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Leaf age affects the seasonal pattern of photosynthetic capacity and net ecosystem exchange of carbon in a deciduous forest

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ABSTRACT

Temporal trends in photosynthetic capacity are a critical factor in determining the seasonality and magnitude of ecosystem carbon fluxes. At a mixed deciduous forest in the south-eastern United States (Walker Branch Watershed, Oak Ridge, TN, USA), we independently measured seasonal trends in photosynthetic capacity (using single-leaf gas exchange techniques) and the whole-canopy carbon flux (using the eddy covariance method). Soil respiration was also measured using chambers and an eddy covariance system beneath the canopy. These independent chamber and eddy covariance measurements, along with a biophysical model (CANOAK), are used to examine how leaf age affects the seasonal pattern of carbon uptake during the growing season. When the measured seasonality in photosynthetic capacity is represented in the CANOAK simulations, there is good agreement with the eddy covariance data on the seasonal trends in carbon uptake. Removing the temporal trends in the simulations by using the early season maximum value of photosynthetic capacity over the entire growing season overestimates the annual carbon uptake by about 300 g C m^{-2} year^{-1} – half the total estimated annual net ecosystem exchange. Alternatively, use of the mean value of photosynthetic capacity incorrectly simulates the seasonality in carbon uptake by the forest. In addition to changes related to leaf development and senescence, photosynthetic capacity decreased in the middle and late summer, even when leaf nitrogen was essentially constant. When only these middle and late summer reductions were neglected in the model simulations, CANOAK still overestimated the carbon uptake by an amount comparable to 25% of the total annual net ecosystem exchange.

Key-words: Ameriflux; canopy model, leaf age; maximum carboxylation rate (V_{cmax}).

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INTRODUCTION

Over 100 long-term eddy covariance studies of carbon dioxide exchange between vegetation and the atmosphere are being conducted across the globe (Running *et al.* 1999; Valentini *et al.* 2000). To interpret and simulate the temporal behaviour of the net ecosystem exchange of carbon (N_{EE}, the net exchange of carbon between vegetation and the atmosphere, with negative values indicating an uptake by vegetation) in these ecosystems requires an understanding of the time evolution of the processes controlling its components: respiration and photosynthesis. The net photosynthetic rate of a canopy is a complex function of leaf area, solar radiation, canopy architecture, canopy microclimate, photosynthetic capacity and stomatal conductance, all of which may vary diurnally, daily, seasonally and annually (Baldocchi, Falge & Wilson 2001). The temporal modulation of these parameters, and the resulting photosynthetic rate, is a major factor in determining the ability of vegetation to exert control on the carbon cycle. It is also vital to understand the precision with which biogeochemical and ecological models need to depict the temporal variability of these parameters at specific locations to accurately simulate gross primary production, and thus net ecosystem exchange of carbon, within an acceptable level of accuracy.

Modelling studies have demonstrated the importance of accurately representing canopy architecture and 'leaf clumping' in estimating N_{EE} (Baldocchi & Harley 1995; Baldocchi & Meyers 1998), but in forests, these characteristics usually change little in time scales of less than 1 year. The relative importance of accurately estimating leaf area and its temporal changes over an annual cycle can be inferred from modelling studies and long-term carbon exchange experiments over different ecosystems (Baldocchi & Meyers 1998; Law *et al.* 2000). Previous studies in forest canopies have shown the short-term response of canopy CO_2 fluxes to solar radiation and other meteorological variables (Goulden *et al.* 1997; Anthoni, Law & Unsworth 1999; Greco & Baldocchi 1996), including several studies demonstrating the temporal evolution of these responses over an annual cycle in evergreen forests (Dang, Margolis & Collatz 1998; Hollinger *et al.* 1994; Hollinger *et al.* 1999). In addition to possible changes in leaf area or climate, these temporal patterns may reflect changes in photosynthetic capacity, which are often neglected in modelling studies in both evergreen and deciduous forests.

Although there is an extensive history of gas exchange measurements on single leaves of tree species, there are fewer studies demonstrating how photosynthesis (Jurik 1986; Reich, Walters & Ellsworth 1991; Sullivan, Bolstad & Vose 1996; Porte & Loustau 1998; Raulier, Bernier & Ung 1999) or photosynthetic capacity (Wilson, Baldocchi & Hanson 2000a, 2000b) of mature species responds to leaf ageing over the season, and only a limited number of studies have evaluated these temporal changes in direct relation to independent measurements of whole-canopy fluxes within an entire annual cycle (Dang *et al.* 1998; Law *et al.* 2000). In particular, there has been little study on how changes in photosynthetic capacity affect N_{EE} in deciduous forests during an entire cycle of leaf development, maturity and senescence.

Previous modelling studies of forested canopies have demonstrated a very high sensitivity of canopy carbon fluxes to the estimated photosynthetic capacity (Aber, Reich & Goulden 1996; Dang *et al.* 1998; Law *et al.* 2000). However, in most modelling studies, photosynthetic capacity was not estimated independently from the validation data set (Arenth *et al.* 1998), was obtained from literature values at different sites or in controlled experiments (Amthor *et al.* 1994; Williams *et al.* 1996), was highly empirical (Aber *et al.* 1996; Frolking *et al.* 1996), was obtained from very few samples (Harley & Baldocchi 1995) or was assumed from leaf nitrogen estimates (Aber & Federer 1992; Aber *et al.* 1996). The studies were usually isolated to brief periods in the growing season and/or photosynthetic capacity was assumed invariant with time. Exceptions include Dang *et al.* (1998) and Law *et al.* (2000), which are studies in coniferous evergreen forests where photosynthetic capacity was evaluated at the measurement site and was allowed to vary over the season in model simulations.

A previous study in a deciduous forest in the south-eastern United States (Walker Branch Watershed, Oak Ridge, TN, USA) simulated N_{EE} using independently measured estimates of parameters, as described by Farquhar, von Caemmerer & Berry (1980), that represent photosynthetic capacity (Harley & Baldocchi 1995). Simulated output was compared with eddy covariance during an isolated measurement period (Baldocchi & Harley 1995). Because sampling of photosynthetic capacity was limited to just two trees and was over only a few weeks, this effort was necessarily limited in addressing the influence of photosynthetic capacity on the magnitude and seasonal variability of N_{EE} in this forest. Also, continuous estimates of soil respiration, which could be used to separate above- and below-ground contributions to N_{EE}, were not available.

Subsequent experiments at this site have addressed some of the previous limitations in scaling photosynthetic capacity in time and space and evaluating its effect on net ecosystem exchange. Spatially and temporally extensive leaf gas exchange measurements and 'A/C_i curves' have been performed over 2 years, characterizing the photosynthetic capacity of this forest more completely (Wilson *et al.* 2000a). Species inventories have been performed in the region surrounding the eddy covariance tower, to assist in scaling leaf-level measurements to canopy scale (Hanson *et al.* 2001; Wilson *et al.* 2001). An eddy covariance system at the forest floor is used to independently estimate soil respiration (Wilson & Meyers 2001). Soil respiration estimates are valuable because the deviation between measured and simulated estimates of N_{EE} may result from differences in either assimilation rate or respiration rate. Soil respiration is typically several times greater than other respiratory sources at Walker Branch (Hanson *et al.* 1993; Edwards & Hanson 1996) and other forests (Mahli, Baldocchi & Jarvis 1999; Law *et al.* 2000); thus, it is important to verify that this component is simulated accurately before evaluating whole-canopy fluxes.

