

Measuring and modelling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought

D. BALDOCCHI

Atmospheric Turbulence and Diffusion Division, NOAA, PO Box 2456, Oak Ridge, TN 37831, USA

ABSTRACT

Forests in the south-eastern United States experienced a prolonged dry spell and above-normal temperatures during the 1995 growing season. During this episode, nearly continuous, eddy covariance measurements of carbon dioxide and water vapour fluxes were acquired over a temperate, hardwood forest. These data are used to examine how environmental factors and accumulating soil moisture deficits affected the diurnal pattern and magnitude of canopy-scale carbon dioxide and water vapour fluxes. The field data are also used to test an integrative leaf-to-canopy scaling model (CANOAK), which uses micrometeorological and physiological theory, to calculate mass and energy fluxes. When soil moisture was ample in the spring, peak rates of net ecosystem CO₂ exchange (N_E) occurred around midday and exceeded 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Rates of N_E were near optimal when air temperature ranged between 22 and 25°C. The accumulation of soil moisture deficits and a co-occurrence of high temperatures caused peak rates of daytime carbon dioxide uptake to occur earlier in the morning. High air temperatures and soil moisture deficits were also correlated with a dramatic reduction in the magnitude of N_E . On average, the magnitude of N_E decreased from 20 to 7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ as air temperature increased from 24 to 30°C and the soil dried. The CANOAK model yielded accurate estimates of canopy-scale carbon dioxide and water vapour fluxes when the forest had an ample supply of soil moisture. During the drought and heat spell, a cumulative drought index was needed to adjust the proportionality constant of the stomatal conductance model to yield accurate estimates of canopy CO₂ exchange. The adoption of the drought index also enabled the CANOAK model to give improved estimates of evaporation until midday. On the other hand, the scheme failed to yield accurate estimates of evaporation during the afternoon.

Key-words: carbon dioxide; drought; evaporation; net ecosystem carbon exchange; photosynthesis; stomatal conductance; temperate hardwood forest.

Correspondence: D. Baldocchi. E-mail: baldocchi@atdd.noaa.gov

INTRODUCTION

The eastern deciduous forest biome of North America has a temperate and humid climate (Trewartha 1968). Nevertheless, drought, soil moisture deficits and heat spells are common occurrences during the growing season (Karl & Young 1987; Cook, Kablack & Jacoby 1988; Huang & van den Dool 1993). A particularly severe dry and hot spell occurred in the region between the central Great Plains and the Atlantic coast during the summer of 1995 (Livezey & Tinker 1996). In eastern Tennessee, where we conduct field studies over a broad-leaved forest, July was abnormally dry and its mean temperature was among the 25 warmest in the last 100 years (Livezey & Tinker 1996).

Soil moisture deficits and high-temperature stress can have several impacts on physiological processes of plants. Soil moisture deficits can cause reductions of cell expansion, leaf area development, photosynthesis, stomatal conductance and transpiration (Hinckley, Lassoie & Running 1978b; Schulze 1986; Kramer & Boyer 1995; Cornic 1994). High leaf temperatures (exceeding 30 °C) can damage chlorophyll-proteins in the thylakoid membrane, inactivate photosystem II and promote respiration (Björkman 1981; Harley & Tenhunen 1991).

The focus of the work reported here is the impact of drought and heat stress on canopy-scale carbon dioxide and water vapour exchange rates over a temperate, broad-leaved forest. Limitations on carbon assimilation, when soil moisture is lacking, caused by non-stomatal or stomatal factors (Schulze 1986; Gollan, Passioura & Munns 1986; Cornic 1994; Dreyer 1996). Non-stomatal limitation of photosynthesis occurs when the photochemical conversion efficiency of photosystem II or the mesophyll conductance to CO₂ diffusion decreases (Cornic 1997; Dreyer 1996; Dickson & Tomlinson 1996).

The non-stomatal component of photosynthesis in oaks (*Quercus* species) has a distinctive sensitivity to drought. Activities of photosystem II (e.g. the photochemical efficiency of light conversion and electron transport) remain normal at dehydration levels beyond those experienced in the field (Dreyer *et al.* 1993, 1996; Epron & Dreyer 1993). The CO₂ concentration at the chloroplast (C_c) of oaks also remains constant (or increases) under drought conditions. This latter observation suggests that

mesophyll conductances diminish as the soil dries. In contrast, many herbs experience a lowering of C_c when dehydrated, which is a response indicative of stomatal closure (Cornic 1994).

There is ample evidence that stomatal limitations on photosynthesis are associated with a hormonal signal (abscisic acid, ABA) sent from the roots (Gollan, Passioura & Munns 1986; Tardieu & Davies 1992; Dreyer 1996). When ABA signals lead to stomatal closure, the CO₂ concentration at the chloroplast is reduced. A stomatal-induced reduction in chloroplast CO₂ concentration reduces carboxylation rates (Cornic 1994) and alters the kinetic properties of the enzyme Rubisco. An increase in the rate of photorespiration (relative to carboxylation) and a lowering of the optimum temperature for photosynthesis are two outcomes of changing Rubisco properties (Cornic 1994).

Stomatal limitations upon photosynthesis also restrict transpiration since water and carbon dioxide molecules diffuse through stomata. One consequence of a reduction in transpiration is an increase in sensible heat transfer and leaf temperature. This change forces a negative feedback on net photosynthesis because respiration rates increase exponentially in response to rising leaf temperatures (Harley & Tenhunen 1991). Another feedback involves a linkage between transpiration, vapour pressure deficits and stomatal conductance (Schulze 1986). Low transpiration rates, during sunny, warm and dry summertime periods, enable the development of a deep convective boundary layer. Deep boundary layers are difficult to humidify, so they foster high vapour pressure deficits (Jacob & deBruin 1992). This sequence of events can either promote evaporation (Baldocchi & Vogel 1996) or feed forward to reduce transpiration further since stomatal closure is frequently correlated with increasing humidity deficits (Schulze 1986; Collatz *et al.* 1991).

There is no guarantee that drought- and heat-stress-related concepts developed on herbs or saplings will apply to forest communities. Several physiological and structural attributes of trees enable them to respond to drought differently from herbs. First, stomata of *Quercus* close during drought to prevent cavitation and xylem dysfunction (Cochard, Breda & Granier 1996). What stimulates this closure, however, is unknown because the level of ABA in xylem sap of oaks is not elevated during drought (Triboulot *et al.* 1996). Secondly, mature trees store significant amounts of water in their sapwood and can tap various sources of soil moisture (Dawson 1996; Dickson & Tomlinson 1996). This attribute affects the phase between the diurnal trends of forest transpiration and available energy (Goulden & Field 1994; Williams *et al.* 1996). Thirdly, many temperate forests experience drought after full leaf expansion occurs (Dreyer 1996). This occurrence prevents a feedback on canopy photosynthesis through a modulation of leaf area; an exception to this corollary includes the case of tulip poplar (*Liriodendron tulipifera*) which drop leaves during drought. Fourthly, the mixed species amalgamation of a forest contains species that

avoid, tolerate or are adapted to drought and heat stress through phenotypic plasticity (Abrams & Mostoller 1995). Consequently, the theoretical response of one tree species to drought and heat stress may not represent the response by a mixed forest stand.

Many studies exist on how photosynthesis and transpiration of leaves of broad-leaved forest species respond to soil moisture deficits (e.g. Hinckley *et al.* 1978a,b; Dougherty *et al.* 1979; Tenhunen *et al.* 1984, 1990; Weber & Gates 1990; Abrams 1994; Dreyer *et al.* 1994; Kubiske & Abrams 1994; Abrams & Mostoller 1995). In contrast, data on how the carbon dioxide and water fluxes of temperate forest ecosystems respond to periods of soil moisture deficit and heat spells are relatively meagre. Most studies on this topic are confined to Mediterranean vegetation, and to transpiration measurements using sap flow methods (Goulden & Field 1994; Loustau *et al.* 1996) or hydrological balances (Nizinski & Saugier 1989; Sala & Tenhunen 1996). Few investigators have employed the eddy covariance method to study carbon dioxide and water vapour fluxes over drought-stressed forests (Goulden *et al.* 1996a; Greco & Baldocchi 1996; Valentini *et al.* 1996). Consequently, the effects of drought and heat stress on canopy photosynthesis and transpiration of forests tend to be inferred from models (Tenhunen *et al.* 1990; Sala & Tenhunen 1996; Williams *et al.* 1996).

Long-term eddy flux studies provide data spanning a variety of soil moisture and temperature conditions (e.g. Wofsy *et al.* 1993; Goulden *et al.* 1996a,b; Greco & Baldocchi 1996; Valentini *et al.* 1996). At Oak Ridge, Tennessee, we have been conducting nearly continuous measurement of canopy carbon dioxide and water vapour fluxes over a temperate broad-leave forest since October 1994. During the 1995 growing season, an extended period with soil moisture deficits was observed at our research site after May. Precipitation totals during June, July and August were 33, 107 and 37 mm *below* normal, respectively. Only May experienced above-normal rainfall (36.5 mm) during the growing season. The summer drought also corresponded with a period of above-normal air temperatures. Mean air temperatures were 1.1, 2.4 and 3.8 °C above normal during June, July and August.

The objectives of this paper are: (a) to examine the effects of environmental forcing variables (available sunlight and temperature) and soil moisture deficits on the diurnal trends and magnitudes of canopy-scale carbon and water vapour fluxes of a broad-leaved temperate forest; (b) to test a canopy-scale carbon dioxide and water vapour flux model (CANOAK) over a range of soil moisture and temperature conditions, and (c) to use the model to interpret how carbon dioxide and water vapour fluxes respond to interacting or non-linear perturbations in their environment.

With regard to data analysis, I test the following hypothesis: model parameters used to compute photosynthesis and stomatal conductance can be regarded as independent of soil moisture deficits during the early phase of a drought. This idea, if supported by field data, would simplify the assignment of model parameters for landscape

assessments of mass and energy fluxes. As an alternative hypothesis, I test the following hypothesis: stomatal conductance can be adjusted using a drought index based on the ratio between cumulative precipitation and potential evaporation.

