

Measuring and modelling seasonal variation of carbon dioxide and water vapour exchange of a *Pinus ponderosa* forest subject to soil water deficit

B. E. LAW,* M. WILLIAMS,† P. M. ANTHONI,‡ D. D. BALDOCCHI§ and M. H. UNSWORTH‡

*Department of Forest Science, 328 Richardson Hall, Oregon State University, Corvallis, OR 97331; †The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543; ‡College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331; §Atmospheric Turbulence and Diffusion Division, PO Box 2456, Oak Ridge, TN 37831 and Department of Environmental Science, Policy and Management, 151 Hilgard Hall, University of California, Berkeley, CA 94720, USA

Abstract

We conducted ecosystem carbon and water vapour exchange studies in an old-growth *Pinus ponderosa* forest in the Pacific North-west region of the United States. The canopy is heterogeneous, with tall multiaged trees and an open, clumped canopy with low leaf area. Carbon assimilation can occur throughout relatively mild winters, although night frosts can temporarily halt the process and physiological factors limit its efficiency. In contrast, carbon assimilation is often limited in the 'growing season' by stomatal closure associated with high evaporative demand (D) and soil water deficits. All of these factors present a challenge to effectively modelling ecosystem processes. Our objective was to generate an understanding of the controls on ecosystem processes across seasonal and annual cycles from a combination of fine-scale process modelling, ecophysiological measurements, and carbon and water vapour fluxes measured by the eddy covariance method. Flux measurements showed that 50% and 70% of the annual carbon uptake occurred outside the 'growing season' (defined as bud break to senescence, ~ days 125–275) in 1996 and 1997. On a daily basis in summer, net ecosystem productivity (NEP) was low when D and soil water deficits were large. Whole ecosystem water vapour fluxes (LE) increased from spring to summer (1.0–1.9 mm d⁻¹) as conducting leaf area increased by 30% and as evaporative demand increased, while evaporation from the soil surface became a smaller portion of total LE as soil water deficits increased. The models underestimated soil evaporation, particularly following rain. In the SPA model, varying the temperature optimum for photosynthesis seasonally resulted in overestimation of carbon uptake in winter and spring, showing that in coniferous forests, assumptions about temperature optima are clearly important. Daily estimates of soil surface CO₂ flux from measurements and site meteorological data demonstrated that modelling of soil CO₂ flux based on an Arrhenius-type equation in CANPOND overestimated CO₂ respired from the soil during drought and when temperatures were low.

Keywords: biogeochemistry, carbon exchange, evaporation, latent heat exchange, micro-meteorology, models, net ecosystem production, physiological ecology, transpiration

Received 23 May 1999; resubmitted 11 November and accepted 15 December 1999

Introduction

Explaining vegetation–atmosphere interactions in the context of global change is a challenging task that requires a combination of long-term terrestrial ecosystem

measurements of carbon, energy and water exchange and process-based models to scale estimates to landscapes and regions.

We conducted our studies in an old-growth pine forest located in a semiarid region where environmental factors strongly limit ecosystem processes. Ponderosa pine

Correspondence: B. E. Law, tel +1/541-737-6111, fax +1/541-737-2540, e-mail lawb@fsl.orst.edu

(*Pinus ponderosa*) is a wide-ranging species in western North America (Elias 1980). These forests exist in continental and montane habitats subject to considerable seasonal variation in climate; they are typically exposed to freezing winter temperatures, low annual precipitation (<600 mm, Franklin & Dyrness 1979), and large soil water deficits and vapour pressure deficits (D) during the summer growing season. Low-elevation coniferous forests in the Pacific North-west differ from most northern temperate conifers in that these forests do not experience winter dormancy and are capable of carbon uptake when temperatures rise above freezing (Havranek & Tranquillini 1995). Because of the summer drought conditions, most carbon gain in these systems has been thought to occur outside of the typical 'growing season', defined as bud break to senescence (Emmingham & Waring 1977). In terms of modelling, the ponderosa pine ecosystem is challenging because of these characteristics, coupled with the heterogeneous open canopy.

In this paper, we used two process-orientated models of vegetation-atmosphere interactions—SPA and CANPOND—to explain controls on ecosystem processes. These models have been validated previously with eddy covariance data in temperate deciduous forests (Baldocchi & Harley 1995; Williams *et al.* 1996; Baldocchi 1997; Williams *et al.* 1997). We parameterized the models with measurements made at the ponderosa pine site, and operated them over two years of contrasting climatic conditions. This is the first study on an extensive forest type in the Pacific North-west that combines multiple years of measurements of whole ecosystem fluxes and component fluxes (e.g. soil-surface CO₂ flux, soil evaporation), and fine-scale process modelling to understand ecosystem function. Few studies have tested and calibrated fine-scale process models over multiple years, which allows evaluation under changing climatic patterns. With this approach, we evaluated the dynamics of photosynthetic capacity, and the influence of factors such as moisture deficits on canopy and soil processes. We also investigated the amount of detail and complexity required to simulate these systems effectively.

Materials and methods

Study site

Hourly measurements of carbon and water vapour fluxes of a ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) forest were compared with model results over 1996 and 1997. The Metolius site is located in a Research Natural Area (44°30'N, 121°37'W, elevation 940 m) on the east side of the Cascade Mountains near Sisters, Oregon.

The stand consists of old (~250 y), young (~45 y) and mixed-age patches of ponderosa pine. The dominant trees have a mean height of 33 m, and the canopy is relatively open (LAI < 2). The understorey vegetation is sparse with patches of bitterbrush (*Purshia tridentata*) and bracken fern (*Pteridium aquilinum*), and a groundcover of strawberry (*Fragaria vesca*). The sandy loam soils are low in nutrients. Soil texture analysis indicates the soil is 73% sand, 21% silt, and 6% clay. The site experiences warm, dry summers and wet, cool winters with intermittent snow cover.

Environmental measurements

We made continuous eddy covariance measurements to determine half-hourly fluxes of CO₂ and water vapour above the forest canopy (47 m height, 14 m above the canopy) in 1996 and 1997, and below the canopy (2 m height) periodically over the two years. Above-canopy wind speed and temperature were measured with a three-dimensional sonic anemometer (Solent model 1012 R2, Gill instruments, Lymington, England), and above- and below-canopy water vapour and CO₂ fluctuations were measured with open-path infrared gas analysers (NOAA ATDD, Oak Ridge, TN) that respond to frequencies up to 15 Hz. In July 1996 (days 187–205), wind velocity and virtual temperature fluctuations were measured at 2 m height with a three-dimensional sonic anemometer (Solent 1012 R2, Gill Instruments, Lymington, England), and in March, May and August 1997 (days 78–89, 129–151 and 220–234), we used a Campbell Scientific three-dimensional sonic anemometer (Model CSAT-3, Campbell Scientific Inc., Logan, UT). Full details of the instrumentation and flux corrections are reported in Law *et al.* (1999a, 1999b) and Anthoni *et al.* (1999).

The CO₂ and water vapour fluxes were corrected for density fluctuations arising from variations in temperature and humidity (Webb *et al.* 1980) and for influences of horizontal wind speed on virtual temperature (Schotanus *et al.* 1983). The data were screened to remove possible eddy covariance instrumentation and sampling problems (Law *et al.* 1999a). Fluxes were also rejected when inconsistently large CO₂ fluxes were observed. After screening, about 75% of the above-canopy carbon flux and 85% of the water vapour fluxes remained available for further analysis. Data gaps were filled based on an empirical relationship with environmental variables where Michaelis–Menten model parameters were determined seasonally from valid flux data from surrounding days (Anthoni *et al.* 1999; appendix A). During turbulent conditions, the change in CO₂ storage, determined from profile measurements in the canopy airspace (1, 4, 31, 46 m), was combined with above-canopy flux measure-

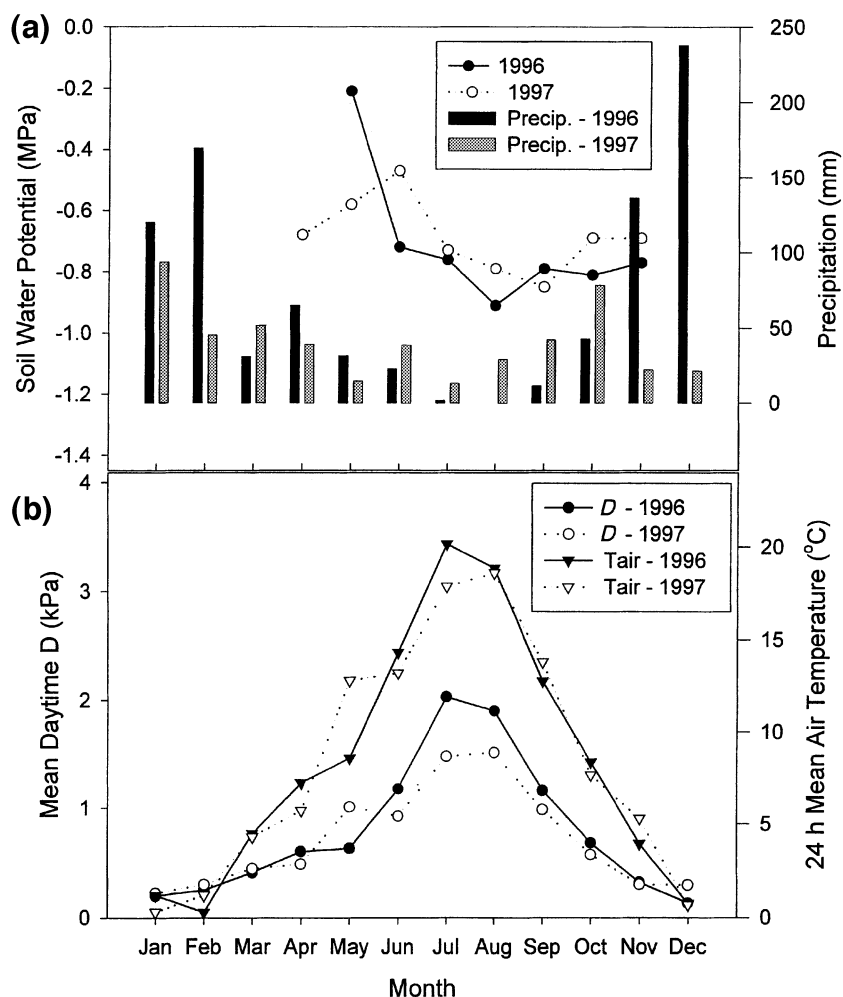


Fig. 1 (a) Mean soil water potential in 1996 and 1997, calculated from predawn leaf water potential by accounting for gravitational effects, and monthly summed precipitation; (b) Mean daytime vapour pressure deficit (D) and 24 h mean air temperature (T_{air}).

ments to estimate NEP. Calm periods lead to accumulation of CO_2 in the area and to a large change in storage in the early morning hours. During those conditions the carbon exchange was modelled from functional relationships with radiation and D when more turbulent conditions existed (Anthoni *et al.* 1999). We have used these procedures for consistency among our studies involving flux data and model evaluation.

