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Extrapolating leaf CO₂ exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation

Abstract Over the last 4 years, two data sets have emerged which allow increased accuracy and resolution in the definition and validation of a photosynthesis model for whole forest canopies. The first is a greatly expanded set of data on the nitrogen-photosynthesis relationship for temperate and tropical woody species. The second is a unique set of long-term (4 year) daily carbon balance measurements at the Harvard Forest, Petersham, Massachusetts, collected by the eddy-correlation technique. A model (PnET-Day) is presented which is derived directly from, and validated against, these data sets. The PnET-Day model uses foliar nitrogen concentration to calculate maximum instantaneous rates of gross and net photosynthesis which are then reduced for suboptimal temperature, photosynthetically active radiation (PAR), and vapor pressure deficit (VPD). Predicted daily gross photosynthesis is closely related to gross carbon exchange at the Harvard Forest as determined by eddy-correlation measurements. Predictions made by the full canopy model were significantly better than those produced by a multiple linear regression model. Sensitivity analyses for this model for a deciduous broad-leaved forest showed results to be much more sensitive to parameters related to maximum leaf-level photosynthetic rate (A_{max}) than to those related to light, temperature, VPD or total foliar mass. Aggregation analyses suggest that using monthly mean climatic data to drive the canopy model will give results similar to those achieved by averaging daily eddy correlation measurements of gross carbon exchange (GCE).

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Introduction

Predicting the effects of global change on forest ecosystem function requires the development of simple, generalizable, well-validated, data-based models that can be run for large regions using only simple driving variables. Such models should be derived directly from existing physiological data on component processes, such as photosynthesis and respiration, and should accurately predict the measured rates of function of intact systems. Rigorous parameterization and validation increase the likelihood of accurate predictions for modified climate regimes.

In a previous paper (Aber and Federer 1992), a simple model of whole forest carbon and water balance (PnET) was presented and validated against annual net primary productivity data for ten forests throughout North America, and for monthly or annual water balance data for three forested watersheds. The photosynthesis routine in this model was based on data available at that time relating maximum rates of net leaf-area-based photosynthesis (A_{max}) to weight-based foliar N concentration. Limitations in this model included a mixing of units in the prediction of A_{max} and the limited number of observations available for parameterizing this relationship. Validations of seasonal carbon flux were not possible because of a lack of data on monthly carbon exchange by forest systems.

Over the last four years, two unique data sets have emerged which overcome these limitations. The first is a greatly expanded set of data on the nitrogen-A_{max} relationship for temperate and tropical woody species (Reich et al. 1991b, 1992). The second is a unique long-term (4 year) record of daily carbon exchange by a deciduous forest at the Harvard Forest in central Massachusetts (Wofsy et al. 1993) made using the eddy-correlation technique (Baldocchi et al. 1988; Verma 1990).

The purposes of this paper are: (1) to present a simple model (PnET-Day) of seasonal changes in whole forest canopy photosynthesis driven by daily climatic data, (2) to validate this model against the 4-year, eddy-correlation data set available for the Harvard Forest; (3) to examine the effects of four different methods of aggregating daily climate data and model output to estimate monthly carbon balances; and (4) to test the sensitivity of the model to changes in both driving variables (e.g., temperature) and input parameters (e.g., foliar N concentration).

Methods

Model structure

General

The structure of the model presented here (PnET-Day, Fig. 1) is similar to the photosynthetic routines in the Forest-BGC (Running and Coughlan 1988; Running and Gower 1991) and TCX (Bonan 1993) models, but differs from those in the explicit use of foliar N levels to determine A_{max}. Response functions for radiation intensity, temperature and vapor pressure deficit are used with daily mean climate drivers for these variables to calculate realized A_{max} for leaves at the top of the canopy. A layered canopy is then simulated, with both radiation intensity and specific leaf weight (SLW) declining with canopy depth. Leaf respiration is a function of A_{max} and temperature, and is calculated separately for daytime and nighttime temperatures. Maximum (summer) and minimum (winter) leaf mass are input parameters. The onset of canopy development in spring is driven by a growing degree day sum algorithm, and canopy senescence results from negative carbon balances in autumn. Both of these are responsive to weather patterns unique to specific years. The model assumes no significant water stress but is intended to replace the photosynthesis routine in the original PnET which performs full water balance and water stress calculations.
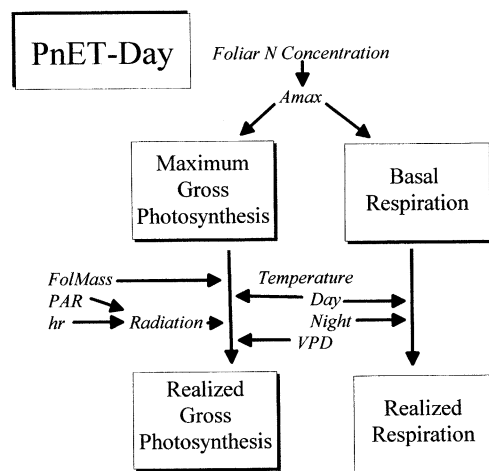

Fig. 1 Structure of the PnET-Day model. Foliar N determines A_{max} which is then separated into potential gross photosynthesis and dark respiration. Potential gross photosynthesis is reduced for suboptimal conditions of light, temperature and vapour pressure deficit (VPD) to give realized gross photosynthesis. Light levels in the simulated layered canopy are determined by ambient photosynthetically active radiation (PAR), cumulative leaf area index (LAI) and the light attenuation constant. Respiration is modified by temperature using a Q_{10} function

Model algorithms and parameters (Table 1)

Model parameters can be divided between those that are generalized and should apply to any species within the broad-leaved deciduous and needle-leaved evergreen groups, and those that need to be specified for an individual site or canopy.

Generalized parameters

Instantaneous A_{max} as a function of foliar N (AmaxA, AmaxB). In a broad context, all wild C3 species demonstrate a common linear relationship between foliar N concentration (g N.g^{-1} leaf) and A_{max} (nmol CO_2 g^{-1} leaf s^{-1}, Field and Mooney 1986; Reich et al. 1991a, 1992), making the use of photosynthesis-N relationships in modeling canopy gas exchange rates (e.g., Reich et al. 1990; Aber and Federer 1992) a powerful, generalized approach. However, this relationship varies between species, or functional groups of species, and species-specific or group-specific relationships predict observed patterns better than a single, general one (Reich et al. 1994, 1995). Given this, we could attempt to aggregate species specific curves (if available) for each tree species in each simulated system for use at the canopy level. However, in keeping with the goal of model generality, data used here are summarized for two groups, broad-leaved deciduous and needle-leaved evergreen, that show different relationships (Fig. 2; Reich et al. 1995) consistent with their differences in leaf morphology and life-span (Reich et al. 1992, 1994).