The first hypothesis stems from several studies of leaf photosynthesis and tree water balance. First, stomatal conductances of North American oak and maple are an empirical and multiplicative function of leaf photosynthesis and relative humidity (Weber & Gates 1990; Harley & Baldocchi 1995). Secondly, a popular, photosynthesis-dependent stomatal conductance algorithm (Collatz *et al.* 1991) is a function of electron transport and light-energy conversion efficiency. In oak species, these two photosynthetic processes have little sensitivity to soil moisture deficits (Epron & Dreyer 1993; Dreyer *et al.* 1995; Dreyer 1996). Thirdly, the stomatal conductance algorithm of Collatz *et al.* (1991), as applied to maple, possesses a proportionality constant that is insensitive to drought (Weber & Gates 1990). Only under extreme drought conditions is there evidence that the constant of proportionality between stomatal conductance and photosynthesis may need to be adjusted (Tenhunen *et al.* 1990; Sala & Tenhunen 1996).

MATERIALS AND METHODS

The field site is located on the United States Department of Energy reservation near Oak Ridge, Tennessee (latitude 35° 57' 30"; longitude 84° 17' 15"; 365 m above mean sea level). Johnson & van Hook (1989), Hutchison & Baldocchi (1989), Baldocchi & Harley (1995) and Greco & Baldocchi (1996) describe details of the site and the experimental set-up. For completeness we present a brief overview of the key site and experimental design features.

Site characteristics

Micrometeorological measurements of carbon dioxide, water and energy exchange rates were made over a mixed-species, broad-leaved forest, growing in the eastern North American deciduous forest biome. The forest stand consists of oak (*Quercus alba* L., *Q. prinus* L.), hickory [*Carya ovata* (Mill.) K. Koch], maple (*Acer rubrum* L.), tulip poplar (*Liriodendron tulipifera* L.) and loblolly pine (*Pinus taeda* L.). The forest has been growing since agricultural abandonment in 1940. The mean canopy height was about 26 m. The peak leaf area index of the canopy typically occurs by day 140 and reaches about 4.9 (Hutchison *et al.* 1986). In 1995, the site experienced a hail storm on day 135. That storm shredded many leaves in the vicinity of the research tower and reduced peak leaf area index to about 4.

The soil is classified as a Fullerton series, Typic Paleudult, otherwise described as an infertile cherty silt-loam. Soil moisture of the top 0.15 m soil and litter layer was measured weekly using the gravimetric method. Pre-dawn leaf water potential was measured periodically to obtain an integrated measure of the soil water potential in

the root volume of understory saplings. Using a pressure chamber, water potential was measured on six to eight leaves (these data were obtained at a site 6 km from the Walker Branch field on leaves of *Acer rubrum* and *Liriodendron tulipifera*).

Physiological studies of American and European oak species indicate that photosynthesis and stomatal conductance are not limited by pre-dawn water potentials confined between 0 and -0.5 MPa (Hinckley *et al.* 1978a; Epron & Dreyer 1993). On the basis of this criterion, field data suggest that ample soil moisture was available to the forest between leaf-out (around day 90) and mid-June (around day 170) (Fig. 1). By July (days 184–214), soil moisture deficits became detectable, as volumetric moisture content dropped below 0.20 m³ m⁻³ and pre-dawn water potential dropped below -0.50 MPa. Data in Fig. 1 indicate that appreciable soil moisture deficits persisted until day 250, despite occasional rain showers in August.

Measurement theory and instrumentation

Flux densities of CO₂, water vapour and sensible heat between the forest and the atmosphere were measured using the eddy covariance technique (see Baldocchi, Hicks & Meyers 1988). This method evaluates vertical flux

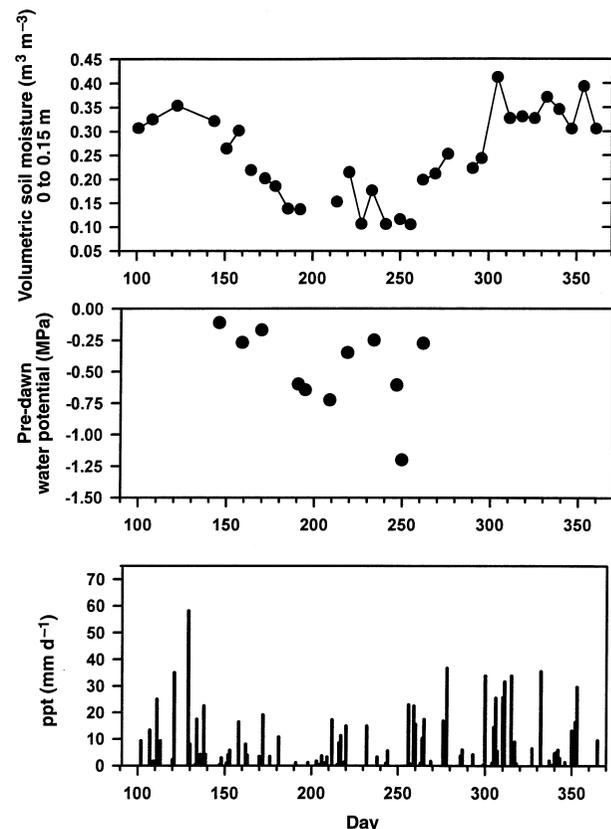


Figure 1. The day-to-day variation of volumetric soil moisture (a), pre-dawn water potential (b) and precipitation (c) during the 1995 growing season at a broad-leaved deciduous forest site near Oak Ridge, TN.

densities of scalars between the forest and the atmosphere by measuring the mean covariance between vertical velocity (w') and scalar (c') fluctuations (e.g. temperature, water vapour and CO₂). The sign convention adopted by atmospheric scientists is used to define the direction of the flux. Positive flux densities represent mass and energy transfer into the atmosphere, and away from the surface. Negative covariance values denote the reverse.

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 (model SWS-211/3K, Applied Technology, Boulder, CO). Carbon dioxide and water vapour fluctuations were measured with an open-path, infrared absorption gas analyser (Auble & Meyers 1992).

Micrometeorological data were sampled and digitized 10 times s⁻¹. In-house software was used to process the measurements. The software computed mass and energy flux covariances for half-hour intervals. Prior studies indicate that the instrument response characteristics, their sampling rates and sampling duration were adequate for measuring mass and energy fluxes above this forest canopy (Anderson *et al.* 1986).

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. Wind velocity axes were rotated numerically to compute flux covariances aligned normal to the mean wind streamlines (see Baldocchi, Hicks & Meyers 1988).

The fast response CO₂/water vapour sensor was calibrated monthly against gas standards. The calibration standards for CO₂ were prepared by NOAA's Climate Monitoring and Diagnostic Laboratory. The water vapour channel was referenced to a dew point hygrometer. With several years of experience, we have found that the calibration sensitivity of this sensor varies by less than 5%, on average, over a month.

Ancillary environmental data were sampled at 1 s intervals and were logged on digital data loggers (model CR-21x, Campbell Scientific, Logan Utah). Soil heat flux density was measured using three soil heat flux plates [model HFT-3, Radiation Energy Balance systems (REBS), Seattle, Washington]. The heat flux plates were buried 0.01 m below the soil surface. Soil temperature was measured with two multi-level thermocouple probes. Temperatures were measured at 0.02, 0.04, 0.08, 0.16 and 0.32 m below the soil surface. Photosynthetically active photon flux density and the net radiation balance were measured above the forest with a quantum sensor (model LI-190S, LiCor Inc., Lincoln, NE) and a net radiometer (model 7, REBS, Seattle, Washington), respectively. A rotating shadow band, fabricated in-house, was used to assess the fraction of diffuse to total incoming insolation. Air temperature and relative humidity were measured above the canopy with a temperature/humidity probe (HMP-35 A, Vaisala, Helsinki, Finland).

Canopy heat storage was calculated from measurements of the temporal change of bole and air temperature and humidity. Bole temperature was assessed using three thermocouple probes; they were inserted 1 cm into the trunk of a tree at breast height. The multiplicative coefficient for computing canopy heat storage was calculated to be 38.8 W m⁻² °C⁻¹, on the basis of stand biomass and the specific heats of cellulose and water.

Solar radiation components were measured under the canopy to assess the amount of sunlight intercepted by the canopy and to infer leaf area index. Solar radiation sensors were mounted on an instrument package that traversed across a 20 m domain. This experimental approach was needed to obtain a spatially representative measure of the subcanopy light environment. A Beer's Law relationship, calibrated using data from previous studies at this site (Baldocchi *et al.* 1984), was used to infer canopy leaf area index from measurements of photosynthetic photon flux interception.

Over a tall forest, the CO₂ flux density measured by an eddy covariance system does not always equal the net biotic CO₂ exchange (Wofsy *et al.* 1993; Hollinger *et al.* 1994; Greco & Baldocchi 1996). A bias error can occur when CO₂ is stored in or withdrawn from the layer of air below the eddy flux system. Storage is most likely to be significant at night when the thermal stratification of the atmosphere is stable and winds are weak and intermittent. A withdrawal of previously stored CO₂ is most likely to occur after daybreak, when convective turbulence resumes and CO₂ is rapidly vented from the canopy into the planetary boundary layer.

The CO₂ storage term equals the integration, with respect to height, of the time rate of change of the CO₂ concentration profile. This term was estimated, by finite difference, with a CO₂ profile measurement system. An automatically controlled solenoid sampling system directed air into an infrared gas analyser (model LI 6262, LiCor Inc., Lincoln, NE). Air was sampled from four levels above and within the forest (36, 18, 10 and 0.75 m). Air from each level flowed through the analyser for 30 s and data were acquired 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 analyser.

CO₂ flux densities presented in this paper represent the net ecosystem exchange rate (N_E), which is the conjugate of the sum of the eddy covariance and storage measurements. Hence, these values are positive when carbon is gained by the ecosystem. I stress that N_E must not be confused with the net flux density of carbon dioxide across the interface between the biosphere and the atmosphere (F_c).

