, we employed an approach that combined stand-level eddy covariance flux measurements and a biophysical model, CANOAK. The eddy covariance flux measurement data are used to validate a biophysical model, CANOAK (Baldocchi and Harley, 1995; Baldocchi, 1997) on annual to multi-year times scales. We then use the model to quantify the impact of weather patterns and changes in plant structure and physiological capacity on annual and decadal scale fluxes of carbon dioxide, water vapor and sensible heat. Specific questions we address include: (1) how well does a biophysical model work over a spectrum of time scales, ranging from hours to years?; (2) how does weather, over a 17 year period, affect inter-annual variability of carbon and water fluxes?; (3) what are the dominant time scales of variance that are associated with the flux densities of carbon dioxide and water vapor over the period of a decade?; and 4) what are the roles of canopy structure, phenology, photosynthetic capacity and turbulence parameterization on annual time scale fluxes?

2. Materials and methods

2.1. Site characteristics

The experimental field site is located on the United States Department of Energy reservation near Oak Ridge, Tennessee (lat. 35° 57′ 30 N″; long. 84° 17′ 15W″; 335 m above mean sea level). The mean annual rainfall is 1372 mm and the mean annual air temperature is 13.9°C. The soil is classified as a Fullerton series, Typic Paleudult, otherwise described as an infertile cherty silt–loam.

The site is classified as an Eastern, mixed-species, broad-leaved deciduous forest. The predominant species in the forest stand are oak (*Quercus alba L.*, *Q. prinus L.*), hickory (*Carya ovata* (*Mill.*) *K. Koch*), maple (*Acer rubrum L.*, *A. saccharum*), tulip poplar (*Liriodendron tulipifera L.*), black gum (*Nyssa sylvatica* Marsh) and loblolly pine (*Pinus taeda L.*). In 1999, our team conducted a population survey within the flux footprint of the meteorological tower. Six transects, radiating 500 m from the central meteorological tower along axes of the predominant wind (22, 67, 112, 205, 247 and 292 degrees), were studied. Along each transect the species and basal area were evaluated in 10 m circular plots that were spaced every 100 m. The average species composition along these transects, on a basal area basis, was 14% pine, 16% maple, 5% hickory, 11% tulip poplar, 41% oak and 13% other deciduous species (data of Eva Falge, unpublished).

The forest has been growing since agricultural abandonment in 1940. When surveyed in 1979 the forest was 22.5 m tall and had a leaf area index of 4.9 (Hutchison et al., 1986). At present, the mean canopy height is about 26 m. The peak leaf area index is about 6.0 and typically occurs by day 140. Over the past few years, leaf out has occurred between day 90 and day 110 and leaf senescence has occurred between days 280 and 300.

2.2. Measurements, instrumentation and flux density calculations

A suite of CO_2, water vapor and sensible heat flux densities and meteorological and soil physics variables were measured concurrently. A set of micrometeorological instruments was supported 36.9 m above the ground (10 m over the forest) on a walk-up scaffold tower. Wind velocity and virtual temperature fluctuations were measured with a three-dimensional sonic anemometer (Applied Technology, Boulder, CO). Carbon dioxide and water vapor fluctuations were measured with an open-path, infrared absorption gas analyzer (Auble and Meyers, 1992).

Micrometeorological data were sampled and digitized ten times per second. In-house software was used to process the measurements. The software computed covariances between velocity and scalar fluctuations over half-hour intervals. Turbulent fluctuations were calculated from the difference between instantaneous and mean quantities. Mean velocity and scalar values were determined, in real-time, using a digital recursive filter. The digital filter algorithm employed a 400 s time constant. Extensive tests have shown that flux covariances computed with this time constant yield values that agree within 2% of covariances computed with conventional Reynolds' averaging.

The fast response CO_2/water vapor sensor was calibrated against gas standards. The calibration standards for CO_2 were traceable to those prepared by NOAA's Climate Monitoring and Diagnostic Laboratory. The output of the water vapor channel was referenced to a dew point hygrometer. Corrections for density fluctuations to CO_2 and water vapor fluctuations were applied to the scalar covariances that were measured with the open path sensor.

The CO_2 storage term was estimated, by finite difference, with a CO_2 profile measurement system. An automatically-controlled, solenoid sampling system directed air into an infrared gas analyzer (model LI 6262, LiCor Inc. Lincoln, Nebraska). Air was sampled from four levels above and within the forest (36, 18, 10, 0.75 m). Air from each level flowed through the analyzer for 30 s and data were sampled during the last 20 s of sampling. This scheme allowed a direct measurement of the profile every 120 s. The gas measurement system was automatically calibrated each day at midnight by passing gases of known concentration through the analyzer.

Photosynthetically active photon flux density and the net radiation balance were measured above the forest with a quantum sensor (LICOR model LI-190S) and a net radiometer (Swissteco Model S-1 or REBS model 6), respectively. A more detailed experimental design was implemented at the forest floor because the solar radiation field below a forest canopy is highly variable. To account for this variability, measurement of solar radiation components were made using an instrument package that traversed slowly across a prescribed domain; the measurement domain is 30 m long under the temperate deciduous forest.

Air temperature and relative humidity were measured with appropriate sensors (Vaisala, model HMP-35A). These sensors were shielded from the sun and aspirated. Wind speed and direction was measured with a propeller wind speed/direction monitor (RM Young model 05701). Static pressure was measured with a Vaisala model PTB101B sensor.

Soil heat flux density was measured by averaging the output of three soil heat flux plates (REBS model HFT-3, Seattle, WA). They were buried 0.01 m below the surface and were randomly placed within a few meters of the flux system. Soil temperatures were measured with two multi-level thermocouple probes. The sensors were spaced logarithmically at 0.02, 0.04, 0.08, 0.16 and 0.32 m below the surface. Three thermocouples were used to measure bole temperatures. Those sensors were placed about 1 cm into the bole and were azimuthally space across a tree at breast height. Canopy heat storage was calculated by measuring the time rate of change in bole temperature in the tree trunks. Ancillary meteorological and soil physics data were acquired and logged on Campbell CR-21x data loggers. The sensors were sampled every second and half-hour averages were computed and stored on a computer, to coincide with the flux measurements.

Additional information on the application of the eddy covariance method and shorter-term measurements of mass and energy exchange at this site are reported in companion papers by Greco and Baldocchi (1996), Baldocchi (1997), Baldocchi et al., (2000b) and Wilson and Baldocchi (2000).

2.3. Biophysical modeling of trace gas fluxes

CANOAK is a one-dimensional, multi-layer biosphere–atmosphere gas exchange model that computes water vapor, CO_2 and sensible heat flux densities and the microclimate within and above the forest. The model consists of coupled micrometeorological and eco-physiological modules. The micrometeorological modules compute leaf and soil energy exchange, turbulent diffusion, scalar concentration profiles and radiative transfer through the canopy. Environmental variables, computed with the micrometeorological module, in turn, drive the physiological modules that compute leaf photosynthesis, stomatal conductance, transpiration and leaf, bole and soil/root respiration. The model has been described and tested for summer length studies in Baldocchi and Harley (1995) and Baldocchi (1997). A brief overview is provided below.

2.3.1. Micrometeorology

The conservation budget for a passive scalar provides the foundation for computing scalar fluxes and their local ambient concentrations. We assumed that the a canopy is horizontally homogeneous and environmental conditions are steady. Based on this assumption, the scalar conservation equation was evaluated as an equality between the change, with height, of the vertical turbulent flux (F) and the diffusive source/sink strength, $S(C,z)$:

$$\frac{\partial F(C,z)}{\partial z} = S(C,z). \tag{1}$$

The diffusive source strength was computed using a resistance-analog relationship:

$$S(C,z) = - a(z)\frac{(C(z) - C_i)}{r_b(z) + r_s(z)} \tag{2}$$

where $a(z)$ is the leaf area density ($m^2\ m^{-3}$), $(C(z) - C_i)$ is the potential difference of scalar concentration or heat content between air outside the laminar boundary layer of leaves and the air within the stomatal cavity (mol mol^{-1}), r_b is the boundary layer resistance to molecular diffusion ($mol^{-1}\ m^2\ s^1$), and r_s is the stomatal resistance ($mol^{-1}\ m^2\ s^1$).

The light environment on sunlit and shaded leaves in a forest is very distinct and the response of many biophysical processes to that light is highly non-linear (Jarvis, 1995). We evaluated Eq. (2) at particular levels in the canopy on the basis of the radiation balance on the sunlit (p_{sun}) and shaded (p_{shade}) leaf fractions.

The transfer of photons through the canopy was simulated to evaluate the flux densities of visible, near infrared and longwave radiation, the probability of sunlit and shaded leaves, as well as photosynthesis, stomatal conductance, and leaf and soil energy balances. The radiative transfer model was derived from probabilistic theory (Norman, 1979). The radiative transfer model assumes that foliage is randomly distributed in space and the sun is a point source. In this case the probability of beam penetration was calculated using a Poisson distribution:

$$P_0 = \exp\left(-\frac{L\ G}{\sin \beta}\right) \tag{3}$$

where L is leaf area index, β is the solar elevation angle and G is the foliage orientation function. G represents the direction cosine between the sun and the mean leaf normal. For the ideal case, in which leaves have a spherical angle distribution, G is constant and equals one-half.

Typically, native vegetation has clumped foliage (Baldocchi and Collineau, 1994). In these circumstances, the Poisson probability density function is inadequate for computing probabilities of photon transmission through vegetation. Instead, the Markov model can be employed (Myneni et al., 1989) to compute the probability of beam penetration:

$$P_0 = \exp\left(-\frac{L\ G\Omega}{\sin \beta}\right) \tag{4}$$

where Ω is a clumping factor and ranges between zero and one.

Mathematically, the probability of sunflecks is equal to derivative of P_0 with respect to L times the average cosine of the leaf-sun angle (Gutschick, 1991). Integration of the sunfleck probability with respect to leaf area index yields the sunlit leaf area.

The probability of diffuse radiation penetration was computed by integrating equations for the probability of beam penetration over the sky's hemisphere. The scattering of light was computed for the visible and near infrared wavebands using the slab, 'adding' approach of Norman (1979).