Daily averaged Amax (AmaxFrac). Maximum instantaneous rates of net photosynthesis are not generally maintained throughout an entire day. In order to run PnET-Day on daily to monthly time-steps an average daily A_{max} is needed. Reductions in gas exchange rates correlated with increasing evaporative demand are well known, and addressed in the model through the DVPD variable (see below, "Effects of vapor pressure deficit"). However, even on days of apparently non-limiting VPD, maximum early morning rates are not maintained throughout the day. In addition to periods of less than saturating irradiance, several poorly understood factors, which may include end-product inhibition, more negative xylem water potentials and inherent circadian rhythms, combine to yield a daily averaged Amax which is below the maximum, early morning instantaneous rate. For example, Ellsworth and Reich (1992) observed on days of low (and ostensibly non-limiting) evaporative demand that achieved daily leaf level carbon gain for sugar maple was 77% of that possible based solely on light limitation to photosynthesis, while on days of high evaporative demand achieved carbon gain was 57% of that possible. Other studies show similar values for this ratio under non-VPD limiting conditions (Table 2). In the PnET model AmaxFrac is set to 0.76, the mean of measured values for 11 eastern deciduous species.

Basal leaf respiration (BaseFolRespFrac, RespQ10). Maximum net photosynthetic rate (A_{max}) is divided into a maximum gross photosynthetic rate and a basal respiration rate (at 20°C) by Base-FolRespFrac which describes respiration as a fraction of A_{max}. Realized respiration is calculated separately for average daytime and nighttime temperatures using a Q_{10} specified by RespQ10. Data from 31 temperate tree species (Walters et al. 1993; P.B. Reich, unpublished work) yield an average value for this ratio of close to 0.1, the same value used in the original PnET model. The Q_{10} for respiration is assumed equal to 2.

Light absorption and photosynthetic response curve (k, HalfSat). Light attenuation in forest canopies is generally described by the Beers-Lambert exponential decay equation ($y=e^{-k \cdot LAI}$). Jarvis and Leverenz (1983) reviewed the available data and concluded that k in needle-leaved forests falls between 0.4 and 0.65 and is about 20% higher (0.5–0.8) in broad-leaved forests. Pierce and Running (1988) calculated a k of 0.52 on average for eight Montana needle-leaved stands. From data presented by Bolstad and Gower (1990) we calculate k of around 0.45 for Norway spruce and European larch (calculated to the point where 80% is extinguished, k goes up

Table 1 List of parameters required to run the PnET-Day model with values derived for needle-leaved evergreen and broad-leaved deciduous forests.

Generalized Parameters

	Needle-leaved Evergreen	Broad-leaved Deciduous	Definition and units
AmaxA	5.3	−46	/Intercept - Coefficients for A_{max} calculation
AmaxB	21.5	71.9	\Slope - (nmol $CO_2.g^{-1}.s^{-1}$)
AmaxFrac	0.76	0.76	Daily A_{max} as fraction of instantaneous
HalfSat	200	200	Half saturation light intensity (μmoles.$m_{-2}.s^{-1}$)
k	0.5	0.58	Light attenuation constant
BaseFolRespFrac	0.1	0.1	Dark respiration as fraction of A_{max}
RespQ_{10}	2	2	Q_{10} for leaf respiration
PsnTMin	2	4	/Minimum and optimum daytime temperatures
PsnTOpt	24	24	\for Dtemp calculation (°C)
DVPD1	0.05	0.05	/Coefficients for
DVPD2	2	2	\DVPD as a function of VPD

Site-specific parameters

|	Harvard Forest		
	Pine	Deciduous	
FolNCon.	1.1	2.2	Foliar N (% by weight)
SLWMAx	280	100	Specific leaf weight (g m^{-2})
SLWdel	0	0.2	Change in SLW with canopy mass (g m^{-2} g)
GDDFolStart	900	100	Growing degree days to start foliar production
GDDFolEnd	1600	900	Growing degree days to complete foliar production
SenescStart	270	270	Day of year after which leaf drop can occur
FolMassMax	800	300	Site specific max. summer foliar biomass (g m^{-2})
FolMassMin	460	0	Site specific min. winter foliar biomass (g m^{-2})
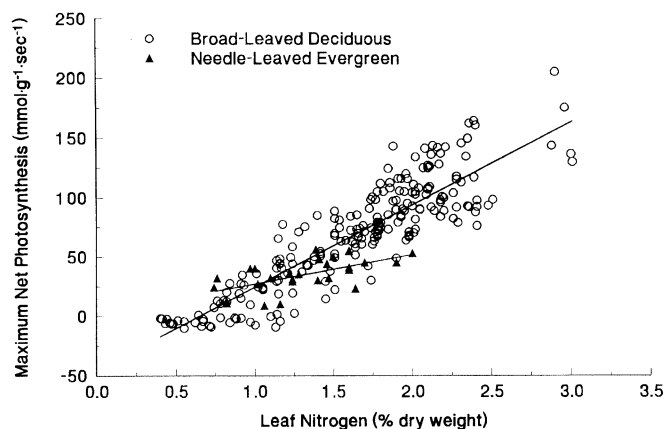
Fig. 2 Relationship between foliar N concentration and A_{max} for broad-leaved deciduous and needle-leaved evergreen species (data from Reich et al. 1995)

Table 2 Data for the ratio of daily averaged A_{max} to instantaneous, early-morning A_{max} for several eastern deciduous forest species