This study proceeds in the following manner:

1. the temporal evolution of photosynthetic capacity, which was determined by solving for the parameters described by Farquhar *et al.* (1980) from leaf gas exchange data, is incorporated into the biophysical model CANOAK;
2. using physiological parameterizations, we evaluate the ability of CANOAK to independently replicate eddy covariance fluxes (above and below canopy);
3. we evaluate if including the seasonality in photosynthetic capacity provides sufficient improvement in model prediction to recommend that the effect is an important consideration, and
4. we evaluate model performance in predicting seasonal trends during a year with (1998) and without (1997) low soil water content.

MATERIALS AND METHODS

Site

Measurements were made continuously in a mixed temperate deciduous forest in Oak Ridge, TN, USA (Walker Branch Watershed; 35°57′30″ N, 84°17′ 15″ W, 365 m above sea level) from 1995 to 1999. The site is located in the southern section of the temperate deciduous forest biome in the eastern United States. The canopy height is approximately 26 m above the ground and maximum leaf area index is about 6. Dominant trees range from 60 to 120 years in age. The most prevalent dominant trees in the forest are *Quercus* spp. (oak) and *Acer* spp. (maple), and the remainder are primarily *Nyssa sylvatica* Marsh (blackgum), *Liriodendron tulipifera* L (tulip poplar), *Pinus* spp. (pine) and *Carya* spp. (hickory). The site is in hilly terrain, and the upwind fetch of forest extends several kilometres in all directions. A more detailed description of the canopy architecture, species composition, climate and soil properties are provided by Luxmoore *et al.* (1981), Hutchison & Baldocchi (1989), Johnson & van Hook (1989), Wilson & Baldocchi (2000) and Hanson *et al.* (2001).

Eddy covariance and environmental measurements

Eddy covariance instrumentation was placed on a scaffold tower 36·9 m above the ground (about 10 m above the canopy). In 1999, a second eddy covariance system was beneath the canopy, 2 m above the forest floor (Wilson *et al.* 2001). This second system was beneath nearly all vegetation, providing estimates of soil respiration. Wind velocity and virtual temperature fluctuations at both locations were measured with three-dimensional sonic anemometers (Applied Technology, Boulder, CO, USA). Fluctuations in water and CO_2 were measured with an open-path, infrared absorption gas analyser, developed at NOAA/ATDD (Auble & Meyers 1992), which was calibrated monthly.

Vertical flux densities were evaluated each half-hour by computing the mean covariance of water and sensible heat fluctuations with the fluctuating vertical velocity (Baldocchi *et al.* 1988; Wilson & Baldocchi 2000). Fluctuations of velocity and scalars from the mean were determined from the difference between the instantaneous values and the mean scalar quantities. Mean scalar values were determined using a digital recursive filter with a 400 s time constant. Corrections were made for the effect of density fluctuations (Webb *et al.* 1980). CO_2 concentrations were measured sequentially at four heights using a LI 6262 (Li-Cor Inc., Lincoln, NE, USA) analyser to compute the storage contribution to N_{EE} (Greco & Baldocchi 1996). The system received a zero and span calibration at least once a day.

Although other independent methods (chambers) have indicated that scalar flux estimates derived from eddy covariance may be biased during nocturnal periods at this site (Baldocchi *et al.* 2000) and others (Lavigne *et al.* 1997), daytime estimates of respiration are often in agreement with chamber estimates (Baldocchi *et al.* 2000). Furthermore, eddy covariance estimates of water fluxes concur well with long-term catchment water balance studies in the watershed (Wilson *et al.* 2001). The annual water balance is likely to be insensitive to accurate nocturnal estimates of evaporation, which may suggest that the daytime eddy covariance estimates at this site are acceptable. The focus of this study is during periods when carbon exchange is dominated by assimilation (daytime); therefore, nocturnal periods are not considered in the analysis. An energy imbalance of about 20% is present at Walker Branch, but this is not unusual, even in flat terrain (Twine *et al.* 2000). There was no evidence of changes in the extent of energy budget closure over the growing season, which suggests that any bias in scalar flux estimates applies equally across the growing season.

Environmental and meteorological variables were averaged over half-hour intervals and logged on digital data loggers (model CR-21x; Campbell Scientific, Inc., Logan, UT, USA). Temperature and relative humidity were measured with a temperature/humidity probe (HMP-35 A; Vaisala, Helsinki, Finland). Photosynthetically active radiation (PAR) was measured above and below the canopy with a quantum sensor (model LI-190S, Li-Cor). The sensor below the canopy was placed on a moving tram to average PAR over a horizontal transect of 20 m. Soil temperature was measured at five levels using two multi-level thermocouple probes.

Prior to 1998, soil water content was measured weekly in the upper 60 cm from gravimetric measurements and time-domain reflectometers (TDR; Soil Moisture Equipment Corp., Santa Barbara, CA, USA) (Wilson & Baldocchi 2000; Wilson *et al.* 2000a; Hanson *et al.* 2001). Subsequently, soil water content was measured continuously using water content reflectometers at four soil depths (Model CS615; Campbell Scientific) and logged on a CR10X data logger (Campbell Scientific). The different instrument types were also collocated as a check against the factory-supplied calibrations. Soil water content was converted to soil water potential based on retention curves developed at the site (Hanson *et al.* 1998). Soil water content was also simulated using the algorithms in the Terrestrial Ecosystem Hydrology Model (TEHM), which have been validated previously near this site (Luxmoore & Huff 1989), including the period of this study (Hanson *et al.* 2001).

Because of anomalous turbulence statistics or instrument malfunction, 22% of the daytime carbon flux data in the 2 years of this study were missing or rejected. Statistical methods using the remainder of the data set were used to fill these data gaps, a procedure that is not expected to create a high level of uncertainty in flux estimates (Baldocchi & Wilson 2001).

Two detailed species inventories were conducted. In one study encompassing 635 trees, species composition was determined from 30 inventory plots (10 m radius) within a 700 m radius of the tower used for eddy covariance measurements (Wilson *et al.* 2001). A second study of 729 individual trees was conducted about 2000 m from the measurement tower (Hanson *et al.* 2001). The relative contributions of species were similar in both studies and the results of the two studies were combined.

