Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models

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Abstract

Net ecosystem productivity (NEP), net primary productivity (NPP), and water vapour exchange of a mature *Pinus ponderosa* forest (44°30′ N, 121°37′ W) growing in a region subject to summer drought were investigated along with canopy assimilation and respiratory fluxes. This paper describes seasonal and annual variation in these factors, and the evaluation of two generalized models of carbon and water balance (PnET-II and 3-PG) with a combination of traditional measurements of NPP, respiration and water stress, and eddy covariance measurements of above-and below-canopy CO_2 and water vapour exchange. The objective was to evaluate the models using two years of traditional and eddy covariance measurements, and to use the models to help interpret the relative importance of processes controlling carbon and water vapour exchange in a water-limited pine ecosystem throughout the year. PnET-II is a monthly time-step model that is driven by nitrogen availability through foliar N concentration, and 3-PG is a monthly time-step quantum-efficiency model constrained by extreme temperatures, drought, and vapour pressure deficits. Both models require few parameters and have the potential to be applied at the watershed to regional scale. There was 2/3 less rainfall in 1997 than in 1996, providing a challenge to modelling the water balance, and consequently the carbon balance, when driving the models with the two years of climate data, sequentially. Soil fertility was not a key factor in modelling processes at this site because other environmental factors limited photosynthesis and restricted projected leaf area index to ~1.6. Seasonally, GEP and LE were overestimated in early summer and underestimated through the rest of the year. The model predictions of annual GEP, NEP and water vapour exchange were within 1–39% of flux measurements, with greater disparity in 1997 because soil water never fully recharged. The results suggest that generalized models can provide insights to constraints on productivity on an annual basis, using a minimum of site data.

Keywords: carbon allocation, eddy covariance, micrometeorology, net ecosystem production, photosynthesis, respiration

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Introduction

Climatic variation and management practices influence carbon uptake, storage and release by forests (Cohen *et al.* 1996), and water vapour exchange with the atmosphere, which can affect micro- and meso-scale climate (Pielke

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et al. 1993). Models of gross ecosystem production (gross photosynthesis, GEP), net primary production (NPP) and net ecosystem production (NEP) are being driven with daily meteorological data and remotely sensed vegetation characteristics to provide regional to global estimates of vegetation–atmosphere interaction (Prince & Goward 1995; Hunt *et al.* 1996). Until advanced sensors

and techniques are developed and made available, there is no direct way of evaluating model predictions at 0.25 km^2 scale and larger. Alternatively, eddy covariance measurements of CO_2 and water vapour fluxes (LE) and complementary field measurements of ecosystem process rates can provide a means of evaluating model estimates of LE, GEP, NEP, NPP and respiration by ecosystem components.

We conducted our study at a ponderosa pine (*Pinus ponderosa* Laws.) site in Oregon that is a member of the AmeriFlux and Fluxnet networks of flux sites. At these sites, suites of measurements are being made at various levels of organization for estimating carbon and water vapour exchange and for parameterizing and validating ecosystem models to improve estimates across larger spatial scales.

In this study, we used two years of eddy covariance measurements of CO_2 and water vapour fluxes and traditional measurements of respiration, leaf area index (LAI) and NPP to check assumptions and predictions made by two generalized models of ecosystem processes, PnET-II and 3-PG. We chose these models because they require few parameters and have the potential for watershed to regional applications through parameterization with GIS coverage of vegetation type, climate and topography (Aber *et al*. 1995; Coops *et al*. 1998). When driven by local meteorological data, the models were able to match seasonal measurements of GEP acquired through eddy covariance measurements in a temperate deciduous forest (Aber *et al*. 1995; Waring *et al*. 1995). Once the models have been evaluated with several measures of ecosystem function in a range of forest types, we will have confidence in broader applications of the models.

The models predict carbon uptake and respiration at monthly or longer time steps, applying principles developed from numerous comparative studies including whole ecosystem daily and annual carbon balances. Both models use monthly summaries of weather data. PnET-II assesses canopy photosynthetic capacity based on nitrogen status while 3-PG is primarily driven by quantum efficiency and environmental constraints on gross photosynthesis. PnET-II and 3-PG both limit photosynthesis and alter carbon allocation based on constraints from environmental factors, in particular soil water availability and soil fertility, and climatic variables: subfreezing temperatures, vapour pressure deficit (D), and limited precipitation during some months. Both models are able to provide some estimate of GEP under equilibrium conditions where soil carbon content and litterfall accumulation are in apparent balance. More detailed parameterization is needed for 3-PG (e.g. local allometric equations for biomass, soil fertility, approx-imate stand age, maximum quantum efficiency) than for PnET-II.

Our research site offers a challenging test for these models because the dominant species are evergreen conifers that have the potential to continue photosynthesis throughout the year. However, carbon uptake is constrained in winter by subfreezing conditions and reduced solar radiation, and in summer by soil water deficits and extreme vapour pressure deficits when incident solar radiation levels are high. The soils are relatively infertile, thus nutrient deficiencies play an important role in carbon allocation only for a few months when other factors are not limiting.

Our objectives are to evaluate the models using traditional and eddy covariance measurements and determine sensitivity of key model parameters, and to use the models to help interpret the relative importance of processes controlling carbon and water vapour exchange in a water-limited pine ecosystem throughout the year.

Materials and methods

Site description

The site is a ponderosa pine forest in central Oregon, located in the Metolius Research Natural Area (44°30′ N, 121°37′W, elevation 940 m). The pine forest extends at least 12 km in all directions. The site consists of about 27% old trees (~250 years), 25% younger trees (~45 years) and 48% mixed-age trees. The understorey is sparse with patches of bitterbrush (*Purshia tridentata*), bracken fern (*Pteridium aquilinum*) and strawberry (*Fragaria vesca*).

Most of the precipitation in the region occurs between October and June, with the summer months lacking effective precipitation (normally ~20 mm July through August). Winters on the eastside of the Cascade Mountains are cool, and there is a large diurnal variation in temperature in summer, typical of the semiarid region. Snow cover in the winter is intermittent, reaching a maximum depth of about 50 cm. Freezing temperatures occur mostly at night and early morning.

Soil at the site is a sandy loam (73% sand, 21% silt, and 6% clay; Law *et al*. 1999a) and is classified as a light-coloured andic inceptisol that is low in nutrients. Soil water-holding capacity to 1 m depth is 163 mm (S. Remillard, pers. comm.). Surface litter was scant in the old stands (194 g m^{-2}), and averaged 38% less than litter mass in the young stands (315 g m^{-2}).

Environmental measurements

Using the eddy covariance method, we made continuous flux measurements on a tower 14 m above the canopy

and 2 m above the soil surface to determine half-hourly sensible and latent heat fluxes (LE, evaporation from surfaces and transpiration), and CO_2 fluxes in 1996 and 1997. Details on the instrumentation, flux corrections and calculations were reported in Law *et al*. (1999a,b) and Anthoni *et al*. (1999). We summarize methods here to briefly explain processing of the flux data. The data were screened to remove possible eddy covariance instrumentation and sampling problems (Law *et al*. 1999a). After screening, about 75% of the above-canopy carbon flux and 85% of the water vapour fluxes were available for further analysis. During turbulent conditions, the change in CO_2 storage, determined from profile measurements in the canopy airspace, was combined with above-canopy flux measurements 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.