The interdependence between sources and sinks ($S(C,z)$) and scalar concentrations ($C(z)$) requires the use of a turbulent diffusion model. A Lagrangian turbulence transfer scheme (Raupach, 1988; Baldocchi, 1992) was used to compute turbulent transport and diffusion. A dispersion matrix was computed using a stochastic differential equation that tracked the diffusion of an ensemble of fluid parcels. The algorithm accounts for inhomogeneity of turbulence statistics inside the canopy and the impact of atmospheric thermal stability on the variance of vertical velocity fluctuations. A turbulence diffusion model, based on the Lagranian framework, is preferred to 'K-theory' because counter-gradient transport occurs in this forest (Meyers and Baldocchi, 1991). Leaf boundary layer resistances for molecular compounds were computed using the Sherwood number based on flat plate theory (Schuepp, 1993). Under free convection, we computed the Sherwood number as a function of the Grasshof number and the leaf to air temperature difference (see Schuepp, 1993). To simulate wind speed, we applied the logarithmic wind law above the canopy and the exponential wind profile within it.

Leaf temperature was calculated by solving the leaf energy balance (Paw, 1987). This information was used to determine enzymatic rates associated with carboxylation, electron transport, and respiration and to evaluate transpiration, sensible heat fluxes and infrared emission.

Soil constitutes the lowest boundary of a canopy-scale, water vapor, CO_2 and trace gas exchange model. Flux densities of convective and conductive heat transfer and evaporation at the soil/litter boundary and soil temperature profiles were computed using a ten layer numerical soil heat transfer model (Campbell, 1985). Surface energy fluxes were computed using an analytical solution to a surface's energy balance. Soil evaporation was computed using an algorithm reported in Mahfouf and Noilhan (1991):

$$E_s = \frac{\rho_a}{R_{soil}}(\varphi \cdot q_{sat}(T) - q_a) \tag{5}$$

where R_{soil} is the resistance of the soil to evaporation, φ is the relative humidity of the soil matrix, q_a is the mixing ratio of the air and q_{sat} is the saturated mixing ratio. For these calculations we assumed R_{soil} was 816 s m^{-1} and that the vapor pressure at the evaporating site was 85% of the saturation vapor pressure ($\varphi\ q_{sat}\ (T)$).

2.3.2. *Eco–physiology: photosynthesis, respiration and stomatal conductance*

The biochemical equations for the carbon exchange processes are taken from Farquhar et al. (1980). Leaf photosynthesis (A) is a function of the carboxylation (V_c), oxygenation (V_o, photorespiration) and dark respiration (R_d) rates of CO_2 exchange between the leaf and the atmosphere (all have units of μmol m^{-2} s^{-1}).

$$A = V_c - 0.5\ V_o - R_d. \tag{6}$$

The term: $V_c - 0.5\ V_o$ is expressed by Farquhar et al. (1980) as:

$$V_c - 0.5\ V_o = [\min W_c, W_j]\left(1 - \frac{\Gamma}{C_i}\right) \tag{7}$$

where the term W_c represents the rate of carboxylation when ribulose bisphosphate (RuBP) is saturated and W_j is the carboxylation rate when RuBP regeneration is limited by electron transport. The variable, Γ, is the CO_2 compensation point in the absence of dark respiration (mol mol^{-1}) and C_i is the intercellular CO_2 concentration (mol mol^{-1}).

Stomatal conductance was computed with the algorithm of Collatz et al. (1991), which couples it to leaf photosynthesis and relative humidity.

$$g_s = \frac{m\ A\ rh}{C_s} + g_0. \tag{8}$$

The coefficient m is a dimensionless slope, rh is relative humidity at the leaf surface, g_0 is the zero intercept, C_s is the CO_2 concentration at the leaf

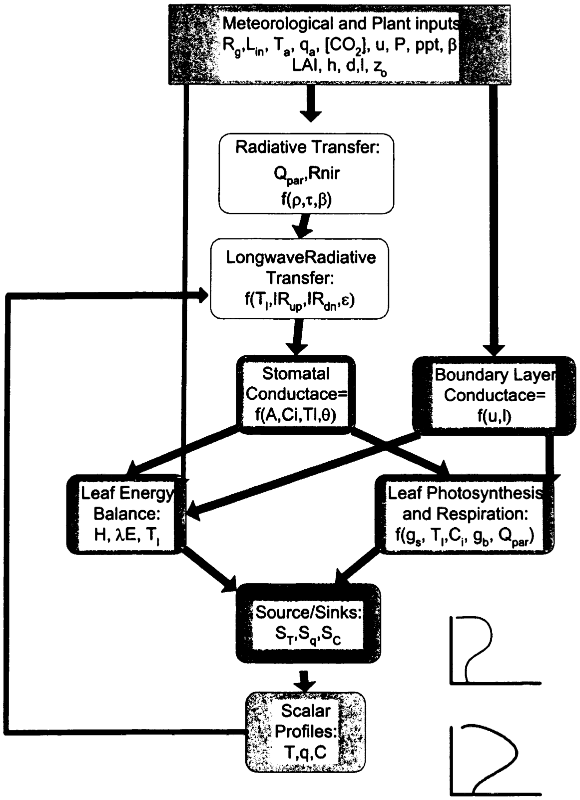

Fig. 1. Schematic of flow chart of the model algorithms used by CANOAK. The model is driven with hourly information on solar radiation (R_g), infrared radiation (L_{in}), air temperature (T_a), humidity (q_a), carbon dioxide (CO_2), wind speed (u) and pressure (P). Solar elevation (β) is computed for a known time, longitude and latitude. Plant inputs include photosynthetic capacity (V_{cmax}), leaf area index (L), canopy height (h), leaf size (l), aerodynamic roughness (z_o) and zero plane displacement (d) heights. Radiation profiles of photosynthetically active (Q_p) and near infrared radiation (R_{nir}) are computed through the canopy as a function of leaf reflectance (ρ, transmittance (τ) and sun angle. Upward and downward directed flux densities of long wave radiation are computed as a function of leaf temperature (T_l) and its thermal emissivity (ε). The light information is used to generate an initial estimate of stomatal conductance (g_s) and the wind speed data is used to estimate leaf boundary layer conductances. Next this information is used to compute leaf energy balance terms (sensible heat, H, and latent heat flux (λE) densities and leaf temperature), photosynthesis (A) and respiration (R_d). Next source and sink strengths of temperature (S_T), water vapor (S_q) and CO_2 (S_c) are computed, followed by computations of scalar profiles, using the Lagrangian diffusion model. New information on A, T_l and humidity are used to revise the computations of stomatal conductance. The sequence of computations is repeated until equilibrium is achieved.

surface and A (μmol m^{-2} s^{-1}) is leaf photosynthesis.

Respiration provides energy for metabolism and synthesis. At the leaf level, we assessed dark respiration as a function of V_{cmax} (Collatz et al., 1991) or its surrogate leaf nitrogen (Vose and Bolstad, 1999) and temperature. A typical value for R_d equals 0.015 times V_{cmax}. An Arrenhius equation was used to adjust respiration rates for temperature. For the species under study respiration rates double with a 10°C increase in temperature (Vose and Bolstad, 1999). Soil respiration was computed with a relation based on the Arrhenius equation (Hanson et al., 1993).

2.4. Model architecture, parameterization, and validation

Fig. 1 shows a flow chart of the model components and their links. A suite of external meteorological variables drive the model. These variables include shortwave radiation, air temperature, relative humidity, wind speed, CO_2 concentration and local time. Based on the local time, longitude and latitude, the model first computes the sun angle. Next the model computes photon transport through the foliage space. These computations produce estimates of flux densities of visible, near infrared and infrared radiation and the fractions of sunlit and shaded leaf area. Computations are performed by abstracting the canopy into 40 layers of equal leaf area. Solar radiation information is used to produce an initial estimate of stomatal conductance. In turn, these products are used to compute leaf photosynthesis, leaf energy fluxes (latent and sensible heat), leaf temperature, and respiration. Information on scalar source/sink strengths (water vapor, heat and CO_2) and turbulent mixing are used to compute scalar profiles of temperature, humidity and CO_2 within and above the canopy. Iterations are performed on revised estimates of long wave radiation emission, stomatal conductance and scalar source-sink strengths for heat, water vapor and CO_2 until equilibrium is achieved between the flux profiles and their local scalar fields.

Two key plant input parameters in CANOAK are leaf area index and the maximum carboxyla-

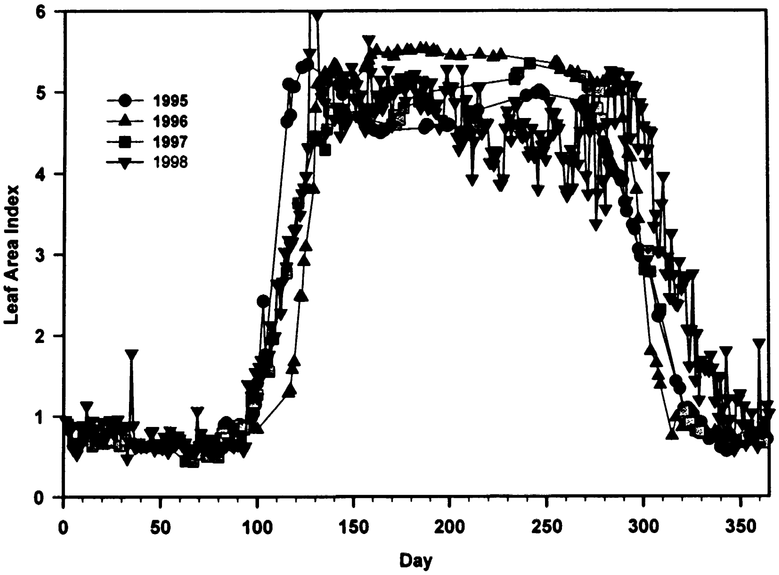

Fig. 2. Seasonal variation in leaf area index for the years 1995 through 1998.

tion rate, V_{cmax}. Seasonal changes in leaf area were derived from measurements of light transmission and litter collection since 1995 (Fig. 2). Estimates of bud-break, in prior years, were assumed to correspond with the day when mean soil temperature exceeded the mean annual temperature of 13°C. We have tested this concept using data from temperate deciduous forests across the FLUXNET network. We found that 75% of the variance in the date of budbreak was predicted using a linear regression between the day that the mean soil temperature equaled the mean annual temperature (Fig. 3). Full leaf was assumed to occur 30 days after bud break.