SPECIES	RATIO	SOURCE
Acer rubrum	0.75	Reich et al. 1990
Prunus serotina	0.75	"
Quercus ellipsoidallis	0.68	"
Rubus spp.	0.70	"
Q. rubra	0.75	Kruger and Reich 1993
Q. rubra	0.81	"
Acer saccharum	0.77	Ellsworth and Reich 1992
Prunus serotina	0.71	Harrington et al. 1989
Cornus spp.	0.63	"
Q. alba	0.73	Dougherty 1977
Castanea spp.	0.83	Abrams et al. 1990
Q. prinis	0.91	"
Q. rubra	0.88	"
Q. ilicifolia	0.75	"
Mean	0.76	(SE=0.015)

if calculated nearer the ground). Ellsworth and Reich (1993) found a k of 0.6 for sugar maple, while Caldwell et al. (1986) found a k of 0.6 for an oak woodland in Portugal. Kira et al. (1969) reported 0.5–0.65 for two hardwood forests. Using these values we arrive at an average k value of 0.58 for broad-leaved deciduous species and 0.50 for needle-leaved. No attempt is made to model changes in leaf angle or in k within the canopy. The photosynthetic response curve used in PnET-Day is derived in Aber and Federer (1992). Values for HalfSat, the light level at which realized canopy photosynthesis is half of A_{max}, are derived from the data sets used in the A_{max} calculations and suggest a constant value across species of 200 μE.

Temperature response (PsnTMin, PsnTOpt). These variables are expressed in terms of daytime temperatures (half way between the maximum and mean daily values). A symmetrical parabolic rela-

tionship is used here, as derived in Aber and Federer (1992). The maximum temperature for photosynthesis is assumed to be PsnT-Opt plus the difference between PsnTOpt and PsnTMin.

Effects of vapor pressure deficit (DVPD1, DVPD2). Leaf gas exchange in most species is sensitive to air dryness, generally expressed as vapor pressure deficit. We examined existing data for six eastern deciduous tree species (three *Quercus* species, two *Acer* species and *Prunus*, Reich and Hinkley 1980; Reich et al. 1990; Ellsworth and Reich 1992; Kruger and Reich 1993) and found a consistent decline in net photosynthetic rate and leaf conductance with increasing VPD, especially above 1 kPa. To effectively but simply capture this non-linear pattern, and to aggregate the effects of partial days above 1 kPa, we use a power function (DVPD1 × VPD^{DVPD2}) with the values given below. This formula-

tion also allows for a linear response from 0 kPa as described for western conifers (e.g. Running 1980, Monson and Grant 1989) by setting the exponent (DVPD2) to zero. This equation then becomes equivalent to the equation used in the original PnET (Aber and Federer 1992).

Site-specific parameters

The following variables are site-specific and ideally should be determined for the area of the forest sampled by the eddy flux system. However, the dimensions of the average tower footprint are not known with precision, and so we rely on parameters which were measured either spatially across the Harvard Forest (Martin and Aber 1995) or point data gathered within the Harvard Forest (e.g., Magill et al. 1995).

Foliar N concentration (FolNCon). Martin and Aber (1995) have applied high spectral resolution remote sensing to the Harvard Forest site to produce images of estimated foliar N concentration for the Prospect Hill tract, a 400-ha area of mixed hardwood/pine forest and pine and spruce plantations that includes the eddy correlation tower. Values in mixed hardwood/pine stands around the tower area range from below 2.0% to over 2.4%. Until field validation of these estimates within a known footprint for the tower can be made, a value of 2.2% is used in the model.

Specific leaf weight (SLWMax and delSLW). Photosynthesis and respiration are calculated on a per unit mass basis, while light extinction through the canopy is a function of leaf area (LAI, m^2 m^{-2}). Specific leaf weight (SLW, g m^{-2}) is used to convert foliar mass to area. Several studies (Ellsworth and Reich 1993; Aber et al. 1990) have shown that foliar nitrogen per unit area declines with canopy depth, and that this occurs by changes in SLW, rather than changes in N concentration per unit foliar mass. Changes in SLW are generally small in needle-leaved species compared with broad-leaved. In the model, SLWMax is the SLW at the top of the canopy, and SLWDel is the change in SLW with canopy depth (expressed as total foliar mass above a given layer). Data are from Ellsworth and Reich (1993) and Aber et al. (1990).

Timing of leaf-out and senescence (GDDFolStart, GDDFolEnd, SenescStart). These variables determine the timing of leaf out and the earliest time at which foliar senescence can occur. The first two are expressed as total accumulated growing degree days calculated as all mean temperatures above 0°C. There is very little quantitative data on the timing of initiation and completion of foliar expansion as a function of climatic variables although the potential for obtaining these relationships from simultaneous climate monitoring networks and satellite remote sensing (e.g., AVHRR data) is high. The values used here (Table 1) are calculated from mean climatic data for the Harvard Forest assuming a normal completion of leaf expansion by mid-May for hardwoods, and late-june for pines at that site. Senescence is determined by the dropping of any foliage which shows a negative carbon balance on any given day after that specified by SenescStart. This eliminates the premature senescence of foliage due to a single very dark or cold day in mid-summer. The actual factors which trigger and control leaf senescence are not yet clearly known.

Leaf Mass (FolMassMax, FolMassMin). These two variables determine the maximum and minimum foliar mass which can occur during the year. FolMassMin is 0 for deciduous forests. FolMass-Max for the Harvard Forest hardwood and pine stands used here are averages of several years of field data from pine and oak-maple stands at that site (Aber et al. 1993; Magill et al. 1995).

Driving variables – climate

Temperature and PAR

Two independent climate data sets are used in the validations and predictions that follow. The first set, referred to as the NOAA record, consists of daily maximum and minimum temperature
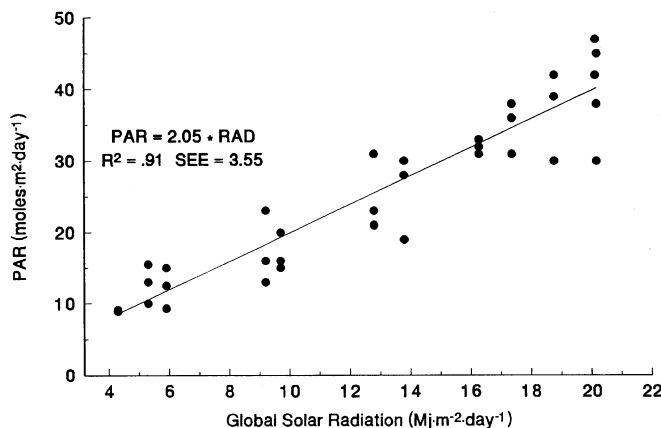

Fig. 3 Relationship between mean daily global solar radiation predicted at monthly intervals for the Harvard Forest by Ollinger et al. (1994) and monthly averaged measured daily values of PAR from the eddy correlation tower at the Harvard Forest

measured using a mercury thermometer in a small clearing outside the main Harvard Forest office, Petersham, Massachusetts. These data are used for aggregation runs at the monthly time step. The NOAA data set does not include solar radiation, which we instead derived for the NOAA runs following Ollinger et al. (1994). It was necessary to convert these mean monthly data from global radiation (joules) to photosynthetically active radiation (PAR, moles). A regression (Fig. 3) of monthly averaged daily total PAR (mol m^{-2} day^{-1}) measured at the eddy flux tower (see below) during 1991–1993 against mean monthly radiation estimated by Ollinger et al. (1994, joules m^{-2} day^{-1}), yielded a conversion of 2.0513 from 10^6 joules to moles.