Meteorological variables were calculated as half-hourly averages from measurements made at the top of the tower (air temperature, vapour pressure deficit, precipitation, diffuse and direct photosynthetically active radiation (PAR), global solar radiation, net radiation). Half-hourly measurements of soil temperature (15 cm depth) were made with thermocouple probes at 18 locations, and a profile of soil temperature was measured continuously near the tower. Sapwood temperature was measured half-hourly on six trees for estimating sapwood respiration. Soil moisture was measured at 0–30 cm and 0–100 cm depths in several locations using automated and manual time domain reflectometry (Campbell

Scientific, Logan, UT; Tektronix, Beaverton, OR). Seasonal weather data are summarized in Fig. 1.

Ecological measurements

We made several physiological and soil measurements periodically through the year for model input parameters, and to evaluate components of whole ecosystem fluxes. We measured assimilation rates in relation to leaf internal CO_2 repeatedly ($A-C_i$ curves; Law *et al.* 1999a), in order to provide the models with estimates of maximum carboxylation rates (V_{cmax}). Other periodic gas exchange measurements included (i) photosynthetic light response for calculating apparent quantum efficiency for CANPOND; and (ii) foliage and stem respiration, and soil surface CO_2 fluxes for estimating hourly ecosystem respiration (R_e) from meteorological data (Law *et al.* 1999a). Foliage samples were collected from the canopy profile seasonally for total nitrogen content to parameterize the models.

Table 1 Comparison of general features of the SPA and CANPOND models.

	CANPOND	SPA
Temporal resolution	Half-hourly	Half-hourly
NEP calculated as	GEP – R_e	GEP – R_{foliage} – (chamber $R_{\text{soil}} + R_{\text{wood}}$)
Influenced by	GEP = $f(\text{LAI}, V_{\text{cmax}}, J_{\text{max}}, \text{CO}_2, T)$ $R_{\text{soil}}, R_{\text{wood}} = f(T)$ $R_{\text{foliage}} = f(T, V_{\text{cmax}})$	GEP = $f(\text{LAI}, \text{foliar N}, V_{\text{cmax}}, J_{\text{max}}, \text{CO}_2, T)$ $R_{\text{foliage}} = f(T, \text{foliar N})$
Strategy	Farquhar model of leaf-level photosynthesis linked with Ball–Berry stomatal conductance models; biochemical model coupled with turbulent and radiative transfer models; integrated over multiple canopy layers	Farquhar model of leaf-level photosynthesis and Penman–Monteith equation for leaf-level transpiration linked with stomatal conductance (g_s) model that optimizes daily carbon (C) gain per unit leaf N; hydraulic resistances for each of 10 canopy layers determine limitations to water transport
Key reference	Baldocchi & Meyers (1998)	Williams <i>et al.</i> (1996)

To identify the onset of water stress, we measured predawn leaf water potential bi-weekly to monthly through the growing season. We scaled data to ground level (to account for gravitational effects) for estimates of soil water potential (Ψ_s , Fig. 1). Daily estimates of soil water potential for input to SPA were derived from interpolation between measurement dates. Tree height, height-to-base-of-live-crown, diameter, sapwood radius and wood increment were determined at 45 plots (8 m radius) across the site, and on a 10 000 m² plot (Law *et al.* 2000a; Law *et al.* 1999a). These data were used to estimate productivity, leaf-area profile, and wood respiration. We also measured the relative water content of sapwood periodically in 1996 to determine the change in sapwood water storage, which can contribute as much as 50% of transpired water (Waring *et al.* 1979).

Leaf-area index (one-sided LAI; m² leaf m⁻² ground) is a critical parameter of many process models. We estimated LAI from optical measurements at 5 m intervals over a 10 000 m² plot with a LAI-2000 Plant Canopy Analyser (PCA; LICOR, Lincoln, NE). We also measured needle clumping within shoot, and clumping at scales larger than shoot (Chen 1996; Law *et al.*, in press) to correct for these effects on LAI. The seasonal change in LAI was calculated from the fractional change in monthly litterfall and the optical estimates of summer maximum LAI. The mean vertical profile of leaf-area density (LAD), used as input to the multilayer models, was calculated from the PCA measurements, canopy geometry and spatial distribution of trees on the plot using a 3-D radiative transfer model (Law *et al.*, in press). Understorey LAI was estimated using the line intercept method within a 1 m × 1 m frame at 13 plot locations (Law *et al.* 1999b). Because most of the understorey was

Fragaria vesca (flat, planophile leaves), LAI was estimated to be the same as the percentage cover.

The soil–plant–atmosphere model (SPA)

Model description. In previous studies, we have developed a model of the soil–plant–atmosphere continuum (SPA) that estimates CO₂ exchange and transpiration rate of plant canopies. Details of model components are described in Williams *et al.* (1996). The model incorporates 10 canopy layers and operates at a 30-minute time-step. This spatial and temporal detail allows the model to resolve the interaction between microclimate and physiology at fine temporal scales for comparisons with flux measurements. A general comparison of the features of SPA and CANPOND is shown in Table 1.

The SPA model employs some well-tested representations of ecophysiological processes, such as the Farquhar model of leaf-level photosynthesis (Farquhar & Von Caemmerer 1982), and the Penman–Monteith equation to determine leaf-level transpiration. These two processes are linked by a unique model of stomatal conductance (g_s) that optimizes daily carbon (C) gain per unit leaf N, within the limitations of canopy water storage and soil-to-canopy water transport. This hydraulic component is a strength that is unique to this model, allowing us to examine in detail the influence of soil moisture constraints and atmospheric conditions on canopy processes in the water-limited forest.

A model assumption is that maximum carboxylation capacity (V_{cmax}) and maximum electron transport rate (J_{max}) are proportional to foliar N concentration. The V_{cmax} is calculated from A/C_i curves with CO₂ concen-

Table 2 Key parameters for the SPA model. Seasonal values encompass the range used to parameterize the model during the specified period. When values were not changed seasonally, they appear in the first column only. V_{cmax} was $37.8 \times \text{foliar N}$, and J_{max} was $49.0 \times \text{foliar N}$.

Description	July 96	March 97	May 97	August 97	Reference
LAI (m ² projected m ⁻² ground)*	1.6	1.1	1.1	1.6–1.8	Law <i>et al.</i> (in press)
Canopy height (m)	9–33				Law <i>et al.</i> (1999a)
Foliar N (g m ⁻² leaf area)	4.3	4.0 to 4.1	4.3	4.2–4.3	This study
V_{cmax} (μmol CO ₂ m ⁻² s ⁻¹)**	163	151–155	163	159–163	This study
J_{max} (μmol m ⁻² s ⁻¹)**	210	196–201	210	206–210	This study
Leaf specific hydraulic conductivity (mmol m ⁻¹ s ⁻¹ MPa ⁻¹)	20.0				Williams <i>et al.</i> (1996)
Minimum sustainable leaf water potential (MPa)	-2.25	-2.25	-2.25	-2.25	This study
Soil water potential (MPa)	-0.72 to -0.79	-0.25	-0.35 to -0.47	-0.75 to -0.82	This study
Soil-root hydraulic conductance (mmol m ⁻² s ⁻¹ MPa ⁻¹)	25.0				Williams <i>et al.</i> (1996)

*LAI includes understorey, which peaked at 0.2 in summer.

** V_{cmax} and J_{max} were calculated from the summer maximum A/C_i curves, adjusting the values to the concentration at the carboxylation site.

trations adjusted to concentration at the carboxylation site. This calculation of V_{cmax} is different from that in CANPOND.

We modified the model to introduce a radiation subroutine that calculates sun-lit and shaded fractions of the foliage in each canopy layer (Norman & Hesketh 1980). Sun-lit fractions receive both incident direct and diffuse radiation, while the shaded fractions receive only diffuse radiation. For each layer, the model calculates gas exchange separately for the sun-lit and shaded fractions, then sums the two values to give a prediction for the whole layer. The SPA model does not transport heat and mass between the soil and canopy layers in this implementation.

Soil evaporation is predicted as a function of D measured at 1 m, and an estimate of soil resistance, based on the hourly variation in the thickness of the dry surface soil layer (l_d) (Choudhury & Monteith 1988). After rain, l_d is reduced to 0.0001 m (at this point the resistance to soil water flux is minimized). At each time-step, the thickness of soil from which evaporated water is drawn (assuming water content of $0.5 \text{ m}^3 \text{ m}^{-3}$ soil) is calculated and l_d increased accordingly. This increases the resistance to further water fluxes. Based on parameters provided by Choudhury & Monteith (1988), soil porosity was set at 0.4 and tortuosity at 2.0.

The SPA model has been applied and validated in arctic, temperate, montane and tropical ecosystems (Williams *et al.* 1996; Williams *et al.* 1997; Williams *et al.* 1998). These studies indicate that relatively simple site descriptions of canopy features, plant and soil hydraulic parameters, and atmospheric and soil conditions can

describe the majority of the variability in CO₂ and LE fluxes in terrestrial ecosystems. In a sense, they demonstrate how well bioenergetics and mass conservation can be used to describe biological functioning, with a minimum of plant variables.

Model parameters and driving variables. In our initial model application, we started from a standard parameterization developed at Harvard Forest, MA, for a mixed *Quercus*–*Acer* stand (Williams *et al.* 1996). The changes we made to model parameters were governed by the availability of site-specific data (Table 2). These included a threshold leaf water potential value for cavitation (–2.25 MPa, our minimum measured mid-day leaf water potential), bi-weekly to monthly Ψ_s and estimates of total root length. Daily LAI, foliar N and soil water potential were derived from interpolation or curves fitted to measurements. The seasonal leaf N contents ranged from 3.8 to 4.3 g m⁻² leaf area. The summer maximum V_{cmax} , adjusted to concentration at the carboxylation site (Williams *et al.* 1996), was $56.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. J_{max} and V_{cmax} were derived from fitting the Farquhar model to $A-C_i$ curves for our site. The temperature response functions for photosynthesis were held constant throughout the year using the same parameters applied in a deciduous forest (Williams *et al.* 1996). We assumed that photosynthetic rates peak between 20° and 25 °C, while the rate at 10 °C was ~85% of the maximum rate. Foliar dark respiration for the Farquhar model was calculated from foliar N as $0.0825 \mu\text{mol C g}^{-1} \text{ N s}^{-1}$ at 10 °C, with a temperature response defined by a Q_{10} of 2.0 (Reich *et al.* 1998). For radiation computations, leaf reflectance (0.05 PAR, 0.35

Table 3 Key parameters for the CANPOND model.