Half-hourly measurements of climatic variables made at the top of the flux tower included air temperature (T_{air}), vapour pressure deficit (D), incident photosynthetically active radiation (PAR), and rainfall. Monthly climate summaries used to drive both models are shown in Fig.1.Three meteorological stations at the forest floor measured soil temperature (T_s, 15 cm depth), soil water content (θ) in 0–30 cm soil layer, and throughfall of precipitation.

Ecophysiology

Respiration by foliage (R_f) and wood (R_w), and soil surface CO_2 fluxes (R_s) were measured periodically through both years using chambers and portable infrared gas analysers. Further descriptions of the respiration measurements and methods for estimating hourly ecosystem respiration from equations developed at the site are described in Law *et al*. (1999a,b).

Gross ecosystem productivity (GEP), or gross carbon uptake was calculated from:

$$GEP = NEP - R_e, \qquad (1)$$

where NEP was calculated from eddy flux measurements, and R_e was from chamber estimates of ecosystem respiration. In the calculation of GEP from flux data, we assume that R_e is negative (a loss of CO_2 from the ecosystem; Anthoni *et al*. 1999). Gross ecosystem production should equal the net rate of carboxylation and oxygenation by the enzyme Rubisco. It does not include dark respiration and is not

equivalent to chamber measurements of net assimilation (Goulden *et al*. 1998).

The methods used to estimate foliage, wood and root production in 1996 are reported in Law *et al*. (1999a). We repeated these measurements to obtain NPP estimates for 1997 in this study. The above-ground net primary production (ANPP) was determined from mensuration measurements of stem diameter, growth increment and height, and from foliage biomass per age class and leaf area index measurements. Allometric equations that were developed on-site were used to estimate current and previous stemwood and branch biomass, and wood production (Law *et al*. 1999a).

Leaf area index was previously determined from optical measurements with a Sunfleck Ceptometer (1996; Decagon Devices, Pullman, WA; Law *et al*. 1999a) and a LAI-2000 (1997; LICOR, Lincoln, NE; Law *et al*. in prep.). The maximum projected LAI of the tree canopy in summer averaged $1.6 \pm 0.1 \, m^2$ leaf m^{-2} ground. Foliage turnover rate (P_f), a parameter in both models, was estimated from the fraction of total dry mass of foliage on 10 shoots that had expanded that year. Foliage samples were collected from top, mid-and lower canopy to determine mean specific leaf area (SLA) and nitrogen concentration per unit leaf area for model parameterization. Annual foliage production was calculated from LAI, SLA and foliage turnover.

Below-ground production was estimated assuming steady-state conditions from annual soil surface CO_2 flux minus annual litterfall carbon (Nadelhoffer & Raich 1992) and that 50% of carbon allocated below-ground was used for root production. Although this is an old-growth forest with minimal recent disturbance, the assumption that carbon storage is in steady state is probably violated (Gower *et al*. 1996). Thus, the accuracy of the root productivity estimate is uncertain.

Predawn water potential (Ψ_p) measurements were made periodically with a pressure chamber through the growing seasons of both years in order to identify changes in water stress, and to evaluate the models. Photosynthetic light response was measured in early summer (before drought stress) with a LICOR 6400 (Law *et al*. 1999a,b), and maximum quantum-efficiency, necessary for parameterizing 3-PG, was calculated from the slope of the photosynthetic light response curve as PAR approached zero.

3-PG model structure

The 3-PG model is described in detail in Landsberg & Waring (1997). In summary, the model calculates GEP from utilizable absorbed photosynthetically active radiation ($\phi_{p.a.u.}$) and a canopy quantum efficiency coefficient (α). $\phi_{p.a.u.}$ is obtained by reducing the values of absorbed
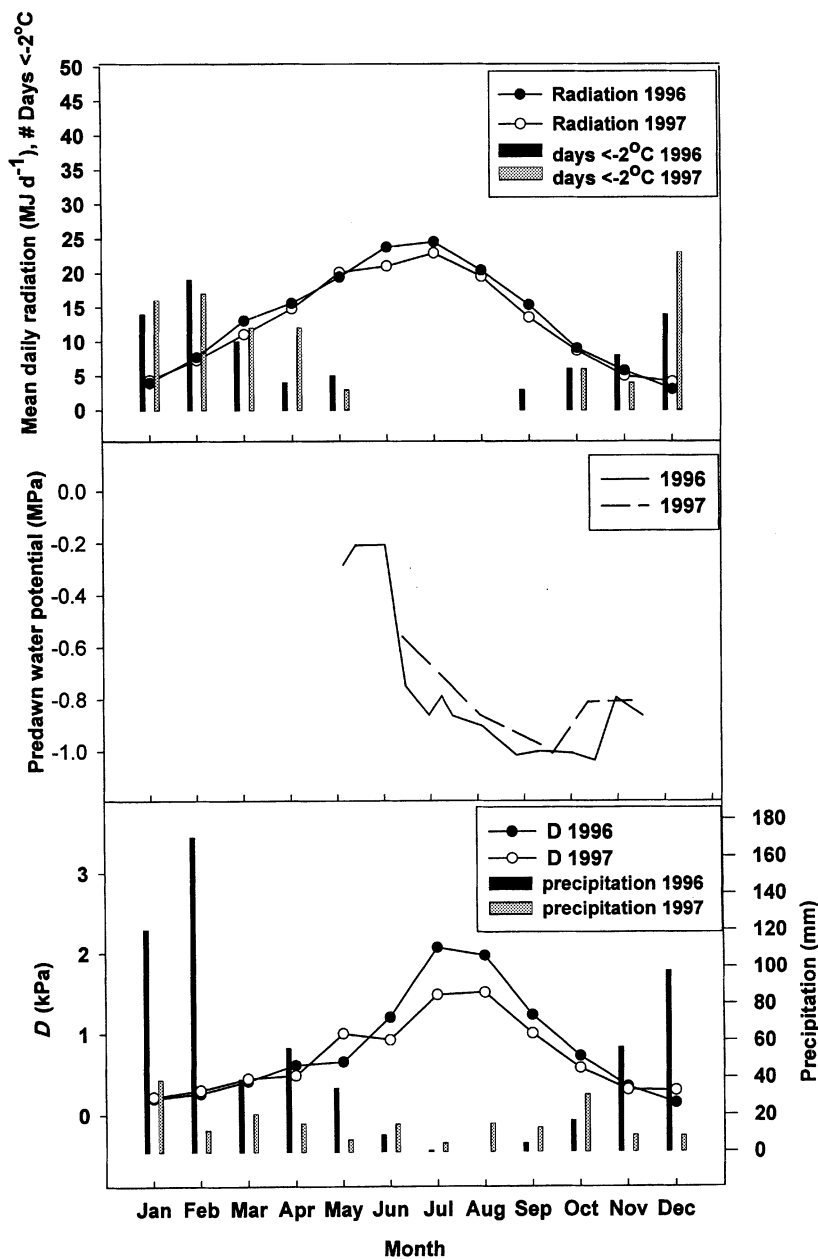
Fig. 1 Mean daytime radiation and number of days with subfreezing temperatures at the ponderosa pine site for 1996 and 1997 (top), predawn leaf water potential (middle), and mean daytime vapour pressure deficit (*D*) and precipitation (bottom).

photosynthetically active radiation ($\phi_{p.a.}$) by amounts determined by linear modifiers — dimensionless factors with values varying between zero and unity. The modifiers reflect constraints imposed on the utilization of radiation absorbed by leaves because of stomatal closure caused by high *D*, soil drought (defined by the ratio of the amount of water in the root zone to the maximum storage, θ_{max}), or the effects of subfreezing temperature (T_f) (Waring *et al.* 1995; Landsberg & Waring 1997).