CANOAK AND PHYSIOLOGICAL PARAMETERIZATIONS

CANOAK is a one-dimensional, multi-layer biosphere-atmosphere model that computes water vapour, CO_2 and sensible heat flux densities. The model has been described and tested during the growing season in Baldocchi & Harley (1995) and Baldocchi (1997). Baldocchi & Wilson (2001) discuss simulated carbon and energy fluxes using a 20 year climate record. The model consists of coupled micrometeorological and eco-physiological modules. The micrometeorological modules compute leaf (sunlit and shaded) and soil energy exchange, turbulent (Lagrangian) diffusion, scalar concentration profiles and radiative transfer through the canopy using observed meteorological conditions above the canopy. The physiological modules are driven by physiological parameters that are obtained directly from extensive chamber measurements performed at the site. The predicted micrometeorology drives leaf photosynthesis and respiration, stomatal conductance and transpiration at 40 canopy layers. Canopy leaf area profiles were assumed to follow a beta distribution, with a heavier concentration of leaves near the canopy top (Hutchison & Baldocchi 1989).

N_{EE} in CANOAK is obtained by summing each component of the carbon flux: bole and soil/root respiration, and leaf photosynthesis and respiration. Physiological and phenological parameterizations are required to estimate each of these canopy source-sink strengths for CO_2 (leaf, bole/stem, soil/root) and these parameterizations are detailed in the following sections.

Leaf-level parameterizations

The photosynthesis parameters described by Farquhar *et al.* (1980) – maximum carboxylation rate (V_{cmax}), maximum rate of electron transport (J_{max}) and dark respiration (R_d) – were estimated from measurements on nearly 800 leaves on 65 trees, encompassing 12 different species, in 1997 and 1998 (Wilson *et al.* 2000a, 2000b). Measurements were made within the sunlit crowns of nine mature dominant trees, representing five of the more prevalent dominant species in this forest (Table 1). The methodology and kinetic parameters used to estimate V_{cmax} are discussed thoroughly in Wilson *et al.* (2000a, 2000b).

Three important results are summarized from the study of Wilson *et al.* (2000a) that are directly relevant for the incorporation of measurements into CANOAK. Firstly, V_{cmax} was not typically constant over the growing season, generally increasing rapidly during leaf expansion, reaching an early-season maximum, followed by a slow decline during late summer and a more rapid decline in autumn. Figures 1 and 2 show the values of V_{cmax} at 25 °C in the two mature *Quercus alba* L. and three mature *Acer rubrum* L. trees during the growing seasons in 1997 and 1998. Figure 3 shows a composite mean value of V_{cmax} over the two years for sunlit leaves of the six most commonly measured mature trees (two *Q. alba*, one *Quercus prinus* L., two *A. rubrum*, one *Acer saccharum* Marsh.). Secondly, species differences in V_{cmax} were present (Table 1; Figs 1 and 2) and were generally correlated with differences in leaf nitrogen per unit area (N_a). However, because N_a was constant over much of the season while V_{cmax} often decreased, the relationship between V_{cmax} and N_a was seasonally dependent (i.e. dependent on leaf age).

Three spatial and temporal attributes of V_{cmax} were addressed when the measurements were incorporated into CANOAK. Firstly, the vertical distribution of V_{cmax} was required. V_{cmax} was assumed to decrease linearly with canopy depth from the maximum value at the top of the canopy to just over a third of that value at the forest floor – an assumption generally supported by measurements (Table 2) (Wilson *et al.* 2000a). To simplify the discussion, V_{cmax} in this paper always refers to the values at the top of the canopy, but V_{cmax} scaled linearly with canopy depth from this value.

A second requirement was an estimate of the magnitude of V_{cmax}. Because it was greater in *Quercus* spp. than in *Acer* spp., an estimate of the relative species contributions was necessary to approximate the magnitude of a mean canopy value of V_{cmax}. The relative species contributions were determined from a composite of two species inventory studies (Wilson *et al.* 2001; Hanson *et al.* 2001). The species measured for gas exchange in this study comprised 75% of the cumulative basal area of the larger trees (greater than 0·1 m in diameter) in this forest (Table 1). Of the remaining 25% of basal area in the forest that was not considered in computing a canopy V_{cmax} value, the most important species not measured for gas exchange were *L. tulipifera* (9·4%) and *Pinus* spp. (6·3%). Twelve other species represented a total of less than 10% of the canopy basal area. The magnitude of V_{cmax} was determined from the species-specific values of N_a weighted by the relative species contribution to the total basal area of the measured species (Table 1). The early season value of V_{cmax} estimated in this way was within 2% of the value obtained directly from the mean V_{cmax} estimates shown in Table 1.

The third requirement in CANOAK was an estimate of the temporal change in V_{cmax} over the growing season. Differences in the magnitude of V_{cmax} between *Quercus* spp. and *Acer* spp. were apparent, but tree-to-tree variation and

Table 1. Measured maximum rate of carboxylation (V_{cmax}) and leaf nitrogen per unit area (N_a) during the early summer period (June 1–July 1) for sunlit leaves of five mature tree species. Data was collected at 25 ± 2·5 °C and V_{cmax} was normalized to 25 °C (Wilson *et al.* 2000a). The number of trees (Trees) and total number of leaves sampled (*n*) during this period in 1997 and 1998 are shown. Also shown is the relative contribution of each species to the total canopy basal area (% canopy), for trees >0·1 diameter at breast height

Species	V_{cmax} (μmol m^{-2} s^{-1})	N_a (g m^{-2})	Trees	*n*	% canopy
Quercus alba	60·0	1·99	2	45	22
Quercus prinus	63·1	1·92	2	24	32
Acer Rubrum	37·6	1·50	3	34	10
Acer saccharum	42·8	1·50	1	9	3
Nyssa sylvatica	39·2	0·95	1	6	8

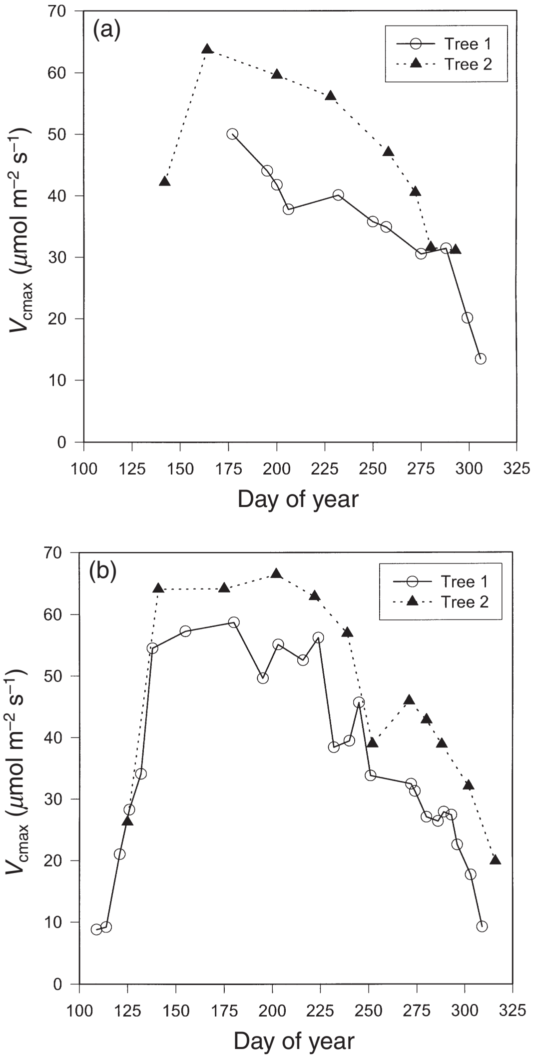

Figure 1. V_{cmax} for two mature *Q. alba* trees over the 1997 (a) and 1998 (b) growing seasons.

