Global Change Biology (1996) 2, 183–197

Seasonal variations of CO_2 and water vapour exchange rates over a temperate deciduous forest

SUSANNA GRECO* and DENNIS D. BALDOCCHI†
**University of Tuscia, Department of Forest Science and Environment, Via S. Camillo de Lellis, 01100 Viterbo, Italy,*
†Atmospheric Turbulence and Diffusion Division, National Oceanic and Atmospheric Administration, PO Box 2456 Oak Ridge, TN 37831, USA.

Abstract

Long-term and direct measurements of CO_2 and water vapour exchange are needed over forested ecosystems to determine their net annual fluxes of carbon dioxide and water. Such measurements are also needed to parameterize and test biogeochemical, ecological and hydrological assessment models. Responding to this need, eddy covariance measurements of CO_2 and water vapour were made over a deciduous forest growing near Oak Ridge, TN, between April 1993 and April 1994. Periodic measurements were made of leaf area index, stomatal resistance, soil moisture and pre-dawn leaf water potential to characterize the gas exchange capacity of the canopy.

Four factors had a disproportionate influence on the seasonal variation of CO_2 flux densities. These factors were photon flux densities (during the growing season), temperature (during the dormant season), leaf area index and the occurrence of drought. The drought period occurred during the peak of the growing season and caused a significant decline in daily and hourly CO_2 flux densities, relative to observations over the stand when soil moisture was plentiful.

The annual net uptake of carbon was calculated by integrating flux measurements and filling missing and spurious data with the relations obtained between measured CO_2 fluxes and environmental forcing variables. The net flux of carbon for the period between April 1993 and April 1994 was -525 g C m^{-2} y^{-1}. This value represents a net flux of carbon from the atmosphere and into the forest. The net annual carbon exchange of this southern temperate broadleaved forest exceeded values measured over a northern temperate forest (which experiences a shorter growing season and has less leaf area) by 200 g C m^{-2} y^{-1} (cf. Wofsy *et al.* 1993).

The seasonal variation of canopy evaporation (latent heat flux) was controlled mostly by changes in leaf area and net radiation. A strong depression in evaporation rates was not observed during the drought. Over a broadleaved forest, large vapour pressure deficits promote evaporation and trees in a mixed stand are able to tap a variety of deep and shallow water sources.

Keywords: biosphere–atmosphere interactions, carbon dioxide, CO_2 fluxes, ecophysiology, eddy covariance, micrometeorology, temperate broadleaved forest

Received 25 June 1995; revision accepted 10 October 1995

Introduction

Yearly changes in atmospheric carbon dioxide concentrations result from fluxes of carbon dioxide into and out of the atmosphere. Yet, direct measurements of annual and seasonal carbon and water vapour fluxes over terrestrial ecosystems are rare (e.g. Wofsy *et al.* 1993; Vermetten *et al.* 1994). Most of our knowledge on terrestrial and global carbon budgets stem from matching long-term measurements of carbon dioxide concentrations with indirect estimates of carbon dioxide fluxes (Tans *et al.* 1990; Potter *et al.* 1993; Lloyd & Farquhar 1994; Maisongrande *et al.* 1995; Conway *et al.* 1995) or from monitoring temporal changes in biomass (Kauppi *et al.* 1992).

Direct and long-term measurements of canopy-scale carbon dioxide and water vapour fluxes are needed over various ecosystems to inform us about their seasonal

Correspondence: Dennis Baldocchi, fax +1-423-576-1327, e-mail baldocchi@atdd.noaa.gov

variation and magnitude. Canopy-scale carbon dioxide and water vapour flux measurements are also needed to quantify the effect of environmental and physiological forcing factors on these fluxes and to provide data for the testing of ecosystem carbon and water balance models.

Annual carbon and water budgets of temperate broadleaved forests are of particular interest. These forests cover a significant portion of the terrestrial biosphere (McGuire *et al.* 1992), they experience distinct periods and patterns of carbon gain and carbon and water loss over the course of a year and they may be a major sink of carbon dioxide in the northern hemisphere (Ciais *et al.* 1995). Yet, most published reports on net carbon dioxide and water vapour exchange over temperate broadleaved forests come from short studies during the summer growing season (Verma *et al.* 1986; Baldocchi & Harley 1995) or from non-contiguous campaigns over the course of a year (Hollinger *et al.* 1994). Only one team has published long-term measurements of CO_2 fluxes over a broadleaved forest. Wofsy *et al.* (1993) reported 3 years of CO_2 flux measurements at Harvard Forest. They showed that a northern temperate forest is accumulating carbon on a yearly basis and at rates greater than estimates derived from carbon balance models.

Long-term carbon dioxide flux measurements at one northern, temperate forest site (i.e. Harvard Forest) is insufficient to understand the carbon balance of all temperate forests. Southern broadleaved forests, for instance, have greater leaf area indices (Hutchison *et al.* 1986; Wofsy *et al.* 1993) and they experience a longer growing season. These factors have the potential to cause more carbon uptake to occur at sites in the warmer and wetter south-eastern deciduous biome (for example, a growing season with 30 extra days can contribute an additional 150–300 g C m^{-2} to the carbon balance of a forest over the course of a year, if daily carbon uptake rates between 5 and 10 g C m^{-2} day^{-1} are maintained). Southern forests also experience periodic droughts. During dry years, there may be a significant reduction of net canopy carbon uptake, as stomatal closure reduces photosynthesis and warm temperatures promote respiration (Hinkley *et al.* 1978; Tenhunen *et al.* 1984). However, we have no information on how dry and wet years may affect the annual carbon balance of these forests.

This paper reports on a year-long measurement study of CO_2, water and energy exchange over a broadleaved deciduous forest growing in the south-eastern deciduous biome of North America. The objective of this report is to examine the seasonality of canopy-scale carbon dioxide and water vapour fluxes and to construct an annual budget on the net carbon flux between the biosphere-atmosphere. We also explore the ramifications of drought on daily carbon dioxide and water vapour fluxes during the growing season.

Materials and methods

(a) Site characteristics

Micrometeorological measurements of carbon dioxide, water and energy exchange rates were made over a mixed deciduous forest, representative of the eastern North America deciduous forest biome. The field site was located on the United States Department of Energy reservation near Oak Ridge, TN (lat. 35° 57′ 30′; long. 84° 17′ 15′; 365 m above mean sea level). The surrounding area is vegetated with an uneven stand of oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.) and loblolly pine (*Pinus taeda*) that developed after agricultural abandonment in 1940.

Information on leaf area profiles, leaf angle distributions, species composition, soil composition and forest stocking densities have been reported by Hutchison *et al.* (1986) and Johnson and van Hook (1989). In brief, the mean canopy height was about 24 m and its peak leaf area index of the canopy was about 4.9 (Hutchison *et al.* 1986).

Soil moisture of the top 15 cm soil and litter layer was measured weekly using the gravimetric method. Periodically, we measured pre-dawn leaf water potential to obtain an integrated measure of the soil water content in the root volume of understory saplings. Using a pressure chamber, water potential was measureed on six to eight leaves (typically leaves of *Acer rubrum* and *Liriodendron tulipifera*).

(b) Measurements and Instrumentation

The eddy covariance technique was used to measure flux densities of CO_2, water vapour and sensible heat between the forest and the atmosphere (see Baldocchi *et al.* 1988 for details). This method evaluates vertical flux densities of CO_2 (F_c), latent (LE) and sensible heat (H) between the forest and the atmosphere by measuring the mean covariance between vertical velocity (w') and scalar (c') fluctuations. Turbulent fluctuations were determined from the difference between instantaneous and mean scalar quantities. Mean scalar values were determined, in real-time, using a digital recursive filter with a 400 s time constant. Positive flux densities represent mass and energy transfer into the atmosphere and away from the surface. Negative values denote the reverse.

Details of the experimental setup are described by Baldocchi and Harley (1995). For completeness we present a brief overview of the key design features of the experiment. A set of micrometeorological instruments was suspended 35 m above the ground (and 11 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 per second. In-house software was used to process the measurements. The software computed mass and energy flux covariances for half-hour intervals and numerically rotated wind velocity axes to compute flux covariance that were aligned normal to the mean wind streamlines (see Baldocchi *et al.* 1988). Computations of power spectra and co-spectra indicate that the instrument response characteristics, its sampling rate and sampling duration were adequate for measuring fluxes above this forest canopy (see Anderson *et al.* 1986; Auble & Meyers 1992).

The CO_2 sensor was calibrated bi-weekly against gas standards that were traceable to the National Bureau of Standards. Water vapour calibrations were referenced to a dew point hygrometer.

Proper interpretation of experimental results and use of the data for model evaluation requires simultaneous measurements of environmental variables and energy balance components. Soil heat flux density was measured using three soil heat flux plates (REBS model HFT-3, Seattle, WA) buried 0.01 m below the surface. Soil temperature was measured with multi-level thermocouple probes, spaced logarithmically at 0.02, 0.04, 0.08, 0.16 and 0.32 m below the soil surface. Shortwave radiation, photosynthetically active photon flux density and the net radiation balance were measured above the forest with a pyranometer (Eppley model 0–48, Newport, RI), a quantum sensor (LICOR model LI-190S, Lincoln, NE) and a net radiometer (REBS model 6, Seattle, WA), respectively. Air temperature and relative humidity were measured above the canopy and near the forest floor with appropriate sensors (Campbell model 207, Logan, UT). Wind speed and direction was measured with a propeller wind speed/direction monitor (RM Young model 05701, Traverse City, MI).