The model assumes the ratio of net (P_N) to gross ecosystem production (NPP/GEP) is 0.47 (Waring *et al.*

1998). Unlike PnET-II, 3-PG computes tree growth over years. It uses a submodel derived from the −3/2 power law (Drew & Flewelling 1977; Landsberg & Coops 1999) and stem growth rates to calculate changes in stem number per unit area with stand development over time (self-thinning). The model uses an equation based on published allometric ratios for different species to determine the allocation of carbon to foliage and stems and to constrain tree growth patterns (Meyers 1938). It also reduces tree growth with age, caused by physiological limitations (Mencuccini & Grace 1996; Ryan & Yoder 1997).

Table 1. Variables for 3-PG model

Description	Symbol	Value	Reference
Canopy quantum efficiency (mol C mol^{-1} photon)	α	0.04	This study
Days < −2 °C month^{-1}	T_d	Meteorological data	This study
Soil fertility, 0 (poorest) to 1.0 (best)	S_f	Sandy loam, 0.4	This study
Maximum leaf stomatal conductance (ms^{-1})	g_{smax}	0.005	This study
Maximum canopy conductance (ms^{-1})	g_{max}	0.02	Kelliher *et al.* (1995)
Boundary layer conductance (ms^{-1})	g_b	0.2	Landsberg & Waring 1997;
Light extinction coefficient	κ	0.5	Runyon *et al.* 1994; Soil water
Water holding capacity (mm)	θ_c	163–300	163 mm to 1 m depth this study
Foliage turnover rate (%)	P_f	25	This study
Foliage leaf mass (kg) equation with tree diameter (mm)	A_f	$D_f = 2.4 \times 10^{-5}$ dbh$^{2.575}$	This study
Specific Leaf Area (kg m^{-2} projected)	σ_f	3.1	This study
Wood density	σ_w	400 kg m^{-3}	This study
Stemwood biomass (kg) equation with tree diameter (mm)	B_s	$B_s = 5 \times 10^{-6}$ dbh$^{2.97}$	Yield tables for site class 32m@100 years; Meyer 1938

In this study, we added a temperature optimum (T_{opt}) equation to the model that takes into account seasonal variation in temperature that may reduce the quantum efficiency of light conversion into photosynthate:

$$T_f = \frac{(T_{mean} - T_{min})}{(T_{opt} - T_{min})} \times \frac{(T_{max} - T_{mean})}{(T_{max} - T_{opt})}^{\left[\frac{(T_{max} - T_{opt})}{(T_{opt} - T_{min})}\right]}, \quad (2)$$

where T_{opt} was 20 °C (Hadley 1969; Monson & Grant 1989), T_{min} 0 °C, and T_{max} 40 °C. The T_f value is between 0 and 1, and is applied as modifier to $\phi_{P.a.}$

The model uses a monthly time step and requires as input data total short-wave (375–2500 nm) incoming radiation (ϕ_s), monthly mean daytime vapour pressure deficit (D), total monthly precipitation, and number of days per month when mean night-time air temperatures reached below –2 °C (Table 1).

Starting values of foliage, stem and root mass are also required, appropriate to the age of the stand at the start of a run, together with appropriate allometric equations and some soil water parameters. Leaf area index (LAI) is determined from foliage mass and input values of specific leaf area (σ_f, m^2 kg^{-1}). In this study, we ran the model for a 50-y-old pine forest with 550 trees ha^{-1} matching the dominant age of the present understorey pine.

The 3-PG model was not designed to estimate heterotrophic respiration and thus NEP. In this paper, we estimated annual NEP from:

$$\text{NEP} = \text{GEP} + R_a + R_h, \quad (3)$$

assuming R_a and R_h are negative values (a loss from the ecosystem, as in eqn 1). The model assumes that 47% of GEP is used for production leaving 53% for autotrophic respiration (R_a). R_h of fine roots (R_{hroot}) was estimated as equal to annual fine root production,

assuming steady state conditions. Fine root production was assumed to be the difference between total root production and coarse root production estimated from allometric equations for Douglas fir (Santantonio *et al.* 1977; Gholz *et al.* 1979). Heterotrophic respiration of litter ($R_{hlitter}$) was calculated from the inverse of mean residence time (MRT), which was computed as soil carbon content to 1 m depth divided by annual litterfall carbon for each year (Landsberg & Gower 1996).

PnET-II model structure

PnET-II is a general, lumped-parameter model of interactions between carbon, nitrogen and water balances in forest ecosystems. Core functions in PnET-II include a linear relationship between foliar N concentration and maximum photosynthetic rate (A_{max}). Conductance is assumed to be related linearly to A_{max} such that transpiration and water-use efficiency are linear functions of vapour pressure deficit. Transpiration is then A_{max} divided by water-use efficiency. This set of relationships provides a simple and direct interaction between nitrogen status of a site (foliar N), carbon gain and transpiration. Evaporation of rain and snow is an empirical constant expressed as a fraction of precipitation (set to 15% for Metolius). That fraction of precipitation is assumed to evaporate from canopy and soil surfaces. There is also a fast flow fraction (10%) which moves snowmelt or rainfall through the soil and below the rooting zone (estimated macropore flow).

PnET-II includes a dynamic allocation of carbon to foliage, wood and roots and includes all plant respiration terms to allow calculation of NPP. The model calculates soil respiration from an exponential temperature response equation developed for temperate forests

Description	Value	Reference
Latitude (°)	44.5	This study
Minimum temperature for photosynthesis (°C)	−2	Jones (1992)
Specific Leaf Weight (g m^{-2})	310	This study
Foliar nitrogen concentration (%)	1.35	This study
Foliage turnover rate (%)	25	This study
Water holding capacity (mm)	163–300	This study

Table 2 Variables for PnET-II model. Values listed here are those which were changed from previous runs. Other variables are as defined for red pine (*Pinus resinosa*) in Aber *et al.* (1995).

(Kicklighter *et al.* 1994). Respiration in foliage is expressed as a fraction of A_{max} multiplied by a Q_{10} value. Wood maintenance respiration is a fraction of gross photosynthesis. Allocation to roots is a function of allocation to foliage. Wood production is essentially a residual term, consisting of carbon remaining after allocation to foliage and roots has been met. Allocation to foliage is determined by the carbon balance of foliage at different levels in the canopy in the previous year. NEP is calculated as the balance between net photosynthesis and the sum of the respiration terms. This version has been validated against daily and annual carbon balances and monthly water balances at both the Harvard Forest and the Hubbard Brook Experimental Forest (Aber *et al.* 1995).