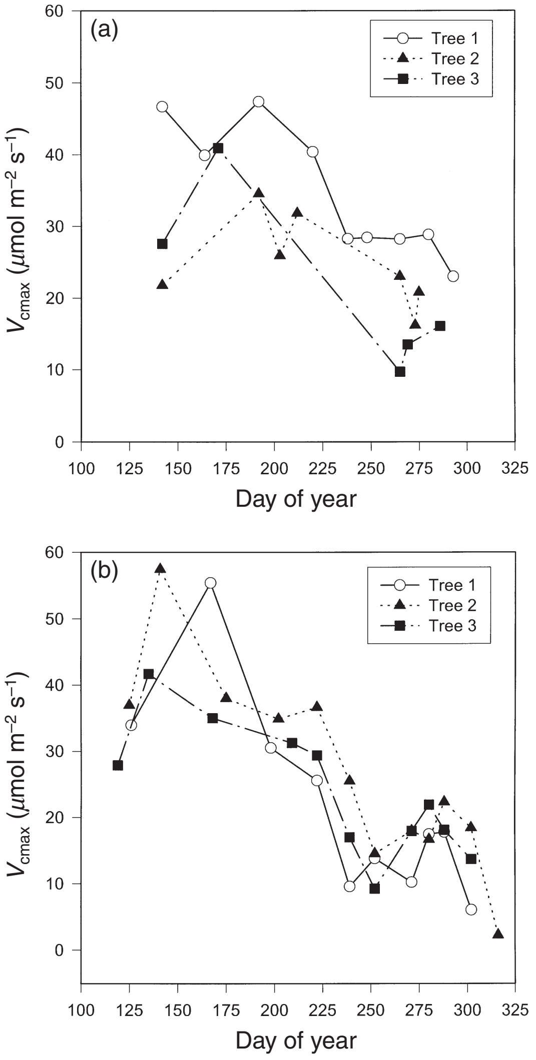

Figure 2. V_{cmax} for three mature *A. rubrum* trees over the 1997 (a) and 1998 (b) growing seasons.

Table 2. Measured maximum rate of carboxylation (V_{cmax}) and leaf nitrogen per unit area (N_a,) during the early summer period (June 1–July 1) for leaves of saplings near the forest floor. Data was collected at 25 ± 2·5 °C and V_{cmax} was normalized to 25 °C (Wilson *et al.* 2000a). The number of trees (Trees) and total number of leaves sampled (*n*) during this period in 1997 and 1998 are shown. Also shown is the relative contribution of each species to the total subcanopy (trees < 0·1 m diameter at breast height) basal area (% subcanopy).

Species	V_{cmax}(μmol m^{-2} s^{-1})	N_a(g m^{-2})	Trees	*n*	% subcanopy
Fagus grandifolia J.F. Ehrh.	15·2	0·60	1	7	1
Acer rubrum	18·1	0·69	6	10	29
Quercus rubrum	20·8	0·91	3	9	2
Oxydendrum arboreum L.	21·2	0·66	2	6	8
Cornus florida L.	20·9	NA	4	7	19
Sassafrass albidum (Nutt.) Nees	22·3	0·61	3	6	2
Quercus sp.	23·2	0·99	4	5	3
Liridendron tulipifera	23·3	0·77	1	6	< 1
Carya sp.	26·1	1·04	3	4	1
Prunus serotina Ehrh.	29·9	0·87	2	5	5

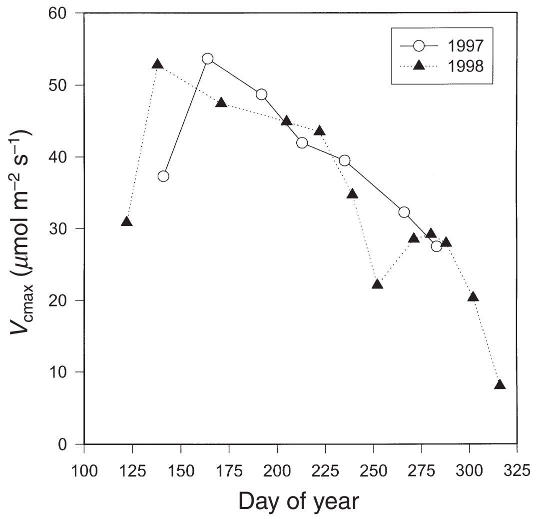

Figure 3. Mean V_{cmax} in 1997 and 1998 of the six most commonly measured mature trees in the study (two *Q. alba*, one *Q. prinus* L., two *A. rubrum*, one *A. saccharum* Marsh.). Symbols represent the mean of data collected within a 2 week period.

limited sampling precluded a detailed evaluation of species differences in seasonality. Therefore, although the magnitude of V_{cmax} was estimated based on relative species contributions, the complexity associated with temporal changes in V_{cmax} precluded a detailed analysis of species differences. Instead, seasonal trends relative to the early season maximum were evaluated after grouping all data together, and not computing species-specific contributions. Temporal changes in V_{cmax} over the growing season were estimated based on four general periods discussed in Wilson *et al.* (2000a) (Fig. 4). These periods are: (i) leaf development; (ii) the late spring maximum; (iii) the summer decline, and (iv) autumnal senescence. Although these periods represent a necessary oversimplification, they depict the general trends of measured photosynthetic capacity across species in this forest (Fig. 3).

During the period of leaf development, V_{cmax} was assumed to scale with canopy leaf area index. Figure 5 shows the relationship between V_{cmax} and whole-canopy leaf area index, using data from an extensively measured *Quercus alba*. There was an approximately linear increase in V_{cmax} with leaf area, followed by an additional increase in V_{cmax} over the next week after leaf area had fully developed. Although the relationship was not linear over the whole range of increase in V_{cmax}, linearity was assumed as an approximation, partially because V_{cmax} reaches maximum values at least a week earlier in other species, especially maples (Figs 1 and 2; Wilson *et al.* 2000a).