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 one cm into the trunk of a tree at breast height. Ancillary environmental data were sampled at 1 s intervals and were logged on Campbell CR-7 and CR-21x data loggers.

The solar radiation field below a forest canopy is highly variable. To account for this variability, measurements of solar radiation components were made using an instrument package that traversed across a 30 m domain. Measurements of PAR interception were used to infer seasonal changes of canopy leaf area index. Exponential relationships derived from previous studies at this site (Baldocchi *et al.* 1984) were used for this purpose.

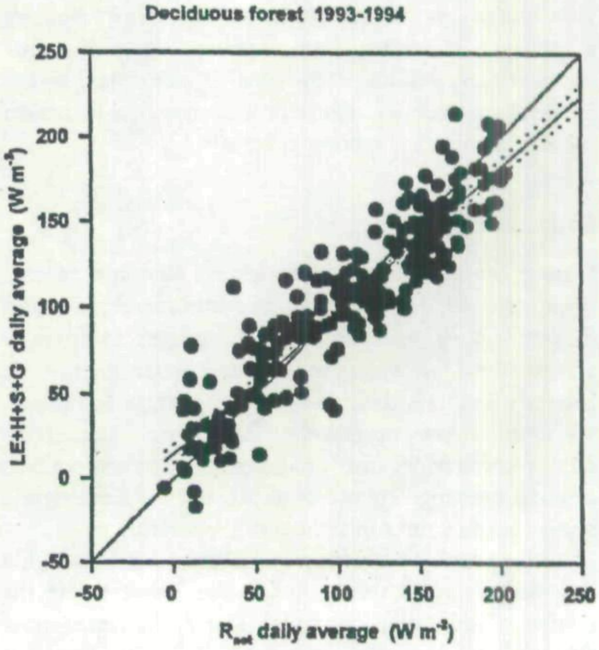

Fig. 1 Test of the energy balance closure. The daily averaged net radiation flux density (R_n) is plotted against the sum of its partitioning components, latent heat (*LE*), sensible heat (*H*), soil heat (*S*) and canopy heat storage (*G*).

Quality of the eddy flux data was tested by checking power and co-spectra of the turbulence measurements and by examining our ability to close the surface energy balance.

The ability to close the surface energy balance—the difference between measurements of net radiation flux density (R_n) and its partitioning into latent (*LE*), sensible (*H*) and soil heat flux (*S*) densities and canopy heat storage (*G*) is shown in Fig. 1 for daily integrated fluxes. Over the course of a year, we encountered a wide the range of wind directions and fair and foul weather. Yet, the amount of scatter observed in Fig. 1 for daily flux measurements is relatively constrained. We also found that closure of the surface energy balance was independent of wind direction (data not shown).

For the days with valid data, the mean, standard error and standard deviation of net radiation flux density were 106, 3.7 and 56 W m^{-2}, respectively. Corresponding statistics for the summation of the energy balance components were 104, 3.4 and 51 W m^{-2}, respectively. From calculations of Student's paired *t*-test, we conclude that there was no significant difference between net radiation and its partitioning into *LE*, *H*, *S* and *G*. These data demonstrate the power that sampling large population pools has to reduce standard errors of the estimate.

This favourable closure of the surface energy balance encourages continued and additional long-term flux measurement studies at this site. It also establishes a figure of merit on the bias error we can expect with such measurements over a non-perfect site.

(c) Data analysis

During the annual experiment, vast amounts of data were acquired. To reduce the data into manageable and digestible bites, we evaluated daily integrated fluxes of carbon dioxide, water vapour and solar energy. To properly evaluate daily and annually integrated fluxes, we found it was necessary to have nearly continuous data records since the processes that control carbon dioxide exchange (photosynthesis and respiration) are non-linear functions of light and temperature.

It is impossible to take perfect and reliable data 24 h a day, seven days a week, month after month; over the course of this year-long pilot study we experienced several breakdowns and acquired direct flux measurements on 244 days. To evaluate daily fluxes we adopted an approach that combined measurements with interpolation and empirical data synthesis (see Wofsy *et al.* 1993; Vermetten *et al.* 1994). First, we screened the data. Data were rejected when sensor outputs were out of range or when sensors were broken, being repaired or being calibrated. We also rejected data when its magnitude exceeded the daily mean plus/minus three times its standard deviation. Numerical schemes were used to fill and adjust missing and suspect data. Hourly gaps of meteorological data were filled via interpolation between earlier and later measurements.

Missing mass and energy flux data were treated in a different way. Missing values of net radiation (R_n), latent (LE) and sensible heat (H) exchange and CO_2 (F_c) flux were estimated using empirical regressions, determined from field data taken during this study and the 1992 field season (Baldocchi & Harley 1995). Missing values of R_n were estimated as a function of photosynthetic photon flux density (Q_p) and missing LE and H-values were estimated as functions of R_n. During the growing season, missing CO_2 flux (F_c) data was estimated as a function of photosynthetic photon flux density during the day and as a function of air temperature at night. During the winter dormant period, missing F_c data was evaluated as a function of air temperature. The temperature-dependent respiration function was based on data selected from windy and well-mixed periods (when friction velocity (u^*) exceeded 0.2 m s^{-1}).

Over a tall forest, the CO_2 flux density measured by an eddy covariance system does not always equal the net biotic CO_2 exchange during the period of integration (see Wofsy *et al.* 1993; Hollinger *et al.* 1994; Baldocchi & Vogel 1996). A bias error can occur when CO_2 is stored in or withdrawn from the layer of air below the eddy flux system. Storage is most likely to be significant during the night when the atmosphere is stably stratified and winds are weak. A withdrawal of previously stored CO_2 is most likely to occur after daybreak, when convective turbulence resumes and CO_2 is rapidly vented from the canopy into the planetary boundary layer.

The CO_2 storage term equals the integration, with respect to height, of the time rate of change of the CO_2 concentration profile:

$$F_{\text{storage}} = \int_0^{z_r} \frac{\partial c(z)}{\partial t} \partial z, \qquad (1)$$

where the integration is between the ground surface and the reference measurement height (z_r). During this pilot study, we did not measure the CO_2 concentration profile above and within the forest. Consequently, we approximated this storage term using a discrete representation:

$$F_{\text{storage}} = \frac{\Delta c(h)\, z_r}{\Delta t}. \qquad (2)$$

Delta (Δ) $c(h)$ over Δt refers to the temporal change in CO_2 concentration measured over a 30 minute period at the reference measurement height. A detailed analysis by Hollinger *et al.* (1994) and by us indicates that use of eqn (2) is justified over a tall forest since CO_2 concentration profiles in a forest tend to be well-mixed.

Over a 24-h interval, the discrete estimate of mean storage term was close to zero (Fig. 2a); its mean value over the course of a year was -0.20 g C m^{-2} d^{-1} and its standard deviation and standard error were 2.32 g C m^{-2} d^{-1} and 0.16 g C m^{-2} d^{-1}, respectively. Hence, potential errors arising from the discrete estimate of CO_2 storage should be small. To re-inforce this point, we also present data on the storage CO_2 term that was measured recently with a four-layer CO_2 gradient system (Baldocchi, unpublished). These new and direct measurements of the CO_2 storage term are closer to zero than our simple and discrete estimate from the 1993–94 study (Fig. 2b); mean and standard deviation of the CO_2 storage term in Fig. 2b are -0.0292 and 0.24 g C m^{-2} d^{-1}, respectively.

Results and discussion

The daily carbon flux between a forest and the atmosphere equals the net ecosystem exchange (NEE), where NEE is the sum of gross photosynthesis (P_{gross}) and respiratory processes associated with leaves (dark and photo-respiration), wood construction and maintenance, roots and microbes (Ruimy *et al.* 1996).

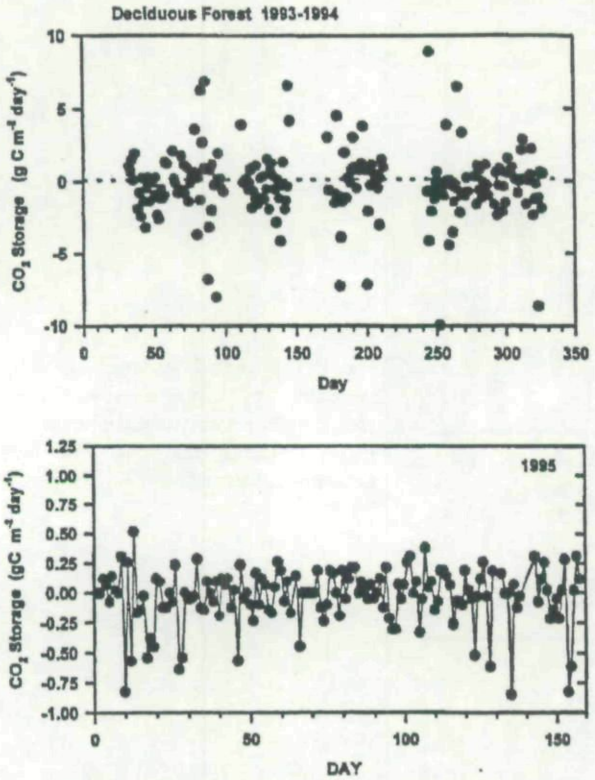

Fig. 2 (a) A discrete estimate of the storage of CO_2 in the air mass under the eddy flux system. Calculations are based on the time rate of change of CO_2 concentration measured with an open-path infrared gas analyser. (b) Measurement of the storage of CO_2 in the air mass under the eddy flux system. Measurements were made with a continous closed path infrared gas analyser that sequentially sampled air at one level above the canopy (35 m) and three levels within the canopy (0.75, 9, 22 m). These measurements were made between 1 January and 6 June 1995 (Baldocchi, unpublished data).

$$F_c = NEE\ P_{\mathrm{gross}} + R_{\mathrm{dark}} + R_{\mathrm{photo}} + R_{\mathrm{wood}} + R_{\mathrm{roots}} + R_{\mathrm{micro}}. \qquad (3)$$

Ecologists also define NEE as the sum of net primary productivity (NPP) and microbial respiration (to be consistent with micrometerological sign convention, we assigned negative values to P_{gross}, NPP and NEE when they depleted CO_2 from the atmosphere).