Model calculations

The CANOAK model was used to calculate fluxes of carbon dioxide and water vapour between the vegetation and the atmosphere (Baldocchi & Harley 1995). The primary

test of the model was against a set of data 3 weeks long and confined to a period during the growing season when soil moisture was ample and air temperature was mild. Consequently, an additional test of the model is warranted over a wider range of soil moisture and temperature conditions. For the sake of clarity, a brief description of the model follows.

CANOAK is a multi-layer, canopy photosynthesis/evaporation model. The model consists of coupled micrometeorological and physiological modules. The micrometeorological model computes 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 models that compute leaf photosynthesis, stomatal conductance, transpiration and leaf, bole and soil/root respiration.

The CANOAK model assumes that the canopy is horizontally homogeneous and environmental conditions are temporally steady. This assumption allows the conservation equation, for a given scalar, 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, $S(c,z)$:

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

The diffusive source strength was modelled using a resistance-analogue relationship:

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

where $a(z)$ is the leaf area density, $[c(z) - c_i]$ is the concentration difference between the air outside the laminar boundary layer of leaves and the air within the stomatal cavity, r_b is the boundary layer resistance to molecular diffusion, r_s is the stomatal resistance and ρ_a is air density. Summing Eqn 1 with respect to height, and adding the trace gas flux density over the soil, yields the canopy-integrated flux density.

Model inputs, algorithms and parameters

The model is driven by a minimal number of external variables that are measured easily. Environmental inputs include incident photosynthetic photon flux density (Q_p), air temperature, wind speed, relative humidity and CO_2 concentration. Plant structural variables include leaf area index, leaf angle orientation, an index of spatial dispersion and canopy height.

The leaf boundary layer resistance, in Eqn 2, was computed using mass transfer theory, reviewed by Schuepp (1993), for a flat plate. Under forced convection, this resistance is a function of the size of the leaf, wind speed and the kinematic and thermal diffusivities of the air. Under calm winds and free convection, an alternative algorithm was used, which is a function of the leaf-air temperature difference.

The scalar concentration field above and within the forest canopy was calculated with a Lagrangian random walk model (Raupach 1988). A dispersion matrix was calculated using the random walk algorithm of Thomson (1987) for a reference turbulence regime and near-neutral condition. When used in subsequent computations, the dispersion matrix was adjusted according to friction velocity and atmospheric stability.

Stomatal conductance, the inverse of resistance, was computed as a function of leaf photosynthetic rate (A) and relative humidity (h) and CO_2 concentration (C_s) at the surface of a leaf (Collatz *et al.* 1991):

$$g_s = \frac{1}{r_s} = m \frac{A h}{C_s} + g_0, \quad (3)$$

where m is a scaling factor and g_0 represents the cuticular conductance.

Leaf photosynthetic rates (A) were computed with a system of equations that describe 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) CO_2 concentrations. The biochemical equations for the carbon exchange processes were taken from Farquhar, von Caemmerer & Berry (1980), Farquhar & von Caemmerer (1982), and Harley & Tenhunen (1991). An analytical solution of the coupled leaf photosynthesis-stomatal conductance model is described by the author (Baldocchi 1994).

The radiative transfer through the canopy volume must be computed to assess leaf photosynthesis, leaf energy balance and the proportions of sunlit and shaded leaf area. The radiative transfer model was derived from probabilistic theory (Ross 1981; Myneni, Ross & Asrar 1989). Since leaves of this forest are clumped, I dispensed with the Poisson probability model and substituted it with the Markov model:

$$P_0 = \exp\left(-\frac{f G \Omega}{\sin \beta}\right), \quad (4)$$

where P_0 is the probability of beam penetration, f is cumulative leaf area, G is the cosine between the mean leaf normal and a beam emanating from the sun, β is the solar elevation angle and Ω is the Markov index of foliage dispersion. The Markov clumping factor was assessed using radiative transfer data obtained from this field site. The clumping factor was equal to 0.84. Photon scattering was computed using algorithms published by Norman (1979).

Fluxes of carbon dioxide, water vapour and sensible heat transfer are non-linear functions of many environmental forcing variables. Model calculations were performed separately for sunlit and shaded leaf fractions to evaluate the expected value of bio-physical functions properly (Norman 1979). The radiative transfer model was used to evaluate the probability of leaves being sunlit or shaded. 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 average cosine of the leaf–sun angle (Ross 1981; Myneni, Ross & Asrar 1989).

Leaf transpiration, sensible heat transfer, and leaf temperature were computed with an analytical solution of the leaf energy balance. The equations and analytical solution used for this exercise are reported by Paw U (1987).

The soil surface constitutes the lowest boundary of the canopy CO₂ and water vapour 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 with an analytical energy balance model. 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. Heat conduction into the soil and the temperature profile of the soil were computed using a 10 layer numerical heat transfer model (Campbell 1985).

The maximum carboxylation rate (V_{cmax}), the maximum rate of electron transport (J_{max}), and the dark respiration rate (R_{d}) are needed at a reference temperature to compute leaf photosynthesis and stomatal conductance. These data were derived from a prior study on oak leaves (*Quercus alba*). Information on the leaf photosynthesis measurements made at this site are presented in Harley & Baldocchi (1995) (see Table 1). Photosynthetic parameters (V_{cmax} , J_{max} and R_{d}) were scaled according to height in the canopy as a function of the leaf area-to-mass ratio. This variable is a surrogate for leaf nitrogen, which correlates with photosynthetic capacity (Ellsworth & Reich 1993; Harley & Baldocchi 1995; Abrams & Mostoller 1995). The vertical variation of the leaf area-to-mass ratio is based on data from Hutchison *et al.* (1986) and 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 & Tenhunen (1991) were used.

Table 1. A list of model variables used by the CANOAK model to estimate fluxes of carbon dioxide and water vapour over a temperate broad-leaved forest

Variable	Temperate broad-leaved forest
latitude	35.9
longitude	84.3
leaf area index	4.0
canopy height (m)	26
V_{cmax} at 311 K ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	73
J_{max} at 311 K ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	170
stomatal factor, m	9.5
Ω	0.84
R_{b} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at 298 K	0.34
Activation energy (E_{a})	51609

Bole respiration was computed using algorithms from Edwards & Hanson (1996) and biomass information from Johnson & van Hook (1989).

RESULTS AND DISCUSSION

Diurnal patterns of carbon dioxide and water vapour fluxes

Measurements

The impact of the drought and heat spell on carbon dioxide and water vapour fluxes is documented and assessed by examining the dynamic evolution of their mean diurnal patterns. This approach is used because soil moisture deficits impose distinct patterns on the diurnal course of leaf carbon and water exchange (Hinckley *et al.* 1978b; Schulze 1986; Korner 1994). Mean diurnal patterns of carbon dioxide and water vapour fluxes were determined by binning fluxes by time and averaging them over 2 week periods. Bin averaging, by time, was used because it reduces the sampling error of the measurements (Moncrieff, Mahli & Leuning 1996). This averaging approach is also appropriate for deriving data sets for model testing because model calculations represent ensemble averages of measurements.

To identify periods experiencing drought, a water stress index was implemented (Fig. 2). The index is defined as the ratio between cumulative precipitation and cumulative potential evaporation. Potential evaporation was approximated with the Priestly Taylor equation. This algorithm equals $1.26 s/(s + \gamma) R_{\text{n}}$ (s is the slope of the saturation vapour pressure–temperature relation, γ is the psychrometric constant and R_{n} is the net radiation flux density). Summing for the index started on day 110, when the soil profile was replenished with water.

Five cases, encompassing a spectrum of well-watered and dry, and cool and hot periods, were chosen for the study. These cases are from periods when the average net radiation balance was similar (Fig. 3a) so that there was no significant difference in the amount of energy available to drive carbon dioxide uptake and evaporation.

The first case contains data averaged over days 141–154 and represents a period when photosynthetic capacity was maximal (Greco & Baldocchi 1996), air temperatures were moderate (Fig. 3b), and soil moisture was ample (the water stress factor exceeded 1) (Fig. 2). The second case contains data for the period between days 168 and 181. This case represents a period after maximal photosynthetic potential had occurred (Greco & Baldocchi 1996), but when air temperatures were still moderate and soil moisture was ample. The third case contains data between days 197 and 210. At this time, soil moisture deficits were beginning and air temperatures were high and above normal. The fourth case includes data averaged over the period between days 225 and 238. In this period very warm midday air temperatures (32 °C) were experienced (Fig. 3b) and the upper soil layer was drying out. Finally, the fifth case contains data averaged over the period between days 239 and 252. During

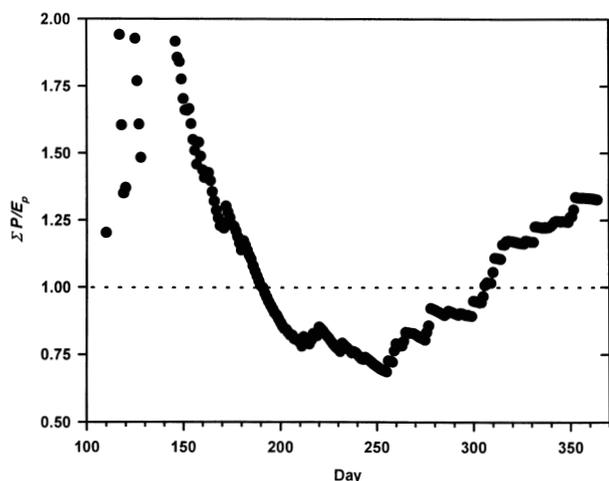


Figure 2. Seasonal variation of the canopy drought stress index during the 1995 growing season at a broad-leaved deciduous forest site near Oak Ridge, TN. The index is defined as the ratio between cumulative precipitation (ΣP) and potential evaporation (E). Summing started after the leaf area index reached 3. The Priestly Taylor equation was used to estimate potential evaporation.

this time, the forest experienced moderate air temperatures, but the lowest pre-dawn water potentials, as the forest had experienced a prolonged period of soil moisture deficit (Figs 1 & 2).