The second climatalogical data set, referred to as the tower record, was collected as part of a long-term measurement program initiated during April 1990 (Wofsy et al. 1993; Goulden et al. 1995). The tower meteorological observations were made simultaneously with the eddy-correlation CO_2 exchange observations at a forested site 1.6 km northeast of the main Harvard Forest office. A 30-m tower (Rohn 25G), extending 6–10 m above a mixed oak-maple canopy, was instrumented with an array of meteorological sensors. Supplemental instrumentation and data acquisition equipment were installed in a climate-controlled hut 20 m from the tower base. Throughout the investigation, air temperature at 30 m (aspirated thermistor), incident PAR (silicon quantum sensor), and soil surface temperature (potted thermistors), were logged at 0.5 Hz. Half-hour means were calculated from these data and further aggregated to daily maximum and minimum temperature, and total daily incident PAR.

For input to PnET-Day from either the NOAA or tower data sets, mean daily temperature is taken as the average of the maximum and minimum, and day and night temperatures are calculated as the average of the mean and the maximum and minimum temperatures, respectively.

Hours of daylight per day (hr)

This variable is calculated using an algorithm for daylength as a function of day of year and latitude drawn from Smith (1974). Total daily PAR (moles m^{-2} d^{-1}) is divided by hr*.0036 to give mean daily instantaneous PAR (μmoles m^{-2} s^{-1}).

Vapor pressure deficit (VPD)

This variable is calculated assuming that the atmosphere is saturated at the daily minimum temperature. VPD then the difference between the saturated vapour pressure at the daytime (not maximum) temperature and the minimum temperature (as in PnET, Aber and Federer 1992).

Validation

Two approaches are taken to determining how well the PnET-Day model predicts carbon balances at the Harvard Forest. First, predicted gross carbon exchange (GCE, equivalent to gross photosynthesis) is compared with the tower GCE, calculated as the sum of measured net carbon exchange (NCE) and estimated total forest respiration, derived as a function of temperature using nighttime tower flux measurements. As a test of the degree to which a full canopy model improves upon a simple statistical model, a statistical model is derived and also tested for goodness of fit with the tower data.

The Harvard Forest eddy-correlation data set

The net exchange of CO_2 by the forest surrounding the meteorological tower was measured from January 1991 through December 1994 using the eddy correlation method (Baldocchi et al. 1988; Verma 1990; Wofsy et al. 1993; Fan et al. 1995; Goulden et al. 1995). A three-dimensional sonic anemometer was used to measure the vertical wind velocity at 30 m height, 6–10 m above the canopy. The raw signals were digitized at 4 Hz and logged for subsequent analysis. The CO_2 mixing ratio at 30 m height was analyzed by drawing 6–8 l min^{-1} of air down a 50-m tube and through a closed path infrared gas analyzer (IRGA), a process that introduced a lag of several seconds. Following an adjustment for this lag, we calculated the net CO_2 exchange as the 30-min covariance of vertical wind and linearly detrended CO_2 concentration. We compensated for errors associated with sonic alignment and local topography by rotating the flux to the plane with zero mean vertical velocity (McMillen 1988). A series of simulations, laboratory tests, and spectral analyses indicated a small underestimation of flux due to the loss of high-frequency CO_2 fluctuations. (The 90% response determined by CO_2 addition on the tower was faster than 1 s.) We corrected for this error by increasing the measured CO_2 flux in proportion to the underestimation of sensible heat flux associated with a simulated reduction in the high frequency response of the temperature detector (Leuning and King 1992; Goulden et al. 1995). This correction was generally small (< 10%).

The eddy-correlation method measures the net exchange of CO_2 through a plane at 30 m height. This flux may differ from that into and out of organisms if the quantity of CO_2 stored between the forest floor and the plane at 30 m changes. In order to more directly assess the flux into plants and soils, we measured the quantity of CO_2 stored below 30 m by frequently sampling the mixing ratio at eight heights through the canopy (Wofsy et al. 1993). This change in CO_2 storage was then added to the eddy flux to calculate net carbon exchange (NCE; positive values represent net movement of carbon into the ecosystem).

This flux is similar to the total ecosystem respiration during well-mixed nocturnal periods, and the sum of photosynthesis and respiration during the day. Respiration from soil heterotrophs and plant maintenance is strongly controlled by temperature (Jarvis and Leverenz 1983). Seasonal relationships were derived between soil temperature and ecosystem respiration using an overall Q_{10} of 2.2 (Goulden et al. 1995). Hourly estimated respiration rates were summed for each day and added to net ecosystem flux measurements to estimate GCE. GCE is equal to the combined rate of RUBISCO carboxylation and oxygenation (Goulden et al. 1995).

Predictions for total daily respiration from the entire ecosystem obtained by this method can be compared with similar estimates for soil-only respiration using the equations of Kicklighter et al. (1994) and mean daily air temperature (Fig. 4). The tower-based estimates average 34% higher than the generalized equation from Kicklighter et al. (1994). This could result from site-specific conditions surrounding the tower area, and from the inclusion of above-ground plant respiration in the tower data. The Kicklighter equation predicts respiration from soils only.