Seasonal variations in leaf area index, incident sunlight, temperature, precipitation and soil moisture are expected to exert control on the net transfer of carbon dioxide and water vapour between vegetation and the atmosphere because these variables control photosynthesis, respiration and transpiration. Leaf area determines the amount of available photosynthetic and transpiring material and the amount of incident photosynthetically active radiation that is intercepted by the forest. The amount of absorbed sunlight establishes an upper limit for canopy photosynthesis (McMurtrie *et al.* 1992; Ruimy *et al.* 1996) and evaporation (Verma *et al.* 1986). Temperature affects rates of enzyme kinetics associated with photosynthesis and respiration. Finally, precipitation and soil moisture affect the hydration of trees and leaves, stomatal conductance and the flow of nutrients into the roots. Before we present the seasonality of carbon dioxide and water fluxes, we first examine how these climate and plant variables varied during the experiment.

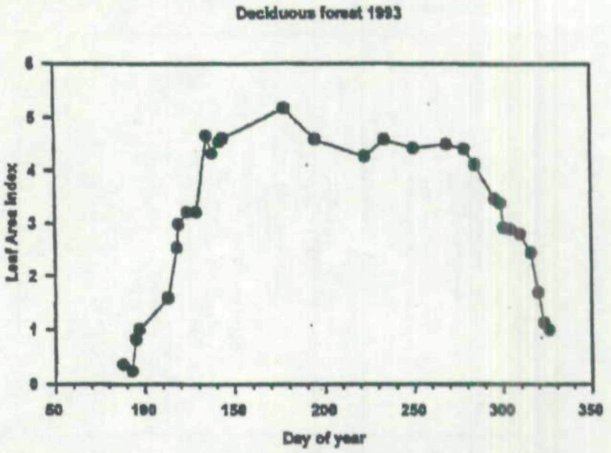

Fig. 3 The seasonal trend of leaf area index. It was estimated by applying measurements of PAR penetration through the canopy to Beer's law function for the probability of radiation penetration through foliage.

(a) Seasonal trends in canopy architecture and environmental variables

Figure 3 shows the inferred seasonal pattern of leaf area index (LAI) during the 1993 growing season. Leaf bud break initiated around Day 95. After which leaves expanded rapidly and they achieved full leaf area expansion by Day 135 (maximum leaf area indexed equaled about 5.1). Leaf area index was relatively invariant until Day 270, then leaves started to senescence and abscise. By Day 330, the canopy was bare until the next spring.

The seasonal variation of photosynthetically active radiation (PAR) is presented in Fig. 4. Peak summertime values of the daily integrated quanta flux approached 60 mol (quanta) m^{-2} d^{-1}, while peak wintertime values approached 20 mol (quanta) m^{-2} d^{-1}. Day to day variations of incident PAR, during the growing season, were almost as great as the annual amplitude. The amount of incident PAR on adjacent sunny and cloudy days often differed by 40 mol (quanta) m^{-2} d^{-1}.

The 30-year, mean, annual, air temperature near Oak Ridge, TN is 13.9°C. During the 1993 and 1994 experimental period mean daily air temperatures ranged between –6 and 29°C and mean soil temperatures (at

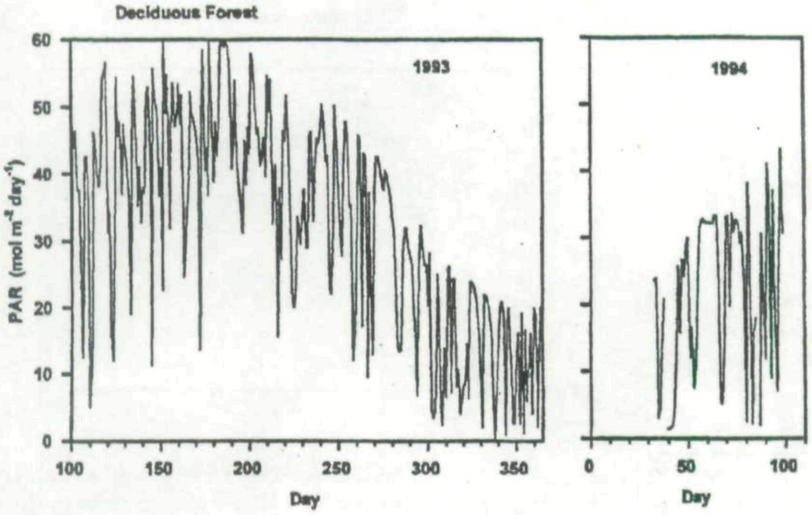

Fig. 4 The annual variation of daily summed photosynthetically active radiation (or photosynthetic photon flux density) during the 1993 and 1994 experimental period.

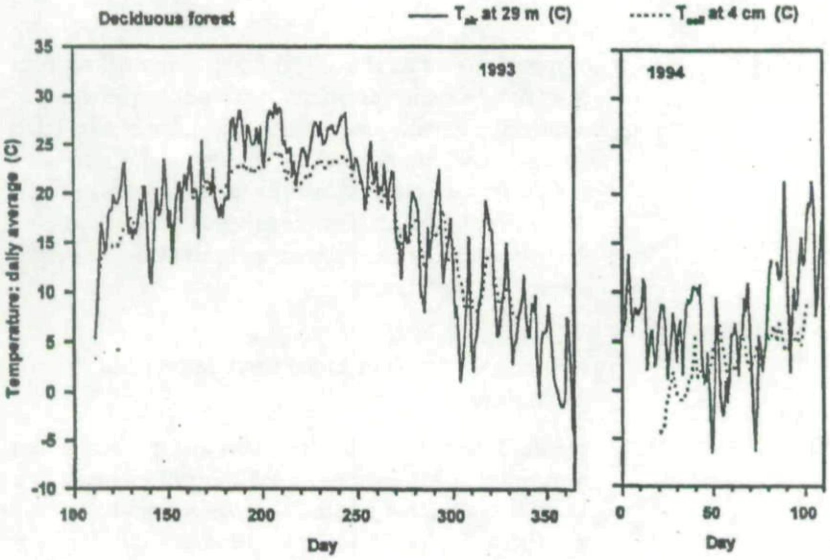

Fig. 5 The annual variation of mean daily air and soil temperature. Air temperature was measured at 29 m and soil temperature was measured at 4 cm.

4 cm) varied between –4 and 25 C (Fig. 5). The frost-free period lasted over 200 days and ranged between April 1 and November 1. Climatologically, the frost-free periods lasts about 195 (± 20) days and ranges between April 13 and October 25. In contrast, the Harvard Forest site often has frozen soils well into April (Mike Goulden, personal communication).

The total precipitation during this year-long experiment was 1583 mm. This value exceeded the mean annual precipitation total of 1350 mm. Despite the abundance of precipitation, it was not uniformly distributed during the 1993 growing season (Fig. 6). Regular rain fell in the spring (April and May). The summertime growing season, however, was punctuated by periods of drought and excessive heat (hourly air temperatures often exceeded 35 C). Monthly precipitation totals for June and July 1993 were about 40% of the climatic mean values; precipitation totals during June, July and August were 46, 50 and 82 mm, respectively; in comparison, the mean precipitation for these months is 105, 137 and 95 mm, respectively. Towards the end of the growing season, above normal precipitation occurred, giving us a chance to examine how carbon dioxide fluxes of the forest responded to a replenishment of soil moisture before leaf senescence.

Pre-dawn water potential and volumetric soil moisture were measured to chronicle and quantify the severity of the drought. At the peak of the drought, pre-dawn leaf water potentials near –1.8 MPa (Fig. 7) and volumetric soil moisture measurements below 0.20 m^3 m^{-3} were recorded (Fig. 8). Periods with pre-dawn water potential below –1.0 MPa revolved around days 194, 197, 208 and

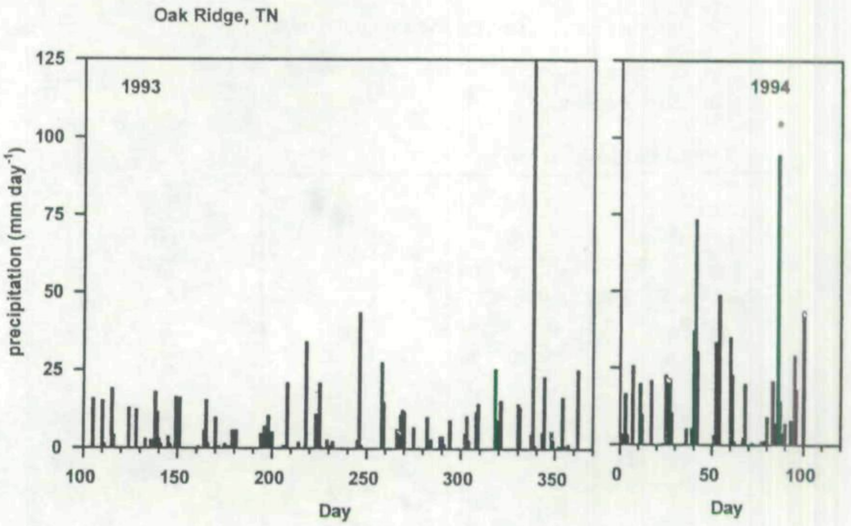

Fig. 6 The record of precipitation at the Oak Ridge, TN meteorological station during the 1993 and 1994 experimental period.