Description	Value	Reference
Latitude	44°29'N	Law <i>et al.</i> (1999a)
Longitude	121°37'W	Law <i>et al.</i> (1999a)
Maximum LAI (m ² projected m ⁻² ground)*	1.8	Law <i>et al.</i> (1999a)
Canopy height (m)	34	Law <i>et al.</i> (1999a)
V_{cmax} at 25°C (μmol m ⁻² s ⁻¹)	73	This study, Middleton <i>et al.</i> (1998), Sullivan <i>et al.</i> (1997)
J_{max} (μmol m ⁻² s ⁻¹)	170	Middleton <i>et al.</i> (1998), Sullivan <i>et al.</i> (1997)
Ball–Berry constant, k	8.0	Harley & Baldocchi (1995)
Apparent quantum yield (mol CO ₂ (mol quanta) ⁻¹)	0.04	Law <i>et al.</i> (1999b)
Shoot clumping factor, Ω	0.83	Law <i>et al.</i> (in press)
Needle clumping within shoot, γ	1.29	Law <i>et al.</i> (in press)
Soil surface CO ₂ flux at 25°C (μmol m ⁻² s ⁻¹)	3.9	Law <i>et al.</i> (1999b)
Q_{10} for foliage respiration	2.0	Harley & Baldocchi (1995)
Q_{10} for sapwood respiration	2.02	Harley & Baldocchi (1995)
Base temperature for photosynthesis, T_b (K)	311	Collatz <i>et al.</i> (1991)
Activation energy, E_a for CO ₂ (J mol ⁻¹)	65, 120	Lloyd & Taylor (1994)
Soil resistance to evaporation (s m ⁻¹)	816	Camillo & Gurney (1986)

*LAI was varied seasonally, as in SPA.

NIR) and soil reflectance (0.05 PAR, 0.12 NIR) were estimated from spectral reflectance data for a nearby ponderosa pine site (Goward *et al.* 1994) and transmittance values were taken from the literature (Norman 1979). Radiation absorption by the canopy was determined from Beer's Law with an assumed extinction coefficient of 0.5. The canopy wind profile is generated from measurements of windspeed above the canopy, and an exponential relationship is used to calculate wind attenuation within the canopy, which influences leaf temperature and gas exchange rates (exponent was set to 4, as in Williams *et al.* 1996). SPA assumes that the air within the canopy is well mixed with the atmosphere, and so turbulent transport is not simulated. In each canopy layer, we use a steady-state approximation to determine leaf temperature, based on radiation, latent heat and sensible heat exchange. We generated hourly driving variables for the model from the site meteorological data.

The CANPOND model

Model description. CANPOND is a 1-D multilayer biosphere–atmosphere gas exchange model that computes water vapour and CO₂ flux densities (Table 1). There are 30 canopy layers and 10 soil layers. Model details are described in Baldocchi & Meyers (1998). The micro-meteorological module computes leaf and soil energy exchange, turbulent transfer, carbon and water vapour profiles and radiative transfer through the canopy. Environmental variables, in turn, drive the physiological modules that compute leaf photosynthesis, stomatal

conductance, transpiration, and respiration by foliage and woody tissue, and soil CO₂ flux (respiration by roots and microbes). The strengths unique to this model are the coupled turbulent transfer and radiative transfer features and how they interact to influence CO₂ and water vapour exchange.

The radiative transfer computations provide probabilities of sun-lit and shaded leaves for calculations of photosynthesis, leaf energy balance, and turbulent transfer of CO₂, water vapour and sensible heat. Stomatal conductance is calculated as a function of assimilation, relative humidity, and CO₂ concentration at the leaf surface (Collatz *et al.* 1991). The model assumes a horizontally homogeneous canopy and temporally steady environmental conditions, allowing the conservation equation for CO₂ or water vapour to be expressed as the equality between the change in concentration with height and the diffusive source/sink strength. The diffusive source strength is modelled from leaf area density with respect to height, concentration difference between the air outside the laminar boundary layer of leaves and within stomata, boundary layer resistance to molecular diffusion, stomatal resistance and air density. The change in concentration summed over the canopy layers is combined with soil fluxes and bole respiration to estimate whole ecosystem NEP and LE fluxes with an hourly time-step.

Soil CO₂ flux rates are computed with an Arrhenius equation (eqn 10 in Hanson *et al.* 1993; Lloyd & Taylor 1994), using chamber measurements of a mean base flux rate of 3.9 μmol m⁻² s⁻¹ at 25°C (Law *et al.* 1999a, 1999b). Flux densities of conductive and convective heat transfer and evaporation at the soil/litter boundary and soil

temperature profiles were computed with a 10-layer soil heat transfer model (Campbell 1985). Surface energy fluxes were computed using an analytical solution to a surface's energy balance. Soil evaporation was computed with an algorithm from Mahfouf & Noilhan (1991):

$$E_s = \frac{\rho}{R_{\text{soil}}} (\varphi \cdot q_{\text{sat}}(T) - q_a), \quad (1)$$

where R_{soil} is the resistance of soil to evaporation, ρ is air density, φ is relative humidity of the soil matrix, q_a is the water vapour mixing ratio of air, T is soil temperature, and q_{sat} is the saturated mixing ratio (Baldocchi & Meyers 1998).

The model has been tested with eddy covariance data in a temperate broadleaf forest (Baldocchi 1997), boreal coniferous forests (Baldocchi & Vogel 1996), and with below-canopy energy fluxes measured at our pine site and a boreal coniferous site (Baldocchi *et al.* 1999). These studies indicated that the model provided accurate estimates of whole ecosystem LE and NEP when water was not limiting, but during drought conditions, a cumulative drought index adjustment to stomatal conductance coefficients improved estimates of LE in the afternoon. The below-canopy studies indicated that the model provided accurate estimates of energy fluxes above the forest floor, an encouraging finding because soils play a major role in the energy fluxes of this open-canopy forest (Baldocchi *et al.*, in press).

Model parameters and driving variables. The CANPOND model was parameterized with plant structural variables (LAI, leaf angle orientation, an index of spatial distribution, and canopy height) and leaf function (V_{cmax} and J_{max} parameters of the Farquhar photosynthesis model) derived from physiological data acquired at this site (Table 3). V_{cmax} , computed from the site A/C_i curves as a function of temperature (Baldocchi & Meyers 1998), was $73 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 25°C . The apparent quantum yield ($0.04 \text{ mol CO}_2 (\text{mol quanta})^{-1}$) was estimated from our light response curves. The key parameters for modelling plant functioning with CANPOND are seasonal LAI, and V_{cmax} . Other model parameters are scaled to these values or they represent the vegetation functional type (e.g. canopy height, roughness length, zero plane displacement). To initialize the model with a minimum of site parameters, the Q_{10} for foliage respiration, R_d , was maintained at 2.0 from a previous parameterization (Harley & Baldocchi 1995), close to the value of 2.1 measured at the site (Law *et al.* 1999a). Similarly, the Q_{10} for sapwood respiration was maintained at 2.02, whereas the measured value was 2.2.

For aerodynamic calculations, the roughness length was set at 13.3% of canopy height and zero plane displacement was assumed to be 65% of canopy height

(Pereira & Shaw 1980). As in the SPA model, an exponential relation was used to calculate wind speed within the canopy, and the attenuation coefficient was set at 2.6, a reasonable assumption for open-canopy forests with leaf area indices less than two (Pereira & Shaw 1980). Environmental driving variables include incident PAR, air and soil temperature, wind speed, relative humidity and CO_2 concentration.

For radiative transfer computations, the Markov clumping factor for this forest ($\Omega=0.83$) and needle clumping within shoot ($\gamma=1.29$) were derived from our field measurements (Law *et al.*, in press). As in the SPA model, we used leaf and soil reflectance and transmittance values from spectral data at a nearby ponderosa pine site (Goward *et al.* 1994). The resistance to soil evaporation for calculations (eqn 2) was assumed 816 s m^{-1} for dry soil and 232 for wet sandy soil following rain (Camillo & Gurney 1986).

Model analysis. Because eddy covariance data were incomplete through both years, we compared estimates of daily NEP, GEP, and LE using days with less than 25% of the flux data missing, following screening, to minimize the effect of using filled data. We removed days when rain occurred between 21.00 hours on the previous day and 21.00 hours of the day of rain because of the effects on the flux instruments. The atmosphere is inherently turbulent, and one-hour eddy fluxes have sampling errors ranging from 15 to 40% (Vickers & Mahrt 1997). Although both models operate on a half-hourly time-step, we chose to compare model estimates with flux data on a daily basis (Baldocchi *et al.* 1988; Anthoni *et al.* 1999). Models are ensemble representations, so it is reasonable to compare model results with daily sums of eddy flux data. We evaluated model performance across seasons by comparing modelled and measured daily NEP, GEP and LE within 3-month periods (Jan–Mar, Apr–Jun, Jul–Sep, Oct–Dec) using regression analysis.

We capitalized on model strengths by testing hypotheses using robust features of both models. The coupling of turbulent transfer, radiative transfer and biochemistry are unique to CANPOND, while SPA has strong hydraulic features. We used both models to test hypotheses about canopy carbon uptake and transpiration in relation to the influences of water availability and D . CANPOND calculates NEP, GEP, and R_e directly, whereas we combined chamber estimates of respiration with SPA GEP to predict NEP. The two are related by:

$$\text{GEP} = \text{NEP} - R_e, \quad (2)$$

where R_e is total ecosystem respiration. Because nocturnal eddy covariance measurements were often limited by low turbulence conditions, we replaced all nocturnal flux