Average diurnal patterns of net ecosystem carbon exchange for the five periods identified above are shown in Fig. 4. When soil moisture was ample in the spring, peak rates of net ecosystem CO_2 exchange (N_E) occurred around midday and their magnitude exceeded $20 \mu\text{mol m}^{-2} \text{s}^{-1}$. Two weeks later, under similar environmental and soil moisture conditions, the magnitude of peak rates of net ecosystem carbon dioxide exchange diminished to below $20 \mu\text{mol m}^{-2} \text{s}^{-1}$.

There are few data on the seasonal evolution of photosynthetic capacity of an oak forest, but our pilot study (Greco & Baldocchi 1996) and data presented here suggest that N_E of a south-eastern, broad-leaved forest peaks between days 140 and 150. In contrast, N_E of a northern hardwood forest peaks after day 160 (Goulden *et al.* 1996b) since leaf-out is delayed as one moves north. Peak values of N_E over agricultural crops, such as corn and soybeans, also occur later in the growing season (Rochette *et al.* 1995, 1996), as these herbaceous plants must grow from seeds.

The accumulation of soil moisture deficits caused peak rates of daytime carbon dioxide uptake to occur earlier in the morning and the maximum value to decrease. By the fifth period (days 239–252) the magnitude of peak daytime rates of N_E was reduced, relative to the first period, by half. Peak values of N_E during the drought equalled $11 \mu\text{mol m}^{-2} \text{s}^{-1}$, as compared to $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the first period. I also note that rates of N_E were lower during case five than during the preceding period (days 225–238). This point is noteworthy because air temperatures were several

degrees lower during the fifth period. In the absence of drought, this condition would reduce the potential for respiratory losses from the forest.

With regard to nocturnal respiration, there was no discernible ranking of carbon efflux values with respect to nocturnal air temperature and soil moisture. This lack of an observed relationship between respiration, temperature and drought may be a consequence of the lower accuracy of measurements of nocturnal CO_2 fluxes (Lee *et al.* 1996; Moncrieff *et al.* 1996).

Mean diurnal patterns of latent heat flux density (LE) are shown in Fig. 5. There was no appreciable difference between evaporation rates in the well-watered case and the period between days 197 and 211, when the drought stress factor first became less than 1. Furthermore, evaporation rates were higher between days 224 and 238 than during the well-watered reference period, despite the limited availability of soil moisture during the latter period. The heat spell enhanced vapour pressure deficits, which promote evaporation over temperate forests (Baldocchi &

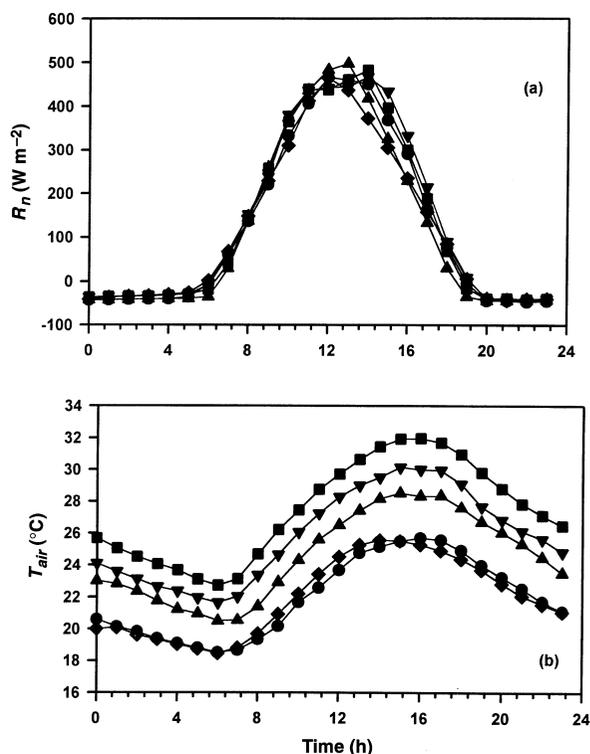


Figure 3. Mean diurnal patterns of meteorological variables over a temperate broad-leaved forest. The data were sorted by hour and were averaged for 2 week periods. (a) Mean diurnal patterns of net radiation. (b) Mean diurnal patterns of air temperature. ●: well-watered conditions and moderate air temperature (days 141–154); ◆: well-watered conditions, moderate air temperature and sub-maximum photosynthetic capacity (days 168–182); ▼: moderate soil moisture deficits (water stress index equalled 0.84) and above-normal air temperature (days 197–210); ■: water stress index equalled 0.77 and above-normal air temperature (days 225–238); ▲: water stress index equalled 0.72 and moderate air temperature (days 239–252).

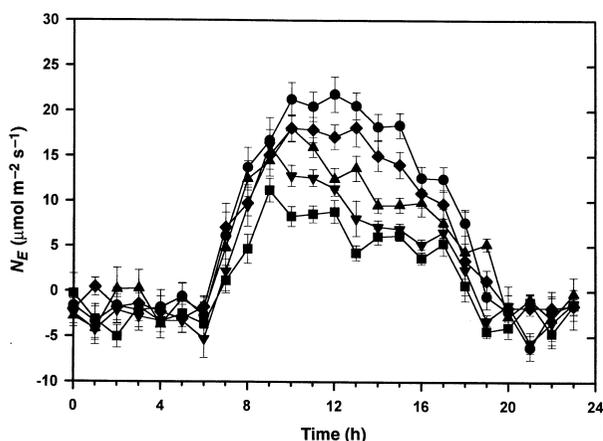


Figure 4. Mean diurnal patterns of net ecosystem CO₂ exchange. The data are averaged according to time of day, for 2 week periods. Five test cases are presented for varying conditions of soil moisture, temperature and photosynthetic capacity. ●: well-watered conditions and moderate air temperature (days 141–154); ◆: well-watered conditions, moderate air temperature and sub-maximum photosynthetic capacity (days 168–182); ▲: moderate soil moisture deficits (water stress index equalled 0.84) and above-normal air temperature (days 197–210); ▼: water stress index equalled 0.77 and above-normal air temperature (days 225–238); ■: water stress index equalled 0.72 and moderate air temperature (days 239–252).

Vogel 1996), despite the potential for stomatal closure when humidity deficits are large. By day 239, the drought was peaking. Only then were the daily patterns of LE negatively affected, as compared to the well-watered case. At this stage of the drought, midday and afternoon rates of LE were 50–75 W m⁻² lower than values measured earlier in the growing season.

Model calculations

Figures 6a and b present a test of the CANOAK model for case 2, a period with ample soil moisture and moderate air temperature. The diurnal patterns of CO₂ and water flux calculations correspond to field measurements. Furthermore, mass flux densities, derived from the CANOAK model, overlap field measurements for many periods of the day. This test adds to the growing number of studies that demonstrate an ability to model forest-stand fluxes of carbon and water under well-watered conditions (Amthor *et al.* 1994; Baldocchi & Harley 1995; Aber, Reich & Goulden 1996; Williams *et al.* 1996). Only during the night do measurements and model calculations diverge appreciably. However, disagreement between calculations and measurements may not be a result of invalid respiration calculations by the model. It is widely suspected that nocturnal measurements of CO₂ fluxes are error-prone under stable conditions and low wind speeds (Lee *et al.* 1996; Moncrieff, Mahli & Leuning 1996) despite the attempt to measure the storage of CO₂ in the canopy air space.

Two schemes were tested for calculating stomatal conductance when the trees were subjected to soil moisture deficits. One method assumed that high-temperature effects on photosynthesis induced limitations to stomatal conductance. The other methods adjusted the *m* coefficient of the stomatal conductance algorithm (Eqn 3).

Tenhunen *et al.* (1990) pioneered the concept of adjusting the proportionality coefficient between stomatal conductance and photosynthesis as a function of soil moisture for Mediterranean forests. However, they did not derive an explicit means for evaluating the drought factor; they defined it by matching model calculations and gas exchange measurements. Williams *et al.* (1996) chose to compute the soil water balance and model water transport through the xylem. Their approach has merit, for it is more mechanistic. However, it requires more model parameters, some of which are difficult to obtain. Since information on xylem hydraulic conductivity is not widely available, I decided not to use their approach. Instead, I adjusted stomatal conductance using a multiplicative water stress index derived from the plant water balance. The water stress index is simply a function of cumulative precipitation and equilibrium evaporation after day 110.

Figure 7 presents a test of the CANOAK model for the period when the soil moisture profile was beginning to be depleted; the water stress factor was 0.78 and pre-dawn water potentials approached –0.5 MPa. Here, we observe that there was general agreement between measured and calculated carbon dioxide and water vapour fluxes through most of the day, as long as the *m* coefficient was scaled by the water stress index. In particular, the model was able to mimic how environmental stresses caused maximum car-

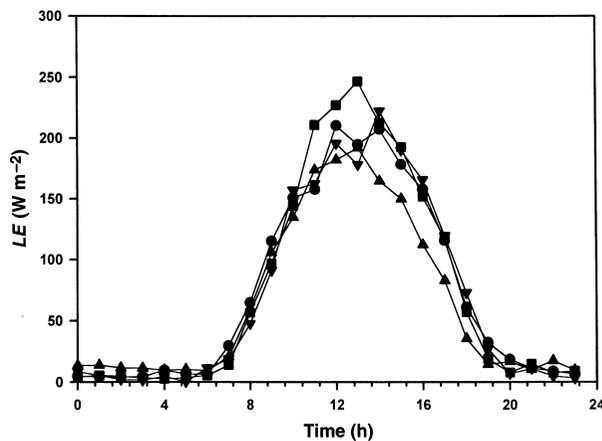


Figure 5. Mean diurnal patterns of canopy latent heat exchange. The data are sorted by hour and were averaged for 2 week periods. Four test cases are presented for varying conditions of soil moisture, temperature and photosynthetic capacity. ●: well-watered conditions and moderate air temperature (days 141–154); ▼: moderate soil moisture deficits (water stress index equalled 0.84) and above-normal air temperature (days 197–210); ■: water stress index equalled 0.77 and above-normal air temperature (days 225–238); ▲: water stress index equalled 0.72 and moderate air temperature (days 239–252).