Foliar N concentration is fixed as an input parameter. Canopy phenology is driven by a growing degree-day parameter. The canopy is divided into 50 equal layers by leaf mass. Light attenuated through the canopy using the Beers–Lambert equation, and specific leaf weight can vary with depth in canopy. Potential gross photosynthesis in each layer is a function of A_{max}, shading from above, temperature and vapour pressure deficit. Potential transpiration is calculated as potential gross photosynthesis divided by water-use efficiency (a function of vapour pressure deficit). A water balance routine uses a soil water release parameter to determine the maximum rate of transpiration attainable without water stress. If the potential transpiration exceeds this value, then both gross photosynthesis and transpiration are reduced from the potential values.

Parameters used in these simulations of ponderosa pine are the same as those published for red pine (*Pinus resinosa*; Aber *et al.* 1995) with the addition of five site-specific variables (Table 2). PnET-II is not generally run as a calibrated model, thus we did not calibrate model equations in this study. In contrast, 3-PG was calibrated to some extent to reach an equilibrium LAI that was close to measured values.

For PnET-II and 3-PG, we compared model estimates with flux measurements of monthly and annual NEP, GEP and LE (transpiration plus evaporation from the surface and foliage) and measurements of annual above-ground NPP in both years.

Model sensitivity tests

An annual water balance that assumed roots had access to water in the upper surface metre (163 mm) proved inadequate to match measured LE. We determined with the models that ~300 mm of soil water-holding capacity was required to support the leaf area measured at the site. Thus we tested the sensitivity of both models to soil water-holding capacity using the measured value to 1 m depth (163 mm), and higher values (e.g. 300 mm ± 20%). We ran 3-PG with a temperature response function (20 °C ± 20%) to determine sensitivity of the model to the effect of temperature limitation on GEP and ANPP. Finally, we varied the target LAI and soil water holding capacity in both models, foliar N in PnET-II, and quantum efficiency (α), soil fertility (S_f), and maximum stomatal conductance (g_{smax}) in 3-PG by ± 20% from the reference values of each variable (LAI = 1.8, θ_c = 300 mm, α = 0.04 mol CO_2 mol^{-1} photon, N = 1.35%, S_f = 0.4, g_{smax} = 0.005 m s^{-1}).

Results and discussion

Climate

Monthly climate data for the site are shown in Fig. 1 and summarized in Table 3. Sub-freezing temperatures were frequent in winter, particularly at night, an important consideration when modelling photosynthesis by conifers. Air temperatures dropped below freezing on 132 days in 1996, and 134 days in 1997, and the mean night-time temperatures were below freezing on 47 nights in 1996, and 62 nights in 1997. There was a large diurnal variation in air temperatures in summer, typical of semiarid regions. The mean of daily maximum D in July through September was higher in 1996 than in 1997 (2.8 and 2.3 kPa; Table 3) as a result of more frequent cloud cover and subsequently reduced temperatures in 1997. Total precipitation in 1996 was 595 mm, a wetter than normal year, with no precipitation in July and

Table 3 Annual climate data for the *Pinus ponderosa* site during two years. The D_{max} is the average of maximum daytime vapour pressure deficit during the dry season (July through September).

	1996	1997
Total annual incident PAR (MJ m^{-2})	2377	2313
Annual shortwave radiation (MJ m^{-2})	5390	5351
Annual mean air temperature (°C)	8.4	8.5
Mean night-time air temperature <0 °C (# days)	47	62
Soil temperature, 15 cm depth, Jul. – Sep. (°C)	14.4	14.2
Soil water content, 0–30 cm depth, Jul. – Sep. (m^3 m^{-3})	0.10	0.11
Annual precipitation (mm)	595	188
D_{max} (kPa) Jul. – Sep.	2.8	2.3

August. Although total annual precipitation in 1997 was low (188 mm), it was fairly evenly distributed throughout the year. Minimum soil water content to 1 m depth reached about 0.11 m^3 m^{-3} in summer 1996 and 0.12 m^3 m^{-3} in 1997, and recharged in the winter months to about 0.24 m^3 m^{-3}.

Ecophysiology and flux measurements

Bud elongation began in mid-May both years, needles were fully elongated by mid-August, and most of the leaf litterfall occurred in October. Foliage retention by *P. ponderosa* at this site is three to four years. Foliar N concentration ranged from a maximum of 1.35% ± 0.15 in summer to 1.19% ± 0.29 in May. Apparent maximum quantum-efficiency was 0.04 mol C mol^{-1} PAR in early summer. The foliar N and quantum-efficiency were lower than values observed in a heavily thinned ponderosa pine stand 5 km away where the trees are growing in full sun with a complement of nitrogen-fixing understorey species (0.05 mol C mol^{-1} PAR; B. Bond, pers. comm.). We measured foliar N profiles at the thinned site on Day 208 (1.45% ± 0.29), close to the measurement date at our site. Although the average foliar N was not significantly different from our site, it might help explain differences in photosynthetic rates.

Predawn leaf water potential (Ψ_p), an indicator of soil water availability, decreased through summer in both years, with values reaching about –1.0 MPa in August and September (Fig. 1). Although this value suggests water stress, it is not as extreme as observed values in previous years in the area; at a nearby ponderosa pine site that had been thinned (LAI = 0.7), Ψ_p reached –1.8 MPa in 1990 when annual rainfall was 540 mm (Runyon *et al*. 1994). Annual LE from flux measurements at our site was 434 ± 65 mm in 1996 and 400 ± 60 mm in 1997 in spite of two-thirds less rainfall (Table 4). The high LE compared with rainfall (188 mm) in 1997, and moderate predawn water potential values in summer suggest that deep roots accessed soil water that is not

accounted for in the surface metre. As plant water stress increased in late summer and evaporative demand declined from its peak, LE decreased (Figs 1 and 2). LE flux decreased from an average of 1.9 mm d^{-1} in spring to 1.4 mm d^{-1} in late summer. These values are relatively low compared with other ecosystems such as *Larix gmelinii* in eastern Siberia (2.3 mm d^{-1} ; Arneth *et al*. 1996), and are comparable to a boreal black spruce forest during the growing season (2 mm d^{-1} ; Jarvis *et al*. 1997).

Gross ecosystem production estimated from eddy flux and chambers varied little from year to year (1208 ± 184–1262 ± 195 g C m^{-2} y^{-1}; Table 4). Ecosystem respiration was greater in 1997 (996 ± 199 g C m^{-2} y^{-1}) than in 1996 (885 ± 177 g C m^{-2} y^{-1}), largely because of increased soil CO$_2$ fluxes in the summer of 1997 when rainfall was more frequent, and may have stimulated microbial respiration in the litter and surface soil (Nakane 1994).

Annual NEP was 324 ± 168 and 266 ± 177 g C m^{-2} y^{-1} in 1996 and 1997 (Table 4), lower than NEP in Florida slash pine (600–740 g C m^{-2} y^{-1}; Clark *et al*. 1999) where climate is less constraining on carbon uptake, but comparable to other temperate and boreal forests (Goulden *et al*. 1998; Hollinger *et al*. 1999). NPP (foliage+wood) was 413 and 400 g C m^{-2} y^{-1} in 1996 and 1997, suggesting that annual heterotrophic respiration (R_h = NPP – NEP) was approximately 22–34% of NEP.