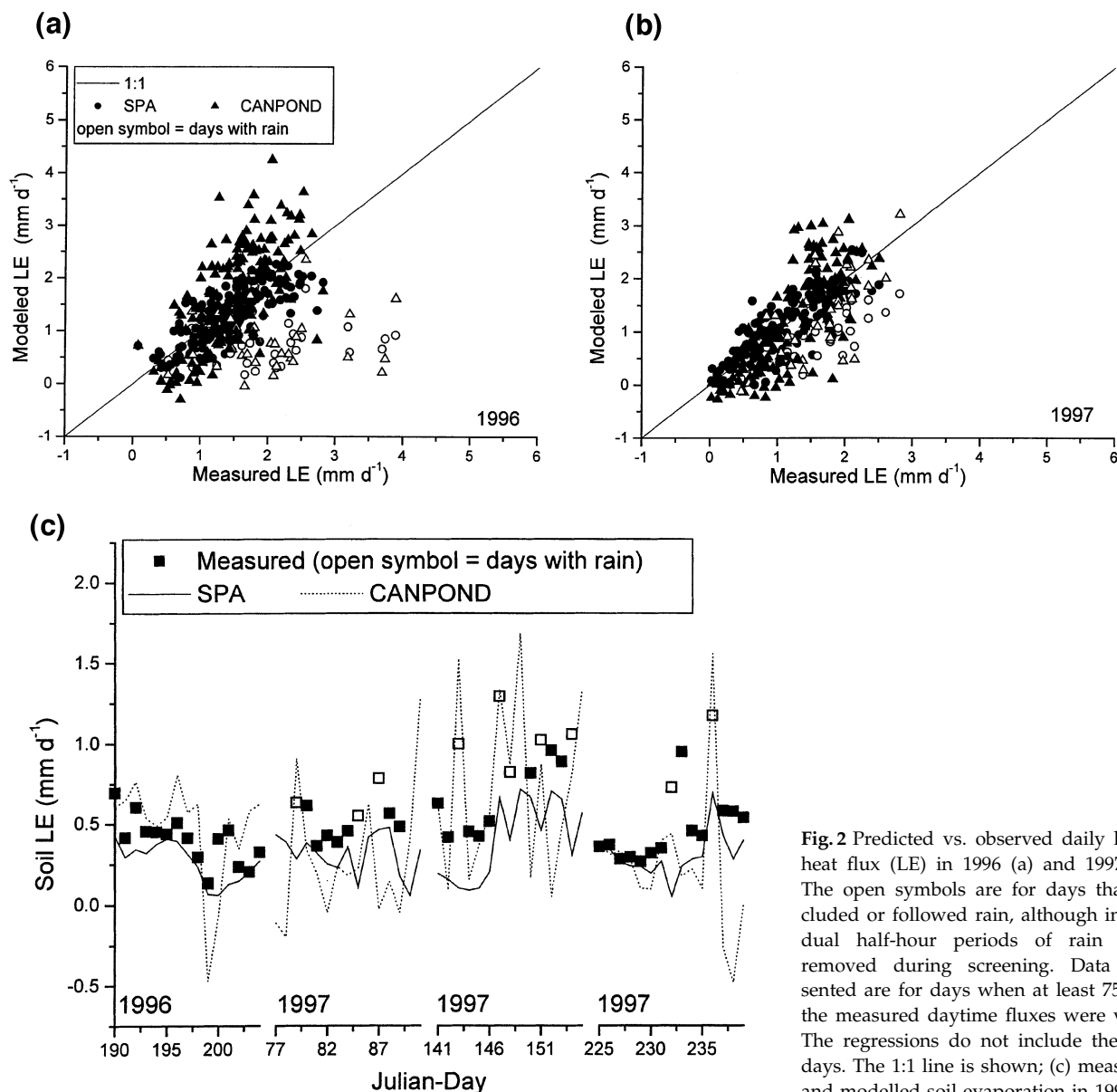


Fig. 2 Predicted vs. observed daily latent heat flux (LE) in 1996 (a) and 1997 (b). The open symbols are for days that included or followed rain, although individual half-hour periods of rain were removed during screening. Data presented are for days when at least 75% of the measured daytime fluxes were valid. The regressions do not include the rain days. The 1:1 line is shown; (c) measured and modelled soil evaporation in 1997.

data with hourly chamber estimates of R_c . The chamber estimates were from measurements of foliage, soil and woody tissue respiration periodically through 1996–97, which were scaled to the site using interpolation of measurements that had been normalized to a common temperature, and temperature response equations developed on-site (Law *et al.* 1999a). Therefore, the comparisons of 24-h NEP include respiration estimates from chambers in both the nocturnal flux data and the SPA model estimates of NEP.

Sensitivity to seasonal change in the temperature optimum for photosynthesis. The temperature optimum (T_{opt}) for

photosynthesis may be lower in spring than in summer (i.e. high rates of photosynthesis may occur at temperatures under 10°C), but cold soil temperatures (daily mean $<5^\circ\text{C}$) may limit water uptake, stomatal conductance, and thus carbon uptake by the trees (DeLucia 1986; Day *et al.* 1991; Sperry 1993; Kramer & Boyer 1995). Plant resistance to water flow in *Pinus contorta* and *Picea engelmannii* seedlings increased abruptly at soil temperatures $\sim 7^\circ\text{C}$, nearly doubling as soil temperature fell from 12 to 7°C (Running & Reid 1980; Kaufmann 1975). Using SPA, we compared model output assuming a constant T_{opt} through the year with output assuming an optimum that we varied seasonally. The variable T_{opt} (between 15

Table 4 Regression coefficients for predicted versus observed daily gross ecosystem production (GEP), net ecosystem production (NEP), and latent heat flux (LE) for 1996 and 1997. Rain days were not included in the comparisons. The intercept is *a*, the slope is *b*, and RMSE is the root mean-square error. The standard error (SE) and *P*-value are for the comparison of the slope to 1 and intercept to 0. * indicates statistical significance.

Variable	<i>a</i>	SE	<i>P</i>	<i>b</i>	SE	<i>P</i>	<i>r</i> ²	RMSE
SPA								
GEP 1996	1.95	0.23	0.00*	0.54	0.05	0.00*	0.46	0.63
GEP 1997	1.29	0.19	0.00*	0.67	0.04	0.00*	0.65	0.75
NEP 1996	0.37	0.09	0.00*	0.63	0.06	0.00*	0.49	0.69
NEP 1997	0.47	0.09	0.00*	0.45	0.07	0.00*	0.28	0.72
LE 1996	0.27	0.07	0.00*	0.72	0.05	0.00*	0.60	0.32
LE 1997	0.21	0.06	0.00*	0.83	0.05	0.00*	0.69	0.33
LE _b 1996	0.12	0.05	0.04	0.44	0.11	0.00*	0.54	0.07
LE _b 1997	0.09	0.05	0.11	0.48	0.09	0.00*	0.43	0.12
CANPOND								
GEP 1996	-0.03	0.41	0.94	1.07	0.09	0.46	0.51	1.12
GEP 1997	0.46	0.40	0.25	0.89	0.09	0.25	0.44	1.55
NEP 1996	0.10	0.11	0.37	0.54	0.07	0.00*	0.30	0.89
NEP 1997	1.02	0.14	0.00*	-0.17	0.10	0.00*	0.02	1.09
LE 1996	-0.12	0.16	0.46	1.23	0.10	0.02	0.49	0.70
LE 1997	-0.30	0.11	0.01*	1.27	0.09	0.00*	0.61	0.60
LE _b 1996	0.37	0.08	0.00*	0.57	0.17	0.03	0.43	0.11
LE _b 1997	0.18	0.13	0.16	0.17	0.22	0.00*	0.02	0.28

and 30 °C) was calculated from the mean maximum temperature of the preceding two weeks. Thus, the optimum changed daily, but it was dampened.

The influence of drought and D. We compared model output from SPA using the interpolated soil water potential measurements with output when we assumed that there were no drought constraints on carbon uptake. In simulating no drought constraints, we ran SPA with soil water potential set to -0.01 MPa every day. We also evaluated measured and modelled NEP and LE as a function of *D* in summer, and GEP in relation to LE.

Results and discussion

The climate of the two years was markedly different, which gave us the unique opportunity to evaluate model results for contrasting environmental conditions at the same site. Total precipitation was 867 mm in 1996, a wetter than normal year, and it was 488 mm in 1997. Only 13 mm of rain fell in Jul to Sep 1996, but precipitation was more evenly distributed through 1997, with 84 mm occurring in Jul to Sep (Fig. 1). The maximum daily air temperatures, daily *D*, and incident radiation in summer 1997 were lower, with more frequent cloud cover, than in 1996. Sub-freezing air temperatures (<-2 °C) occurred on 24 and 30 days in 1996 and 1997.

Over the course of the year in 1996, sapwood relative water content (RWC) decreased from 90% in the autumn of 1995 when recharge of sapwood occurs with rainfall, to its lowest point of 56% the following summer when evaporative demand was high. The RWC decreased by 22% over a two-week period in July. Similar seasonal patterns in sapwood water storage and *D* were observed in 500-y-old *Pseudotsuga menziesii* in Oregon (Waring & Running 1978). When RWC changed from day-to-day, the sapwood probably supplied a large portion of transpired water. Thus, stem capacitance, a component of the SPA model's hydraulic system, may be more critical in the application of the model to forests subject to summer drought.

Seasonal LAI is an important model variable when comparing predictions with flux measurements across seasons. We found that LAI peaked in mid-August (1.8 ± 0.2 , including understorey LAI of 0.2), about 90 days later than the maximum foliar N content was reached ($4.3 \pm 0.15 \text{ g m}^{-2}$).

Carbon uptake occurred during the winter months, though it was low (averaged $1 \text{ g C m}^{-2} \text{ d}^{-1}$). Maximum GEP ($6\text{--}7 \text{ g C m}^{-2} \text{ d}^{-1}$) was reached in Jun 1996 and May 1997, when *D* was relatively low, soil water was still plentiful, and the highest maximum assimilation rates per unit leaf area were measured (e.g. $21 \mu\text{mol m}^{-2} \text{ leaf s}^{-1}$). GEP remained fairly constant or decreased through summer as soil water deficits increased, and then declined in October as the days shortened and

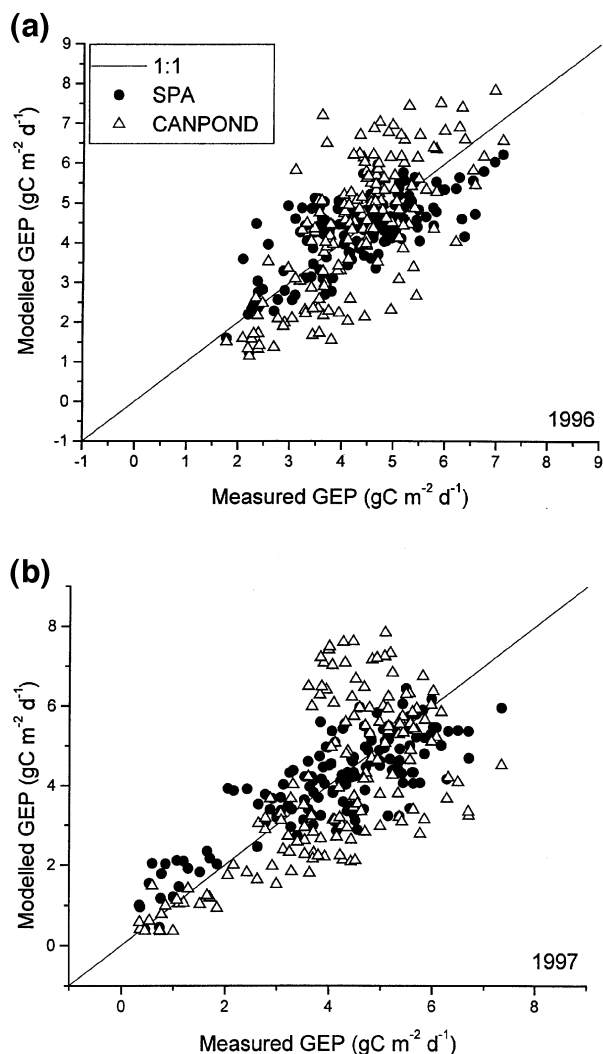


Fig. 3 Predicted vs. observed daily gross ecosystem productivity (GEP) in 1996 (a) and 1997 (b). The 1:1 line is shown.

minimum LAI and canopy N were reached. Maximum monthly NEP ($48\text{--}50\text{ g C m}^{-2}$) also occurred in Jun 1996 and May 1997, when temperatures were moderate, water was not limiting, and respiration rates were not as high as in summer. Approximately 50% and 70% of annual NEP occurred outside the typical 'growing season' (bud break to senescence, \sim days 125–275) in 1996 and 1997, confirming expectations from leaf-level measurements on conifers in the Pacific North-west. Leaf gas exchange measurements showed photosynthesis at temperatures near freezing, and reduced photosynthesis in summer with increased D and water stress, as observed in other leaf-level studies on conifers in the Pacific North-west (Law & Waring 1994). In mid-summer, large D and increasing soil water deficits ensured that maximum rates of carbon uptake occurred earlier in the morning, with increased respiration and reduced NEP by mid-day.