For the remainder of the growing season, V_{cmax} was calculated from the product of three terms that could vary over the growing season:

$$V_{cmax} = V_{cmaxopt} \times A_{fact} \times S_{fact}, \qquad (1)$$

where $V_{cmaxopt}$ (μmol m^{-2} s^{-1}) is the optimal value of V_{cmax} with adequate soil water potential, determined directly from the mean canopy value of N_a (Wilson *et al.* 2000a):

$$V_{cmaxopt} = -\,15\cdot 3 + 39\cdot 7\, N_{a}, \qquad (2)$$

where N_a is in g m^{-2} and A_{fact} and S_{fact} are unitless factors accounting for leaf age and soil water potential (Eqns 3 & 4) independent of changes in leaf nitrogen.

The second period shown in Fig. 4 is of approximately 5–6 weeks duration, beginning after full leaf expansion, and represents an optimal phase of maximum photosynthetic capacity in late spring when V_{cmax} was determined by the canopy value of N_a (1·75 g m^{-2}). During this period, it was assumed there was no reduction in V_{cmax} resulting from leaf ageing ($A_{fact} = 1$). Gas exchange data shows some indication that the approximate duration of this period was up to several weeks longer in *Quercus* spp. (Fig. 1) and often shorter in *Acer* spp. (Fig. 2), but an approximate mean duration was chosen, as represented in Fig. 4.

During the third period (between days 175 and 285), the effect of leaf age reduced V_{cmax} through the factor A_{fact}:

$$A_{fact} = [2\cdot 48 - 6\cdot 0 \times 10^{-3}\, D_{oy}], \qquad (3)$$

where D_{oy} is the day of the year, between 175 and 320. The expression A_{fact} was determined from the residual of the regression with N_a as shown in Wilson *et al.* 2000a. Because leaf nitrogen did not change over this period, $V_{cmaxopt}$ (Eqn 2) was identical to the maximum values in the first period.

The fourth period encompassed a more rapid decline in V_{cmax}, including the period of autumnal senescence. The decrease in V_{cmax} was partially explained by decreases in N_a and $V_{cmaxopt}$ (mean canopy value of N_a decreased from 1·75

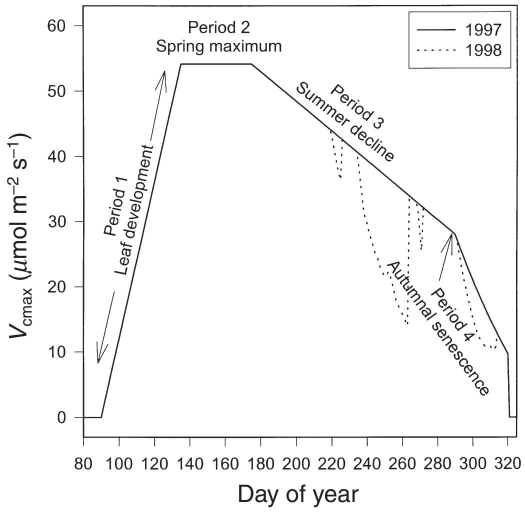

Figure 4. The seasonal parameterization of V_{cmax} in the CANOAK simulations during a year without (1997, solid line) and with (1998, dashed line) periods of low soil water potential. The parameterizations during period 1 differ slightly between the two years because of differences in leaf area, but is not shown in order to clarify the main points. Data is from Wilson *et al.* (2000a).

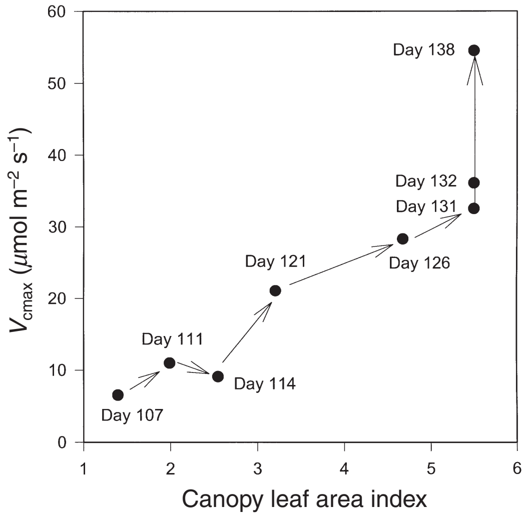

Figure 5. Relationship between V_{cmax} and canopy leaf area index during leaf development in 1998. Arrows show the temporal progression. V_{cmax} was estimated from gas exchange data on a *Q. alba* tree and leaf area index was estimated from radiation transmission through the whole canopy.

to 1·05 g m^{-2} between days 285 and 320), but also involved the additional independent effect of leaf age (i.e. both V_{cmaxopt} and A_{fact} decreased during this period).

In addition to the seasonal trends, there was an apparent reduction in V_{cmax} during periods of low soil water potential (Wilson *et al.* 2000a). The residual between V_{cmax} during days with low soil water potential in 1998 and estimates of V_{cmax} using Eqn 1 were used to formulate a stress function:

$$S_{\text{fact}} = \min\,[1{\cdot}55 + 0{\cdot}44\psi_{\text{soil}}, 1{\cdot}0], \qquad (4).$$

where ψ_{soil} is the water potential (MPa) in the upper 30 cm of soil. S_{fact} was determined as a function of ψ_{soil} after averaging all data for each day and evaluating the residual, assuming $S_{\text{fact}} = 1$. When the stress function was less than unity, r^2 of Eqn 4 was 0·96 ($n = 8$ d).

Figure 6 shows the continuous estimates of soil water potential using the TEHM algorithm (Luxmoore & Huff 1989) and the periodically measured values. Soil water content was lower in 1998, and in contrast to 1997, S_{fact} was not always 1 (S_{fact} in 1998 is shown at the bottom of Fig. 6). Figure 4 (dashed lines) shows the value of V_{cmax} used in CANOAK during 1998, which resembles the general characteristics observed in the data (Fig. 3) (Wilson *et al.* 2000a).

Other important parameters in the model of Farquhar *et al.* (1980) that could be deduced from the gas exchange measurements were the maximum rate of electron transport ($J_{\max}$), dark respiration (R_{d}) and the temperature dependencies of V_{cmax}, $J_{\max}$ and R_{d}. The ratio between $J_{\max}$ and V_{cmax} at 25 °C was set to the mean found in the measurements (2·70), although there was inconclusive evidence that this ratio increases slightly throughout the season (Wilson *et al.* 2000a). The only evidence of seasonality in R_{d} was the larger magnitude (an increase by a factor of three, from 0·5 to 1·5 μmol m^{-2} s^{-1} at 25 °C) during leaf development, which was incorporated into the simulations during this period. The parameters describing the activation energy for V_{cmax} and R_{d} (Farquhar *et al.* 1980) were determined from temperature response surfaces (Wilson *et al.* 2000a). The temperature response of V_{cmax} and R_{d} were measured periodically and did not change appreciably over the growing season. Because $J_{\max}$ was only evaluated at 25 °C, the activation energy for $J_{\max}$ was estimated directly from the equations provided by Farquhar *et al.* (1980) and Leuning (1997).