Data on leaf photosynthetic properties were derived using an environmentally controlled cuvette system (LICOR 6400) on oak leaves (*Quercus alba; Q. prinus*), maple (*Acer rubrum*) and black gum (*Nyssa sylvatica*) (Harley and Baldocchi, 1995; Wilson et al., 2000a). Values of photosynthetic model parameters are listed in Table 1. These rate coefficients are scaled according to leaf temperature, position in the canopy and time of year. We used the algorithm of Harley and Tenhunen (1991) to adjust V_{cmax} with temperature, relative to an optimal temperature (311 K). We

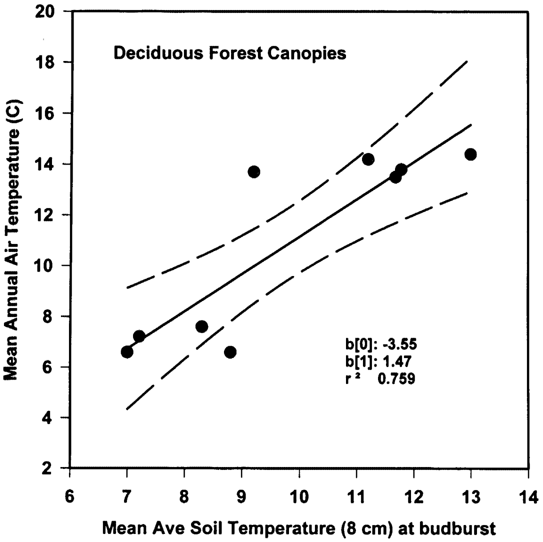

Fig. 3. The relation between mean annual air temperature and the mean soil temperature at budbreak. This relation is used to trigger phenological onset of leaf out during the multi-year calculations. The data come from field sites near Oak Ridge, TN, Borden, Ontario, Solling, Denmark, and Bloomington, Indiana.

Table 1
Parameter values used by the CANOAK model in the simulations of canopy CO_2, water vapor and energy exchange

Parameter	Value	Units
V_{cmax}(311°K)[a]	73	$\mu mol\ m^{-2}\ s^{-1}$
J_{max}	2.32 V_{cmax}	–
R_d	0.0046 V_{cmax}	–
LAI max	6	
Canopy height	26	m
Leaf length	0.10	m
Stomatal conductance factor	9.5	
Quantum yield	0.22	
Markov clumping factor	0.84	

[a] V_{cmax} at 25°C is 39 $\mu mol\ m^{-2}\ s^{-1}$.

note that the reference value of V_{cmax} at 311 K is equal to 39 umol $m^{-2}\ s^{-1}$ at 25°C and corresponds with the geometric mean of data for white and chestnut oak, red maple, sugar maple and black gum around day 225 (Wilson et al., 2000a). Other biochemical rate constants, used for photosynthesis, such as the maximum rate of electron transport (J_{max}) and dark respiration rate (R_d), were scaled to the maximum carboxylation rate (V_{cmax}) (e.g. Wullschleger, 1993; Wilson et al., 2000a). We varied V_{cmax} with depth in the canopy to reflect its dependency on vertical variations in specific leaf weight and leaf nitrogen content. For the purposes of these computations we assumed that V_{cmax} decreased linearly with depth in the canopy. Seasonal variations in V_{cmax} were linked to seasonal changes in leaf area index. The seasonal change in photosynthetic capacity was computed to vary as a fraction of full leaf area, which is a simpler representation of the results reported by Wilson et al. (2000a).

As long as environmental driving data are available, models can produce information on fluxes as they may occur 24 h a day, 365 days a year. In contrast, much meteorological flux data must be rejected due to instrument malfunction and limitations imposed by constraints on the application of the eddy covariance method (Foken and Wichura, 1995; Baldocchi et al., 2000b). Of course it is impossible to expect perfect data capture over the course of a year or many years. Fortunately, gaps in the meteorological data were typically less than a few percent of the total. When gaps in the meteorological record occurred, they were filled using redundant instruments or with interpolation. Applying strict acceptance/reject criteria to the flux measurement record caused about 40% of the data to be rejected. We used the gap filling procedure of Falge et al. (2000) to generate missing data and to construct a continuous dataset. Using gap-filled data to test the model does not introduce any bias since we are able to sample statistical population with adequate redundancy to produce a robust estimate of the population mean (Falge et al., 2000; Lianhong Gu, personal communication).

3. Results and discussion

3.1. Model testing

Science is based on the foundation of the proposition and testing of hypotheses. Yet, rarely are we able to prove a hypothesis, rather we must try and falsify a theory (Popper, 1959). Ecosystems are hierarchal and multi-scaled. In practice, no trace gas exchange model will pass the stringent falsification criteria, which has been advocated by Popper (1959). So how does one make progress? Rastetter (1996) argues that we must test models with scale appropriate data.

Biophysical models, such as CANOAK, produce information that represents the mean response to a set of environmental conditions. To perform faithful tests between model computations and eddy flux measurements, we averaged the eddy flux measurements over 2 weeks periods. Averaging of eddy flux data is needed to reduce the run-to-run variability that is associated with individual periods (Moncrieff et al., 1996). Natural variability generally ranges between 10 and 30% and is due to the stochastic nature of turbulence and spatial variability of the vegetation. Two-week periods were chosen because this period is an appropriate length whereby phenological or physiological changes are minimal, as deduced by its correspondence with a spectral gap in the long-term flux measurement record (Baldocchi et al., 2000b).

Fig. 4a shows how well calculations of canopy CO_2 exchange, generated by the CANOAK model, were able to reproduce measured temporal patterns and magnitudes of CO_2 exchange. On hourly, daily and seasonal time scales the fidelity between measured and computed values was high. Model performance is quantified in Fig. 4b via a linear regression between measured and computed flux densities. The linear regression through the independent test data and dependent model data yielded a zero intercept of 0.908 μmol m^{-2} s^{-1}, a slope of 1.085 and a coefficient of determination

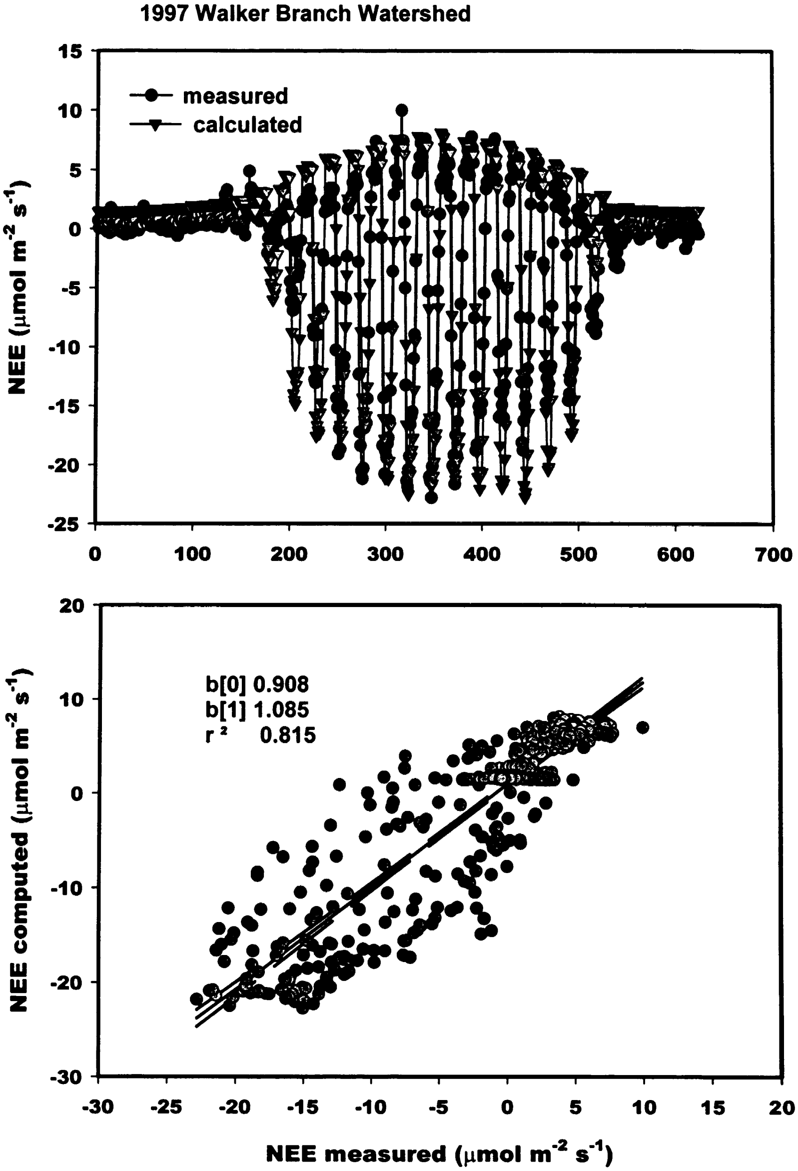

Fig. 4. (a) Mean diurnal patterns of computed and measured rates of net ecosystem–atmosphere CO_2 exchange. The measurements were derived from the eddy covariance method. Calculations were derived from the CANOAK model. The data were bin-averaged by hour for 2 week periods during 1997, a wet year. (b) One to one regression plot between measured and computed flux densities of CO_2 exchange. Negative values represent a loss of carbon from the atmosphere and a gain by the biosphere

(r^2) of 0.815. These statistical parameters suggest that over 80% of the variance in field measurements was accounted for by computations made with the CANOAK model.

Coefficients of variance exceeding 0.80 are becoming a typical figure of merit for tests of biophysical models that couple carbon–water flux sub-models and account for non-linear forcings of photosynthesis, stomatal conductance and respiration by considering the energy balance of sunlit and shaded leaves. A similar and high level of model performance ($r^2 > 0.80$) was achieved by Williams et al. (1996) for a hardwood forest, by Hanan et al. (1998) and Verhoef and Allen (2000) for savanna and Anderson et al. (2000) for cropland, for example.

Another criterion for testing a model is whether or not it computes accurate component fluxes. Our test of the CANOAK model produced an internally-consistent ratio between plant respiration (R_{pl}) and photosynthesis (P_c). Based on independent scaling of leaf and soil fluxes, the ratio between R_{pl} and P_c, on an annual basis, was 0.51. This value in close agreement with assessments by Gifford (1994) and Waring et al. (1998) for growing plants.