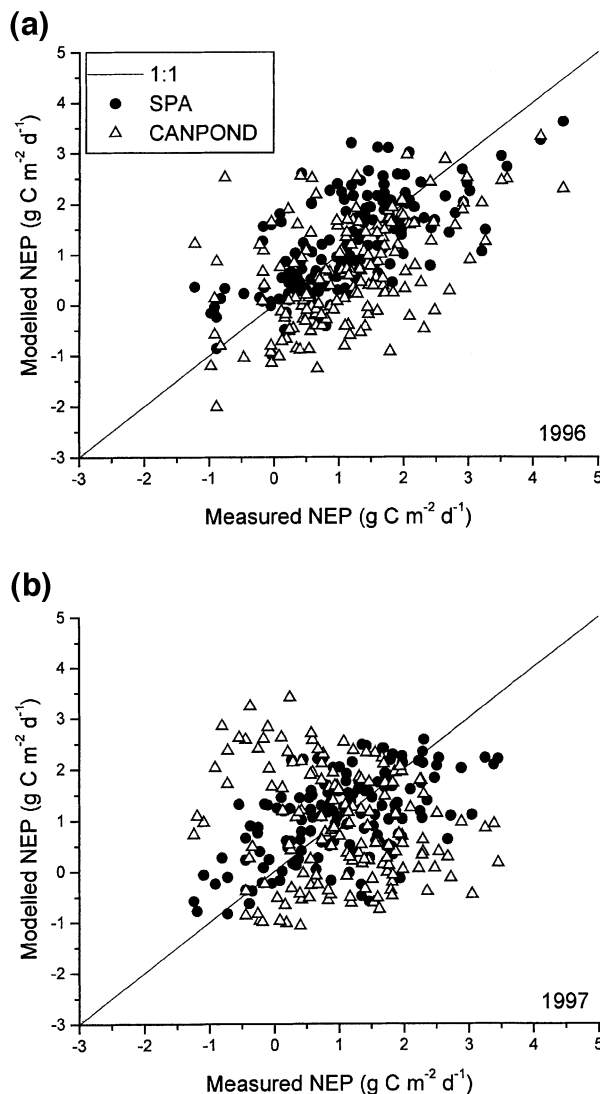


Fig. 4 Predicted vs. observed daily net ecosystem productivity (NEP) in 1996 (a) and 1997 (b). The 1:1 line is shown.

The ecosystem was a net source of CO_2 to the atmosphere in summer 1997, and our chamber data show greater soil fluxes than in summer 1996, suggesting that higher respiration rates occurred with more frequent surface-wetting of soils. Consequently, the combination of photosynthesis during spring and fall when moisture and radiation were high, and proportionately more respiration with higher temperatures and less carbon uptake due to drought that limit NEP in summer appear to result in a large fraction of annual NEP occurring outside the growing season.

Whole ecosystem LE fluxes increased from spring to summer ($1.0\text{--}1.9\text{ mm d}^{-1}$) and averaged 1.8 mm d^{-1} over the growing season. This is slightly less than LE averaged over the growing season in more mesic temperate deciduous forests (2.2 mm d^{-1} ; Wullschlegel *et al.* 1998) and boreal coniferous forests (2 mm d^{-1} ; Jarvis *et al.* 1997).

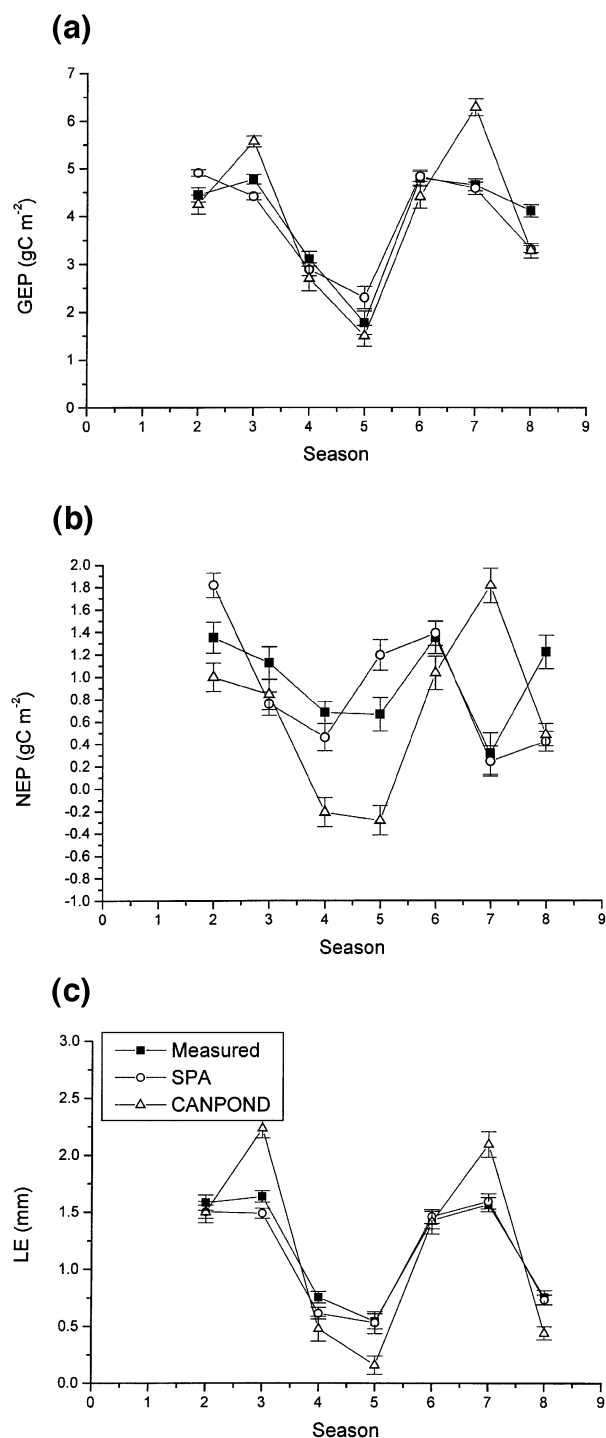


Fig. 5 Means and standard deviations for measured and modelled (a) GEP (b) NEP, and (c) LE for seven three-month periods, where period 1 is Jan–Mar 1996 (missing because of limited data), period 2 is Apr–Jun 1996, and so forth. Means were compared only for days when less than 25% of flux data were filled.

The more open nature of the canopy caused soil evaporation to be a significant component of whole

ecosystem LE. Based on the difference between above- and below-canopy LE measurements, soil evaporation was 44% of LE in early spring, and decreased to 22% and 33% of LE in summer 1996 and 1997. Cool spring temperatures probably limited transpiration when water was plentiful (i.e. atmospheric demand was less than potential rates of supply), and water availability limited soil evaporation in summer while increasing evaporative demand resulted in increased transpiration rates. Thus, in open forest canopies, it is critical to focus modelling efforts on soil contributions to water vapour fluxes. In contrast, errors in model estimates of soil evaporation for a closed-canopy deciduous forest would likely have little impact because values are small and relatively constant year-round (Baldocchi 1997).

Model analysis

First, we compared measurements and models between years using daily data. The modelled and measured LE compared well on days without rain (Fig. 2). Following the rain days, the flux data indicate a higher LE than the models predicted. This could be a result of the difficulty in modelling the rapid change in evaporation that occurs following rain (Mahfouf & Noilhan 1991), which is complicated by the amount of rainfall, and interception by the canopy. The accuracy of flux measurements during and following rain could also be a problem with open-path infrared gas analysers, so we chose to remove rain days from statistical comparisons of modelled and measured variables. SPA explained 60% and 69% of the variation in daily LE in 1996 and 1997, but underestimated LE in both years, and significantly underestimated soil evaporation (Table 4; Fig. 2c). CANPOND estimates of LE compared relatively well with measurements in both years, but there was more variation at high LE values. The model also underestimated soil evaporation (Fig. 2c). Clearly, improved models of soil evaporation are necessary, particularly for applications in open-canopy forests.

Daily total net radiation explained 63% and 64% of the variation in daily LE in 1996 and 1997 with rain days removed, and it explained most of the variation in modelled LE (78% and 84% of the variation in SPA LE; 69% and 78% in CANPOND LE). Solar radiation, air temperature, surface temperature, and humidity influence net radiation. The value of process-orientated models over more empirical modelling based on net radiation is that they are not site-specific, and we can tease out the effects of individual features of climate and soil properties on carbon and water vapour exchange.

There was a reasonable correlation between measured and modelled daily GEP using SPA and CANPOND (Fig. 3, Table 4). In 1996 and 1997, SPA explained 46 and

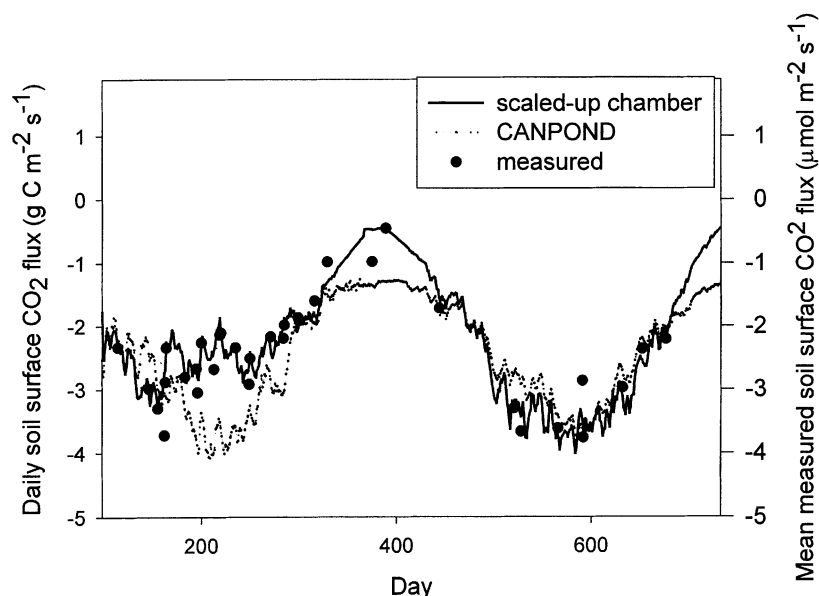


Fig. 6 Soil surface CO₂ flux in 1996 and 1997, compared with modelled soil fluxes from CANPOND. Soil flux measurements were averaged over a day. The scaled-up chamber estimates were developed from a site-specific temperature response equation applied to periodic measurements that had been normalized to a common temperature (Law *et al.* 1999a).