The second set of important parameters needed to estimate the leaf contribution to the carbon flux in CANOAK are coefficients that compute stomatal conductance from the relationship described in Collatz *et al.* (1991):

$$g_s = \frac{mAr_{\text{h}}}{C_s} + g_0 \qquad (5)$$

where g_{s} is the stomatal conductance (mol m^{-2} s^{-1}), A is assimilation rate (mol m^{-2} s^{-1}), C_{s} is the CO$_2$ concentration at the leaf surface (mol mol^{-1}) and r_{h} is the relative humidity; g_{o} and m are the intercept and slope, derived from regression. When the Wilson *et al.* (2000b) data set was used to estimate the slope and intercept in Eqn 5, g_{o} was 0·01 mol m^{-2} s^{-1}, and m was 7·8 ($r^2 = 0{\cdot}85$), which are the values used in this study. Because of the high degree of scatter, we were not able to definitively conclude statistically significant changes in slope (m) with leaf age or during drought.

Soil and bole parameterizations

Soil respiration is parameterized using response surfaces to soil temperature and soil water content from data collected across Walker Branch Watershed (Hanson *et al.* 1993):

$$R_{\text{soil}} = W_{\text{fact}} \times R_{\text{base}} \times Q_{10}{}^{Ts/10} \qquad (6)$$

where R_{base} is 0·50 μmol m^{-2} s^{-1}, Q_{10} is 2·47 and T_{s} is the soil temperature (°C) at 16 cm depth. W_{fact} is a factor to account for soil water content:

$$W_{\text{fact}} = \frac{\Psi_{\min} + \Psi_{\text{S}}}{\Psi_{\min}} \qquad (7)$$

$\psi_{\min}$ was determined empirically (– 7 MPa), and ψ_{s} (MPa) was the measured soil water potential in the upper 30 cm of soil. Bole and stem respiration parameterizations were based on temperature and obtained from measure- ments on 56 trees in the watershed (Edwards & Hanson 1996).

Canopy leaf area

Canopy leaf area index is specified in CANOAK. Leaf area index was inferred from the relative transmission of solar radiation (Wilson & Baldocchi 2000). Independent leaf area estimates were provided from litter baskets. Budburst

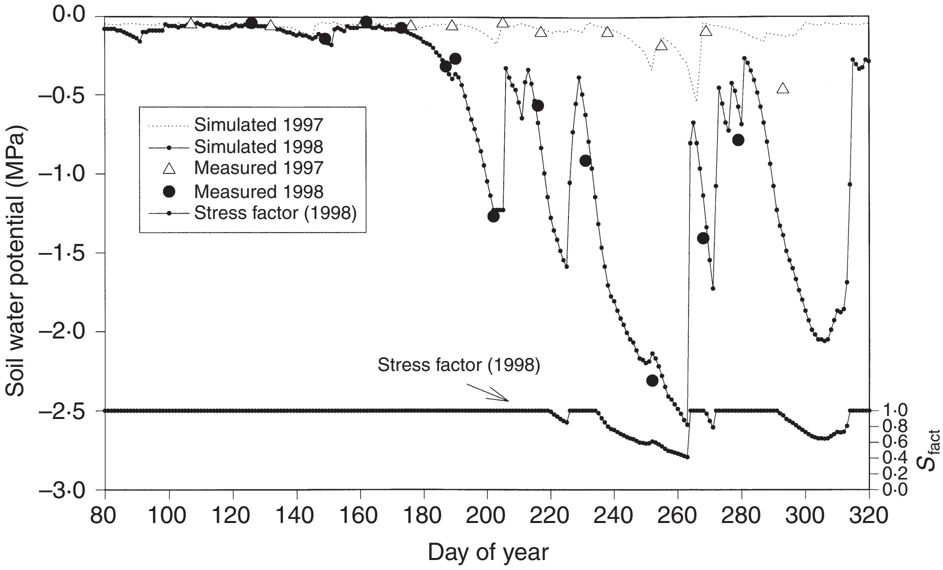

Figure 6. Simulated and measured soil water potential of the upper 30 cm of soil in 1997 and 1998. Shown in the bottom of the graph is the stress factor (S_{fact}, Eqn 4) in 1998. S_{fact} in 1997 was always 1 and is not shown.

during the two years emphasized in this study (1997 and 1998) began just before day 100 and leaf abscission began in some species between day 290 and day 300, but was not fully completed until several weeks later. Maximum leaf area index was almost identical for the two years and was assumed to be 5·5, and leaf area index was constant after leaf development in early spring until the beginning of abscission in autumn.

To evaluate the impact of seasonal changes in V_{cmax}, simulations were performed for the 1997 and 1998 growing seasons, the two years with extensive leaf gas exchange measurements. Three simulations were performed for both years. In the first simulation set, the observed changes in V_{cmax} were used (i.e. Fig. 4). In the second simulation set, the maximum value of V_{cmax} was used throughout the season (i.e. the early season peak in Fig. 4 was assumed to apply throughout growing season). In the third simulation set, V_{cmax} was set to an 'average' growing season value.

RESULTS

Measured and simulated estimates of seasonal N_{EE}

In 1999, when an eddy covariance system beneath the canopy was available to estimate soil respiration, the magnitude and seasonality of daytime soil respiration during the growing season was similar for the independently measured and simulated estimates (Fig. 7). Both methods showed some response to drought following day 250. The total soil respiration estimated by CANOAK during the daytime growing season (days 100–315) in 1999 (313 g C m^{-2}) was close to that measured by eddy covariance (321 g C m^{-2}).

In the first set of simulations, V_{cmax} in CANOAK was allowed to track the measured seasonal pattern shown Fig. 4. The seasonal trend of N_{EE} in these CANOAK simulations follows that measured by eddy covariance fairly well – especially in 1997, the year without low soil water potential (Fig. 8). The cumulative measured annual daytime N_{EE} during the growing season (days 100–315) was –1225 g C m^{-2} year^{-1} in 1997 and –1196 g C m^{-2} year^{-1} in 1998. The simulated values were within 5%: –1241 g C m^{-2} year^{-1} in 1997 and –1251 g C m^{-2} year^{-1} in 1998.

N_{EE} was summed cumulatively starting from day 100. Figure 9 (top two curves) shows the difference between CANOAK estimates of cumulative growing season N_{EE} and eddy covariance estimates of cumulative growing season N_{EE} for each of the two years (i.e. CANOAK cumulative N_{EE} minus eddy covariance cumulative N_{EE}; negative values indicate a model bias for more carbon uptake). CANOAK slightly overestimated (i.e. difference is negative) cumulative N_{EE} relative to measurements before day 150 during both years. After this period early in the year, the cumulative growing season bias in CANOAK relative to the eddy covariance measurements was even smaller during both years.