Fig. 5a shows how well the CANOAK model was able to reproduce temporal patterns and magnitudes of latent heat exchange over the course of a year. By coupling fluxes of carbon and water, the model was able to mimic the temporal pattern of measured latent heat flux densities with high fidelity, too. With regards to reproducing absolute flux densities of latent heat exchange, the model overestimated measurements, on average by 14%; the linear regression through the independent test data and dependent model data yielded a zero intercept of 4.96, a slope of 1.14 and a coefficient of determination (r^2) of 0.83. Similar levels of agreement have been reported by Kellomäki and Wang (1999) for a boreal forest, Anderson et al. (2000) for crop lands and Verhoef and Allen (2000) for savanna.

We are uncertain if the difference between measured and modeled λE reflects errors in the model or the measurement. Measurements of energy balance closure suggest that λE may be low because we underestimate closure of the energy balance by 20–25% (Wilson and Baldocchi, 2000). On the other hand, a comparison between our annual sum of evaporation versus an independent estimate, derived by the hydrologic balance of the watershed agreed, within 5% (Wilson et al., 2001).

The time step at which model calculations are integrated can affect its performance. Leuning et al. (1995), for example, report that the light response curve for canopy CO_2 exchange is curvilinear, when it is quantified using hourly data, but is linear when one uses daily-integrated data. Consequently, the impact of integrating non-linear biophysical processes changes with time step. In Fig. 6 we compare model calculations with daily sums of CO_2 exchange, as this is a common time step used by many biogeochemical models (Cramer et al., 1999). The agreement between model calculations and measurements deteriorate markedly when we compare daily integrals. For example, the coefficient of determination, r^2, drops to 0.55.

Poorer model performance, as deduced by comparisons against daily-integrated flux measurements, does not necessarily result from errors in the model. Previous studies at the Walker Branch Watershed suggest that the eddy covariance method underestimates respiration at night and during the winter (Baldocchi, 1997; Baldocchi and Meyers, 1998; Baldocchi et al., 2000b). At night under stable atmospheric thermal stratification, CO_2 evolved from the understory drains down hill and does not cross the plane of the eddy covariance system that is mounted above the canopy. Another source of variance between measurements and computations can stem from how the flux footprint and the species viewed by the tower varies with wind direction and atmospheric stability (Amiro, 1998).

In order to isolate impacts of nighttime and wintertime measurement error, we examined model performance for daytime periods during the growing season. In this case, biases associated with the slope and the intercept of the regression diminished but scatter increased (slope equal 1.00; intercept equaled -0.36 μmol m^{-2} s^{-1}; r^2 equaled 0.616).

For perspective, Law et al. (2000a) report an r^2 value of 0.51 and a slope of 2.38 when comparing the lumped-parameter PNET II model (Aber et

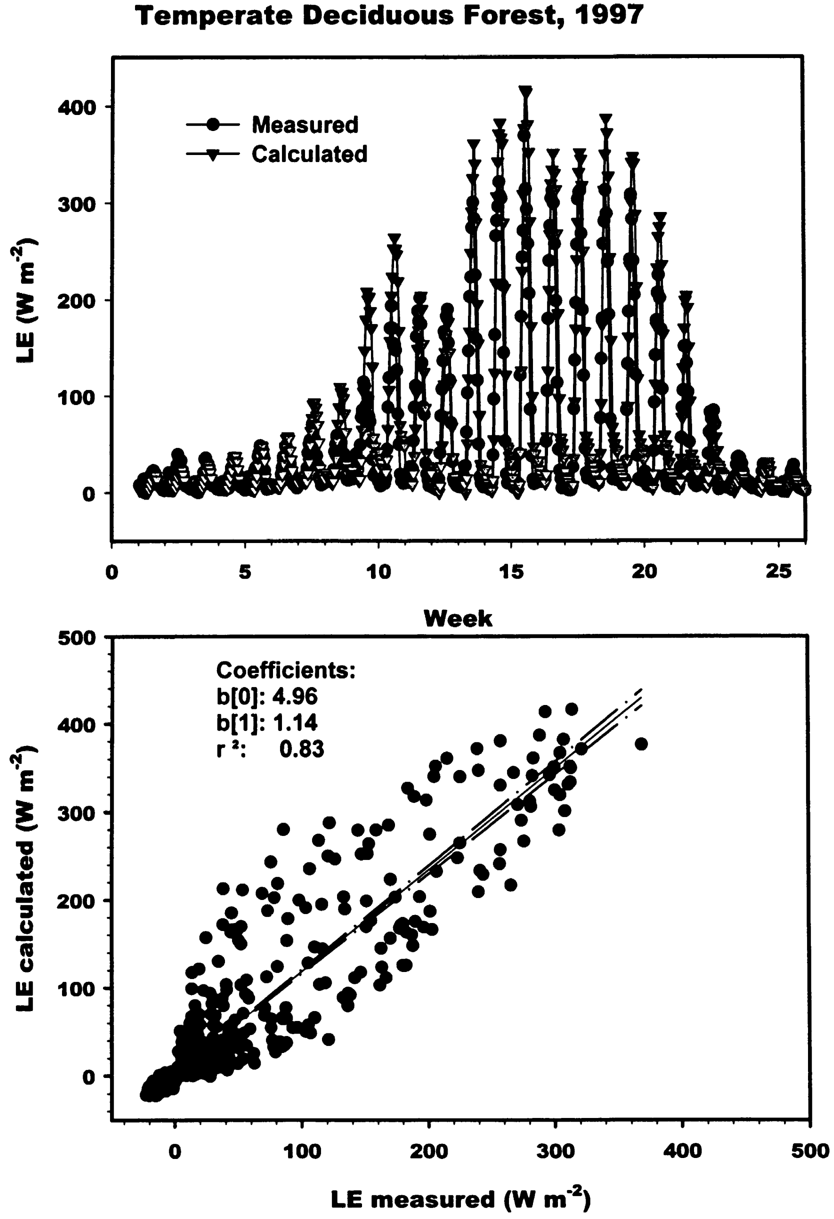

Fig. 5. (a) Mean diurnal patterns of computed and measured rates of latent heat flux. The measurements were derived from the eddy covariance method. Calculations were derived from the CANOAK model. The data were bin-averaged by hour for 2 week periods during 1997, a wet year. (b) One-to-one regression plot between measured and computed flux densities of latent heat.

al., 1996) against daily-integrated flux data from a semi-arid ponderosa pine stand. A version of the CANOAK model, adapted to ponderosa pine, compared against those data and experienced low r^2 values, too (Law et al., 2000a). In contrast, Kellomäki and Wang (2000) found that averaging data over the course of a day improved upon the coefficient of variance when they compared calculated and measured values of net CO_2 exchange over a boreal forest for half-hour and daily time steps over a 25 day period. In their case, r^2 increased from 0.72 to 0.83, when they examined daytime data only and r^2 increased from 0.61 to 0.74 when examined nighttime data.

Despite the favorable agreement between the data and model calculations we cannot claim that we have proven that the CANOAK model is completely successful. Sources of errors in any model test abound and stem from uncertainties in: (1) model parameters; (2) meteorological driving variables; (3) the functional representation of the biophysical system; (4) the time and space resolution of the model and (5) errors in the flux measurements that are used to validate the model.

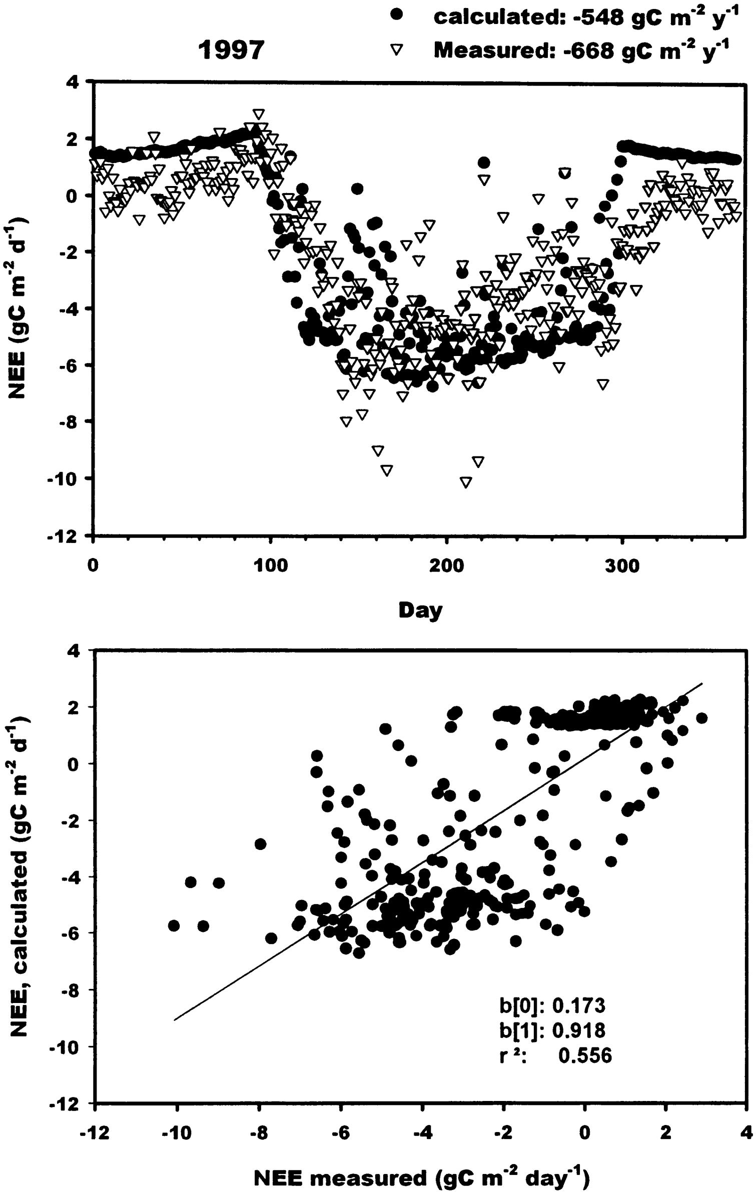

Fig. 6. Comparison between measured and calculated sums of daily CO_2 exchange over a temperate deciduous forest. The data are from 1997. Model calculations were produced with the CANOAK model.