Table 5 Annual climate data, gross (GEP) and net (NEP) ecosystem productivity and water vapor (LE) exchange, ecosystem respiration (R_e), and net primary productivity (NPP) in the *Pinus ponderosa* stand during two years. The summarized climate data are annual incident PAR (Q_o), mean daily air temperature (T_a), soil temperature at 15 cm depth (T_s) from June through September, annual precipitation and the daytime average vapor pressure deficit (D_{av}) during the dry season (June to September). Ecosystem respiration was calculated as the difference between GEP and NEP.

Variable	1996			1997		
	Measured	SPA	CANPOND	Measured	SPA	CANPOND
Q_o (MJ m ⁻²)	2377			2313		
T_a (°C)	8.4			8.5		
T_s (°C)	14.4			14.2		
Jun–Sep Precipitation (mm)	867			488		
D_{av} (kPa)	1.7			1.3		
Jun–Sep GEP (g C m ⁻²)	1208 ± 184	1264	1167	1262 ± 195	1278	1264
NPP (g C m ⁻²)	413			400		
R_e (g C m ⁻²)	885	885	1086	996	996	1077
NEP (g C m ⁻²)	324 ± 168	379	81	266 ± 177	282	187
LE (mm)	436 ± 65	323	361	400 ± 60	346	376
Transpiration		257	301		257	311

65% of the variation in daily GEP [root mean-square error (rmse) = 0.63, 0.75], and CANPOND explained 51 and 44% (rmse = 1.12, 1.55). There was more scatter in predicted vs. observed daily NEP resulting from errors in estimates of the photosynthesis and respiration components (Fig. 4).

Seasonal comparisons. We compared measured and modelled daily carbon and water vapour exchange in three-month periods (Jan–Mar, Apr–Jun, ...) to examine model output in different seasons. Figure 5 shows

comparisons of means for seven three-month periods using only days where flux data were good (<25% filled, excluding Jan to Mar 1996, because of limited data). SPA estimates of GEP were within 10% of the mean measured values ($P > 0.05$), except for winter months, and estimates of NEP were more variable except for spring through summer 1997. It is important to note that SPA NEP includes our scaled-up chamber estimates of respiration.

CANPOND estimates of GEP showed stronger correlations with measurements in the wet season (periods 2 and 4–6). CANPOND estimates of GEP were 12% and

Table 6 Results of sensitivity tests with both models, where key parameter values Tables 1 and 2 were varied independently by $\pm 20\%$. Baseline values of annual GEP and LE are shown. Ψ_s is soil water potential, G_p is leaf specific hydraulic conductivity, R_{soil} is soil resistance to evaporation, and k is the Ball-Berry constant. The models were driven with 1996 climate data only. The percentage changes in annual GEP and LE are shown.

	SPA				CANPOND			
	GEP		LE		GEP		LE	
	+20%	-20%	+20%	-20%	+20%	-20%	+20%	-20%
LAI	7	-8	5	-6	17	-18	12	-14
Foliar N	6	-7	1	-1				
V_{cmax}	0.1	-0.3	0	0.1	18	-17	9	-8
J_{max}	4	-6	1	-1				
Ψ_s	-2	2	-4	4				
G_p	3	-3	6	-7				
R_{soil}					-0.1	0.1	-0.7	-0.6
K					5	-5	15	-15

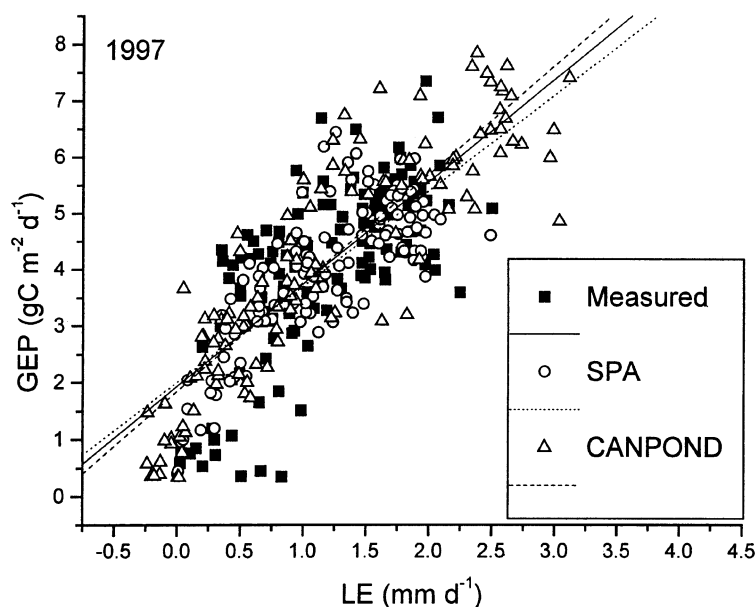


Fig. 7 Daily gross ecosystem productivity (GEP) vs. water vapour flux (LE) in 1996. The slopes were similar (1.8 measured, SPA 1.7, CANPOND 1.9), indicating a strong linkage between carbon uptake and water loss by the ecosystem on a daily basis.

33% greater than the measurement means for Jul to Sep 1996 and 1997 ($P < 0.01$; periods 3 and 7), most likely because the model only considers atmospheric constraints on carbon uptake through the Ball-Berry model. CANPOND also overestimated soil-surface CO_2 fluxes in the dry summer of 1996 and in winter, leading to an underestimation of NEP during these periods, while comparisons with soil CO_2 fluxes were very good in the wetter summer of 1997 (Fig. 6). This shows that the Arrhenius-type soil flux model performs well when water is not limiting and temperatures are not low. The combination of CANPOND overestimating GEP and respiration from soil surfaces during summer droughts also shows the importance of including the limitations of soil water deficits on respiration and gross photosynthesis in models that are applied to water-limited forests. Comparisons between CANPOND NEP and

measurements were generally poor in all seasons ($r^2 = 0.01\text{--}0.40$), underestimating NEP in all seasons except summer 1997 when soil flux estimates were good but GEP estimates were high.

SPA estimates of LE compared well with seasonal means throughout both years (Fig. 5c), with underestimates in Jul. through Dec. 1996. CANPOND estimates of LE were significantly higher than measurement means in Jul. through Sep. in both years (periods 3 and 7), and were significantly lower than measurements through much of the wet season. The Ball-Berry model in CANPOND appears to allow too much transpiration and thus photosynthesis during relatively dry summer growing seasons. Again, this demonstrates the need to include soil water deficits in addition to atmospheric influences in models as constraints on transpiration, evaporation and gross photosynthesis.

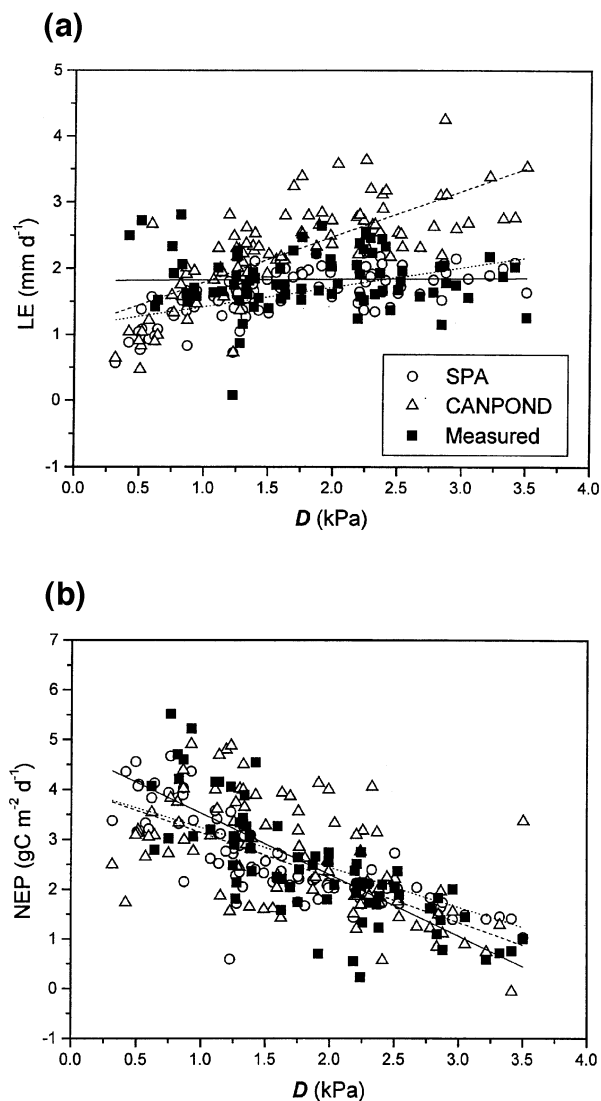


Fig. 8 (a) Measured and modelled daily latent heat flux (LE) vs. mean daylight vapour pressure deficit (D) for days 152–244 in 1996 (Jun–Aug). (b) Measured and modelled daytime net ecosystem productivity (NEP) vs. D . The LE response to higher D is less than proportional.

The model predictions of annual GEP were quite close to measured values, but there was greater disparity between measured and modelled annual NEP as observed in the seasonal data (Table 5). In an earlier study with more generalized models, 3PG and PnET-II, the models performed quite well on an annual basis after doubling the soil water holding capacity and forcing the soil to recharge in the winter (Law *et al.* 2000b). This led us to believe that roots were accessing deep soil water because rainfall alone could not support the observed leaf area, according to the models. The 3PG and PnET-II models include a water balance, which is difficult to

accurately portray in this semiarid ecosystem. The process-based models, SPA and CANPOND, have a strong linkage between carbon and water vapour exchange through leaf metabolic processes, and demonstrate the importance of understanding both atmospheric and soil water limitations to ecosystem processes in drought-prone ecosystems.