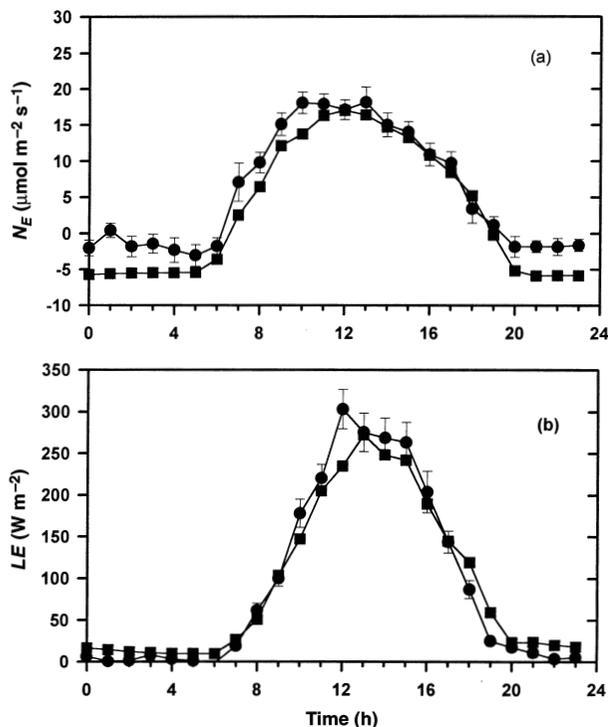


Figure 6. A comparison between measured (●) and simulated (■) values of canopy CO_2 (a) and water vapour (b) exchange. The canopy was well watered in this case (days 168–182) and air temperature was moderate.

bon uptake rates to occur by mid-morning and diminish gradually as the day progressed. Only afternoon estimates of LE differed greatly from measurements.

Figure 8 compares measurements and model calculations for the most severe period of the drought, when the stress factor equalled 0.72 and pre-dawn water potentials were below -1.2 MPa. The CANOAK model was able to mimic the shape of the diurnal pattern of N_E well if the maximum stomatal conductance was adjusted by the water stress factor. Absolute values of calculated N_E , however, overestimated midday and early afternoon fluxes by up to $5 \mu\text{mol m}^{-2} \text{s}^{-1}$. This bias can be due to errors in evaluating photosynthesis, plant or soil respiration. With regard to evaporation, simulations of LE were accurate until noon. After noon, model estimates of LE exceeded measurements by about 50 W m^{-2} . Ignoring the effect of soil moisture deficits on stomatal conductance led to a large overestimate of LE from mid-morning to midnight.

Impact of environmental variables on canopy-scale carbon dioxide exchange rates

Sunlight

When the temperate broad-leaved forest was well supplied with soil moisture, variations in the photosynthetic photon flux density absorbed by the canopy (Q_a) accounted for only 43% of the variance in net ecosystem carbon dioxide

exchange (N_E) (Fig. 9a). Furthermore, N_E was a non-linear function of Q_a . This observation is consistent with data from several temperate forests (Goulden *et al.* 1996b; Valentini *et al.* 1996). The non-linear behaviour of this relationship is noteworthy since it contrasts with the response of N_E to absorbed sunlight that is observed for managed crops. Crops possess a light response curve that is relatively linear and has a coefficient of determination typically exceeding 84% (Baldocchi 1993; Ruimy *et al.* 1995; Rochette *et al.* 1996).

The relatively low carboxylation capacity of oak and maple leaves may cause photosynthetic rates of forests to light-saturate; the mean carboxylation velocity (V_{cmax}) at 25°C is $47 \mu\text{mol m}^{-2} \text{s}^{-1}$ for hardwood forest species and is $90 \mu\text{mol m}^{-2} \text{s}^{-1}$ for dicot crops (Wullschlegel 1993). Using the cited values as a frame of reference, Fig. 10 shows that photosynthetic rates of a broad-leaved forest canopy with relatively low V_{cmax} values (25 and $50 \mu\text{mol m}^{-2} \text{s}^{-1}$) become light-saturated. Only the photosynthesis–light response curve of a canopy with a high V_{cmax} value remains quasi-linear. The theoretical results shown in Fig. 10 are consistent with experimental data surveyed by Ruimy *et al.* (1995).

One source of variation of data in Fig. 9a stems from the impact that sky conditions have on canopy photosynthesis. Several authors (Jarvis, Miranda & Muetzelfeldt 1985; Hollinger *et al.* 1994; Baldocchi & Harley 1995; Rochette

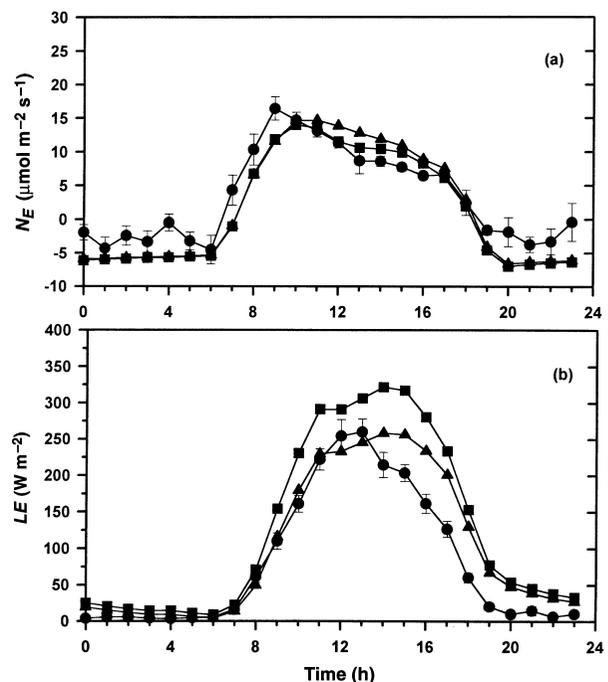


Figure 7. A comparison between measured (●) and simulated values of canopy CO_2 (a) and water vapour (b) exchange for case 4 (days 225–239). The vegetation suffered from soil moisture deficits and was exposed to hot daytime air temperatures in this case. ▲: model calculation with water stress index equal to 0.78; ■: model calculation with water stress index equal to 1.0.

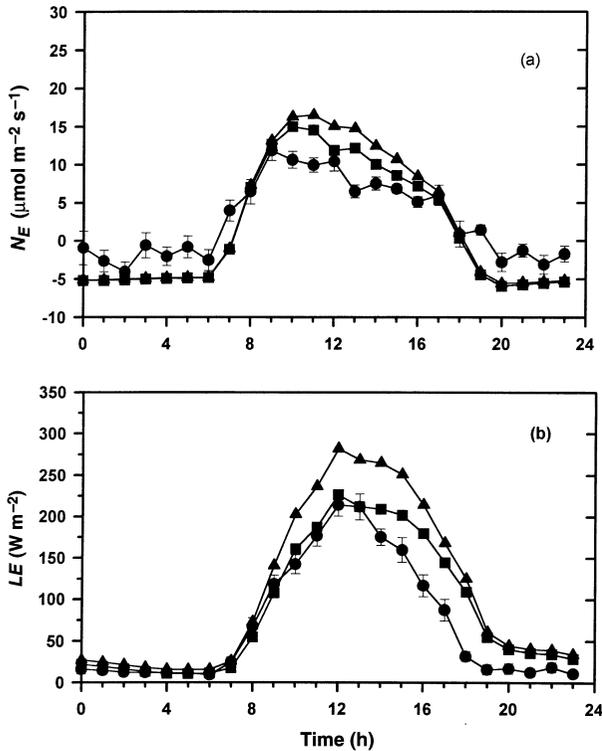


Figure 8. A comparison between measured (●) and simulated values of canopy CO₂ (a) and water vapour (b) exchange for case 5 (days 239–252). The vegetation suffered from soil moisture deficits. ■: model calculation with water stress index equal to 0.72; ▲: model calculation with water stress index equal to 1.0.

et al. 1996) report that radiation use efficiency (the initial slope of the relationship between N_E and Q_a) is higher under cloudy skies than under clear skies. Figure 9b shows that the slope of the N_E – Q_a curve is much steeper when the sky is mostly overcast (diffuse/total > 0.7) than when it is mostly clear (diffuse/total < 0.3). When clear sky conditions are compared with cloudy ones, rates of N_E are diminished by more than half. For example, when Q_a was $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, rates of N_E were 10 and $25 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, under clear and cloudy conditions.

A combination of physical and physiological processes account for this response. The relatively low carboxylation capacity of temperate forest species causes the photosynthetic rates of upper sunlit leaves to be light-saturated on sunny days. Since stomatal conductance scales with $V_{c\text{max}}$, these leaves also experience lower rates of transpiration and warmer temperatures than leaves possessing higher photosynthetic capacities. Consequently, sunlit leaves experience enhanced rates of respiration, which lower rates of net photosynthesis (Baldocchi & Harley 1995).

The results presented in Fig. 9b may have implications for a class of global primary production models. Some global primary production models estimate biospheric rates of carbon assimilation as a product between a radiation use efficiency and a satellite-derived estimate of solar radiation absorbed by canopies (e.g. Ruimy, Saugier &

Dedieu 1994). Few, if any, of these models consider the impact of sky cover on the radiation use efficiency. Sensitivity experiments on global models need to be done to evaluate the impact of cloud cover and atmospheric aerosols on the global carbon balance. Such calculations would also give guidance about whether or when more complex models need to be incorporated into global models. For example, the effect of cloud cover is diminished when daily integrals of N_E are considered instead of hourly integrals (Leuning *et al.* 1995).