Diurnally, NEP approached zero in summer afternoons as vapour pressure deficits reached 2–4 kPa, and as respiration rates increased with temperature. This phenomenon was observed in temperate deciduous forests (Baldocchi 1997) and in boreal forests (Jarvis *et al*. 1997). Models operating even on a daily time-step using mean values of D may miss this limitation on carbon uptake.

The mean residence time of litter, calculated from litterfall and soil carbon, was 36 years in 1996 and 22 years in 1997, resulting in a very low estimate of heterotrophic respiration of surface litter (4 and 10 g C m^{-2} y^{-1}). Microbial activity generally decreases with soil moisture, and thus decomposition of surface litter is very slow in dry ecosystems (Orchard *et al*. 1992).

Table 4 Annual carbon budget (g C m^{-2} y^{-1}) and water vapour exchange (mm y^{-1}) estimated from field measurements and the models, PnET-II and 3-PG, and 95% confidence intervals. The model results were from using soil water holding capacity (θ_c) of 300 mm, and PnET-II results include θ_c set at 163 mm (PnET-II$_{163}$). Measured values of net primary production (NPP) are means for five years (1992–96, 1993–97). Measured R_e is ecosystem respiration from scaled-up chamber measurements of foliage, wood, and soil CO$_2$ flux. Heterotrophic respiration (R_h) was estimated from NPP – NEP. Measured below-ground carbon allocation (C_b) was calculated from the difference between annual soil CO$_2$ flux (683 and 773 g C m^{-2} y^{-1}) and annual litterfall carbon (130 and 216 g C m^{-2} y^{-1}) in 1996 and 1997, respectively. NEP and latent heat flux (LE) was measured by the eddy covariance method.

	1996				1997			
Variable	Measured	3-PG	PnET-II$_{163}$	PnET-II$_{300}$	Measured	3-PG	PnET-II$_{163}$	PnET-II$_{300}$
Foliar NPP	59	64	69	63	51	55	69	63
Wood NPP	77 ± 18	152	173	220	70 ± 9	132	173	251
ANPP	136	216	125	283	121	187	125	314
Total NPP	413	422	367	396	400	362	367	424
GEP	1208 ± 184	899	905	1145	1262 ± 195	770	889	875
NEP	324 ± 168	250	112	289	266 ± 177	209	233	284
R_e	885 ± 177	649	793	856	996 ± 199	561	656	591
R_h	89	172	255	107	134	153	134	140
C_b	553	375	138	307	557	318	138	70
LE	434 ± 65	436	340	472	400 ± 60	300	256	258

Evaluation of 3-PG

Model parameters that are important in each model were varied by ± 20%. In 3-PG, we compared model sensitivity to soil water holding capacity (θ_c), soil fertility (S_f), quantum efficiency (α), LAI, a temperature optimum (T_{opt}), and stomatal conductance (g_{smax}), changing one parameter at a time. The 3-PG model was most sensitive to changes in α, followed by g_{smax}, LAI, T_{opt}, θ_c, and S_f (Table 5). The greatest changes in predicted GEP were from changes in α (–26–24% change), and LE was most affected by LAI (–10–14%). This agrees with studies that have shown a correlation between LE and LAI, particularly when LAI values are less than 3 (Swank & Douglas 1974). A 20% decrease in g_{smax} allowed more conservation of water into summer and thus 15–17% more carbon uptake when LAI was higher in summer. The soil fertility coefficients (S_f; 0.4 ± 0.08) resulted in <1% change in annual GEP and LE. Generally, soil fertility makes little difference in such harsh climates because in most months, other environmental factors more strongly limit photosynthesis and carbon allocation. Without a temperature optimum, GEP was 50–185 g C m^{-2} month^{-1} in January to March, unreasonably high values compared with flux data. Similar results were found in sensitivity tests of a fine-scale model, SPA, when we changed the temperature optimum seasonally and compared results with hourly flux data at our site (Law *et al.* in review).

Because 3-PG adjusts leaf area to site conditions, we ran 3-PG with a range of θ_c values from 163 mm measured to 1 m depth up to 300 mm, and found that 300 mm resulted in an equilibrium LAI of 1.4, close to measured LAI (1.6 ± 0.1). The modelled LAI stabilized at 1.0 for θ_c of 163 mm.

The model typically took about 10 years for LAI to equilibrate within ± 0.1 given initial stand biomass estimates for 50-y-old trees at a mean diameter and 550 trees ha^{-1} density. We ran the mean of 1996 and 1997 weather data for 20 years to allow the model to equilibrate, then ran 1996 and 1997 weather data sequentially. Although trees grow in diameter in the model, no age effect was imposed over the 20-y period. The difference between productivity of a 50- and 70-y-old forest is minimal compared with the actual age distribution observed at the site (45–250-y-old).

The 3-PG assumption of no photosynthesis when temperatures dropped below –2 °C was somewhat overly constrictive because eddy flux data at the pine site indicated carbon uptake can occur when overcast days follow nights of subfreezing temperatures (Fig. 2). We chose as the most realistic parameter values θ_c of 300 mm, S_f of 0.4, and a temperature optimum of 20 °C.

The annual NPP predicted by 3-PG (422 and 362 g C m^{-2} y^{-1} in 1996 and 1997) were close to measured values (413 and 400 g C m^{-2} y^{-1} in 1996 and 1997). Model estimates of stem production were 152 and 132 g C m^{-2} y^{-1} in 1996 and 1997, averaging more than twice field estimates using allometric equations developed at the site (Table 4). This was outside the 95% confidence interval of the measurements (77 ± 18 and 70 ± 9 in 1996 and 1997). Field estimates of production were based on the two prominent age classes. The model was initialized for an even-aged 50-y-old stand. Because the stand consists of 27% old-growth and 48% mixed-age trees and the stand density of the old age class was lower (70 trees ha^{-1}) than the 550 trees per hectare used to parameterize 3-PG, it is not surprising that the model estimates of stem

Table 5 Results of sensitivity analyses with both models, where key model variables were varied independently by $\pm 20\%$. α is canopy quantum efficiency, T_{opt} is the temperature optimum for photosynthesis, θ_c is soil water holding capacity, S_f is soil fertility, and g_{smax} is stomatal conductance. The percentage change in annual GEP and LE are shown for each year (1996/1997), resulting from a 20% decrease (-20%) or increase ($+20\%$) in the model variable.