Model sensitivity. To determine the importance of key model variables to predictions, we conducted sensitivity tests with SPA and CANPOND by varying input parameters by $\pm 20\%$ (Table 6). We independently varied LAI, foliar N, V_{cmax} , leaf-specific hydraulic conductivity (G_p), and Ψ_s in SPA, and we varied LAI, V_{cmax} , R_{soil} , and the Ball-Berry constant in CANPOND. For both models, predictions of annual GEP and LE were most sensitive to LAI. SPA predictions of annual GEP were also sensitive to foliar N, and LE to changes in G_p (Table 6). CANPOND predictions of annual GEP were also sensitive to V_{cmax} (17–18% change in annual GEP), while LE was most sensitive to the Ball-Berry constant (15% change in annual LE). The results suggest that to predict CO_2 and water vapour exchange seasonally, accurate measurements of seasonal foliar N, seasonal LAI, and G_p for SPA, and seasonal LAI, V_{cmax} and the Ball-Berry constant for CANPOND are necessary.

Environmental controls on ecosystem processes. Measured and modelled water-use efficiency of the forest (GEP/LE) were very similar (Fig. 7), and there was a strong linkage between gross carbon uptake and water loss by the forest. Annual GEP and LE didn't vary much between the two years; GEP:LE increased only $\sim 14\%$ between 1996 and 1997, in spite of the large difference in annual rainfall (Table 4). Root access to deep soil water may be buffering the system from year-to-year (Eissenstat & Van Rees 1994), a focus of on-going studies comparing our young and old pine sites.

Daytime LE was fairly constant across a range of D in Jun to Aug 1996 (Fig. 8a), as found by Baldocchi (1997) in a deciduous forest during summer drought. SPA LE followed the same trend, lending support to the hydraulic limitation theory that stomata adjust to maintain a sustainable flow of water through the soil-plant system. In contrast, CANPOND LE is influenced by relative humidity and thus D through the Ball-Berry model. Figure 8(b) shows daytime NEP vs. mean daylight D for the same period. We limited the comparison to the summer to minimize the effect of large differences in radiation on NEP. Modelled and measured NEP decreased with increasing D , and the slopes were similar. This can be partly explained by the strong influence of temperature on respiration, as well as on D .

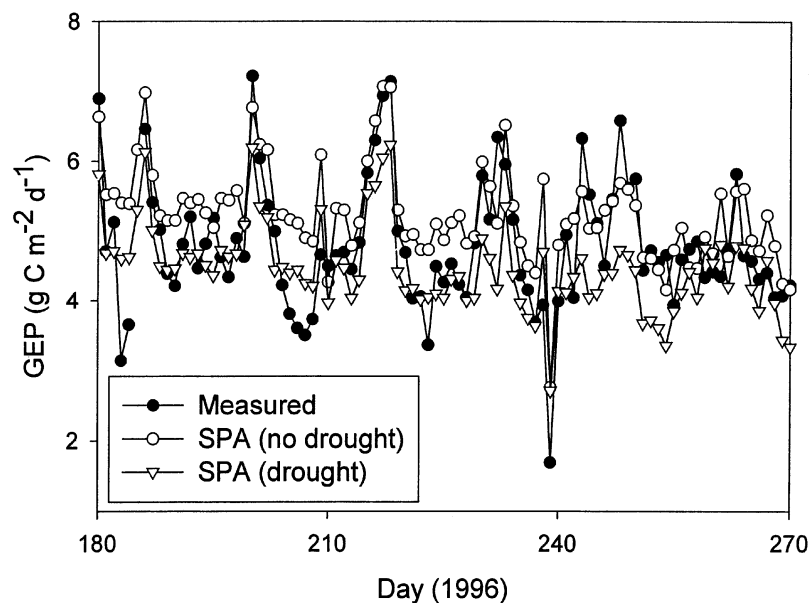


Fig. 9 Daily total GEP with and without drought constraints in SPA. Data are shown for Jul–Sep 1996, when summer drought had occurred. GEP from the ‘no drought’ assumption was 17% higher than when drought was allowed to influence stomatal conductance and carbon uptake.

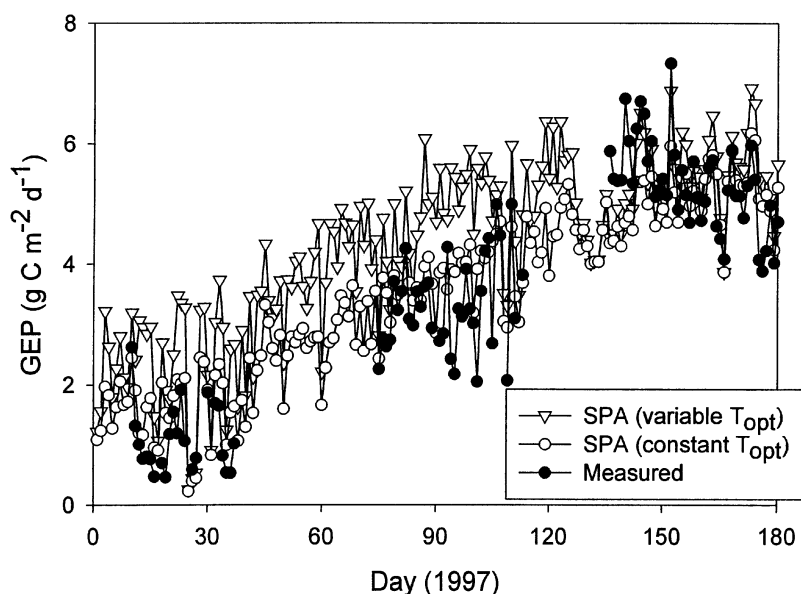


Fig. 10 Daily total GEP with a constant optimum temperature for photosynthesis (T_{opt}) through the year, and changing T_{opt} seasonally as a function of air temperature. Data are shown for Mar to Jun, when GEP from the variable T_{opt} was much higher than measurements and the model output from a constant T_{opt} . Modelled GEP converged in the summer months.

When we assumed no drought constraints using SPA, this increased GEP by 17% Jul to Sep 1996 and 14% in 1997 compared with the baseline runs with drought constraints imposed by site measurements of predawn water potential (Fig. 9). It suggests that soil water deficit limited GEP by this amount based on model assumptions of hydraulic limitations. It also indicates how models without soil water deficit limitations to water use and carbon uptake can overestimate GEP in dry summer months.

Seasonal change in temperature optimum. For our baseline run of SPA, we assumed that the temperature optimum

for photosynthesis was constant throughout the year. When we changed the T_{opt} seasonally in SPA, the lower T_{opt} in spring (15 °C) resulted in substantially increased GEP in Jan to Apr compared with the baseline runs and measurements (Fig. 10), and consistently weaker correlations with measurements in each season ($r^2 = 0.66$ Jan–Mar to 0.13 Apr–Jun) than for the baseline runs. Seasonally, the increase in modelled GEP over the baseline run was 38% in Jan–Mar, 14% Apr–Jun, and 3% in Jul–Sep 1997. It raises interesting questions when modelling across coniferous and deciduous forests. In a deciduous forest (Harvard Forest), the foliage is active during a restricted temperature range, so selecting an

appropriate T_{opt} from within this range is not critical. Our results show that in coniferous forests, assumptions about a temperature optimum for photosynthesis are clearly important. Lowering the temperature optimum in winter and spring assumes that more photosynthesis can occur at lower temperatures, but this may be overly optimistic. Studies show that soil temperatures below $\sim 5^{\circ}\text{C}$ limit water uptake and stomatal conductance, and that spring recovery can be slow (Running & Reid 1980; Jones 1992). Another complicating factor is that our flux data and leaf-level measurements show photosynthesis on overcast days in winter and spring, but not on clear days following similar low night-time temperatures, suggesting that photoinhibition occurs on the clear days. This phenomenon is not accounted for in either of the models. Confirmation of the influence of seasonal temperature optima and soil temperature constraints requires detailed ecophysiology studies, as in our newly initiated studies.

Comparison with other forest ecosystems

Mid-day mid-summer NEP was low ($\sim 5 \mu\text{mol m}^{-2} \text{s}^{-1}$) compared with other temperate forest ecosystems, partly because of D constraints on carbon uptake and increasing ecosystem respiration with increasing temperatures. For example, an old-growth broad-leaved forest that was not subject to high D in summer, and had an LAI at least twice that of our site, had a typical mid-day NEP of $\sim 15 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Hollinger *et al.* 1994). Part of this difference is likely to be due to lower rates of carbon uptake in coniferous vs. broad-leaf deciduous forests (Teskey *et al.* 1995), and long-term water limitations on LAI in the semiarid ponderosa pine ecosystem. The decline in NEP at elevated temperatures and large D has been observed in a boreal deciduous conifer forest (*Larix gmelinii* mid-day mid-summer NEP $\sim 4 \mu\text{mol m}^{-2} \text{s}^{-1}$), where it was concluded that these conditions induced increased soil CO_2 flux and decreased photosynthesis (Hollinger *et al.* 1998).

The length of the photosynthetically active season of evergreen forests is strongly influenced by the length of the frost-free period (Waring & Running 1998). A substantial amount of carbon uptake by coniferous forests outside the 'growing season' is possible at temperatures near freezing, although the rates are very low (Fig. 10; Guehl & Aussenac 1987). Whereas gross carbon uptake of temperate forests in the north-eastern U.S. and boreal forests in summer is primarily controlled by incident radiation (Waring *et al.* 1995; Williams *et al.* 1996; Hollinger *et al.* 1998), GEP is limited by soil water deficit and high D in ponderosa pine, radiata pine (Arneith *et al.* 1999), and beech forests in semiarid climates (Valentini *et al.* 1996). In addition to climatic

limitations on gross carbon uptake, NEP in all of these forests is influenced strongly by factors affecting ecosystem respiration, particularly soil CO_2 flux, which can contribute 70–75% of ecosystem respiration (Law *et al.* 1999a; Mahli *et al.* 1999).

Conclusions

In closed canopy ecosystems, day-to-day variability in productivity and evapotranspiration is driven by changes in irradiance. But in this open canopy system with low LAI, soil water deficits and high atmospheric demand for water appear to have a large impact on canopy and soil processes. Our comparisons of modelled and measured whole ecosystem CO_2 and water vapour exchange, and specific components (soil evaporation, soil surface CO_2 flux) highlight the importance of modelling physical and biological aspects of soils well, including water availability through the root profile. To accurately model ecosystem carbon and water vapour exchange across seasons, seasonal LAI, canopy N, and leaf specific hydraulic conductivity are most critical for SPA, and LAI, V_{cmax} and the Ball-Berry constant are critical variables for CANPOND. There may be compensating errors in model estimates, such as cold soil limitations to stomatal conductance and lower temperature optima for photosynthesis in the cooler months. We plan to address the relative importance of these factors in future studies.