Effects of seasonality in V_{cmax} on N_{EE}

A second set of simulations was performed in both years to quantify the importance of the observed seasonality in V_{cmax}. In these simulations, V_{cmax} was assumed constant and set to the early season maximum value (i.e. value during the second period in Fig. 4) over the entire growing season. This approach substantially overestimated N_{EE} during both growing seasons, except during the late spring and early summer, when V_{cmax} was observed to be near the maximum value (Fig. 10, and compare with Fig. 8). The mean annual overestimate in N_{EE}, defined as the difference between simulations using the maximum value of V_{cmax} to simulations that more closely matched the observed seasonality in V_{cmax}, was 278 g C m^{-2} year^{-1} in 1997 and 388 g C m^{-2} year^{-1} in

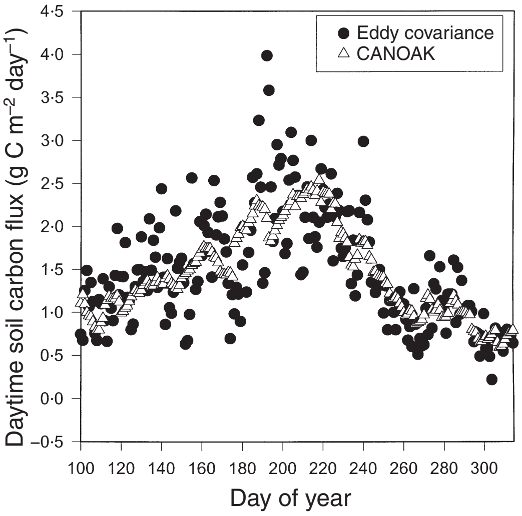

Figure 7. Measured and simulated daily daytime soil respiration during the 1999 growing season.

1998 (Fig. 9), or more than half the total estimated annual N_{EE} at this site (Greco & Baldocchi 1996). A little more than half of this overestimate occurred during leaf development (between days 100 and approximately day 135) and during the period of final senescence (between days 286 and 315). However, the overestimate was 131 (1997) and 188 (1998) g C m^{-2} year^{-1} between days 176 and 285, a period when leaf nitrogen content was not changing and no visible changes in leaf pigmentation were observed.

A second possible simple seasonal representation of V_{cmax} was to assign a single mean value (approximately 39 μmol m^{-2} s^{-1}) over the entire growing season, instead of the maximum value. Compared to using the early season maximum value of V_{cmax}, this simple approach reduced the annual bias in simulated N_{EE} (to within 10% of the annual total). However, on a daily time scale, the performance of this approach shows appreciably less skill relative to the simulations, where V_{cmax} follows the observed temporal pattern. When a single mean V_{cmax} was used instead of the observed seasonality, the mean absolute difference between CANOAK and eddy covariance estimates of N_{EE} increased by 23% (from 1·22 g C m^{-2} d^{-1} to 1·50 g C m^{-2} d^{-1}) and the coefficient of variation (r^2) between simulated and observed daily daytime N_{EE} decreased from 0·70 to 0·57.

Seasonality of N_{EE} during drought

When the maximum value of V_{cmax} was used during periods of low soil water potential in 1998 (after day 230; Fig. 6), the overestimate of N_{EE} was even greater than in 1997 (Fig. 10). Including the leaf age and soil water potential factor in V_{cmax} improved the predictions in 1998 considerably, but still frequently overestimated N_{EE} after day 260 (Fig. 8b). Although CANOAK reduced N_{EE} at the daily time scale during periods of low soil water potential, the approach of simply decreasing V_{cmax} often did not simulate the more extreme midday depression of photosynthesis frequently observed during periods of low soil water content (not shown).

DISCUSSION

Effects of temporal trends in V_{cmax}

Including the observed effect of leaf age on photosynthetic capacity decidedly improved the agreement between independently simulated and measured estimates of N_{EE} over the entire growing season. A similar agreement between simulated and eddy covariance-derived estimates of soil respiration further increases our confidence that CANOAK accurately simulates the individual components of N_{EE} and that it is necessary to consider the seasonal variation in V_{cmax}. Using the early season value of V_{cmax} over the

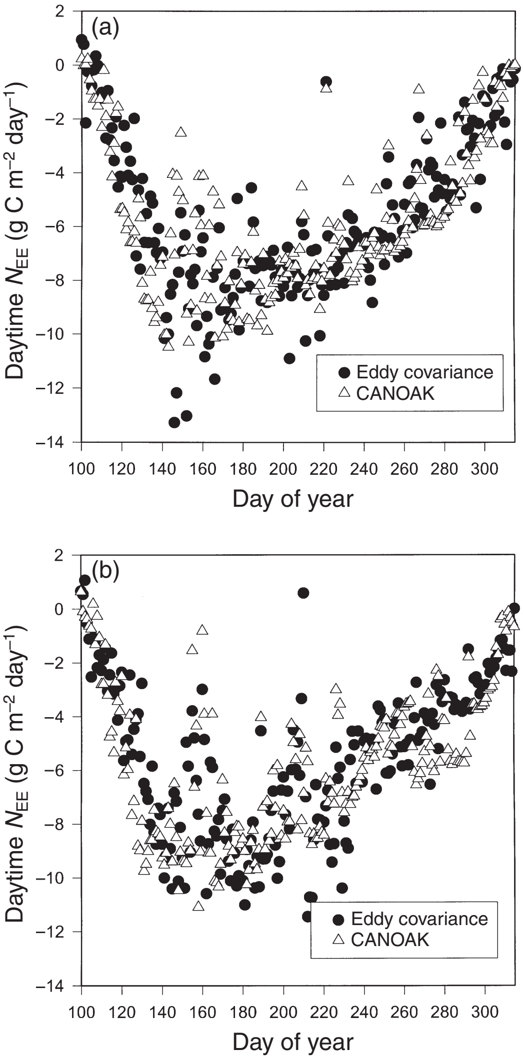

Figure 8. Eddy covariance and CANOAK estimates of daily daytime carbon flux between days 100 and 315, in 1997 (a) and 1998 (b).

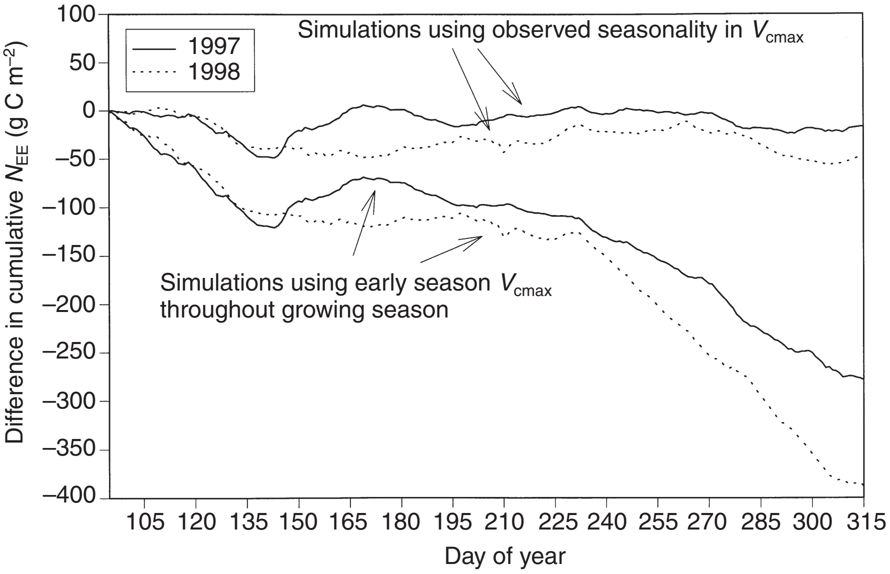

Figure 9. Difference in cumulative N_{EE} between CANOAK and eddy covariance during the growing season, which starts on day 100 (i.e. cumulative N_{EE} simulated by CANOAK minus cumulative N_{EE} measured by eddy covariance).