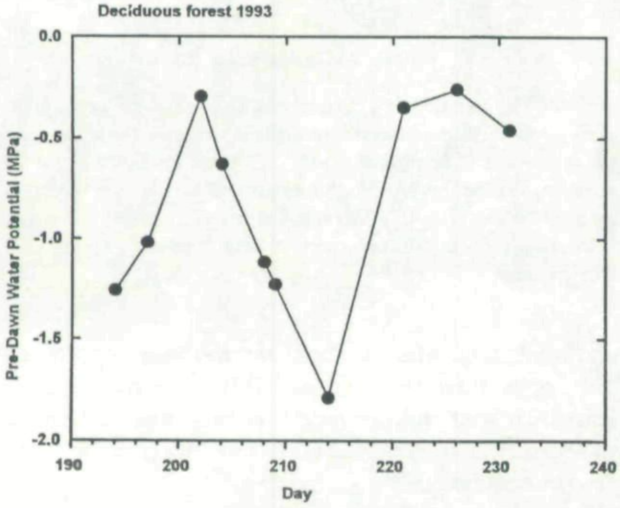

Fig. 7 Periodic measurements of pre-dawn water potential during the 1993 growing season. The measurements were made in the Baldocchi woods, which are across the river and 6 km from the Walker Branch Watershed site.

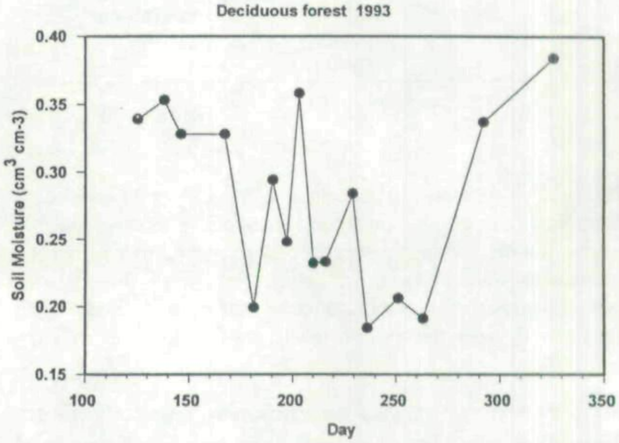

Fig. 8 Gravimetric measurements of soil moisture made at Walker Branch Watershed during the 1993 growing season. We converted the mass-based measurements to a volume basis using the multiplication factor, 1.33 g cm^{-3}, which is the bulk density of the soil in the upper horizon.

214-and periods when soil moisture was below 0.20 m^3 m^{-3} included days 181, 236 and 263.

(b) The influence of environmental variables on daily CO_2 fluxes

Because photosynthesis is a major component of NEE, many ecosystem models scale daily carbon uptake to daily solar radiation (i.e. McMurtrie *et al.* 1992; Waring *et al.* 1993; Maisongrande *et al.* 1995). How well daily fluxes of carbon exchange of a temperate forest are related to daily incident PAR is examined in Fig. 9. The data segregated into groups. One group is associated with measurements were made during the dormant period and the other is associated with data from the growing season (after full-leaf). Net wintertime rates of CO_2 efflux were significant and ranged between 0 and 5 g C m^{-2} d^{-1}. As expected, wintertime CO_2 effluxes were independent of PAR.

Theoretically, canopy respiration rates are a function of temperature (Amthor 1994). However, when we plotted short-term respiration rates against air temperature, we observed a large degree of scatter; the coefficient of determination for a second-order polynomial regression was only 0.152. Much scatter occurred because respiration measurements, averaged over 30 min, have relatively low magnitudes and sampling errors are large, during the winter and at night, due to the intermittency of turbulence. To reduce the effects of sampling uncertainty, we block-averaged the data into 5° C temperature classes. Using averaged data, we observe a much stronger rela-

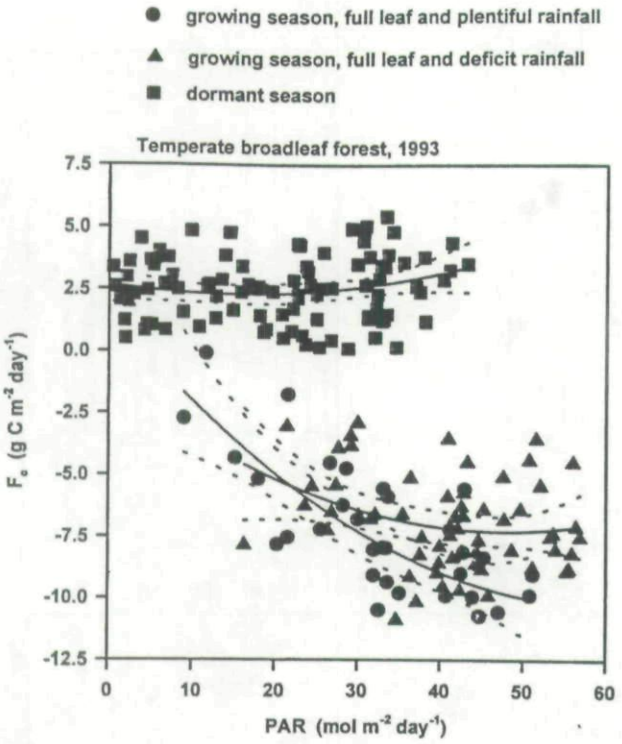

Fig. 9 The relationship between daily CO_2 exchange of a temperate deciduous forest and incident photosynthetically active radiation. Data are segregated according to whether the forest was dormant or at full-leaf. Data from the full leaf period segregated a second time, according to periods when precipitation was plentiful or deficient.

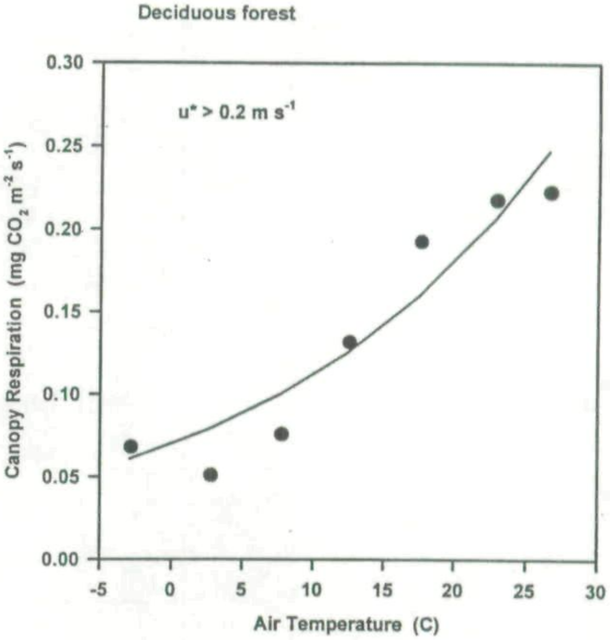

Fig. 10 The relationship between CO_2 exchange rates of a temperate deciduous forest and air temperature. The data were block-averaged according to 5° C temperature ranges to compensate for the effects of intermittent turbulence. We also restricted these data to periods when friction velocity exceeded 0.20 m s^{-1}, to minimize errors in our estimate of the CO_2 storage term.

tionship between canopy respiration and air temperature (Fig. 10). A non-linear regression through block-averaged field data yielded:

$$F_c \, (\mathrm{mg\ CO_2\ m^{-2}\ s^{-1}}) = 0.067 \exp (0.04859\ T_{\mathrm{air}}) \qquad (4)$$

for which the regression accounted for over 90% of the variance.

The Q_{10} coefficient represents the factor respiration increases with a 10 degree increase in temperature. We estimated the Q_{10} to be 1.62. For comparison, this Q_{10} value is lower than our recent measurements over a Canadian boreal jackpine stand (*Pinus banksiana*); there the respiratory Q_{10} value was 2.6 (Baldocchi *et al.* 1996). It is also lower than the Q_{10} value reported for respiration of Harvard Forest (2.1; Goulden *et al.* 1995), but they correlated canopy efflux rates with soil temperature instead of air temperature.

Q_{10} values of plant respiration vary with temperature and season (Amthor 1994). They are near 3 at low temperatures and decrease to about 1 near the high temperature shoulder of the respiration–temperature response curve. Higher Q_{10} values are also associated with growth respiration (Ryan *et al.* 1994). The cited differences among reported Q_{10} values may be reasonable and systematic. Mean air temperatures near Oak Ridge, TN are warmer than air and soil temperatures near Harvard Forest and in Canada. We also used data from the dormant winter period when growth respiration was zero to calculate Q_{10}.

During the growing season, the relation between daily F_c and PAR was influenced by the whether rainfall was plentiful or deficient (Fig. 9). During the periods with plentiful rainfall (May, September and days in August after rain events exceeded 75 mm), daily rates of carbon uptake were well-correlated with PAR – the coefficient of determinations (r^2) was 0.57 – and peak rates of carbon uptake exceeded 12 g C m^{-2} d^{-1}, on sunny days. Sources of variation include the effect of cloud cover on the relationship between canopy carbon uptake and PAR (Jarvis *et al.* 1985; McMurtrie *et al.* 1992) and the folding of variable nocturnal carbon dioxide fluxes into the 24 hour estimate of CO_2 exchange. We also note that the F_c–PAR response curve of a broadleaved forest is curvilinear. This behaviour is consistent with findings by Verma *et al.* (1986), Wofsy *et al.* (1993) and Baldocchi and Harley (1995), but differs with the F_c-PAR response curve of crops, which tend to be linear (Baldocchi 1993; Ruimy *et al.* 1996).