The tower measurements were frequently interrupted by rainfall, calibration, maintenance and data collection, and occasionally for extended periods by equipment failure. In the present analysis we use 538 days with uninterrupted observations for the years 1991–1994. This represents the longest and most continuous eddy-correlation data set available for any forest ecosystem. For the pur-
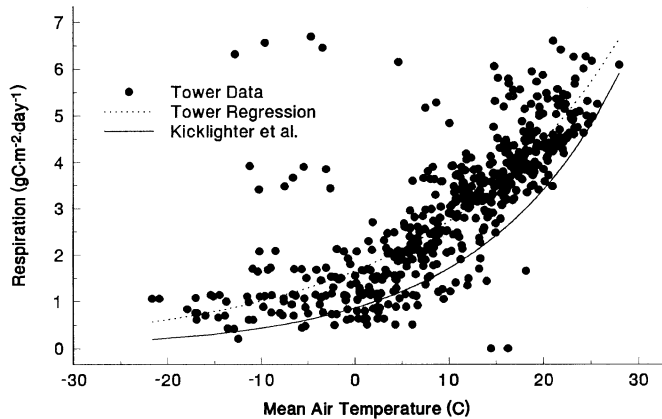

Fig. 4 Comparison of estimated respiration for the days in the eddy correlation data set from the Harvard Forest. Tower data are daily estimates of whole-forest respiration summed from hourly predictions using equations derived on site (Goulden et al. 1995). The Kicklighter et al. (1994) curve is a generalized relationship for soil respiration only derived from several data sets for sites throughout the northeastern United States

poses of model validation we assume that the eddy-flux observations are accurate, although in practice we expect both systematic and random errors. An error analysis indicates an absolute uncertainty during daylight periods of less than 20% (Goulden et al. 1995). Random errors associated with the finite averaging time further limit the accuracy of single 30-minute observations to ± 20% (Baldocchi et al. 1988). Random errors cause appreciable scatter in direct comparisons of simultaneous observations and predictions, but are otherwise unimportant since a large number of 24-hour observations are considered.

A simple statistical model

Simple statistical models can often approach the accuracy of more complex and biologically realistic models. This will occur if the predictions of the more complex model are insensitive to many of the interactions included, or if autocorrelations between driving variables (e.g., VPD and temperature) reduce the effective dimensionality of the model. To test whether the PnET-Day model is overly complex in this way, a simple multiple linear model of GCE versus daily climatic variables was developed for comparison with the full canopy model. Simple linear relationships were used in the statistical model even though it is known that relationships between gross photosynthesis and light and temperature are non-linear. This was done to provide a base-line comparison between this simple model and the full model with physiologically meaningful interactions. Any number of combinations of non-linear interactions could also be tested. The accuracy of such hybrid statistical models should lie between PnET-Day and the statistical model employed here.

Aggregation

One of the purposes of both the tower measurements and the PnET-Day model is to predict total carbon balances over long time periods (months to years). A critical step in arriving at final values for these periods is solving the aggregation problem: how to extrapolate even this relatively complete data set to cover days for which direct measurements are not available.

Four methods of aggregating to a monthly total were compared. The first is to simply take the average of all daily tower GCE measurements within each month. The second also uses the partial data, but applies the model to the daily climate drivers measured at the tower and averages all model predictions within a month. The third averages all of the tower climate data for a

month and uses that average data to run one day of the model, which is then applied to the entire month. The fourth uses the NOAA record of mean monthly climatic to run the model for the average day in each month. Monthly data from this source are derived from a more complete set of daily observations, but have no direct link with tower data.

Sensitivity analyses

Sensitivity analysis allows a clearer understanding of the relative importance of the different parameters and algorithms in the model in controlling daily GCE. It provides insight into which factors are most important in controlling model predictions, and also shows the degree to which errors in parameters or input data will result in errors in prediction. It will also show the extent of short-term change in ecosystem function expected from different changes in climate.

To test the sensitivity of the model to both driving variables (climate) and input parameters (Table 1), the effect of a 10% increase in each variable on predicted GCE over the entire simulation period was recorded. A preliminary test showed that sensitivity responses were symmetrical, that either an increase or decrease resulted in the same relative change in GCE, but with opposite sign. Therefore, results are presented for the 10% increase only.

At a larger scale, the effects of changing species group, and of predicted changes in climate were also tested. For the former, the parameter set was altered to represent a Harvard Forest pine stand and the model was rerun with the monthly averaged NOAA climate data. For the latter, temperature was increased by either 3°C or 5°C (day and night temperature, all months).

Results and discussion

Validation

PnET-Day versus eddy correlation data

All parameter values used in the validation exercise are as derived from field data (Table 1). No adjustments ("tuning" or model calibrations) were made to increase goodness of fit. Agreement between PnET-Day and tower data is generally very good (Fig. 5) [standard error of prediction (SEP)=1.73]. There are no major discrepancies between predicted and observed values, although the model tends to underestimate the highest mid summer GCE rates. This could be corrected by adjusting the A_{max} parameters which control maximum photosynthetic rates within the error limits of the statistical relationship in Fig. 2, but no such post hoc calibrations were carried out in this study. Overall, PnET-Day underestimates mean daily GCE over the entire 4-year period by 0.09 (4.90 versus 4.99) g C m^{-2} day^{-1}.

The eddy-correlation data for winter 1992–1993 show occasional large negative values for GCE associated with high CO_2 efflux during extremely windy periods (Goulden et al. 1995). The respiration term used to convert NCE measured at the tower to GCE is a long-term average function only of temperature and so does not capture the detailed effects of turbulence on the timing of CO_2 flux to the atmosphere.

It is interesting that even during the relatively dry periods in June and July 1991 and June 1993 there is no evidence of water stress. This version of PnET-Day explicitly ignores soil-based deficiencies in water availability,
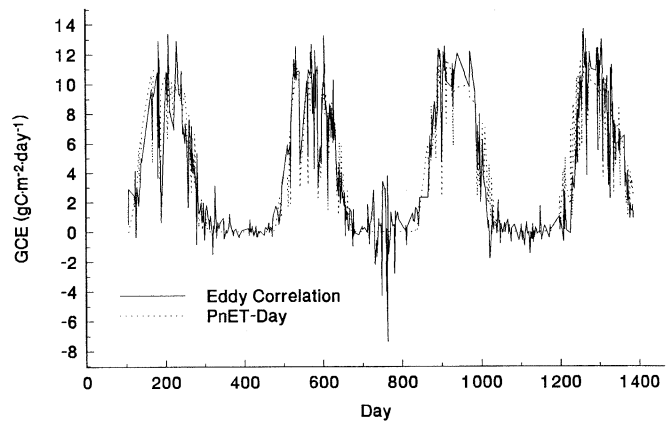

Fig. 5 Time course of gross carbon exchange (GCE) predicted by the PnET-Day model and measured at the eddy correlation tower at the Harvard Forest for the period 1991–1994. Day 1 is 1 January 1991

and yet does not show any systematic disagreement with tower-based GCE measurements in mid-summer, suggesting that soil-based water stress is not a controlling factor at the tower site.