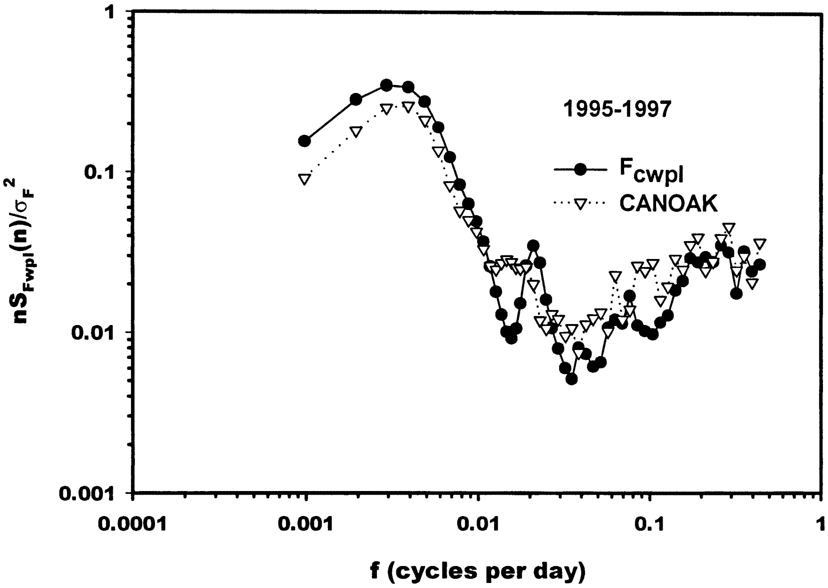

Fig. 7. Fourier transform of CO_2 flux measurements and model calculations over the period 1995–1997

We can conclude that in view of the large number of potential errors, we were able to produce representative and reasonably accurate estimates of CO_2 and water vapor exchange over the course of a year.

3.2. Spectral variability of fluxes

As we attempt to study the metabolism and water balance of forests for periods longer than 1 year, it is prudent to use mathematical tools to interpret the large population of data. One tool is the Fast Fourier Transform (Press et al., 1992). The Fast Fourier Transform converts a stochastic time series into a sum of periodic sine waves. Fourier analysis is thereby able to quantify the amount of variance (or power) that is associated with a particular frequencies or periods and how spectral power varies across a spectrum of frequencies Fig. 7 compares the spectral densities of measured and calculated time series of net ecosystem–atmosphere CO_2 exchange that were acquired over the period 1995–1997. The site experienced summer drought in 1995, while 1996 and 1997 were normal years with ample rainfall. The greatest spectral variance observed in field data was associated with periods on the order of a year (0.003 cycles per day) and less than a week (the time scale of frontal passage, 0.2 cycles per day). A distinct spectral gap occurred at the monthly time scale (0.035 cycles per day). In general, calculations generated by the CANOAK model reproduced most of the significant spectral peaks and their magnitudes over the 3-year time frame by only altering driving weather variables, leaf area index and photosynthetic capacity. The greatest spectral disagreement between the model and data corresponded at the spectral peak with a periodicity of 0.02 cycles per day. This peak was generated by incorporating data with the 1995 summer drought. When one examines spectra from only 1996 and 1997, there is no spectral peak at a periodicity of 0.02 cycles per day (Baldocchi et al., 2000a). Modeling studies by Law et al. (2000a,b) demonstrate the importance of soil moisture deficits on canopy CO_2 exchange on ecosystems that experience seasonal soil moisture deficits. This version of CANOAK does not treat the effect of soil moisture deficits on stomatal conductance, leaf photosynthesis and soil respiration, hence the observed disagreement with measured CO_2 flux densities arises at these time scales.

To understand the power spectra of measured and modeled net CO_2 exchange better, we computed power spectra on two component fluxes, canopy photosynthesis and respiration (Fig. 8). Both variables experience a broad, low frequency seasonal peak ($f \sim 0.005$ cycles per hour), which is driven by temperature, and results in a relatively high and positive covariance between photosynthesis and respiration. At the weekly scale ($f \sim 0.005$) canopy photosynthesis experiences a modest spectral peak, whereas respiration does not, causing a low covariance. The passage of weather fronts and their impact on clouds and light transmission has an important impact on canopy photosynthesis (Baldocchi, 1997; Gu et al., 1999). At daily and sub-daily time scales ($f > 0.03$), both variables experience high spectral power, due to the daily cycles of light and temper-

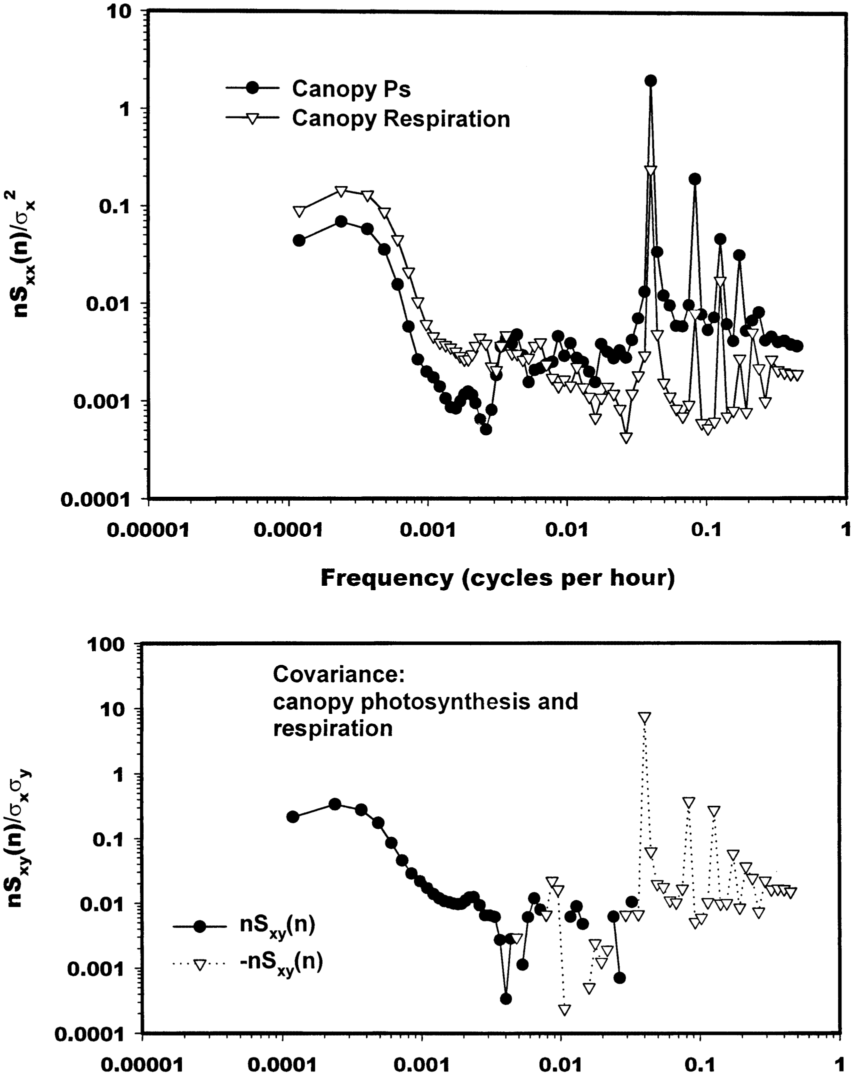

Fig. 8. (a) power spectra of computations of canopy photosynthesis and respiration over the course of a year for a deciduous broadleaved forest. (b) The covariance between canopy photosynthesis and respiration

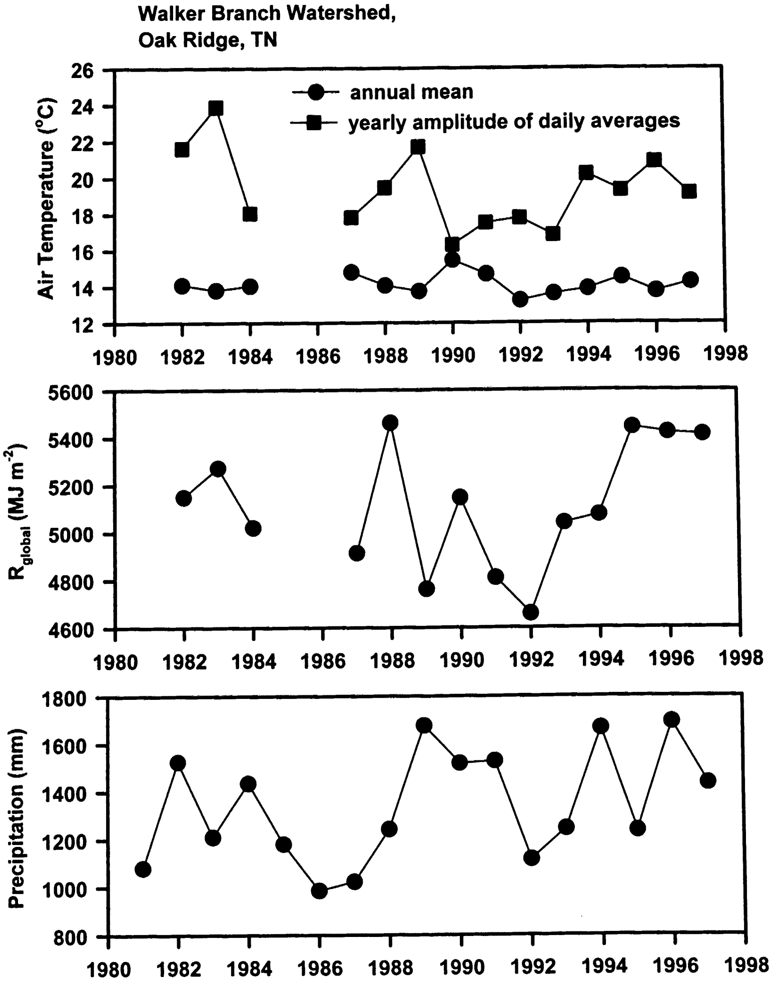

Fig. 9. Interannual variability of air temperature, the yearly amplitude, solar radiation and precipitation at the Walker Branch Watershed forest field site.

ature, but on the daily time scale photosynthesis and respiration negatively co-vary with one, as one process assimilates carbon dioxide and the other expels it.