The amount of quanta intercepted and absorbed by a forest sets the upper limit on the amount of carbon that it can assimilate. As a first approximation, net photosynthesis is the product of the canopy quantum yield and the amount of absorbed PAR (Ruimy *et al.* 1996; McMurtrie *et al.* 1992; Potter *et al.* 1993). The quantum yield of temperate forests is about 0.037 mol C mol^{-1} quanta (Ruimy *et al.* 1996) and about 95% of incoming PAR is intercepted by a broadleaf forest canopy (Baldocchi *et al.* 1984). Applying these values to peak summertime insolation measurements (55 mol m^{-2} d^{-1}) yields an estimate of daytime carbon uptake equaling 1.93 mol C m^{-2} d or 23.2 g C m^{-2} d^{-1}. If we assume canopy respiration occurs at a rate of 0.20 mg CO$_2$ m^{-2} s^{-1} during the summer (Fig. 10), maximal rates of net carbon uptake by the canopy will approach 18.5 g C m^{-2} d^{-1}. It is evident from Fig. 9 that observed sums of carbon uptake by this deciduous forest were below its theoretical optimum. Saturation of the F_c with respect to PAR (Baldocchi & Harley 1995) partly accounts for the failure of this forest to achieve optimal rates of daily carbon uptake when the forest has sufficient soil moisture.

During the dry and hot periods, the correlation between F_c and PAR was very weak (r^2 equalled 0.08). On average (deduced by comparing results from the non-linear regressions), the drought reduced daily carbon uptake by about 30% on sunny days (e.g. when PAR equaled 50 mol m^{-2} d^{-1}). This drought and heat stress-imposed reduction in daily carbon uptake is attributed to physiological reductions in gas exchange rates that are associated with leaf photosynthesis and stomatal conductance (Kubiske & Abram 1994; Tenhunen *et al.* 1989; Schulze 1986; Hinckley *et al.* 1978). High temperatures also causes a concomitant increase in the respiration of plant parts. On dull days (PAR < 25 mol m^{-2} d^{-1}), there was statistical overlap of daily carbon fluxes from wet and dry periods. Lower evapourative demand, temporary re-hydration of the boles and leaves and reduced respiration on dull days provide explanations for this result.

(c) Seasonal trend of diurnal patterns

Daily courses of carbon dioxide and water vapour exchange rates provide information on the importance of physiological factors, relative to climatic forcing. Below we examine the diurnal course of carbon and water vapour fluxes on three contrasting days. Day 144 was a mild (mean daily air temperature, T_{air}, equalled 20.4°C) and sunny spring day when soil moisture was adequate. Day 244 was a hot (mean T_{air} equalled 28.2°C), clear day during the drought period and day 34 was a clear, cool (mean T_{air} equalled 5.7°C) winter day, when the canopy was leafless.

On the well-watered spring day (Fig. 11), canopy CO$_2$ fluxes, latent heat exchange and incident PAR were synchronized. With regard to F_c, photosynthesis began around 06.30 hours. The magnitude of carbon dioxide uptake (negative values) increased with increasing PAR values and achieved a peak value near –2.0 mg CO$_2$ m^{-2} s^{-1} around 13.00 hours. As the afternoon progressed, rates of carbon dioxide uptake slowly decreased until around 19:30 hours, when respiration (positive values) exceeded assimilation. Nocturnal rates of CO$_2$ efflux were on the order of 0.2 mg CO$_2$ m^{-2} s^{-1}. The net daily carbon dioxide flux was –40.6 g CO$_2$ m^{-2} d^{-1} (11.1 g C m^{-2} day^{-1}). With regards to LE and PAR, significant rates of exchange commenced at sunrise and peak values occurred after midday. The respective peak values for LE and PAR were 340 W m^{-2} and 1700 µmol m^{-2} s^{-1}.

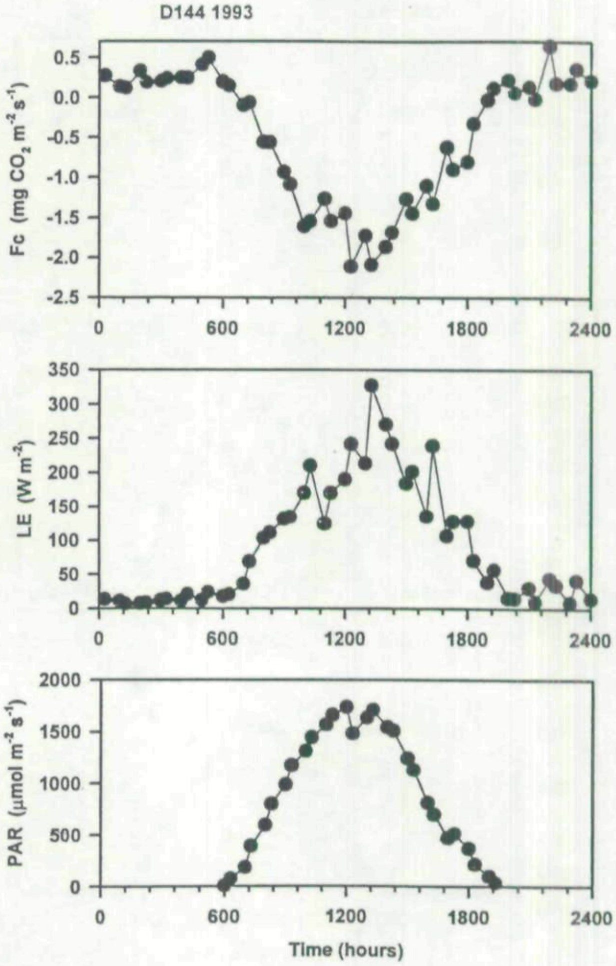

Fig. 11 Diurnal patterns of canopy CO$_2$ and latent heat exchange rates and PAR. The data are from Day 144 and were obtained over a well-watered deciduous forest.

Soil water deficits (e.g. the drought) had a marked impact on the diurnal course of CO$_2$ exchange (Fig. 12). On Day 244, re-hydration of tissue overnight allowed moderate rates of carbon dioxide uptake to occur during morning. Nevertheless, peak CO$_2$ fluxes were earlier and lower than the peak values observed on the well-watered

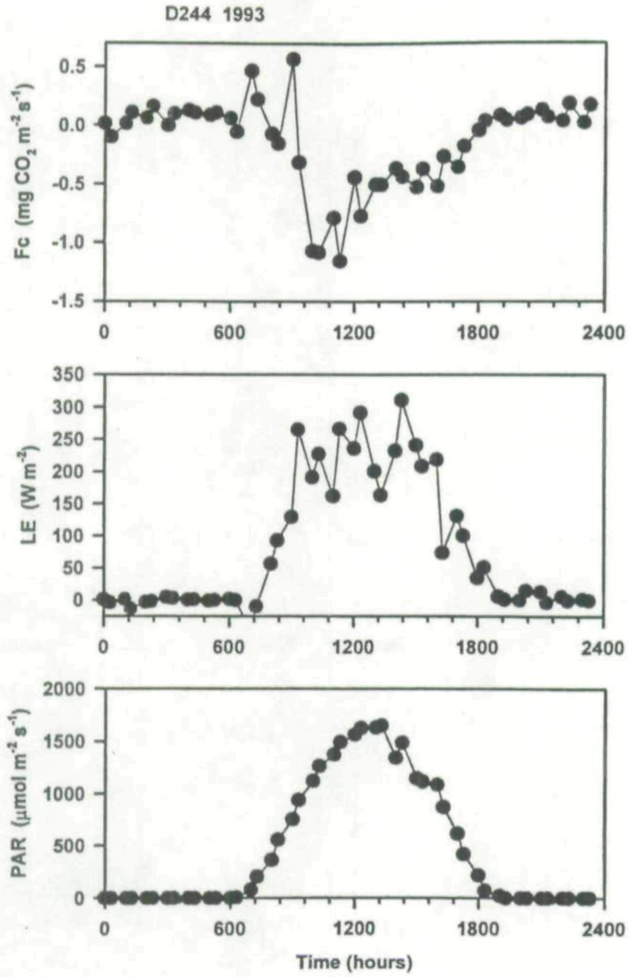

Fig. 12 Diurnal patterns of canopy CO_2 and latent heat exchange rates and PAR. The data are from Day 244 and were obtained over a deciduous forest experiencing soil moisture deficits.