The role of high temperature and soil water deficits on carbon dioxide and water vapour fluxes

Figure 11 explores the relative trade-offs between the effects of air temperature and soil moisture status on N_E , for the period between 1000 and 1400 h (to minimize confounding effects I restricted the data to periods when the mean photosynthetic photon flux density exceeded $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$). Rates of N_E were near-optimal when

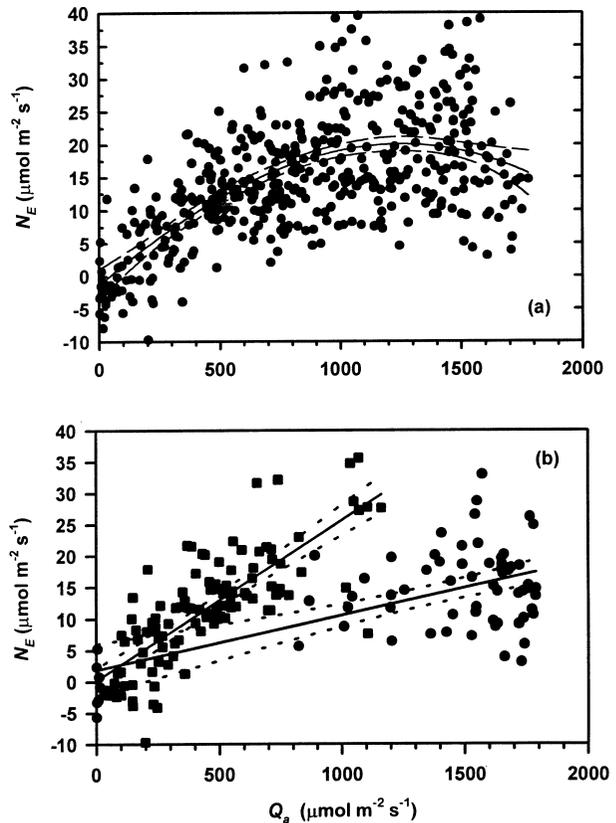


Figure 9. The dependence of net ecosystem carbon dioxide exchange on variations of absorbed photosynthetic photon flux density (Q_a). (a) These data were restricted to a period early in the growing season, after full-leaf and before the onset of the drought. The coefficient of variation for the second-order polynomial regression, fitted through the data, equalled 0.43. (b) The impact of sky conditions on N_E . Data are separated into categories when the ratio between diffuse and total photosynthetic photon flux data was less than 0.3 (■) or greater than 0.7 (●).

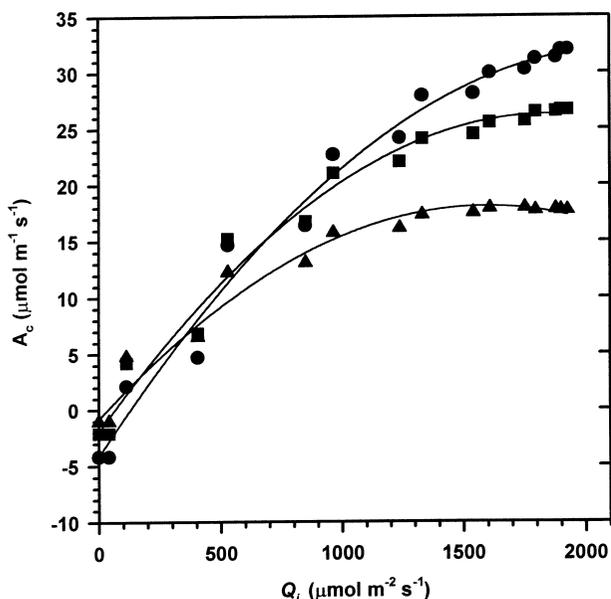


Figure 10. Model calculations on the impact of maximum carboxylation velocity (evaluated at 25 °C) on the relationship between canopy photosynthesis (A_c) and incident photosynthetic photon flux density (Q_i). The data are representative of the case of a well-watered, broad-leaved forest with a leaf area index of 4. ●: V_{cmax} equal to 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$; ■: V_{cmax} equal to 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$; ▲: V_{cmax} equal to 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

air temperature ranged between 22 and 25 °C until day 224. In contrast, higher air temperatures were correlated with a dramatic reduction in the magnitude of N_E (Fig. 11a). On average, the magnitude of N_E decreased from 20 to 7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ as air temperature increased from 24 to 30 °C. This canopy-scale response is similar to the temperature-related reduction of leaf photosynthesis and has also been reported for several oak and maple species (Hinckley *et al.* 1978a).

Model calculations were performed to examine why N_E is so sensitive to temperature. Figure 12 shows that the ratio between canopy respiration and photosynthesis increases from below 0.2 to 0.55 as mean leaf temperature increased from 20 to 32 °C. Increasing temperature promotes respiration over assimilation by causing the relative solubility of CO_2 versus oxygen and the specificity factor of Rubisco to decrease (Farquhar *et al.* 1980; Harley & Tenhunen 1991; Cornic 1994). Higher temperatures also promote root and soil respiration (Hanson *et al.* 1993). An inhibition of photosynthesis due to elevated ozone cannot be discounted (Amthor *et al.* 1994 Tjoekler *et al.* 1995). A covariance among N_E , air temperature and ozone concentration was detected. However, this issue is beyond the scope of this paper and warrants careful statistical scrutiny to obtain defensible results.

After day 225, average midday rates of N_E were statistically independent of air temperature (Fig. 11b) and mean rates were maintained below 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$. A distinct limitation on physiological function seems to have been

imposed on the carbon dioxide exchange rates of the forest, at this stage, by a lack of available soil moisture.

Concluding remarks

Significant variations in the magnitude and diurnal pattern of canopy CO_2 exchange rates occurred as the soil became progressively drier. The dynamic variation of diurnal patterns of N_E , at the stand-scale, resembles data published for a range of well-watered and drought-stressed leaves of hardwood species (Hinckley *et al.* 1978a; Tenhunen *et al.* 1990; Kubiske & Abrams 1992). The cause of these changes is complex and controversial. Cornic (1994), for instance, argues that limitations on photosynthesis during drought are imposed primarily through stomatal closure. He states that limitations occur through a sequence of events linked to a reduction of the CO_2 concentration at the chloroplast and the kinetic properties of Rubisco. The agreement between canopy-scale CO_2 flux measurements and model calculations supports this assertion since I only adjusted the stomatal conductance proportionality constant of the CANOAK model during the drought. Had

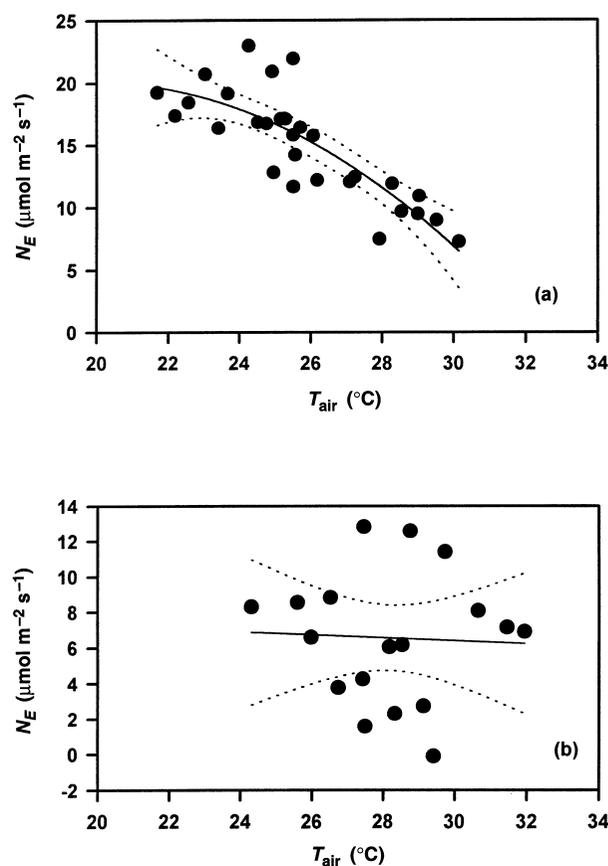


Figure 11. Impact of air temperature on net ecosystem carbon dioxide exchange rates. These data are from midday periods (1000–1500 h). (a) Data are from the period between day 141 and day 224. The forest was either well watered or experiencing the early part of the drought. (b) These data are restricted to the most severe period of the drought (days 225–252).

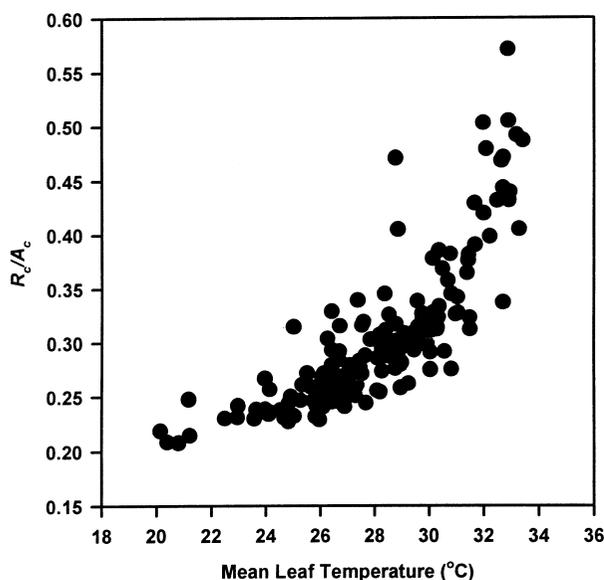


Figure 12. The relation between canopy respiration (R_c , leaf + bole + soil) and photosynthesis (A_c), as a function of leaf temperature. The values were computed with the CANOAK model and are for sunny periods ($Q_a > 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$).

alterations in the mesophyll conductance been large, one would have expected a larger deviation between the measurements and model calculations.