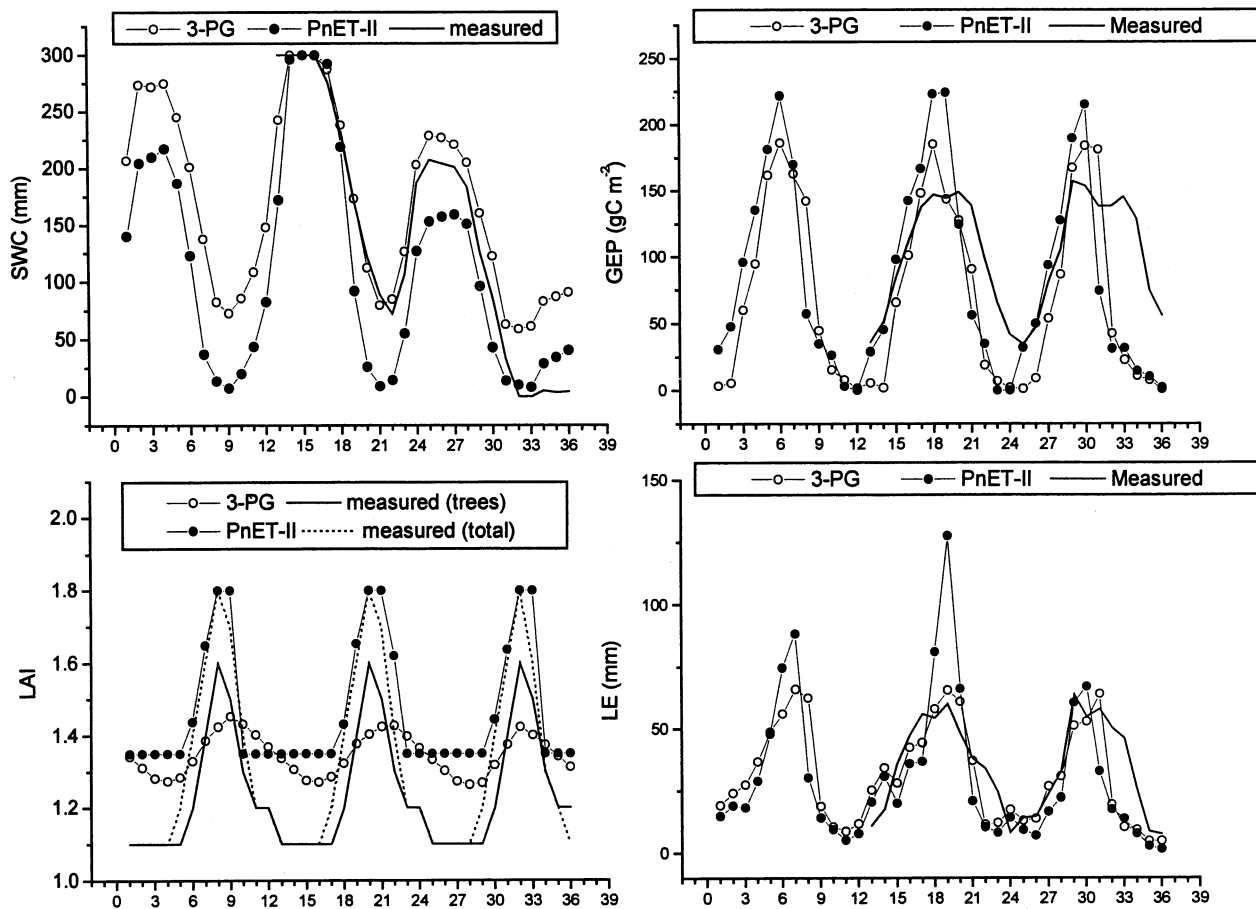| Variable	Reference	3-PG				PnET-II			
		GEP		LE		GEP		LE	
		-20%	$+20\%$	-20%	$+20\%$	-20%	$+20\%$	-20%	$+20\%$
Foliar N (%)	1.35					$-7/-4$	$7/4$	$-3/3$	$2/-1$
LAI	1.8	$4/-11$	$10/-23$	$7/-4$	$14/-10$	$-7/-5$	$7/4$	$-3/3$	$2/-1$
α (mol CO_2 mol^{-1} photon)	0.04	$-26/-16$	$24/12$	$-9/1$	$5/-3$				
T_{opt}	20	$12/7$	$-16/-9$	$3/-2$	$-5/1$				
θ_c (mm)	300	$-9/-4$	$6/6$	$-8/-4$	$5/6$	$-10/-1$	$5/1$	$-12/-1$	$5/1$
S_f	0.4	$-0.4/-0.1$	$0.4/-0.1$	$-0.7/-0.3$	$0.7/0.3$				
g_{smax} (ms^{-1})	0.005	$15/17$	$-11/-14$	$-2/-1$	$2/-0.4$				

Fig. 2 Monthly comparisons of modelled and measured (a) soil water content (SWC, mm) (b) leaf area index (m^2 leaf m^{-2} ground, projected; dotted line is total LAI of understorey and trees) (c) gross ecosystem production (GEP, g C m^{-2} month^{-1}), and (d) water vapour exchange (LE, mm mo^{-1}) using the 3-PG and PnET-II models. Months 1–12 are for the last year of the 15–20 years equilibration of the models with the mean of 1996 and 1997 climate data. Months 13–24 are for 1996 climate, and months 25–36 are for 1997 climate (1996 and 1997 were run sequentially). 'Measured' soil water content was calculated from a simple one-dimensional water balance approach using the difference between measured precipitation and LE, and accounting for runoff when soil water content reached saturation. The model results are for soil water holding capacity set to 300 mm.

production were greater than observed values. The normalized yield table data for a 50–70-y-old stand, however, came close to that predicted by 3-PG (149 g C m^{-2} y^{-1}). The carbon balance for the mixed-age stand, on the other hand, suggests that the model allocated much more carbon to stem production than field estimates indicated, a similar proportion of GEP allocated below-ground (~41% vs. ~45% from field measurements), and slightly more of the below-ground carbon allocation to root production (55% vs. 50% assumed in field estimates; Table 4).

Flux estimates of monthly GEP indicate a rapid increase from January to May and little increase in GEP during the summer months. The 3-PG estimates of monthly GEP increased more sharply from winter to summer and peaked in June, effectively underestimating GEP in fall through spring and overestimating GEP in summer (Fig. 2). Although a high soil water-holding capacity value was used to parameterize the model at the beginning of each year, the model appears to allow stomatal conductance to remain high in summer, using much of the available water (down to 80 mm) and reducing rates of carbon uptake in fall. There was a reasonable correlation between predicted and observed monthly GEP over the 24 months ($r^2 = 0.61$; Table 6). The slope was not statistically different from 1, but the intercept was significantly different from 0. The 3-PG estimates of annual GEP were 26 and 39% lower than flux and chamber estimates in 1996 and 1997, outside the error of measurements (Table 4).

As with GEP, the model generally underestimated monthly LE in autumn to spring (Fig. 2). Our below-canopy flux measurements combined with above-canopy fluxes suggest that ~50% of LE was evaporation from the soil and understorey vegetation in autumn through spring and ~25% in the dry summer months. The model assumes that only 15% of rainfall is intercepted by the canopy (and surface litter in open canopies) and is evaporated, and this amount is combined with transpiration to estimate whole ecosystem LE. Predicted vs. observed monthly LE for the 24 months yielded an r^2 of 0.59, with a statistically nonsignificant slope and intercept (Table 6). On an annual basis, the model estimates of LE were within the error of the flux measurements; 3-PG underestimated LE by 17% in 1997, but values were similar in 1996 (Table 4).

The model assumption that autotrophic respiration, R_a, is 53% of GEP is close to independent estimates for the site using chamber and mensuration data (R_a/GEP = 0.55; Law *et al.* 1999a). The use of a fixed ratio of NPP/GEP allows estimates of root respiration as a function of below-ground NPP, assuming soil carbon storage is at steady state. Annual NEP, calculated from (2), was 250 and 209 g C m^{-2} y^{-1} in 1996 and 1997, lower

than flux estimates (NEP$_f$) by 21 and 23%, respectively, but within the error of measurements (Table 4).