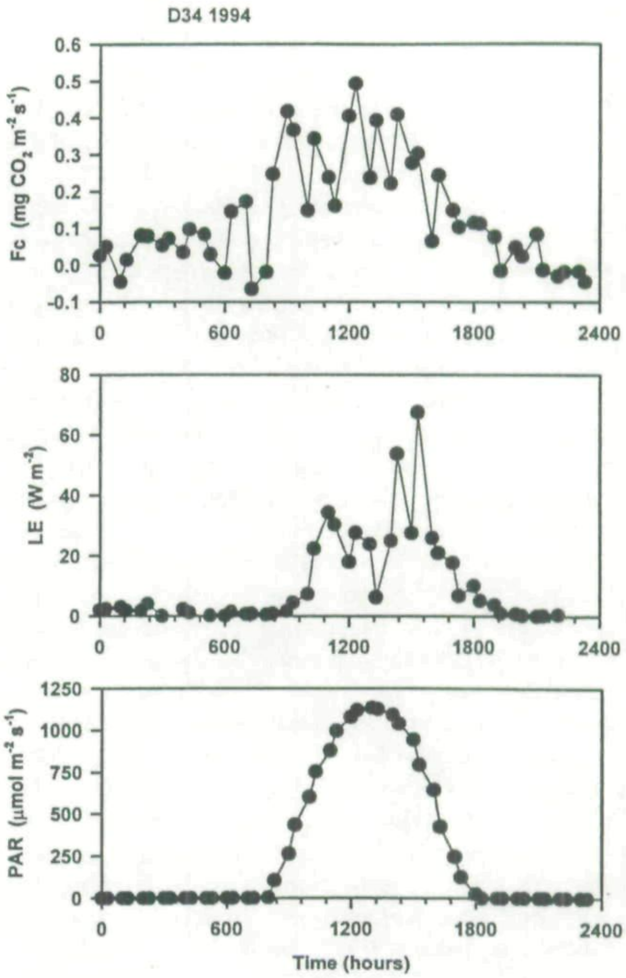

Fig. 13 Diurnal patterns of canopy CO_2 and latent heat exchange rates and PAR. The data are from Day 34 and were obtained over a leafless deciduous forest.

spring day (Fig. 11). As the afternoon progressed, rates of net CO_2 uptake continued to diminish with time, despite abundant sunlight. We also note that a midday depression and afternoon recovery of CO_2 exchange was not observed, as is commonly reported for diurnal course for a droughted Mediterranean oak forests (*Quercus suber*) (Tenhunen *et al.* 1984). After dusk, carbon was lost from the canopy, as canopy respiration (leaves, boles and soil) once again controlled the flux of carbon dioxide.

Surprisingly, maximum *LE* rates were not greatly reduced during this drought-prone period; maximum *LE* exceeded 300 W m^{-2}. On the other hand, *LE* values oscillated considerably despite clear skies and uniform radiational forcing. In earlier work, we observed that high humidity deficits (as associated with hot summer days) promote evaporation rates from this broadleaf forest (Baldocchi & Vogel 1995). The oscillating nature of these data suggest that intricate feedbacks may have occurred between atmospheric demand, the rhizospheric supply of moisture, water storage in the boles and the stomatal control of gas exchange.

Figure 12 also presents data for a case when direct eddy flux measurements detected little nocturnal respiration (00.00–06.00 hours). Instead, a delayed venting of nocturnally respired CO_2 was observed after daybreak when turbulent mixing resumed. This phenomenon has been observed over numerous forest canopies, throughout the world (Wofsy *et al.* 1993; Hollinger *et al.* 1994; Baldocchi *et al.* 1996). Its occurrence emphasizes the need to add short-term CO_2 storage measurements to eddy fluxes when using such data to test carbon balance models on an hourly basis.

The daily patterns of F_c, *LE* and PAR during the winter are presented in Fig. 13. The rates of carbon loss exhibit a distinct diurnal pattern. Low rates occurred during the night, when temperatures were cool and turbulent mixing was weak. Substantial rates of carbon efflux (> 0.4 mg CO_2 m^{-2} s^{-1}) occurred during the day, when a moderate

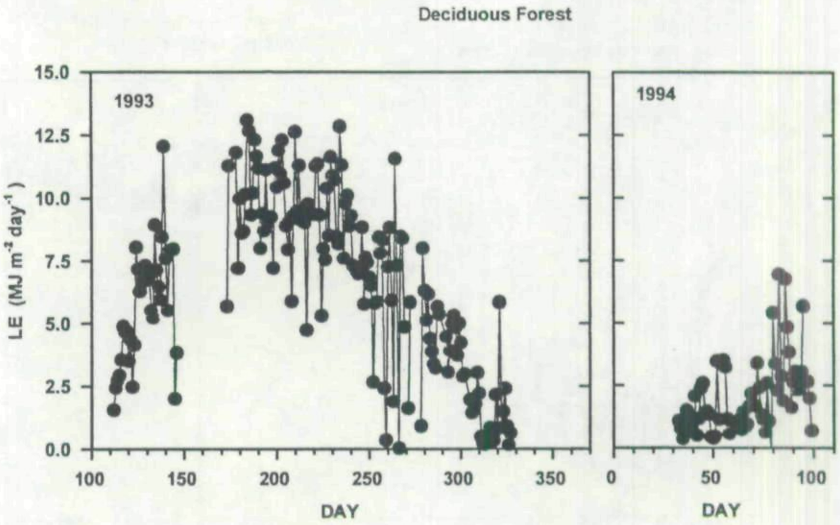

Fig. 14 Seasonal variation of daily integrated latent heat exchange over a temperate deciduous forest.

solar load was able to heat the boles and soil and, thus, modulate respiration. In sum, the net daily carbon dioxide loss on 3 February 1994 was 10.67 g CO_2 m^{-2} d^{-1} (2.91 g C m^{-2} d^{-1}). Hourly rates of latent heat exchange were small (< 80 W m^{-2}) since the air was cool, solar radiation was diminished and no transpiring leaves were present.

(d) Seasonal variation of daily water vapour and CO_2 fluxes

The seasonal course of daily integrated latent heat exchange is presented in Fig. 14. The seasonal cycle of LE was synchronized with the seasonal patterns of leaf area index, PAR and air temperature (Figs 3, 4 and 5). Significant (> 2 MJ m^{-2} d^{-1}) evaporation initiated with springtime leaf expansion. Maximal rates of daily LE occurred about mid-summer and approached 13 MJ m^{-2} d^{-1}, which was about 75% of the daily net radiation load. The low daily rates of LE during the growing season were not associated with the drought, but with cloudy and rainy weather. During the autumn, daily totals of LE diminished as leaves senesced and abscised. Yet, days with great LE occurred after rainstorms when the foliage and soil surfaces were wet. After the canopy was bare, daily evaporation rates were typically less than 2 MJ m^{-2} d^{-1}.

The annual (April 1993 – April 1994) course of daily CO_2 net ecosystem exchange (NEE) is presented in Fig. 15. Negative carbon fluxes (a net loss from the atmosphere and a net gain of carbon by the canopy) started around Day 117 increased with time until the end of May. The commencement of carbon uptake by the canopy was about 22 days after budbreak and after leaf area index exceeded two. Leaf expansion, an increase in photosynthetic capacity (Doughtery *et al.* 1979; Hanson *et al.* 1994) and an increase in daily insolation explain the springtime increase in daily carbon uptake rates.

Maximal rates of carbon uptake occurred by Day 140, when net carbon uptake rate exceeded 11 g C m^{-2} d^{-1}. For comparison, C_3 crops uptake 5 and 20 g C m^{-2} d^{-1} during the growing season (Baldocchi 1994; Ruimy *et al.* 1996) and temperate deciduous and conifer forests uptake between 5 and 10 gC m^{-2} d^{-1} (Wofsy *et al.* 1993; Galoux *et al.* 1981; Vermetten *et al.* 1994). On the other hand, 24 hour sums of carbon uptake over a slow-growing Nathofagus forest (Hollinger *et al.* 1994) and unproductive Douglas fir (*Pseudotsuga menzeii*) (Price & Black 1991) and jackpine (*Pinus banksiana*) stands (Baldocchi *et al.* 1996) are significantly smaller (their daily sums of carbon uptake range between 0 and 2 g C m^{-2} d^{-1}).

Drought periods were generally deleterious to net carbon uptake. In many instances, the drought reduced the daily rate of canopy carbon uptake by 25–30%, as compared to springtime carbon uptake rates that were observed around Day 150 (Fig. 15).

Numerous physiological studies show that reductions in CO_2 assimilation rates and stomatal conductances of oak are associated with low pre-dawn leaf water potentials or low soil water content (Tenhunen *et al.* 1984; Ephron & Dreyer 1993; Hinckley *et al.* 1978; Kubiske & Abrams 1994). Theoretically such reductions have stomatal and non-stomatal origins (Tenhunen *et al.* 1984; Schulze 1986). Tenhunen *et al.* (1984), for example, report that midday depressions in CO_2 uptake rates of droughted *Quercus suber* leaves are due to a decrease in photosynthetic capacity, a decrease in carboxylation efficiency and an increase in the CO_2 compensation point due to increased leaf temperature and respiration. More recent data in the literature suggest that photosynthetic

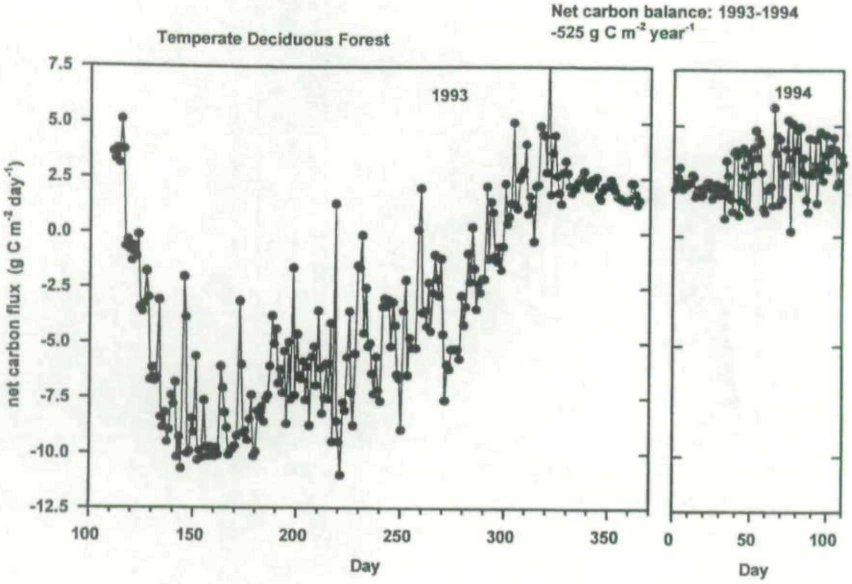

Fig. 15 Seasonal variation of daily integrated carbon exchange over a temperate decidous forest, growing near Oak Ridge, TN. Direct measurements were made with the eddy covariance method. Missing data were filled using empirical relationships determined from the field measurements.

capacities of oak species are independent of water deficits. Ephron & Dreyer (1993), for example, report that the photochemistry of photosystem II (light-driven electron transport and enzymatic reactions requiring ATP and NADPH) is not significantly affected for soil moisture deficits. Strong experimental evidence indicates that soil water deficits trigger a hormonal signal (ABA), which induces stomatal closure and limits carbon uptake (Tardieu & Davies 1992; Gollan *et al.* 1986).