Patterns in differences between PnET-Day and the eddy correlation estimates of GCE could help identify errors in parameterizatin of the PnET model. Residuals (PnET - Tower) were not significantly (P<0.01) related to any of the four driving variables (t_{max}, t_{mni}, PAR, VPD) or to time of year.

Results from the statistical model

The statistical model was developed using daily PAR, average daily temperature (t_{ave}) and VPD. Of these, only average t_{ave} showed a non-linear relationship with tower GCE in single-factor correlations. This resulted from GCE values near zero for all days where $t_{ave} < 0°C$. This was accommodated by setting the statistical model GCE to 0 for all days with $t_{ave} < 0°C$. A multiple linear regression of GCE for all days with tave > 0oC yielded the model:

$$GCE = -3.076 + 0.5344\,(t_{ave}) + 0.005727\,(PAR) - 3.724\,(VPD) \quad (1)$$

Results of the linear model (Fig. 6) show an underestimation of GCE during the growing season, overestimates during spring and fall, and several individual days with large discrepancies between predicted and observed values. Overall the statistical model has an SEP of 2.20, 27% higher than the full model. Residuals show that the statistical model overestimates at low GCE and underestimates at high GCE. These results suggest that the greater complexity of the full canopy model yields significant increases in the accuracy and precision of predictions, but that those increases are not order of magnitude in size. However, the statistical model relies on the availability of a very large, high-quality data set for its derivation and would not be expected to predict accurately for sites other than the one for which it was derived.
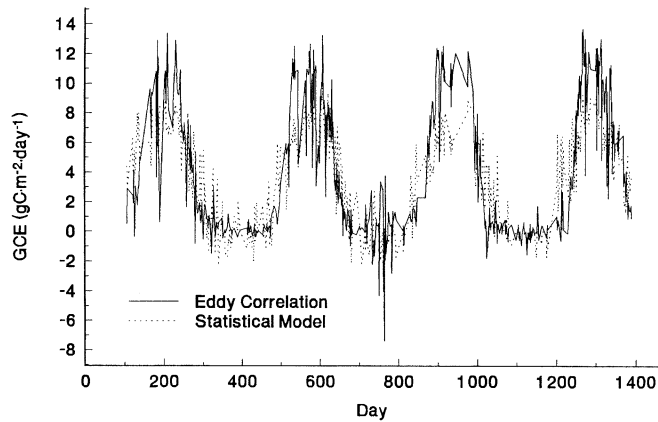
Fig. 6 Time course of measured GCE for the Harvard Forest and predictions from a statistical model based on temperature, PAR and VPD. Day 1 is 1 January 1991
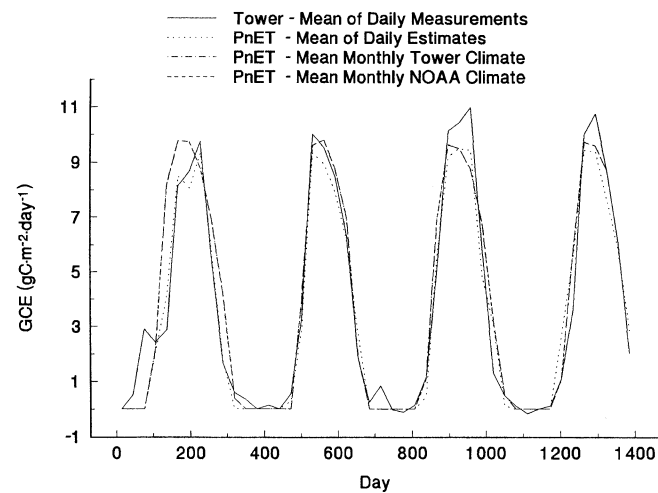

Fig. 7 Results from four different methods of aggregating tower and PnET-Day model results to the monthly level. See text for explanation

The generalized, physiologically-based relationships in PnET-Day should transfer more successfully to the prediction of carbon balances in other stands and under different climatic conditions.

Aggregation

The four aggregation methods (Fig. 7) produced very similar results, with differences occurring mainly in the early spring leaf-out period of 1991. Average daily GCE for the 4-year period ranged only from 3.92 to 4.27 g C m^{-2} day^{-1} for the four treatments. These results suggest that accurate predictions of monthly GCE can be derived using only monthly mean data from nearby weather stations. This type of climatic information is available over wide areas and can be extrapolated to regional data planes for use with geographic information systems (GIS; e.g., Ollinger et al. 1994). Combining PnET-Day with such a GIS would yield spatially explicit estimates of GCE over the region involved.

Table 3 Sensitivity of PnET-Day model to changes in input parameters and driving variables. All values are percent change in mean daily GCE over the entire period of simulation

Parameter/ variable	Percent change in GCE
Input parameters (+10%)	
FolNCon.	+14%
SLWMAx	+6%
SLWdel	−2%
AmaxA	−4%
AmaxB	+14%
AmaxFrac	+9%
HalfSat	−5%
k	−5%
BaseFolRespFrac	+<1%
RespQ_{10}	+1%
PsnTMin	−1%
PsnTOpt	−3%
DVPD1	−<1%
DVPD2	−<1%
GDDFolStart	−<1%
GDDFolEnd	−1%
SenescStart	+3%
FolMassMax	+2%
Climatic variables (+10%)	
Temperature	
(max and min)	+5%
PAR	+5%
VPD	−1%
Climatic variables (absolute)	
Temperature	
(+3oC aboslute)	+16%
(+5OC absolute)	+21%

Sensitivity analyses

GCE predictions were more sensitive to changes in parameters related to A_{max} than to any others (Table 3). Increases of 10% either the foliar N concentration or the AMaxB parameter yielded increases of 14% in GCE. The ratio between realized daily A_{max} and the instantaneous rate (AMaxFrac) was the next most sensitive parameter. These were followed by parameters related to light interception per unit leaf mass and the shape of the photosynthetic response curve (k, HalfSat and SLWmax). Parameters related to foliar respiration, temperature effects, and the timing of leaf out and senescence all showed responses of 3% or less to a 10% change in value.