Evaluation of PnET-II

In PnET-II, we varied foliar N, LAI, and θ$_c$ by ± 20%, independently, for the sensitivity tests (Table 5). Altering either foliar N or LAI by 20% had nearly identical, symmetrical effects on GEP (~7% in 1996, and ~4% in 1997) and LE (1–3% change). In a stand with such low LAI, increasing either A_{max} through foliar N or LAI has the effect of increasing photosynthetic capacity. Using 300 mm as the baseline θ$_c$, a 20% change in θ$_c$ had little effect on GEP (1–10%) and LE (1–12%). The lower response in GEP and LE in 1997 is due to the lower water availability (greater drought stress). In a system where soil water recharge does not occur, as in 1997, precipitation is more important than the storage capacity in simulations by both models. We increased precipitation by 20% in PnET-II, which yielded an increase in GEP by 1% in 1996, and 15% in 1997, when soil water was below capacity all year. PnET-II does not handle large water-holding capacities well. The 300 mm of available water would require 2 m of stone-free soil, fully rooted for water uptake. PnET-II spreads available water over this entire depth, causing equally low soil water potential everywhere. A better algorithm would split the soil into two or more layers to simulate less negative water potential in the upper layer right after rainfall, and hence less water stress.

When PnET-II was run with the soil water-holding capacity of 300 mm (PnET-II$_{300}$), the predicted maximum LAI was 1.8, slightly higher than measured values for trees (1.6), but the same as our estimate for trees plus understorey shrubs and herbs (Fig. 2; Law *et al.* in review (b)). Increasing soil water holding capacity from 163 to 300 mm resulted in a closer comparison of annual values of GEP and NEP with measurements. When θ$_c$ was increased from 163 to 300, modelled annual LE increased by 28% in 1996 to 472 mm, but there was little effect on annual LE in 1997 (256 mm), again because soil water recharge did not occur through the winter of 1996–97. In the following discussion, we compare measurements and predictions from runs with θ$_c$ set at 300 mm. Canopy equilibrium was reached after running the model for 15 years on the mean of 1996 and 1997 climate. Then we ran the model on 1996 and 9997 data sequentially, as for 3-PG.

The correlation between predicted and observed monthly GEP for the 24 months was fair ($r^2 = 0.41$; Table 6). The slope and intercept were not statistically significant, although the standard errors of the estimates were large. The predicted annual GEP was 5% less than measurements in 1996 (within the error of measure-

Table 6 Regression coefficients from predicted vs. observed monthly gross ecosystem production (GEP), net ecosystem production (NEP), and latent heat flux (LE), for 24 months (1996 and 1997). The intercept is a, the slope is b, and RSE is the residual standard 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	a	SE	P	b	SE	P	r^2	RSE
GEP								
3-PG	−58	24	0.02*	1.24	0.21	0.27	0.61	44
PnET-II	−30	32	0.35	1.11	0.29	0.70	0.41	59
NEP								
PnET-II	−34	14	0.02*	2.38	0.50	0.01*	0.51	37
LE								
3-PG	2.1	5.7	0.71	0.82	0.14	0.23	0.59	13
PnET-II	−8.5	9.6	0.39	1.12	0.25	0.63	0.49	22

ments), and 31% less than measured GEP in 1997 (outside the error of measurements).

The correlation between modelled and measured monthly NEP was reasonable ($r^2 = 0.51$; Table 6 and Fig. 3), but the slope and intercept were statistically significant. Again, the standard errors of the estimates were large. The annual predicted NEP values were 11% lower and 8% higher than measurements in 1996 and 1997, within the error of measurements (Table 4).

The annual R_e predictions were within the error of measurement in 1996, but lower than measured values by ~41% in 1997 and outside the error of measurements. In 1997, the predictions of annual foliage respiration were more than 50% greater than measured values, and predicted soil CO_2 fluxes were ~83% lower than chamber estimates, so it appears that the overestimation of foliage respiration was offset to some extent by underestimation of soil CO_2 fluxes in predicting R_e. The carbon budget suggests that although predictions of total NPP were within 8–11% of measured values for both years, too much carbon was allocated to wood production (more than twice measured values and outside the error of measurements), and to foliage production (34 and 55% greater than measured values). The soil CO_2 flux comparisons suggest that not enough carbon was allocated below-ground in the model.

The correlation between predicted and observed monthly LE for the 24 months yielded an r^2 of 0.49 (Table 6). The slope and intercept were not statistically significant, although the standard errors were large. Annually, predicted LE was greater than measurements by 9% in 1996 (within the error of measurements) and less than measurements by 36% in 1997 (outside the error of measurements; Table 4).

Seasonally, PnET-II$_{300}$ predictions of monthly LE, GEP, and NEP were higher than flux measurements in early summer (particularly 1996), and dropped to rates lower than measured values before summer's end when simulated water availability was near zero (Fig. 2). GEP and LE were probably underestimated by PnET-II in 1997 because the simulated water availability never

recovered in the winter of 1996 through spring 1997, and the potential photosynthesis and water balance modules allowed rapid use of available water as incident radiation increased in summer (Fig. 2). If recharge occurred by run-on or subsurface flow of water in early 1997, this might explain the underestimates by the model in 1997.

We applied a simple 1D model to estimate soil water content using the difference between precipitation and measured LE, and assuming run-off occurred if a soil water-holding capacity of 300 mm was exceeded (Plauborg 1995). The results suggest that there was less depletion of soil water in winter 1996/1997, and more recharge in spring 1997 than PnET-II$_{300}$ predicts (Fig. 2a).

To evaluate the monthly water-use efficiency (WUE) from measurements and the models as a function of D, we combined the above-minus below-canopy LE to determine a mean monthly fraction of total LE that was from transpiration, and plotted WUE (GEP/transpiration) vs. D (Fig. 4). It appears that the 3-PG estimates of WUE are lower than flux estimates, but PnET-II values are fairly close to flux estimates. At least for the 3-PG model, this may explain the rapid use of available water, and the resulting underestimation of GEP from late summer to winter.