Leaf stomatal conductance measurements were taken during the summer period on *Quercus alba* (white oak) and *Acer rubrum* (red maple) trees to help interpret how drought affected canopy gas exchange rates. On days preceded by considerable rainfall stomatal conductance reached values between 3.5 and 6.5 mm s^{-1}; in particular, white oak leaves kept their stomata open throughout the day. Under severe drought condition, stomata of both species were open during the morning (stomatal conductance averaged 5.0 mm s^{-1}), but were closed by midday. We submit that it is biased to conclude that all stomata shut in the afternoon during the drought and restricted canopy level fluxes of carbon and water, due to our limited ability to sample leaves throughout the forest crown. During drought, some species in this forest are better able to extract deeper sources of moisture (e.g. oaks), while other species have shallower root systems and are more adversely affected by soil moisture deficits (e.g. maples and tulip poplar) (Paul Hanson, personal communication). Non-complete stomatal closure by constituents of this forest is suggested by the observation that F_c was only reduced by 25–30% (Fig. 9) and by the fact that *LE* was not largely reduced (Fig. 14).

A resumption of regular rainfall occurred in September. This replenishment of soil moisture caused a temporary recovery in daily CO_2 uptake rates. But soon the onset of autumn caused leaf senescence, leaf fall and a gradual reduction in carbon uptake rates. Net carbon loss became a regular event by Day 300. During the winter, carbon was lost from the canopy at a rate ranging between 0 and 5 g C m^{-2} d^{-1}.

We assessed the annual budget of carbon uptake to be −525 g C m^{-2} y^{-1}. This result is subject to scrutiny. Empirical relations were used to fill missing data and nighttime flux measurements may be inaccurate due to reduced turbulent mixing. On the other hand, the observation of a negligible CO_2 storage, over 24 h, and closure of the surface energy balance gives us reasonable confidence in our measurements. Furthermore, combining a large amount of data reduces the sampling error considerably. At this stage it is prudent to assign a conservative estimate of error since the practice of making long-term flux measurements is in its infancy. Based on our ability to close the surface energy balance, errors associated with sensor calibration and instrument drift and Goulden *et al.*'s (1995) assessment of errors associated with long-term CO_2 flux measurements, we assign an error equal to ± 20% of our annual estimate.

The net annual carbon flux of a southern temperate forest is considerably larger than the net carbon flux measured over the northern Harvard Forest, despite the occurrence of drought at our site. In a recent re-evaluation of the data of Wofsy *et al.* (1993), Goulden *et al.* (1995) report that the net carbon exchange of the Harvard Forest was –220 ± 30 g C m^{-2} y^{-1} in 1994. The difference between net carbon fluxes at these two sites is partly due to a longer growing season and larger photosynthetic potential experienced by the Oak Ridge forest. For example, net carbon uptake does not occur at Harvard Forest until

Table 1 Literature survey of net primary productivity (NPP) of temperate deciduous forests and an estimate of net ecosystem exchange (NEE). Soil respiration was estimated using the algorithm of Hanson *et al.* (1993) and site climate data. The annual sum of soil respiration was 560 g C m^{-2} y^{-1}. Edwards *et al.* (1989) reports that roots account for 72% of carbon evolved from the forest floor of Walker Branch Watershed; the complement, 28%, is attributed to microbial respiration. Therefore, the microbial respiration is estimated to be 157 g C m^{-2} y^{-1} and is added to NPP.

Site	Investigator	NPP (g C m^{-2} y^{-1})	NEE (g C m^{-2} y^{-1})
Oak Ridge, TN	Reichle *et al.* 1973	−685	−528
Wisconsin	Janacek *et al.* 1989	−860	−703
temperate deciduous	McGuire *et al.* 1992	−730	−573
Knoxville, TN	Running and Nemani	−590 to −681	−433 to −524
temperate deciduous	Potter *et al.* 1993	−315	−158
temperate deciduous	Warnant *et al.* 1994	−659	−502
temperate deciduous	Foley, 1995	−588	−433

late May, a month later than at Oak Ridge (Goulden *et al.* 1995). Furthermore, the leaf area index (e.g. its photosynthetic potential) of the Oak Ridge forest is about 20% greater than at the Harvard Forest.

Carbon balance estimates from biomass measurements provide a constraint on our carbon flux measurements and help us determine if our direct flux measurements are in the 'ball-park'. Biomass inventories conducted on the Walker Branch Watershed (Edwards *et al.* 1989) indicate that the increment of wood growth at oak-hickory and chestnut oak plots ranged between 310 and 350 g dry weight m^{-2} y^{-1} between 1967 and 1983. Litter accumulation was on the order of 75 g dry weight m^{-2} y^{-1}. Typically, one-half of dry biomass is carbon, so the yearly accumulation of above ground biomass was between 192 and 212 g C m^{-2} y^{-1}. These values are lower than our direct carbon flux measurement, but they neglect the amount of carbon being stored in the soil and the growth of roots. Some fraction of top growth must occur by the roots, for top growth cannot be sustained without an appropriate rooting systems.

If the indirect and direct measures of carbon uptake are correct, they suggest that a large amount of carbon is being stored in the soil or consumed by root growth. On the other hand, if we underestimated nocturnal carbon fluxes by 0.05 mg CO_2 m^{-2} s^{-1}, this small bias error would add to 215 gC m^{-2} y^{-1} if it were multiplied by 12 h per night and 365 days per year. Adding this hypothetical correction value to our annual sum of −525 g C m^{-2} y^{-1}, yields a net canopy carbon flux equaling −310 g C m^{-2} y^{-1}.

We find it instructive to also compare our measurements against carbon balance calculations of temperate deciduous forests, since few model calculations of carbon uptake have been verified. Table 1 shows that literature estimates of NPP of temperate deciduous forests range between −315 (Potter *et al.* 1993) and −860 (Janacek *et al.* 1989) g C m^{-2} y^{-1}. To facilitate a comparison with our data, we converted these values into estimates of net ecosystem exchange (NEE) by adding an annual estimate of heterotrophic respiration to the NPP calculations. Using our soil temperature measurements and the soil respiration algorithm of Hanson *et al.* (1993), we calculated that 560 g C m^{-2} y^{-1} were lost from the soil system at Walker Branch Watershed. Since 28% of soil CO_2 efflux is associated with microbial respiration (Edwards *et al.* 1989), the yearly carbon loss due to heterotrophic respiration equals 157 g C m^{-2} y^{-1}. Adding this heterotrophic respiration estimate to the NPP calculations in Table 1 yields values of NEE ranging between −158 and −703 g C m^{-2} y^{-1} and a geometric mean of −449 g C m^{-2} y^{-1}. The estimated geometric mean of literature NEE values is within the 20% error bound of our annual measurement of −525 g C m^{-2} y^{-1}.

Conclusion

Carbon dioxide and water vapour fluxes of a temperate broadleaved forest vary considerably over the course of a year. The annual budget of net carbon exchange over a temperate deciduous forest was estimated to be −525 g C m^{-2} y^{-1}. Our data represent the second documented measurement of annual carbon exchange over a temperate broadleaved forest (after Wofsy *et al.* 1993). These data are of particular interest, for they show that latitudinal and climatic differences will affect the net carbon balance of a generic temperate deciduous forest. In other words, greater rates of net carbon uptake can occur over a south-eastern forest because the growing season is longer and the photosynthetic capacity of the canopy is greater.

We advocate the continuation of long-term CO_2 flux measurements, at numerous sites, to obtain a sufficiently large pool of data to assess interannual and intra-annual variations in carbon fluxes with better certainty. We also urge that long-term and direct flux measurements be conducted at locations where independent biomass measurements are made.

Acknowledgements

This research was partially supported by the National Oceanic and Atmospheric Administration and the U.S. Department of Energy. Susanna Greco was supported by a Global Change Fellowship, provided by the Bank of San Paolo di Torino.

We are grateful to Dr Detlef Matt and Kevin Birdwell for providing us with climate data, to Dr Tilden Meyers for development of the data acquisition program and to Mark Hall and David Auble for field and calibration assistance. We thank Dr Riccardo Valentini for being a catalyst to do this work and we thank Drs Mike Goulden, Jeff Amthor, Stan Wullschleger and Paul Hanson for their careful reviews of this work and for the many stimulating discussions we've had with them.