entire season substantially overestimates the carbon flux and is not a practical modelling approach for this forest. However, this approach is often implicitly used when modellers extrapolate estimates of V_{cmax} from a short time period to other periods in the growing season (Aber *et al.* 1996; Williams *et al.* 1996; Zeller & Nikolov 2000). Simulations using a single 'mean' value of V_{cmax} over the season inaccurately predict the seasonality of carbon uptake. Furthermore, if a mean representative V_{cmax} over the growing season is known, it is implied that measurements have been performed over the season, and the seasonality should be approximated and incorporated directly into the simulations.

Accurate simulations of N_{EE} over an annual cycle in this deciduous forest require V_{cmax} to vary during leaf development and final senescence, periods in which photosynthetic capacity is expected to change. However, an almost equally large bias – of more than a quarter of the estimated total annual N_{EE} (Greco & Baldocchi 1996) – was introduced if declines in photosynthetic capacity were not considered during the middle and late growing season. During this period, V_{cmax} decreased but leaf development had ceased, leaves remained green, no frost events occurred and there was essentially no reduction in canopy leaf nitrogen content (Wilson *et al.* 2000a). Furthermore, no important changes in dark respiration (R_d) or temperature kinetics of V_{cmax} and R_d were observed.

This study stresses the need to consider temporal changes in photosynthetic capacity in this forest, but no simple method was found to estimate the temporal changes throughout much of the growing season without resorting to extensive gas exchange experiments. V_{cmax} correlated with leaf mass per unit area, and apparently somewhat with whole-canopy leaf area, during leaf development (Wilson *et al.* 2000a). Changing photosynthetic capacity during leaf expansion and senescence can be potentially diagnosed from direct measurements of leaf area or from satellite-derived products that indicate changes in absorbed or reflected radiation within particular wavelengths (White *et al.* 1997). However, the temporal decline in V_{cmax} during middle and late summer, when leaf area is nearly constant, is not correlated with changes in leaf nitrogen, or with other easily measured leaf characteristics over most of the growing season, precluding a simple predictor of temporal patterns in V_{cmax} during the period of leaf maturity. Seasonal changes in the photosynthetic parameters described by Farquhar *et al.* (1980) have not been documented for other deciduous forests, but studies in other deciduous forests suggest that photosynthesis does not decline until a period much closer to senescence (Jurik 1986; Reich *et al.* 1991; Sullivan *et al.* 1996; Raulier *et al.* 1999). Therefore, the widespread importance of reductions in V_{cmax} on N_{EE} during the middle and late growing season in deciduous forests may not be a general result. Alternatively, the need to consider the trends in V_{cmax} associated directly with leaf development and final senescence applies to all deciduous forests.

Effects of drought

CANOAK quantitatively replicated part of the response of N_{EE} to low soil water potential at a daily time scale, simply by reducing V_{cmax} using a stress factor that was related to soil water potential. The inability of CANOAK to depict the more extreme observed diurnal variation in N_{EE} during drought, such as the afternoon depression, emphasizes that this study was not designed to adequately address the suite of physiological processes associated with low soil water content and/or high vapour pressure deficit. The model's difficulties in consistently simulating the diurnal variation during drought also suggests that the relative humidity response in the Collatz *et al.* (1991) relationship may not

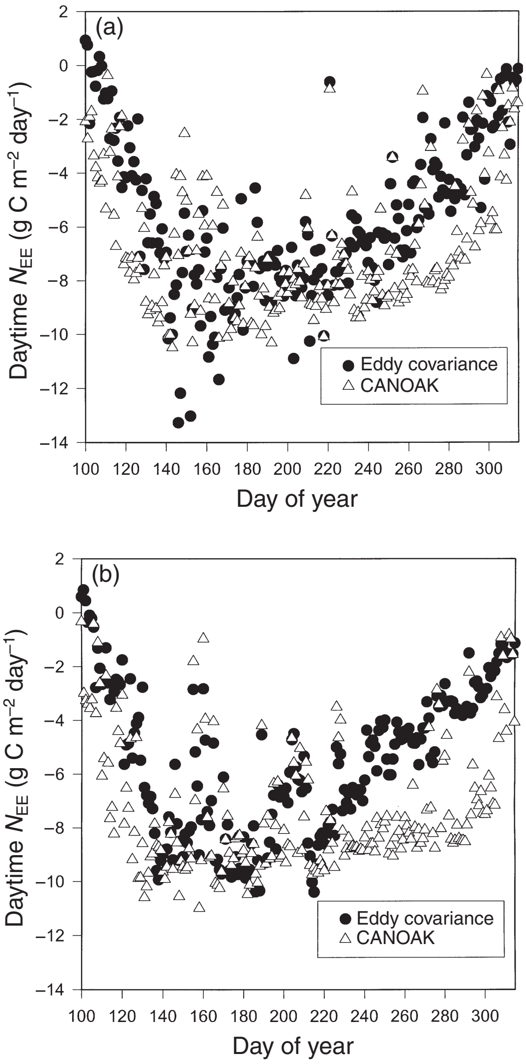

Figure 10. Eddy covariance and CANOAK estimates of daily daytime carbon flux between days 100 and 315 in 1997 (a) and 1998 (b). In these simulations, V_{cmax} was assumed to be constant throughout the growing season at the early season maximum.

sufficiently describe the regulation of stomatal functioning during periods of low soil water content. In the simulations presented here, the slope of the relationship of Collatz *et al.* (1991) algorithm, describing the constraints between stomatal conductance and assimilation rate, was not assumed to vary diurnally or over the season. However, this assumption was based on limited data of leaf response to changes in vapour pressure deficit or relative humidity and is in contrast to the assumption made by Baldocchi (1997). Significant stomatal limitation of single leaves during periods of low soil water content has been deduced quantitatively (Wilson *et al.* 2000b), suggesting that the model may be overestimating stomatal conductance during drought. The regulation of stomatal conductance and gas exchange during drought depends on hormonal signals, the increased resistance for water transport to the roots and/or hydraulic limitations within the tree (Jones 1992; Lowenstein & Pallardy 1998). Insightful algorithms on how to include the effects of hydraulic limitations have been proposed (Williams *et al.* 1996), but are hypothetical and require the parameterization of all the complexities associated with tree hydraulic conductivity and capacitance.

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