Of particular interest in a global remote sensing context are the relative sensitivities of GCE to total leaf biomass and foliar N concentration. Many current models of biosphere-atmosphere exchange (see discussion by Running and Hunt 1993) are based on NDVI (normalized difference vegetation index), which is often assumed to represent spatial differences in green biomass. These results suggest that, at least in closed canopy, broad-leaved deciduous forests, gross photosynthesis is 7 times more sensitive to the foliar N concentration in the foliage displayed, than it is to the total mass of foliage. However, if NDVI in dense canopies (LAI>3) captures concentrations of chlorophyll rather than changes in mass (Myneni et al. 1995), the high correlation between chlorophyll
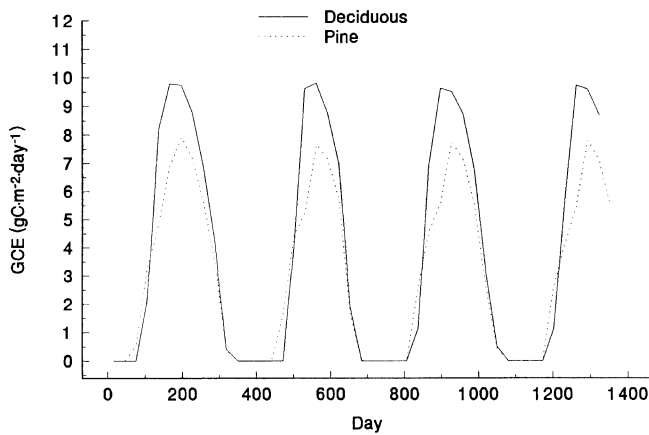
Fig. 8 Effects of species composition on gross carbon exchange. Species composition simulated by changes in vegetation parameters in Table 1 from deciduous to pine
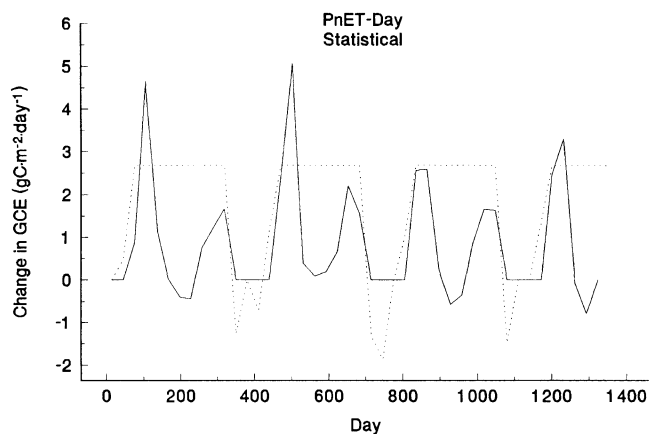

Fig. 9 Relative sensitivity of the full PnET-Day model and the statistical model to changes in climate. Data are expressed as the difference between +5°C run and a control run for each model

and nitrogen concentrations in foliage would allow accurate estimates of carbon exchange (e.g., Waring et al. 1995).

Altering all of the vegetation parameters to run a pine canopy rather than a deciduous canopy (Table 1) reduces predicted gross carbon exchange by about 20% in mid summer (Fig. 8). This results from the lower A_{max} values which are only partially offset by higher SLW. A slight increase in early-spring carbon gain for the pines relative to the hardwood simulation results from the presence of over-wintered foliage. It should be noted that the much lower slope of the A_{max}-N relationship for needle-leaved evergreen species will result in a much lower sensitivity to changes in foliar N concentration.

Predicted GCE for the Harvard Forest is also less sensitive to changes in climate variables than to those determining A_{max} (Table 3). Increases of 10% in PAR and temperature result in 5% increases in GCE. However, if changes in temperature are expressed as absolute increases on the order of those predicted for the next century (3–5°C), increases of 16–21% in GCE are predicted. It must be noted that this assumes no dilution in foliar N

content by increased carbon availability and biomass production, no water stress due to either a longer growing season or reduced rainfall, no acclimation of A_{max} or respiration to altered temperature, and no photoperiodic controls on carbon acquisition and allocation. More complete models which include a full water balance, and carbon and nitrogen allocation routines are required to assess the importance of these system-level feedbacks.

Not only did the PnET-Day and statistical models differ in terms of accuracy of validation, they also gave different results for responses to warming (Fig. 9). While both models predicted increased GCE, the statistical model failed to capture interactions between temperature and other variables, yielding a flat, linear increase across all months when t_{ave} is above 0°C. In contrast, the full model shows both sharp increases in GCE by the extension of the growing season into both late winter and late fall (greatest increases in March-April and October-November), with possible depressions in mid-summer due to temperatures above the optimum for gross photosynthesis. Predicted increases in average daily GCE were 0.81 and 1.76 g C m^{-2} day^{-1} for the PnET-Day and statistical models, respectively.

Conclusions

The results presented here demonstrate that a simple, daily time step model based on physiological measurements at the leaf level can accurately predict seasonal changes in gross carbon exchange by a forest canopy. Predictions made by the full canopy model (PnET-Day) were significantly better than those produced by a multiple linear regression model. Sensitivity analyses predicted that a deciduous stand at the Harvard Forest should be more sensitive to parameters related to maximum photosynthetic rate (A_{max}) than to those related to light, temperature, VPD or total foliar mass. Aggregation analyses suggest that using monthly mean climatic data to drive the canopy model will give results similar to those achieved by averaging daily measurements of GCE within a month.