3.3. Interannual variability

Recent data show that year-to-year swings in the rate of growth of atmospheric CO_2 range between 1 and 5 Gt per year (Keeling et al., 1995). On a land area basis, these values convert to a range between about 10 and 50 gC m^{-2} year^{-1}. One question we can ask with a tested model is: what is the potential year-to-year variability of net ecosystem CO_2 exchange that may have occurred at this site over the time duration of almost two decades? Fig. 9 quantifies the year-to-year variability in air temperature, solar radiation and precipitation that was observed at the site between 1981 and 1998. Mean annual air temperature varied between 13 and 16°C, the amplitude in daily mean air temperature ranged between 16 and 24°C. Incident shortwave solar radiation ranged between 4600 and 5400 MJ m^{-2} year^{-1} and precipitation ranged between 1000 and 1700 mm per year. The theoretical consequences of this variability on interannual variations in net ecosystem CO_2 exchange (NEE) and canopy evapotranspiration are shown in Fig. 10. Based on weather fluctuations alone, the net ecosystem CO_2 exchange of this deciduous forest over a 17 year period ranges between -400 and -650 g C m^{-2} $year^{-1}$ (Fig. 10a). The standard deviation of net CO_2 exchange is about 50 gC m^{-2} $year^{-1}$ and the peak-to-peak span is on the order of 50% of the long-term mean (-527 gC m^{-2} $year^{-1}$). A similar breadth of values was reported in a recent model analysis by Grant et al. (1999) using three years of weather data over a boreal aspen forest and by Kinderman et al. (1996) using the Frankfort Biosphere model for a variety of biomes.

Over the past 2 decades, the mean amount of water evaporated from the forest was estimated to be 771 ± 85 mm, with a range 650 and 900 mm $year^{-1}$ (Fig. 10b). These annual sums of evaporation are high relative to watershed-derived measurements (662 ± 101 mm $year^{-1}$) and eddy flux measurements (Wilson et al., 2001). To identify

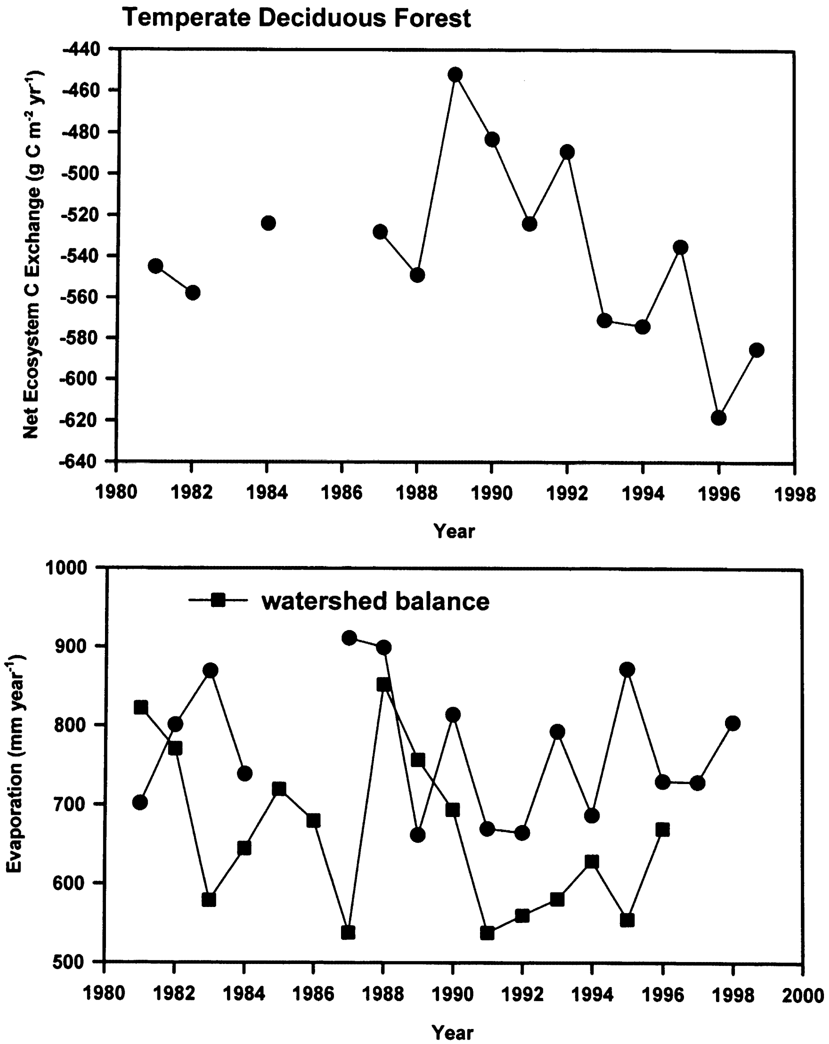

Fig. 10. Interannual variation in canopy CO_2 exchange and evaporation over a temperate deciduous forest. The evaporation data are compared with watershed estimates of evaporation derived from the data of Pat Mulholland (Wilson et al., 2001).

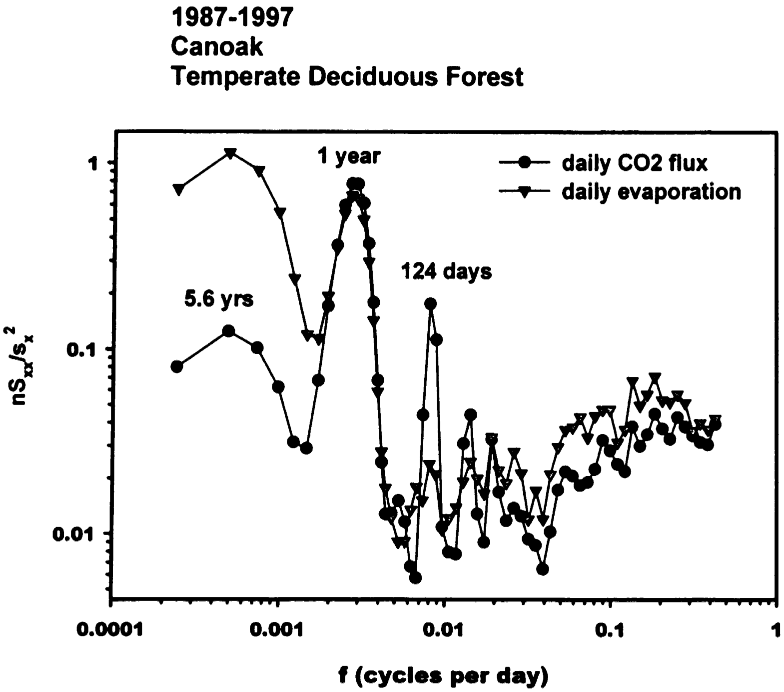

Fig. 11. Power spectra of CO_2 and water vapor exchange over a decade time period. The spectra are based on model calculations of CO_2 exchange and evaporation.

whether the bias is due to how we modeled evaporation from the plant or the soil, we have tested the soil evaporation model with independent measurements (Baldocchi et al., 2000c; Wilson et al., 2000b). In one analysis, we found that measured soil evaporation summed to 93 mm during 1998 and the model computed 117 mm (Wilson et al., 2000b). This difference is too small to account for the 100 mm overestimate in λE we observed with the model (Fig. 10b).

Process-based models lend scientists the ability to ask questions about how a ecosystem responds to perturbations beyond the range of available data. With regards to long-term fluxes, one key question we intend to ask is: what are the dominant scales of variance associated with CO_2 and water vapor exchange over the course of a decade? Using a continuous 10 year meteorological record, we calculate that significant variance occurs in calculations of net ecosystem CO_2 exchange and latent heat exchange (λE) on time scales of 5.6 years, as well as the expected annual, seasonal, weekly and daily cycles (Fig. 11). These data suggest that long-term flux studies need to extend to at least a decade to examine important variance that may be observed in such records. Long-term records are also needed to extend analyses of this type to examine if there is any direct correspondence between year-to-year fluctuations in trace gas fluxes by *El Niño*/*La Niña* events (e.g. Keeling et al., 1995), changes in climate, land use, stand disturbance and stand age.

3.4. Impact of canopy structure on mass and energy fluxes

In our past work we examined the influence of factors such as leaf clumping and turbulent mixing on short time scale (hourly) flux densities of water, heat and CO_2 (Baldocchi and Harley, 1985). Bias errors can occur if these factors are ignored, but the importance of such errors on annual sums of CO_2 exchange have not been quantified. Leaf clumping is a common feature of many native stands. Its effect on photon transfer through the canopy can be accommodated through the use of a Markov model to compute the probability of beam penetration (P_0) through the canopy (Baldocchi and Collineau, 1994; Myneni et al., 1989). Fig. 12 compares computations of net ecosystem CO_2 exchange, summed annually, that consider ((Ω equals 0.84) and ignore clumping of leaves (Ω equals one). On average, the version of the CANOAK model that considers leaf clumping computes a mean of sum of net CO_2 exchange equal to -527 g C m^{-2} $year^{-1}$.