The field data indicate that evaporation rates were similar or higher during the early stage of the drought than during a prior well-watered period (Fig. 5). Without careful scrutiny, this evidence could have led one to conclude that the stomata remained open during the drought. A rationale for this conclusion could be obtained from the fact that the mature and dominant trees are able to tap deeper sources of soil moisture during the early stage of the drought; this conclusion would be consistent with isotopic data from Dawson (1996). Model calculations of evaporation suggest that this conclusion may be misleading. While rates of evaporation were similar across a wide range of available soil moisture, model calculations show that evaporation rates during the drought were appreciably below values that would have occurred otherwise, based on available radiation and the driving potential of the atmosphere for moisture transfer.

The cumulative drought index seems to have promise as a means for adjusting model coefficients during drought, for it enabled the model to yield accurate estimates of canopy CO₂ exchange. Furthermore, adoption of the drought index enabled the CANOAK model to give improved estimates of evaporation until midday. The scheme only failed during the afternoon, when evaporation was overestimated. However, this positive result may be fortuitous since the model scheme is not mechanistic. Consequently, further work is needed to improve upon this scheme. Some critics may argue, from these results, that the diurnal pattern of forest evaporation during drought

should not be modelled as an ensemble of leaves (an assumption that is valid for crops). A tree is an organ with leaves, with a capacity to store water in its boles. The transport of water through these two compartments causes hysteresis between rates of soil water uptake and transpiration (Jones 1982; Williams *et al.* 1996).

To gain credibility, use of the drought stress index must be tested in a wider range of circumstances. It should also be compared with calculations derived from a more rigorous modelling scheme. At present, theoretical methods exist that adjust g_s according to an optimal use of available soil water (Cowan 1982; Makela, Berninger & Hari 1996) and hydraulic transport through boles (Williams *et al.* 1996) and as a function of leaf (Mott & Parkhurst 1991) or canopy transpiration (Monteith 1995). Scaling stomatal conductance according to changes in ABA (e.g. Tardieu & Davies 1992) has promise for herbs, but there is no conclusive evidence showing that it may be valid for oak trees (Triboulot *et al.* 1996).

ACKNOWLEDGMENTS

This research is supported by the U.S. Department of Energy, Terrestrial Carbon Program. Supplemental support was provided by the U.S. Environmental Protection Agency, through a contract from Washington State University. This project was aided by the field and laboratory assistance of my colleagues, Mark Hall, Mark Brewer and David Auble. I thank Dr Detlef Matt for access to the solar radiation data and Dr Tilden Meyers for programming the data acquisition software. I thank Drs Paul Hanson, Jeff Amthor, Erwin Dreyer, Matt Williams and Paul Jarvis and anonymous reviewers for constructive comments on an earlier version of this manuscript and for sobering and insightful discussions on the presentation of the data.

REFERENCES

- Aber J.D., Reich P.B. & Goulden M.L. (1996) Extrapolating leaf CO₂ exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. *Oecologia* **106**, 257–265.
- Abrams M.D. (1994) Genotypic and phenotypic variation as stress adaptations in temperate tree species: a review of several case studies. *Tree Physiology* **14**, 833–842.
- Abrams M.D. & Mostoller S. (1995) Gas exchange, leaf structure and nitrogen in contrasting successional species growing in open and understory sites during drought. *Tree Physiology* **15**, 361–370.
- Amthor J.S., Goulden M.L., Munger J.W. & Wofsy S.C. (1994) Testing a mechanistic model of forest-canopy mass and energy exchange using eddy correlation: carbon dioxide and ozone uptake by a mixed oak-maple stand. *Australian Journal of Plant Physiology* **21**, 623–651.
- Anderson D.E., Verma S.B., Clement R.E., Baldocchi D.D. & Matt D.R. (1986) Turbulence spectra of CO₂, water vapour, temperature and velocity over a deciduous forest. *Agricultural and Forest Meteorology* **38**, 81–99.

- Auble D.L. & Meyers T.P. (1992) An open path, fast response infrared absorption gas analyzer for H₂O and CO₂. *Boundary Layer Meteorology* **59**, 243–256.
- Baldocchi D.D. (1993) A comparative study of mass and energy exchange over a closed (wheat) and an open (corn) canopy: II. Canopy CO₂ exchange and water use efficiency. *Agricultural and Forest Meteorology* **67**, 291–322.
- Baldocchi D.D. (1994) An analytical solution for coupled leaf photosynthesis and stomatal conductance models. *Tree Physiology* **14**, 1069–1079.
- Baldocchi D.D. & Harley P.C. (1995) Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest: model testing and application. *Plant, Cell and Environment* **18**, 1157–1173.
- Baldocchi D.D. & Vogel C. (1996) A comparative study of water vapour, energy and CO₂ flux densities above and below a temperate broadleaf and a boreal pine forest. *Tree Physiology* **16**, 5–16.
- Baldocchi D.D., Matt D.R., Hutchison B.A. & McMillen R.T. (1984) Solar radiation within an oak-hickory forest: an evaluation of extinction coefficients for several radiation components during fully leafed and leafless periods. *Agricultural Forest Meteorology* **32**, 307–322.
- Baldocchi D.D., Hicks B.B. & Meyers T.P. (1988) Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology* **69**, 1331–1340.
- Björkman O. (1981) The response of photosynthesis to temperature. In *Plants and Their Atmospheric Environment* (eds J. Grace, E.D. Ford & P.G. Jarvis), pp. 273–302. Blackwell Scientific Publications, Oxford.
- Campbell G. (1985) *Soil Physics with BASIC*. Elsevier, Amsterdam.
- Cochard H., Breda N. & Granier A. (1996) Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism? *Annales Sciences Forestieres* **53**, 197–206.
- Collatz G.J., Ball J.T., Griwet C. & Berry J.A. (1991) Regulation of stomatal conductance and transpiration: a physiological model of canopy processes. *Agricultural and Forest Meteorology* **54**, 107–136.
- Cook E.R., Koblack M.A. & Jacoby G.C. (1988) The 1986 drought in the southeastern United States: How rare an event was it? *Journal of Geophysical Research* **93**, 14257–14260.
- Cornic G. (1994) Drought stress and high light effects on leaf photosynthesis. In *Photoinhibition of Photosynthesis from Molecular to the Field* (eds N.R. Baker & J.R. Bowyer), pp. 297–313. BIOS Scientific Publications, Oxford.
- Cowan I.R. (1982) Regulation of water use in relation to carbon gain in higher plants. In *Encyclopedia of Plant Physiology: Physiological Plant Ecology*, Vol. 2 (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), pp. 589–614. Springer-Verlag, Berlin.
- Dawson T.E. (1996) Determining water use by trees and forest from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology* **16**, 263–272.
- Dickson R.E. & Tomlinson P.T. (1996) Oak growth, development and carbon metabolism in response to water stress. *Annales Sciences Forestieres* **53**, 181–196.
- Dougherty P.M., Teskey R.O., Phelps J.E. & Hinckley T.M. (1979) Net photosynthesis and early growth trends of a dominant white oak. *Plant Physiology* **64**, 930–935.
- Dreyer E. (1996) Photosynthesis and drought in forest trees. In *Trees – Contributions to Modern Tree Physiology* (eds H. Rennenberg, W. Eschrich & H. Ziegler), pp. 217–240. SPB Academic Publishing, Amsterdam, The Netherlands.
- Dreyer E., Granier A., Breda N., Cochard H., Epron D. & Aussenac G. (1993) Oak trees under drought constraints: ecophysiological aspects. In *Recent Advances in Studies on Oak Decline* (eds N. Luisi, P. Lerario & A. Vannini), pp. 293–322.
- Dreyer E., Tardieu F., Schulze E.-D., Stiller V., Dizengremel P., Sehmer L. & Label P. (1994) Regulation of photosynthetic activity in forest trees during drought. In *EUROSILVA – Contribution to Forest Tree Physiology* (eds M. Bonnet Rasinbert & H. Sanderman), pp. 339–368. INRA, Paris.
- Edwards N.T. & Hanson P.J. (1996) Stem respiration in a closed-canopy upland oak forest. *Tree Physiology* **16**, 433–439.
- Ellsworth D.S. & Reich P.B. (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**, 169–178.
- Epron D. & Dreyer E. (1993) Photosynthesis of oak leaves under water stress: maintenance of high photochemical efficiency of photosystem II and occurrence of non-uniform CO₂ assimilation. *Tree Physiology* **13**, 107–117.
- Farquhar G.D. & von Caemmerer S. (1982) Modeling photosynthetic response to environmental conditions. In *Encyclopedia of Plant Physiology*, Vol. 12B (O.L. Lange, P. Nobel, C. Osmond & H. Ziegler), pp. 549–587. Springer-Verlag, Berlin.
- Farquhar G.D., von Caemmerer S. & Berry J.A. (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* **149**, 78–90.
- Gollan T., Passioura J.B. & Munns R. (1986) Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. *Australian Journal of Plant Physiology* **13**, 459–464.
- Goulden M.L. & Field C.B. (1994) Three methods for monitoring the gas exchange of individual trees: ventilated-chamber, sap-flow and Penman Monteith measurements on evergreen oak. *Functional Ecology* **8**, 125–135.
- Goulden M.L., Munger J.W., Fan S.M., Daube B.C. & Wofsy S.C. (1996a) Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* **271**, 1576–1578.
- Goulden M.L., Munger J.W., Fan S.M., Daube B.C. & Wofsy S.C. (1996b) Measurement of carbon storage by long-term eddy correlation: Methods and a critical assessment of accuracy. *Global Change Biology* **2**, 169–182.
- Greco S. & Baldocchi D.D. (1996) Seasonal variations of CO₂ and water vapour exchange rates over a temperate deciduous forest. *Global Change Biology* **2**, 183–198.
- Hanson P.J., Wullschlegel S.D., Bohlman S.A. & Todd D.E. (1993) Seasonal and topographic patterns of forest floor CO₂ efflux from an upland oak forest. *Tree Physiology* **13**, 1–15.
- Harley P.C. & Baldocchi D.D. (1995) Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest: leaf level parameterization. *Plant, Cell and Environment* **18**, 1146–1156.
- Harley P.C. & Tenhunen J.D. (1991) Modeling the photosynthetic response of C₃ leaves to environmental factors. In *Modeling Photosynthesis – From Biochemistry to Canopy* (eds K. Boote & R. Loomis), pp. 17–39. American Society of Agronomy, Madison, WI.
- Hinckley T.M., Aslin R.G., Aubuchon R.R., Metcalf C.L. & Roberts J.E. (1978a) Leaf conductance and photosynthesis in four species of the oak-hickory forest type. *Forest Science* **24**, 73–84.
- Hinckley T.M., Lassoie J.P. & Running S.W. (1978b) *Temporal and Spatial Variations in the Water Status of Forest Trees. Forest Science Monograph* 20. Washington, DC.
- Hollinger D.Y., Kelliher F.M., Byers J.N., Hunt J.E., McSeveny T.M. & Weir P.L. (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest & the atmosphere. *Ecology* **75**, 134–150.