References

Amthor JS (1994) Plant respiratory responses to the environment and their effects on the carbon balance. In: *Plant-Environment Interactions* (ed. Wilkinson RE) , pp. 501–554. M. Dekker, New York.

Anderson DE, Verma SB, Clement RE, Baldocchi DD and Matt DR (1986) Turbulence spectra of CO_2, water vapor, temperature and velocity over a deciduous forest. *Agricultural Forest Meteorology*, **38**, 81–99.

Auble DL TP. Meyers. (1992) An open path, fast response infrared absorption gas analyzer for H_2O and CO_2. *Boundary Layer Meteorology*, **59**, 243–256.

Baldocchi DD (1993) A comparative study of mass and energy exchange over a closed (wheat) and an open (corn) canopy: II. Canopy CO_2 exchange and water use efficiency. *Agricultural and Forest Meteorology*, **67**, 291–322.

Baldocchi DD BB. Hicks and TP. Meyers. (1988) Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology*, **69**, 1331–1340.

Baldocchi DD, Matt DR, Hutchison BA, McMillen RT (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 DD, Harley PC (1995) Scaling carbon dioxide and water vapor exchange from leaf to canopy in a deciduous forest: model testing and application. *Plant, Cell and Environment*, **18**, 1157–1173.

Baldocchi DD, Vogel C (1996) A comparative study of water vapor, energy and CO_2 flux densities above and below a temperate broadleaf and boreal pine forest. *Tree Physiology* (in press).

Baldocchi DD, Vogel CA and Hall B (1996) Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. *Agricultural and Forest Meteorology* (in press).

Ciais P, Tans PP, Trolier M, White JWC, Francey RJ (1995) A large northern hemisphere terrestrial CO_2 sink indicated by the $^{13}C/^{12}C$ ratio of atmospheric CO_2. *Science*, **269**, 1098–1102.

Dougherty PM, Teskey RO, Phelps JE, Hinckley TM (1979) Net photosynthesis and early growth trends of a dominant white oak. *Plant Physiology*, **64**, 930–935.

Edwards NT, Johnson DW, McLaughlin SB, Harris WF (1989) Carbon dynamics and productivity. In: *Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed* (eds Johnson DW, van Hook RI), pp. 197–232. Springer-Verlag, New York, NY.

Ephron D, Dreyer E (1993) Photosynthesis of oak leaves under water stress: maintenance of high photochemical efficiency of photosystem II and occurrence of non-uniform CO_2 assimilation. *Tree Physiology*, **13**, 107–117.

Field CB, Randerson JT, Malmstrom CM (1995) Global net primary production: combining ecology and remote sensing. *Remote Sensing of the Environment*, **51**, 74–88.

Foley JA (1994) Net primary productivity in the terrestrial biosphere: the application of a global model. *Journal of Geophysical Research*, **99**, 20773–20783.

Galoux A, Benecke P, Gietl G, Hager H, Kayser C, Kiese O, Knoerr KR, Murphy CE, Schnock G, Sinclair TR (1981) Radiation, heat, water and carbon dioxide balances. In: *Dynamic Properties of Forest Ecosystems* (ed. Reichle DE) , pp. 87–204. Cambridge University Press, Cambridge.

Gollan T, Passioura JB, 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 ML, Munger JW, Fan SM, Daube BC, Wofsy SC (1995) Measurement of carbon storage by long-term eddy correlation: Methods and a critical assessment of accuracy. *Global Change Biology* (in press).

Hanson PJ, Wullschleger SD, Bohlman SA, Todd DE (1993) Seasonal and topographic patterns of forest floor CO_2 efflux from an upland oak forest. *Tree Physiology*, **13**, 1–15.

Hanson PJ, Samuelson LJ, Wullschleger SD, Tabberer TA, Edwards GS (1994) Seasonal patterns of light-saturated photosynthesis and leaf conductance for mature and seeling *Quercus rubra* foliage: differential sensitivity to ozone exposure. *Tree Physiology*, **14**, 1351–1366.

Hinckley TM, Aslin RG, Aubuchon RR, Metcalf CL, Roberts JE (1978) Leaf conductance and photosynthesis in four species of the oak-hickory forest type. *Forest Science*, **24**, 73–84.

Hollinger DY, Kelliher FM, Byers JN, Hunt JE, McSeveny TM, Weir PL (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology*, **75**, 134–150.

Hutchison BA, Matt DR, McMillen RT, Gross LJ, Tajchman SJ, Norman JM (1986) The architecture of a deciduous forest canopy in eastern Tennessee, USA. *Journal of Ecology*, **74**, 635–646.

Janecek A, Benderroth G, Ludeke MKB, Kindermann J, Kohlmaier GH (1989) Model of the seasonal and perennial carbon dynamics in deciduous forests controlled by climate variables. *Ecological Modelling*, **49**, 101–124.

Jarvis PG, Miranda HS, Muetzelfeldt RI (1985) Modelling canopy exchanges of water vapor and carbon dioxide in coniferous forest plantations. In: *The Forest–Atmosphere Interaction* (eds Hutchison BA, Hicks BB), pp. 521–542. Reidel, Dordrecht.

Johnson DW, van Hook RI (eds) (1989) *Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed*. Springer-Verlag. New York, NY, 401 pp.

Kauppi PE, Mielikainen K, Kuuseia K (1992) Biomass and carbon budget of European forests, 1971–1990. *Science*, **256**, 70–74.

Kubiske ME, Abrams MD (1994) Ecophysiological analysis of woody species in contrasting temperate communities during wet and dry years. *Oecologia*, **98**, 303–312.

Lloyd J, Farquhar GD (1994) ^{13}C discrimination during CO_2 assimilation by the terrestrial biosphere. *Oecologia*, **99**, 201–215.

Luxmoore RJ, Huff DD (1989) Water. In: *Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed* (eds Johnson DW, van Hook RI), pp. 164–196. Springer-Verlag, New York, NY.

Maisongrande P, Ruimy A, Dedieu G, Saugier B (1995) Monitoring seasonal and interannual variations of gross productivity, net primary production and net ecosystem productivity using a diagnostic model and remotely sensed data. *Tellus*, **47B**, 178–190.

McGuire AD, Melillo JM, Joyce LA, Kicklighter DW, Grace AL Moore B, Vorosmarty CJ (1992) Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochemical Cycles*, **6**, 101–124.

McMurtrie RE, Comins HN, Kirschbaum MUF, Wang YP (1992) Modifying existing forest growth models to take account of effects of elevated CO_2. *Australian Journal of Botany*, **40**, 657–677.

Potter CS, Randerson JT, Field CB *et al.* (1993) Terrestrial ecosystem production: a process model based on global satellite and surface data. *Global Biogeochemistry Cycles*, **7**, 811–841.

Price DT, Black TA (1991) Effects of summertime changes in weather and root-zone soil storage on canopy CO_2 flux and evapotranspiration of two juvenile Douglas fir stands. *Agricultural and Forest Meteorology*, **53**, 303–323.

Reichle DE, Dinger BE, Edwards NT, Harris WF, Sollins P (1973) *Carbon Flow and Storage in a Forest Ecosystem*. In: *Carbon and the Biosphere* (eds Woodwell GM, Pecan EV) , pp. 345–365. Eds Tech. Info. Center.

Ruimy A, Jarvis PG, Baldocchi DD, Saugier B (1996) CO_2 Fluxes over plant canopies and solar radiation: a literature review. *Advances in Ecological Research*, **26**, 1–68.

Running SW, Nemani RR (1988) Relating seasonal patterns of the AVHRR vegetation index to simulated photosynthesis and transpiration of forests in different climates. *Remote Sensing of Environment*, **24**, 347–367.

Ryan MG, Linder S, Vose JM, Hubbard RM (1994) Dark respiration in pines. In: *Pine Ecosystems* (eds Gholz HL, Linder S, McMurtrie R). *Ecological Bulletin*, **43**, 50–63.

Schulze ED (1986) Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. *Annual Review of Plant Physiology*, **37**, 247–274.

Tans PP, Fung IY, Takahasi T (1990) Observational constraints on the global atmospheric CO_2 budget. *Science*, **247**, 1431–1438.

Tardieu F, Davies WJ (1992) Stomatal response to abscisic acid is a function of current plant water status. *Plant Physiology*, **98**, 540–545.

Tenhunen JD, Lange OL, Gebel J, Beyschlag W, Weber JA.(1984) changes in the photosynthetic capacity, carboxylation efficiency, and CO_2 compensation point associated with midday stomatal closure and midday depression of net CO_2 exchange of leaves of *Quercus suber*. *Planta*, **162**, 193–203.

Vermetten AWM, Ganzeveld L, Jeuken A, Hofschreuder P, Mohren GMJ (1994) CO_2 uptake by a stand of Douglas fir: flux measurements compared with model calculations. *Agricultural and Forest Meteorology*, **72**, 57–80.

Waring RH, Runyon J, Goward SN, McCreight R, Yoder B, Ryan MG (1993) Developing remote sensing techniques to estimate photosynthesis and annual growth across a steep climatic gradient in western Oregon, USA. *Studia Forestalia Suecia*, **191**, 33–42.

Warnant P, Francois L, Strivay D Gerard J-C (1994) CARAIB: a global model of terrestrial biological productivity. *Global Biogeochemical Cycles*, **8**, 255–270.

Wofsy SC, Gouldin ML, Munger JW, Fan SM, Bakwin PS, Daube BC, Bassow SL Bazzaz FA (1993) Net exchange of CO_2 in a mid-latitude forest. *Science*, **260**, 1314–1317.