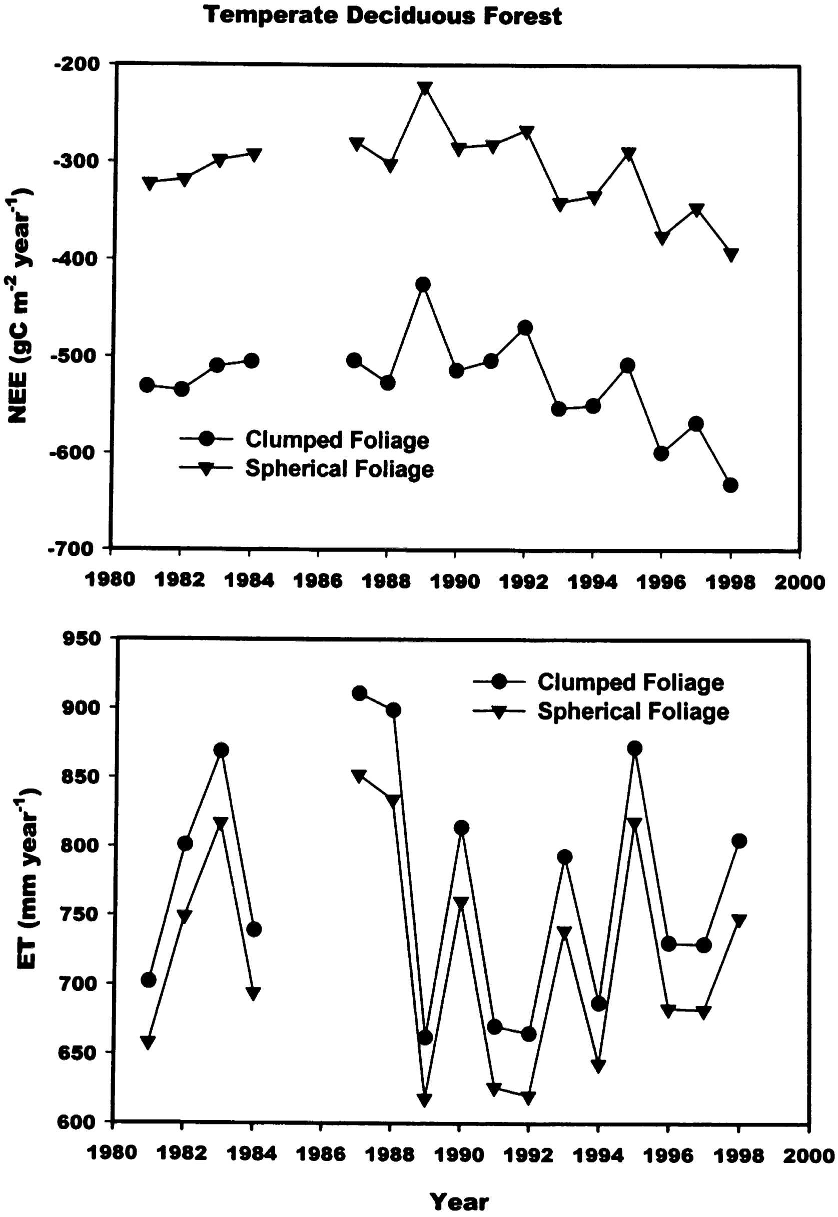

Fig. 12. Comparison between NEE and ET computed with a model that considers the impact of leaf clumping or assumes a random and spherical leaf distribution.

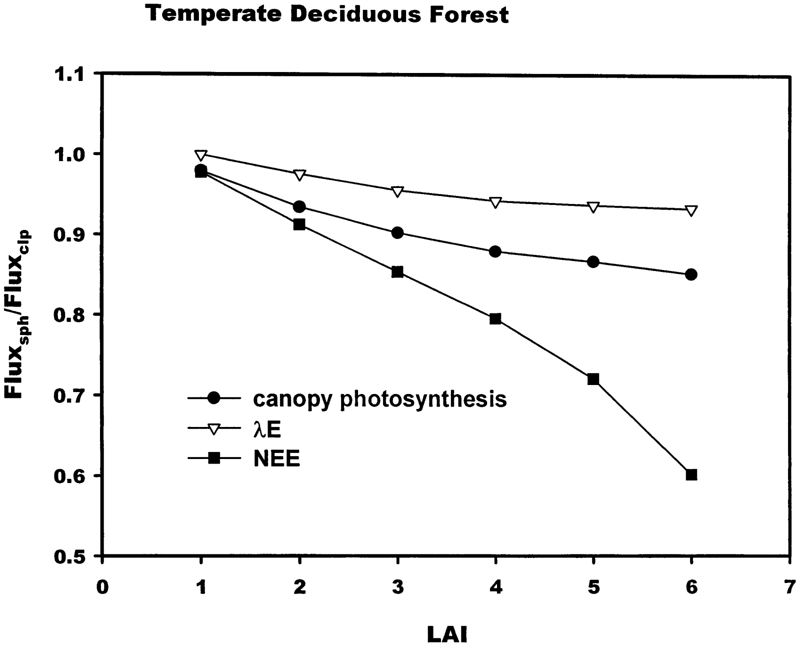

Fig. 13. The relative difference in fluxes computed on the assumption that leaves are distributed in a random manner with a spherical leaf angle distribution versus those that assume the leaves are clumped. The relative fluxes are computed as a function of leaf area index for net primary productivity, evaporation and net CO_2 exchange. Computations were performed for a yearly time series using meteorological drivers from 1997.

In contrast, the version of the model that assumes the leaves are randomly distributed in space (it assumes the leaf angle distribution is spherical) computes net CO_2 exchange to be -309 gC m^{-2} $year^{-1}$, a difference of 218 gC m^{-2} $year^{-1}$. These computations indicate that the systematic difference between the two model schemes amplify when the effect of leaf clumping is considered over an annual basis. Yet if we compare hourly computations leaf photosynthesis based on the model that does and does not consider clumping we find that the mean difference is only 12.5%. (slope: 0.875; zero offset: -0.15 umol m^{-2} s^{-1}; $r^2=0.999$), a value similar with our previous analysis (Baldocchi and Harley, 1995). These results demonstrate the importance of time scale on the question being asked.

The effect of leaf clumping on integrated canopy photosynthesis may vary with leaf area. Recently, we found that clumping had little effect on canopy photosynthesis of a ponderosa pine stand, with a leaf area index of 1.6 (Law et al., 2000b). That observation plus the data shown in Fig. 12 leads us to hypothesize that the effect of clumping on the computations of mass and energy exchange diminish as leaf area index diminishes. We tested this hypothesis by comparing computations of canopy photosynthesis and evaporation on the basis of on two radiative transfer models (Fig. 13). One model assumes the leaves were random in space and their leaf inclination distribution was spherical (the numerator). The other considers the impact of clumped leaves (the denominator). Focusing on canopy photosynthesis we observe that the impact of clumping diminishes as leaf area decreases. As leaf area approaches one, most leaves are sunlit so the impact of re-distributing light through the canopy, as clumping does, has less and less impact on the net flux density of canopy photosynthesis. This finding is consistent with the results of Wang and Polglase (1995). They reported that net primary productivity of tundra, with low leaf area, increased and net primary productivity of a humid tropical forest, with high leaf area, decreases as their clumping factor changed from 0.7 towards one.

Few biogeochemical models consider the impact of clumping on net primary productivity [Wang and Polglase (1995) is one exception]. Based on the model calculations we have presented, there is indirect evidence that the community of biogeochemical models may be underestimating net primary productivity (NPP) of temperate deciduous forests by ignoring clumping. For example, Kicklighter et al. (1999) reports that NPP of temperate deciduous forests, computed from 17 models, averages near 600 gC m^{-2} $year^{-1}$ and ranges between 350 and 1000 gC m^{-2} $year^{-1}$. In comparison, CANOAK-based estimates of net primary productivity are on the order of 1000–1100 gC m^{-2} $year^{-1}$ for a temperate forest near Oak Ridge, TN.

3.5. Impact of micrometeorological representation and heterogeneity on mass and energy fluxes

How much meteorological detail one should incorporate into a carbon–water flux model that is used for ecological and biogeochemical applications remains a key question. Several analyses have shown that it is critical to consider the light environment on sunlit and shaded leaves (Sinclair et al., 1976; Norman and Polley, 1989; De Pury and Farquhar, 1997). It remains inconclusive whether one needs to consider feedbacks between scalar profiles and vegetative sources and sinks (Goudriaan, 1977; Raupach and Finnigan, 1988; Baldocchi, 1992). And no studies have asked this question using data on an annual time scale. Fig. 14 compares flux densities of latent (λE) and sensible heat (H) and net ecosystem CO_2 exchange that were computed using the Lagrangian turbulent diffusion sub-model, that enables CANOAK to consider feedbacks between the local scalar field and source-sink strengths, and a version of the model that assumes that the scalar field is constant. We observe that the inclusion of detailed micrometeorology has little ($< 3\%$) influence on net canopy CO_2 exchange. The impact on λE is seasonal, though small, too, being less than 3%. Scatter and bias are greater for computations during the winter leafless periods, as the stomata are not buffering fluxes from the impact of boundary layer resistances and surface-air humidity differences. On the other hand, the impact of ignoring the impacts of canopy air temperature gradients on sensible heat exchange, H, is large. The model scheme that ignores temperature profiles yields values of H that are about 61% of the reference values.

Computing H correctly has important consequence on meteorological, atmospheric chemistry and biogeochemical problems. Daily growth of the planetary boundary layer, for example, is related to the time course of H. This information is needed to compute clouds and precipitation, the dilution of pollution and CO_2 in the planetary boundary layer (Betts et al., 1996; Denning et al., 1996). The later problem relates to the rectifier effect and how surface layer measurements of CO_2 are interpreted by global circulation inversion models that interpret regional sources and sinks of CO_2 (Denning et al., 1996).

3.6. Impact on length of growing season

Several modeling analyzes (Lieth, 1975; Kinderman et al., 1996) have indicated the importance of growing season length on net ecosystem CO_2 exchange of temperate deciduous forests. Recent analyses of satellite data (Keeling et al., 1995; Myneni et al. 1997) suggest that year-to-year differences in the rate of growth of CO_2 may be affected by the presence or absence of *El Niño* and how it alters the length of the growing season. The impact of growing season duration on net ecosystem CO_2 exchange is quantified in Fig. 15. Model computations indicate that net ecosystem CO_2 exchange increases theoretically by 5.98 gC m^{-2} for each day increase in the length of the growing season. Consequently, a 30 day difference in the length of the growing season can cause net ecosystem CO_2 exchange to range between 450 and 620 g C m^{-2} $year^{-1}$. This value is consistent with the range observed in our decadal simulation.

For perspective, we compare these data with contemporary and published flux measurements and with estimates of net primary productivity from Lieth (1975), who used biomass data across the Eastern Deciduous biome. Drawing on data from the published literature, using broad-leaved deciduous forest sites from across the FLUXNET network, we find that net ecosystem CO_2 exchange varies by 6.47 gC m^{-2} per incremental day of the growing season (Fig. 15). Using biomass measurements, Lieth (1975) estimates that net primary productivity of temperate deciduous forests increases by 5.17 gC m^{-2} for each day increase in the length of the growing season. This value is only 14% lower than our model estimate. We note that biomass-based estimates of net primary productivity are derived from above ground estimates of growth increment and either ignore or make assumptions about below ground allocation of carbon. Despite the encouraging agreement with independent data, we caution the reader that our calculations may not be definitive. Our current soil respiration model is driven only by temperature. It does not consider the impacts of root phenology or soil moisture.