References

Aber JD, Federer CA (1992) A generalized, lumped-parameter model of photosynthesis, evaporation and net primary production in temperate and boreal forest ecosystems. Oecologia 92: 463–474

Aber JD, Wessman CA, Peterson DL, Melillo JM, Fownes JH (1990) Remote sensing of litter and soil organic matter decomposition in forest ecosystems. In: Hobbs RJ, Mooney HA (eds) Remote sensing of biosphere functioning. Springer, Berlin Heidelberg New York, pp 87–103

Aber JD, Magill A, Boone R, Melillo JM, Steudler P, Bowden R (1993) Plant and soil responses to chronic nitrogen additions at the Harvard Forest, Massachusetts. Ecol Appl 3: 156–166

Abrams MD, Schultz JC, Kleiner KW (1990) Ecophysiological responses in mesic versus xeric hardwood specieis to an early-season drought in central Pennsylvania. For Sci 36:970–981

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

Bolstad PV, Gower ST (1990) Estimation of leaf area in fourteen southern Wisconsin forest stands using a portable radiometer. Tree Physiol 7: 115–224

Bonan GB (1993) Physiological control on the carbon balance of boreal forest ecosystems. Can J For Res 23: 1453–1471

Caldwell MM, Meister HP, Tenhunen JD, Lange OL (1986) Quercus coccifera in a Portuguese macchia: measurements in different canopy layers and simulation with a canopy model. Trees Struct Funct 1:25–41

Dougherty PM (1977) Net carbon exchange characteristics of a dominant white oak tree (Quercus alba L.). Ph.D. Dissertation, University of Missouri

Ellsworth DS, Reich PB (1992) Leaf mass per area, nitrogen content and photosynthetic carbon gain in Acer saccharum seedlings in contrasting forest light environments. Funct Ecol 6: 423–435

Ellsworth DS, Reich PB (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96: 169–178

Fan S-M, Goulden ML, Munger JW, Daube BC, Bakwins PS, Wofsy SC, Amthor JS, Fitzjarrald DR, Moore KE, Moore TR (1995) Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy correlation. Oecologia (in press)

Field CJ, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givinish TJ (ed) On the economy of plant form and function. Cambridge University Press, New York pp 25–55

Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsy SC (1995) Measurements of carbon storage by long-term eddy correlation: methods and a critical evaluation of accuracy. Global Change Biol (in press)

Harrington RA, Brown BJ, Reich PB (1989) Ecophysiology of exotic and native shrubs in southern Wisconsin. I. Relationship of leaf characteristics, resource availability and phenology to seasonal patterns of carbon gain. Oecologia 80: 356–367

Jarvis PG, Leverenz JW (1983) Productivity of temperate, deciduous and evergreen forests. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology IV (Encyclopedia in plant physiology, NS, vol 12D). Springer, Berlin Heidelberg New York pp 233–280

Kicklighter DW, Melillo JM, Peterjohn WT, Rastetter EB, McGuire AD, Steudler PA, Aber JD (1994) Aspects of spatial and temporal aggregation in stimating regional carbon dioxide fluxes from temperate forest soils. J Geophys Res 99(D1): 1303–1315

Kira T, Shinozaki K, Hozumi K (1969) Structure of forest canopies as related to their primary productivity. Plant Cell Physiol 10:129–142

Kruger EL, Reich PB (1993) Coppicing alters ecophysiology of Quercus rubra saplings in Wisconsin forest openings. Physiol Plant 89:741–750

Leuning R, King KM (1992) Comparison of eddy-covariance measurements of CO_2 fluxes by open- and closed-path CO_2 analyzers. Boundary Layer Meteorol 59: 297–311

Magill A, Aber JD, Hendricks JJ, Melillo JM, Steduler PA (1995) Plant and soil responses to 6 years of chronic nitrogen additions at the Harvard Forest, Petersham, MA. Ecol Appl (in press)

Martin ME, Aber JD (1995) Estimating forest canopy chemistry and ecosystem function from high resolution remote sensing data. Ecol Appl (in press)

McMillen RT (1988) An eddy correlation technique with extended applicability to non-simple terrain. Boundary Layer Meteorol 43: 231–245

Monson RK, Grant MC (1989) Experimental studies of ponderosa pine. III. Differences in photosynthesis, stomatal conductance and water use efficiency between two genetic lines. Am J of Bot 76: 1041–1047

Myneni RB, Hall FG, Sellers PJ, Marshak AL (1995) The interpretation of spectral vegetation indices. IEEE-IGARS (in press)

Ollinger SV, Aber JD, Federer CA, Lovett GM, Ellis J (1994) Modeling physical and chemiscal climatic variables across the northeastern U.U. for a Geographic Information System. US For Serv Gen Tech Rep (in press)

Pierce LL, Running SW (1988) Rapid estimation fo coniferous forest leaf area index using a portable integrating radiometer. Ecology 69: 1762–1767

Reich PB, Hinkley TM (1980) Water relations, soil ecology fertility, and plant nutrient composition of a pygmy oak ecosystem. 61: 400–416

Reich PB, Abrams MD, Ellsworth DS, Kruger EL, Tabone TJ (1990) Fire affects ecophysiology and community dynamics of central wisconsin oak forest regeneration. Ecology 71: 2179–2190

Reich PB, Uhl C, Walters MB, Ellsworth DS (1991a) Leaf life-span as a determinant of leaf structure and function among 23 Amazonian tree species. Oecologia 86: 16–24

Reich PB, Walters MB, Ellsworth DS (1991b) Leaf age and season influence the relationship between leaf nitrogen, leaf mass per area, and photosynthesis in maple and oak trees. Plant Cell Environ 14: 251–259

Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecol Monogr 63: 365–392

Reich PB, Walters MB, Ellsworth DS, Uhl C (1994) Photosynthesis-nitrogen relations in Amazonian tree species. I. Patterns among species and communities. Oecologia 97: 62–72

Reich PB, Kloeppel B, Ellsworth DS, Walters MB (1995) Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. Oecologia (in press)

Running SW (1980) Environmental and physiological control of water flux through Pinus contorta. Can J For Res 10: 82–91

Running SW, Coughlan JC (1988) A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol Model 42: 125–154

Running SW, Gower ST (1991) FOREST-BGC, a general model for forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. Tree Physiol 9: 147–160

Running SW, Hunt ER (1993) Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. In: Ehleringer JR, Field CB (eds) Scaling physiological processes: leaf to globe. Academic Press, San Diego, pp 141–158

Smith WH (1974) Air pollution – effects on the structure and function of temperate forest ecosystems. Environ Pollut 6: 111–129

Verma SB (1990) Micrometeorological methods for measuring surface fluxes of mass and energy. Remote Sensing Rev 5: 99–115

Walters MB, Kruger EL, Reich PB (1993) Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. Oecologia 96: 219–231

Waring RH, Law BE, Goulden ML, Bassow SL, McCreight RW, Wofsy SW, Bazzaz FA (1995) Scaling net photosynthesis at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. Plant Cell Environ (in press)

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