Differences among the measured data and predictions by the two models can be focused on two processes: GEP and below-ground carbon allocation. Measured GEP is the combination of daytime ecosystem respiration estimated from scaled-up chamber measurements and daytime NEP measured by eddy covariance. It is possible that uncertainties in measurements (chamber error ± 20% and eddy covariance error ± 12%) resulted in overestimates of GEP, but the 3-PG and PnET-II$_{300}$ predictions of GEP were mostly outside the error of measurement. The two models differ considerably in their allocation of carbon to above- and below-ground components. In PnET-II, wood maintenance respiration is a fixed fraction of GEP, foliar respiration is a fraction of A_{max} (0.10) modified by a Q_{10} function (Q_{10} of 2), and root allocation is a function of foliar production, relying on a
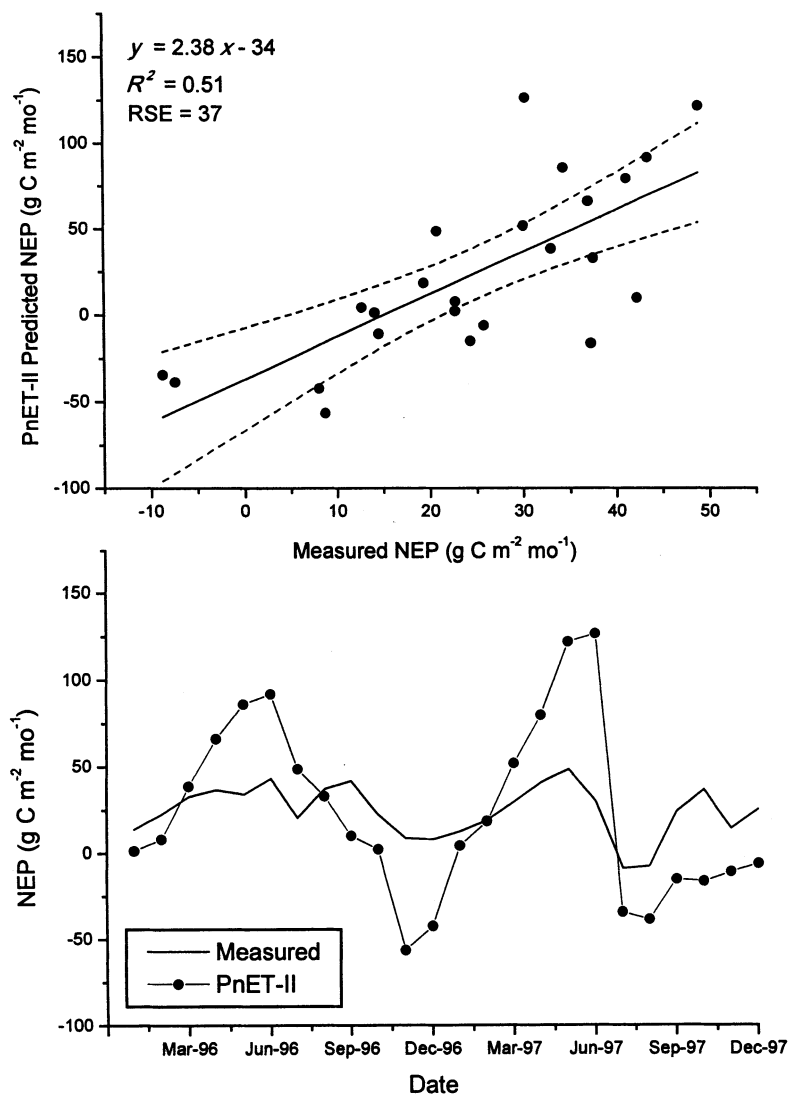
Fig. 3 Measured and modelled net ecosystem productivity (NEP), using PnET-II and parameterized with soil water holding capacity of 300 mm. The regression line and the 95% confidence interval (dashed lines) are shown.

global-scale relationship between these two variables (Raich & Nadelhoffer 1989). Root allocation is divided evenly between production and respiration. Previously, we showed that the Raich and Nadelhoffer equation ($B_{p+c+m} = 130 + 1.92$ litterfall carbon) underestimated below-ground carbon allocation at the site by 32% when compared with the difference between annual soil surface CO_2 flux and litterfall carbon (Raich & Nadelhoffer 1989; Law *et al.* 1999a). An analysis across sites by Gower *et al.* (1996) suggested that use of the Raich and Nadelhoffer equation is not appropriate at specific sites because of differences in allocation patterns associated with species characteristics and resource availability, and violation of certain assumptions (e.g. soil carbon storage is near steady state). The use of the Raich and Nadelhoffer equation in PnET-II could explain the underestimation of root production and overestimate

of wood production compared with measurements. In 3-PG, carbon is allocated as a fraction of total biomass based on local allometric equations; more carbon was allocated below ground by 3-PG than by PnET-II. Clearly, there is still much uncertainty in our understanding of carbon allocation patterns in forest ecosystems.

Conclusions

Although ponderosa pine is a major forest type in the western U.S. (Elias 1980), little is known about the seasonal and annual variation in the carbon cycle of this ecosystem with climate. Net ecosystem productivity peaks in the moderately warm, wet spring and levels off in the dry summer months. The dry growing season and relatively low leaf area (<3 projected LAI) prove
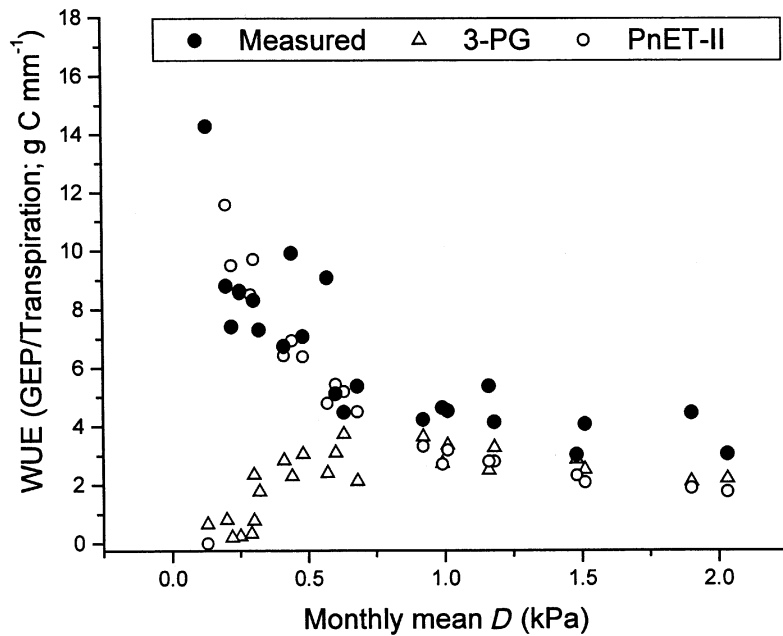
Fig. 4 Measured and modelled water use efficiency (WUE = GEP/transpiration) vs. monthly mean daytime D. Measured GEP was calculated from eqn (1), and transpiration was calculated from the seasonal fraction of above-to below-canopy LE.

challenging to the prediction of seasonal variation in gross and net ecosystem productivity with models.

Simulations with a range of moderate to low soil fertility suggest that environmental factors other than fertility limit carbon assimilation and allocation throughout the year in this semiarid region. In more humid regions, where LAI is high, light levels are low at the bottom of the canopy, and water stress is moderate, foliar N (A_{max}) is the most sensitive variable, as shown with PnET-Day at a temperate deciduous forest (Harvard Forest; Aber *et al.* 1996).

Our model tests show that it is important to characterize soil water availability and water-use well in these ecosystems. The models appear to allow much greater carbon uptake and water use in early summer than actually occurs; then simulated available water becomes negligible and carbon uptake declines in late summer more than observed fluxes indicate. In an ecosystem where soil water recharge does not occur, precipitation appears to be more important than the storage capacity. Both models distribute available water over the entire rooting depth, causing equally low soil water potential everywhere. A better algorithm would split the soil into two or more layers to simulate variation in water potential through the soil profile, allowing less water stress following rainfall.

Because the old-growth ecosystem contained a variety of age classes, it was difficult to apply the 3-PG model assuming a uniform age. Similarly, age-related differences in A_{max} probably limit PnET-II predictions, but to a lesser extent than accurate simulation of soil water availability in this ecosystem.

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