Acknowledgements

This study was funded by NASA (grant #NAGW-4436, NAG5-7531, and W-19389). We are grateful to Steve Van Tuyl and Will Hutchinson for their field assistance, and to Suzanne Remillard for her soil water holding capacity data for the site. We gratefully acknowledge the assistance of the Sisters Ranger District of the US Forest Service in establishing the study site, which is located in a Research Natural Area—an area selected to represent vegetation types in a natural condition.

References

- Arneith PM, Law BE, Unsworth MH (1999) Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. *Agricultural and Forest Meteorology*, **95**, 115–168.
- Arneith A, Kelliher FM, McSeveny TM, Byers JN (1998) Net ecosystem productivity, net primary productivity and ecosystem carbon sequestration in a *Pinus radiata* plantation subject to soil water deficit. *Tree Physiology*, **18**, 785–793.
- Baldocchi DD (1997) Measuring and modeling carbon dioxide and water vapor exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant, Cell and Environment*, **20**, 1108–1122.
- Baldocchi DD, Harley PC (1995) Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. II. Model testing and application. *Plant, Cell and Environment*, **18**, 1157–1173.

- Baldocchi DD, Meyers TP (1998) On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective. *Agricultural and Forest Meteorology*, **90**, 1–25.
- Baldocchi DD, Vogel CA (1996) Energy and CO₂ flux densities above and below a temperate broad-leaved forest and a boreal pine forest. *Tree Physiology*, **16**, 5–16.
- Baldocchi DD, Hicks BB, Meyers TP (1988) Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology*, **69**, 1331–1340.
- Baldocchi DD, Law BE, Anthoni PM (1999) On measuring and modeling energy fluxes above the floor of a homogeneous and heterogeneous conifer forest. *Agricultural and Forest Meteorology*, **102**, 187–206.
- Camillo PJ, Gurney RJ (1986) A resistance parameter for bare-soil evaporation models. *Soil Science*, **141**, 95–105.
- Campbell GS (1985) *Soil Physics with BASIC*. Elsevier, Amsterdam.
- Chen J (1996) Optically-based methods for measuring seasonal variation of leaf area index in boreal conifer stands. *Agricultural and Forest Meteorology*, **80**, 135–164.
- Choudhury BJ, Monteith JL (1988) A four-layer model for the heat budget of homogeneous land surfaces. *Quarterly Journal of the Royal Meteorological Society*, **114**, 373–398.
- Collatz GJ, Ball JT, Grivet C, Berry JA (1991) Regulation of stomatal conductance and transpiration: a physiological model of canopy processes. *Agricultural and Forest Meteorology*, **54**, 107–136.
- Day TA, Heckathorn SA, DeLucia EH (1991) Limitations of photosynthesis in *Pinus taeda* L. (loblolly pine) at low soil temperatures. *Plant Physiology*, **96**, 1246–1254.
- DeLucia EH (1986) Effect of low-root temperature on net photosynthesis, stomatal conductance and carbohydrate concentration in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings. *Tree Physiology*, **2**, 143–154.
- Eissenstat DM, Van Rees KCJ (1994) The growth and function of pine roots. *Ecological Bulletins*, **43**, 76–91.
- Elias TS (1980) *The Complete Trees of North America*. Van Nostrand Reinhold Company, New York.
- Emmingham WH, Waring RH (1977) An index of photosynthesis for comparing forest sites I western Washington. *Canadian Journal of Forest Research*, **7**, 165–174.
- Farquhar GD, von Caemmerer S (1982) Modeling photosynthetic response to environmental conditions. In: *Encyclopedia of Plant Physiology*, Vol. 12B: *Physiological Plant Ecology II. Water Relations and Carbon Assimilation* (eds Lange OL), pp. 549–587. Springer, Berlin.
- Franklin J, Dyrness T (1979) *Natural Vegetation of Oregon and Washington*. OSU Press, Corvallis, OR.
- Goward SN, Huemmrich KF, Waring RH (1994) Visible-near infrared spectral reflectance of landscape components in western Oregon. *Remote Sensing of Environment*, **47**, 190–203.
- Guehl J-M, Aussenac G (1987) Photosynthesis decrease and stomatal control of gas exchange in *Abies alba* Mill. in response to vapor pressure difference. *Plant Physiology*, **83**, 316–322.
- Hanson PJ, Wullschlegler SD, Bohlman SA, Todd DE (1993) Seasonal and topographic patterns of forest floor CO₂ efflux from an upland oak forest. *Tree Physiology*, **13**, 1–15.
- Harley PC, Baldocchi DD (1995) Scaling carbon dioxide and water vapor exchange from leaf to canopy in a deciduous forest: Leaf model parameterization. *Plant, Cell and Environment*, **18**, 1146–1156.
- Havranek WM, Tranquillini W (1995) Physiological processes during winter dormancy and their ecological significance. In: *Ecophysiology of Conifer Forests* (eds Smith WK, Hinckley TM), pp. 95–124. Academic Press, San Diego, CA.
- Hollinger DY, Kelliher FM, Byers JN, Hunt JE, McSeveny TM, Weir PL (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology*, **75**, 134–150.
- Hollinger DY, Kelliher FM, Schulze E-D *et al.* (1998) Forest-atmosphere carbon dioxide exchange in eastern Siberia. *Agricultural and Forest Meteorology*, **90**, 291–306.
- Jarvis PG, Massheder JM, Hale SE, Moncrieff JV, Rayment M, Scott SL (1997) Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest. *Journal of Geophysical Research*, **102**, 28,953–28,966.
- Jones HG (1992) *Plants and Microclimate*. Second edition. Cambridge University Press, Cambridge, pp. 106–130.
- Kaufmann MR (1975) Leaf water stress in Engelmann spruce. Influence of the root and shoot environments. *Plant Physiology*, **56**, 841–844.
- Kramer PJ, Boyer JS (1995) *Water Relations of Plants and Soils*. Academic Press, San Diego, CA.
- Law BE, Waring RH (1994) Combining remote sensing and climatic data to estimate net primary production across Oregon. *Ecological Applications*, **4**, 717–728.
- Law BE, Baldocchi DD, Anthoni PM (1999b) Below-canopy and soil CO₂ fluxes in a ponderosa pine forest. *Agricultural and Forest Meteorology*, **94**, 13–30.
- Law BE, Cescatti A, Baldocchi DD (2000a) Leaf area distribution and radiative transfer in open-canopy forests: Implications to mass and energy exchange. *Tree Physiology*, in press.
- Law BE, Ryan MG, Anthoni PM (1999a) Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biology*, **5**, 169–182.
- Law BE, Waring RH, Anthoni PM, Aber JD (2000b) Measurement of gross and net ecosystem productivity and water vapor exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology*, **6**, 155–168.
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Mahfouf JF, Noilhan J (1991) Comparative study of various formulations of evaporation from bare soil using in situ data. *Journal of Applied Meteorology*, **30**, 1354–1365.
- Mahli Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment*, **22**, 715–740.
- Middleton EM, Sullivan JH, Bovard BD, Deluca AJ, Chan SS, Cannon TA (1998) Seasonal variability in foliar characteristics and physiology for boreal forest species at the five Saskatchewan tower sites during the 1994 Boreal Ecosystem-Atmosphere Study. *Journal of Geophysical Research*, **102**, 28 831–28 828 844.
- Norman JM (1979) Modeling the complete crop canopy. In: *Modification of the Aerial Environment of Crops* (ed. Barfield G), pp. 249–280. American Society of Agricultural Engineers, St. Joseph, Michigan.
- Norman JM, Hesketh JD (1980) Micrometeorological methods for predicting environmental effects on photosynthesis. In:

- Predicting Photosynthesis for Ecosystem Models* (eds Hesketh JD, Jones JW), pp. 9–35. CRC Press, Boca Raton, FL.
- Pereira AR, Shaw RH (1980) A numerical experiment on mean wind structure inside canopies of vegetation. *Agricultural and Forest Meteorology*, **22**, 303–318.
- Reich PB, Walters MB, Ellsworth DS (1998) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia*, **114**, 471–482.
- Running SW, Reid CP (1980) Soil temperature influences on root resistance of *Pinus contorta* seedlings. *Plant Physiology*, **65**, 635–640.
- Schotanus PH, Nieuwstadt FTM, de Bruin HAR (1983) Temperature measurements with a sonic anemometer and its application to heat and moisture fluxes. *Boundary-Layer Meteorology*, **26**, 81–93.
- Sperry J (1993) Winter xylem embolism and spring recovery in *Betula cordifolia*, *Fagus grandifolia*, *Abies balsamea*, and *Picea rubens*. In: *Water Transport in Plants Under Climate Stress* (eds Borghetti M *et al.*), pp. 86–98. Cambridge University Press, UK.
- Sullivan JH, Bovard BD, Middleton EM (1997) Seasonal and canopy position variability in leaf level CO₂ and water fluxes in jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) in Saskatchewan, Canada. *Tree Physiology*, **17**, 553–561.
- Teskey RO, Sheriff DW, Hollinger DY, Thomas RB (1995) External and internal factors regulating photosynthesis. In: *Resource Physiology of Conifers: Acquisition, Allocation, and Utilization* (eds Smith WK, Hinckley TM), pp. 105–142. Academic Press, San Diego, CA.
- Valentini R, DeAngelis P, Matteucci G, Monaco R, Dore S, Scarascia Mugnozza GE (1996) Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biology*, **2**, 199–207.
- Vickers D, Mahrt L (1997) Quality control and flux sampling problems for tower and aircraft data. *Journal of Atmospheric and Oceanic Technology*, **14**, 512–526.
- Waring RH, Running SW (1978) Sapwood water storage: Its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. *Plant, Cell and Environment*, **1**, 131–140.
- Waring RH, Running SW (1998) *Forest Ecosystems – Analysis at Multiple Scales*. Academic Press, San Diego, CA.
- Waring RH, Law BE, Goulden ML *et al.* (1995) Scaling gross ecosystem production at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. *Plant, Cell and Environment*, **18**, 1201–1213.
- Waring RH, Whitehead D, Jarvis PG (1979) The contribution of stored water to transpiration in Scots pine. *Plant, Cell and Environment*, **2**, 309–317.
- Webb EK, Pearman GI, Leuning R (1980) Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society*, **106**, 85–100.
- Williams M, Malhi Y, Nobre A, Rastetter EB, Grace J, Pereira MGP (1998) Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis. *Plant, Cell and Environment*, **21**, 953–968.
- Williams M, Rastetter EB, Fernandes DN *et al.* (1996) Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell and Environment*, **19**, 911–927.
- Williams M, Rastetter EB, Fernandes DN *et al.* (1997) Predicting gross primary productivity in terrestrial ecosystems. *Ecological Applications*, **7**, 882–894.
- Wullschleger SD, Meinzer FC, Vertessy RA (1998) A review of whole-plant water use studies in trees. *Tree Physiology*, **18**, 499–512.