- Huang J. & Van den Dool H.M. (1993) Monthly precipitation-temperature relations and temperature prediction over the United States. *Journal of Climate* **6**, 1111–1132.
- Hutchison B.A. & Baldocchi D.D. (1989) Forest meteorology. In *Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed* (eds D.W. Johnson & R.I. Van Hook), pp. 21–95. Springer-Verlag, Berlin.
- Hutchison B.A., Matt D.R., McMillen R.T., Gross L.J., Tajchman S.J. & Norman J.M. (1986) The architecture of a deciduous forest canopy in eastern Tennessee, USA. *Journal of Ecology* **74**, 635–646.
- Jacob C.M.J. & deBruin H.A.R. (1992) The sensitivity of regional transpiration to land-surface characteristics: significance of feedback. *Journal of Climate* **5**, 683–698.
- Jarvis P.G., Miranda H.S. & Muetzelfeldt R.I. (1985) Modeling canopy exchanges of water vapour and carbon dioxide in coniferous forest plantations. In *The Forest-Atmosphere Interaction* (eds B.A. Hutchison & B.B. Hicks), pp. 521–542. Reidel, Dordrecht.
- Jones H.G. (1982) *Plants and Microclimate*. Cambridge University Press, Cambridge.
- Johnson D.W. & van Hook R.I. (eds) (1989) *Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed*. Springer-Verlag, New York.
- Karl T.R. & Young P.J. (1987) The 1986 Southeast drought in historical perspective. *Bulletin of the American Meteorological Society* **68**, 773–778.
- Korner Ch. (1994) Leaf diffusive conductances in major vegetation types of the globe. In *Ecophysiology of Photosynthesis* (eds E.D. Schulze & M.M. Caldwell), pp. 463–490. Springer, Berlin.
- Kramer P.J. & Boyer J.S. (1995) *Water Relations of Plants and Soils*. Academic Press, San Diego.
- Kubiske M.E. & Abrams M.D. (1992) Photosynthesis, water relations and leaf morphology of xeric versus mesic *Quercus rubra* ecotypes in central Pennsylvania in relation to moisture stress. *Canadian Journal of Forest Research* **22**, 1402–1407.
- Kubiske M.E. & Abrams M.D. (1994) Ecophysiological analysis of woody species in contrasting temperate communities during wet and dry years. *Oecologia* **98**, 303–312.
- Lee X., Black T.A., den Hartog G., Neumann H.H., Nesic Z. & Olenik J. (1996) Carbon dioxide exchange and nocturnal processes over a mixed deciduous forest. *Agricultural and Forest Meteorology* **81**, 12–30.
- Leuning R., Kelliher F.M., dePury D.G.G. & Schulze E.D. (1995) Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies. *Plant, Cell and Environment* **18**, 1183–1200.
- Livezey R.E. & Tinker R. (1996) Some meteorological, climatological and micrometeorological considerations of the severe U.S. heat wave of mid-July 1995. *Bulletin of the American Meteorological Society* **77**, 2043–2054.
- Loustau D., Berbigier P., Roumagnac P., Arruda-Pacheco C., David J.S., Ferreira M.I., Pereira J.S. & Tavares R. (1996) Transpiration of a 64-year-old maritime pine stand in Portugal. 1. Seasonal course of water flux through maritime pine. *Oecologia* **107**, 33–42.
- Makela A., Berninger F. & Hari P. (1996) Optimal control of gas exchange during drought: theoretical analysis. *Annals of Botany* **77**, 461–467.
- Moncrieff J.B., Mahli Y. & Leuning R. (1996) The propagation of errors in long term measurements of land atmosphere fluxes of carbon and water. *Global Change Biology* **2**, 231–240.
- Monteith J.L. (1995) Accommodation between transpiring vegetation and the convective boundary layer. *Journal of Hydrology* **166**, 251–263.
- Mott K.A. & Parkhurst D.F. (1991) Stomatal responses to humidity in air and helox. *Plant, Cell and Environment* **14**, 509–515.
- Myneni R., Ross J. & Asrar G. (1989) A review on the theory of photon transport in leaf canopies. *Agricultural and Forest Meteorology* **45**, 1–153.
- Nizinski J. & Saugier B. (1989) A model of transpiration and soil water balance for a mature oak forest. *Agricultural and Forest Meteorology* **47**, 1–17.
- Norman J.M. (1979) Modeling the complete crop canopy. In *Modification of the Aerial Environment of Crops* (eds W. Barfield & J. Gerber), pp. 249–280. American Society of Agricultural Engineers, St. Joseph, MI.
- Paw U K.T. (1987) Mathematical analysis of the operative temperature and energy budgets. *Journal of Thermal Biology* **12**, 227–233.
- Raupach M.R. (1988) Canopy transport processes. In *Flow and Transport in the Natural Environment: Advances and Applications* (eds W.L. Steffen & O.T. Denmead), pp. 1–33. Springer-Verlag, Berlin.
- Rochette P., Desjardins R.L., Pattey E. & Lessard R. (1995) Crop net carbon dioxide exchange rate and radiation use efficiency in soybean. *Agronomy Journal* **87**, 22–28.
- Rochette P., Desjardins R.L., Pattey E. & Lessard R. (1996) Instantaneous measurement of radiation and water use efficiencies of a maize crop. *Agronomy Journal* **88**, 627–635.
- Ross J. (1981) *The Radiation Regime and Architecture of Plant Stands*. W. Junk, The Hague, Netherlands.
- Ruimy A., Jarvis P.G., Baldocchi D.D. & Saugier B. (1995) CO₂ fluxes over plant canopies and solar radiation: a literature review. *Advances in Ecological Research* **26**, 1–68.
- Ruimy A., Saugier B. & Dedieu G. (1994) Methodology for the estimation of terrestrial net primary production from remotely sensed data. *Journal of Geophysical Research* **99**, 5263–5283.
- Sala A. & Tenhunen J. (1996) Simulations of canopy net photosynthesis and transpiration of *Quercus ilex* L. under the influence of seasonal drought. *Agricultural and Forest Meteorology* **78**, 203–222.
- Schuepp P.H. (1993) Tansley Review no. 59: Leaf boundary layers. *New Phytologist* **125**, 477–507.
- Schulze E.D. (1986) Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. *Annual Review of Plant Physiology* **37**, 247–274.
- Tardieu F. & Davies W.J. (1992) Stomatal response to abscisic acid is a function of current plant water status. *Plant Physiology* **98**, 540–545.
- Tenhunen J.D., Lange O.L., Gebel J., Beyschlag W. & Weber J.A. (1984) Changes in the photosynthetic capacity, carboxylation efficiency, and CO₂ compensation point associated with midday stomatal closure and midday depression of net CO₂ exchange of leaves of *Quercus suber*. *Planta* **162**, 193–203.
- Tenhunen J.D., Sala Serra A., Harley P.C., Dougherty R.L. & Reynolds J.F. (1990) Factors influencing carbon fixation and water use by Mediterranean sclerophyll shrubs during summer drought. *Oecologia* **82**, 381–393.
- Thomson D.J. (1987) Criteria for the selection of stochastic models of particle trajectories in turbulent flow. *Journal of Fluid Mechanics* **180**, 529–556.
- Tjoekker M.G., Volin J.C., Olesksyn J. & Reich P.B. (1995) Interaction of ozone pollution and light effects on photosynthesis in a forest canopy experiment. *Plant, Cell and Environment* **18**, 895–905.
- Trewartha G.T. (1968) *An Introduction to Climate*. McGraw-Hill, New York.
- Triboulot M.B., Fauveau M.L., Breda N., Label P. & Dreyer E. (1996) Stomatal conductance and xylem-sap abscisic acid (ABA) in adult oak trees during a gradually imposed drought. *Annales Sciences Forestiere* **53**, 207–220.
- Valentini R.P., de Angelis G., Matteucci R., Monaco S., Dore & G.E.

- & Scarascia-Mugnozza (1996) Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biology* **2**, 199–208.
- Weber J.A. & Gates D.M. (1990) Gas exchange in *Quercus rubra* (northern red oak) during a drought: analysis of relations among photosynthesis, transpiration and leaf conductance. *Tree Physiology* **7**, 215–225.
- Williams M., Rastetter E.B., Fernandes D.N., Goulden M.L., Wofsy S.C., Shaver G.R., Meillo J.M., Munger J.W., Fan S.M. & Nadelhoffer K.J. (1996) Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell and Environment* **19**, 911–927.
- Wofsy S.C., Goulden M.L., Munger J.W., Fan S.M., Bakwin P.S., Daube B.C., Bassow S.L. & Bazzaz F.A. (1993) Net exchange of CO₂ in a mid-latitude forest. *Science* **260**, 1314–1317.
- Wullschlegel S.D. (1993) Biochemical limitations to carbon assimilation in C₃ plants—a retrospective analysis of the A/C_i curves from 109 species. *Journal of Experimental Botany* **44**, 907–920.

Received 1 November 1996; received in revised form 13 March 1997; accepted for publication 14 April 1997