New data from the EUROFLUX network indicates that gross primary productivity across a range of European conifer and deciduous forests is constant (Valentini et al., 2000). Is this a universal finding or an artifact of the structural and functional attributes of the forests under study in

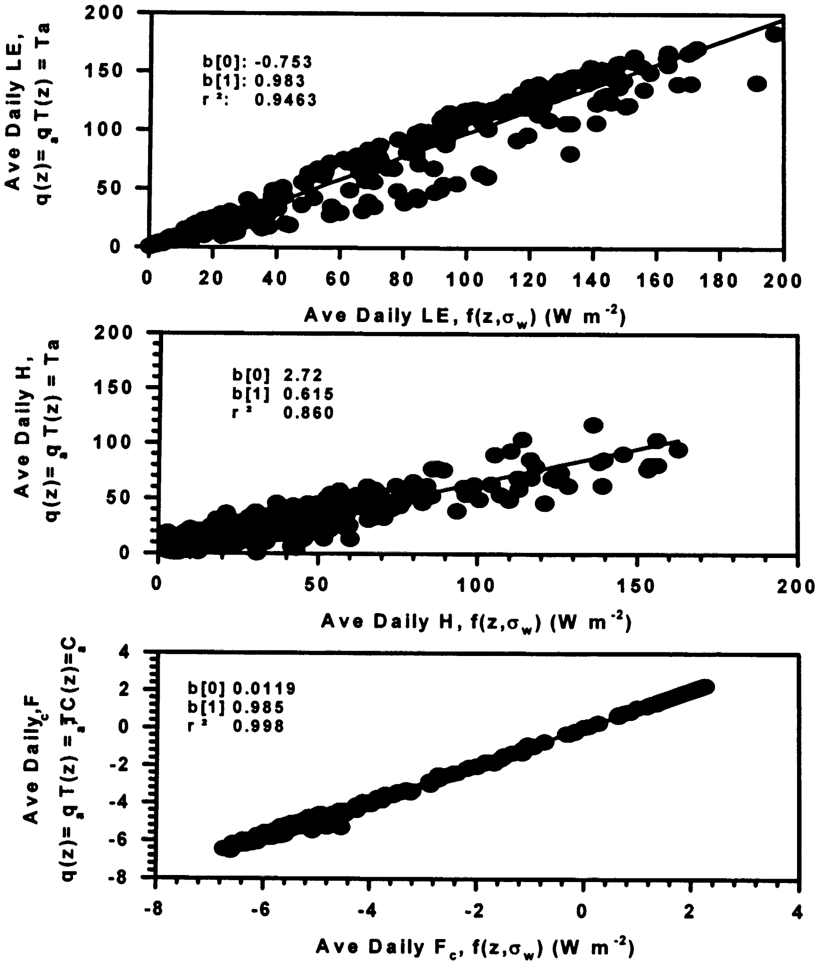

Fig. 14. Role of turbulence parameterisation on daily- integrated fluxes: (a) latent heat exchange; (b) sensible heat exchange; (c) CO_2 exchange.

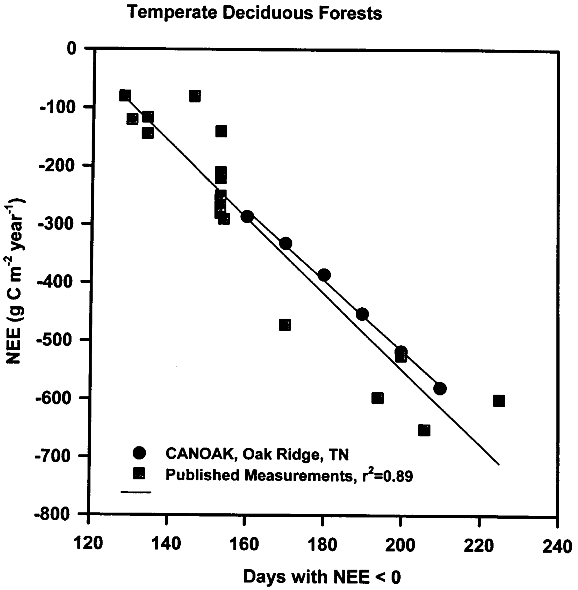

Fig. 15. Impact of growing season length on NEE, published data: aspen, Canada (Black et al., 2000); Harvard Forest, (Goulden et al., 1996); Denmark, (Pilegaard et al., 1996); Japan, (Yamamoto et al., 1999); Italy, (Valentini et al., 2000), Oak Ridge,(Greco and Baldocchi, 1996, Wilson and Baldocchi, 2000); Belgium, (Aubinet, Valentini et al., 2000).

Europe? Here, we use the model to address how gross primary productivity varies with canopy structure (leaf area index), photosynthetic capacity (V_{cmax}) and light interception (the fraction of absorbed quanta, f_{par}). Fig. 16 suggests that canopy photosynthesis is constant when LAI and V_{cmax} are high, but that it diminishes with sparse and non-productive canopies. Most of the European forests had moderate to high leaf area indices (LAI > 3), so they would have corresponded with the upper end of the curve.

4. Conclusions

A biophysical model, CANOAK, was applied to compute fluxes of CO_2 and water vapor exchange over a temperate deciduous forest on annual to decadal time scales. In many regards, the level of agreement between CO_2 and water vapor flux densities generated by the CANOAK model and test data was high, in view of the myriad sources of error that one can encounter while measuring and computing fluxes. With respect to our long-term calculations, our results suggest that varying leaf area, weather drivers and car-

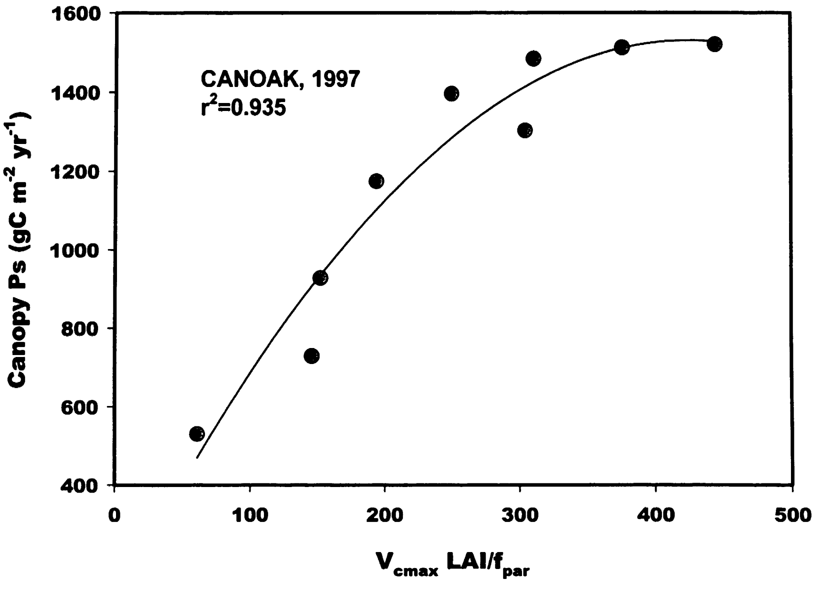

Fig. 16. The relation between canopy photosynthesis and maximum carboxylation velocity, leaf area index and the fraction of absorbed photosynthetic photon flux density.

boxylation capacity (V_{cmax}) with time enables one captures over 80% of the seasonal variation in CO_2 and latent heat fluxes over a temperate deciduous forest. We achieved this level of performance by not altering the model with respects to soil water relations, seasonal changes in the temperature kinetics of photosynthesis and respiration.

This finding is encouraging, considering the results of a recent report by Niinemets et al. (1999), who conclude that: "modeling whole canopy photosynthesis using a single J_{max} (maximum rate of electron transport) versus temperature response curve is not appropriate". In our case, not accounting for acclimation kinetic coefficients with temperature, over the course of the growing season, seems to be of second order importance. However, we cannot conclude whether or not our simulations would have improved had we considered acclimation effects on photosynthetic kinetics based on the accuracy and representativeness of the flux measurements and our lack of temperature kinetic data. In practice we found it difficult to obtain such data in the field as our photosynthesis cuvette system does not allow us to modify leaf temperature over a wide range of temperatures (0–40°C). The CANOAK model will need a set of algorithms for computing fluxes during drought periods.

One reason for the strong performance of the CANOAK model stems from its multi-layer nature and how it considers how non-linear processes such as photosynthesis, stomatal conductance and leaf energy balance vary on the sunlit and shaded fractions. These results are consistent with data from several studies that have shown that the performance of a biophysical trace gas flux model diminishes when a big leaf model is used and when it ignores the distinct microclimate on the sunlit and shaded leaves (Sinclair et al., 1976; De Pury and Farquhar, 1997).

How well the model is perceived to perform, compared to test data, depends on the time scale of the data. We observed a closer correspondence between measurements and model calculations when the comparisons were based on hourly averaged data, rather than daily-integrated data. Bias errors in the measurement of nocturnal fluxes may be one reason for diminished performance at the daily time step.

Applying the model to decadal scale meteorological records produces interannual variability of NEE as large as 200 gC m^{-2} year and produces significant variance of trace gas fluxes on the time scale of 5–6 years. Based on these calculations we argue for the continued and extended operation of ongoing flux measurement networks.

How much detail to incorporate into the model continues to be a relevant question for trace gas flux modeling. The role of clumped leaves on light transfer and the computation of fluxes is a very important factor. Ignoring clumping can cause a 50% error in the estimation of annual carbon fluxes. Impact of canopy microclimate gradients is small on computing canopy CO_2 exchange. In this respect, biogeochemical models that neglect this effect will not have large errors (e.g. Cramer et al., 1999).

Improved attempts to model carbon dioxide and water vapor exchange over decadal and century times scales will require merging of biophysical models, like CANOAK, with phenological models that determine the timing of leaf out and leaf fall, gap-dynamic models that consider populations changes and disturbances and biogeochemical models that consider long stored pools of carbon and their turnover and inter-annual variability in leaf area and leaf nutrient content. This is because models that compute long-term fluxes do not have the luxury of inputting such variables as leaf area and photosynthetic capacity. As one attempts to extend coupled carbon–water flux models to semiarid climates information on soil moisture and its impact on stomatal conductance, photosynthesis and soil respiration is needed (Hanan et al., 1998; Law et al., 2000b).

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