

Seasonal and annual respiration of a ponderosa pine ecosystem

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Abstract

The net ecosystem exchange of CO₂ between forests and the atmosphere, measured by eddy covariance, is the small difference between two large fluxes of photosynthesis and respiration. Chamber measurements of soil surface CO₂ efflux (F_s), wood respiration (F_w) and foliage respiration (F_f) help identify the contributions of these individual components to net ecosystem exchange. Models developed from the chamber data also provide independent estimates of respiration costs. We measured CO₂ efflux with chambers periodically in 1996–97 in a ponderosa pine forest in Oregon, scaled these measurements to the ecosystem, and computed annual totals for respiration by component. We also compared estimated half-hourly ecosystem respiration at night (F_{nc}) with eddy covariance measurements. Mean foliage respiration normalized to 10 °C was 0.20 $\mu\text{mol m}^{-2}$ (hemi-leaf surface area) s^{-1} , and reached a maximum of 0.24 $\mu\text{mol m}^{-2}$ HSA s^{-1} between days 162 and 208. Mean wood respiration normalized to 10 °C was 5.9 $\mu\text{mol m}^{-3}$ sapwood s^{-1} , with slightly higher rates in mid-summer, when growth occurs. There was no significant difference ($P > 0.10$) between wood respiration of young (45 years) and old trees (250 years). Soil surface respiration normalized to 10 °C ranged from 0.7 to 3.0 $\mu\text{mol m}^{-2}$ (ground) s^{-1} from days 23 to 329, with the lowest rates in winter and highest rates in late spring. Annual CO₂ flux from soil surface, foliage and wood was 683, 157, and 54 $\text{g C m}^{-2} \text{y}^{-1}$, with soil fluxes responsible for 76% of ecosystem respiration. The ratio of net primary production to gross primary production was 0.45, consistent with values for conifer sites in Oregon and Australia, but higher than values reported for boreal coniferous forests. Below-ground carbon allocation (root turnover and respiration, estimated as F_s – litterfall carbon) consumed 61% of GPP; high ratios such as this are typical of sites with more water and nutrient constraints. The chamber estimates were moderately correlated with change in CO₂ storage in the canopy (F_{stor}) on calm nights (friction velocity $u^* < 0.25 \text{ m s}^{-1}$; $R^2 = 0.60$); F_{stor} was not significantly different from summed chamber estimates. On windy nights ($u^* > 0.25 \text{ m s}^{-1}$), the sum of turbulent flux measured above the canopy by eddy covariance and F_{stor} was only weakly correlated with summed chamber estimates ($R^2 = 0.14$); the eddy covariance estimates were lower than chamber estimates by 50%.

Keywords: carbon allocation, carbon balance, carbon exchange, eddy covariance, micrometeorology, net primary production, photosynthesis, *Pinus ponderosa*, respiration, vegetation–atmosphere interaction

Received 23 October 1997; revised version received 26 January and accepted 12 February 1998

Symbols

ANPP above-ground net primary production (foliage + wood) ($\text{g C m}^{-2} \text{ground}$)

dbh diameter of tree measured at breast height (1.4 m)

F_{ca} CO₂ flux density measured above the canopy ($\mu\text{mol m}^{-2} \text{ground s}^{-1}$)

F_{cb} CO₂ flux density measured below the canopy ($\mu\text{mol m}^{-2} \text{ground s}^{-1}$)

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F_f	flux density of CO ₂ for foliage (μmol m ⁻² ground s ⁻¹)	GPP	gross primary production (NPP + R _a)
F_{ne}	Eddy covariance estimates of ecosystem CO ₂ flux density at night (nocturnal ecosystem respiration) (μmol m ⁻² ground s ⁻¹)	HSA	hemi-surface area of leaves, half the total leaf surface area (m ²)
F_{nc}	Chamber estimates of ecosystem CO ₂ flux density at night (μmol m ⁻² ground s ⁻¹)	LAI	leaf area index (m ² leaf m ⁻² ground, projected)
F_s	flux density of CO ₂ for soils (μmol m ⁻² ground s ⁻¹)	NEE	net ecosystem exchange of CO ₂ (μmol m ⁻² s ⁻¹) (NEE = NEP = GPP - (R _a + R _h))
F_{stor}	change in CO ₂ storage within the air column of the canopy (μmol m ⁻² ground s ⁻¹)	NPP	net primary production (wood + foliage + roots) (g C m ⁻² ground)
F_w	flux density of CO ₂ for wood biomass in live trees (μmol m ⁻² ground s ⁻¹)	R _a	autotrophic (plant) respiration
		R _h	heterotrophic (microbial plus animal) respiration
		u*	friction velocity (m s ⁻¹)

Introduction

Net ecosystem exchange of carbon (NEE) between forests and the atmosphere has become a focus of global change research because temperate and boreal forests may be storing a large fraction (35% per year) of the carbon released from burning fossil fuels (Tans *et al.* 1990; IPCC 1995). NEE is the small difference of the two large fluxes of photosynthetic CO₂ uptake and the release of carbon to the atmosphere by autotrophic (R_a) and heterotrophic (R_h) respiration. Because NEE is typically an order of magnitude less than photosynthesis or respiration (Goulden *et al.* 1996a), an understanding of biological and physical controls on photosynthesis and respiration is necessary to estimate how NEE will respond to environmental change.

Even though respiration fluxes nearly equal input from photosynthesis, respiration has received much less attention in measuring and modelling. Models of respiration are often simple one or two box models, with respiration represented as a simple function of temperature (e.g. Sellers *et al.* 1997), even though control of respiration is more complicated (Ryan *et al.* 1997). Few studies have made concurrent measurements of component CO₂ fluxes within stands in relation to environmental variables (Jarvis 1995). However, there is increasing evidence that respiration fluxes, particularly from heterotrophs, strongly influence short and long-term NEE (Goulden *et al.* 1996a; Goulden *et al.* 1997).

It would be useful to develop biome-specific parameters, such as the ratio R_a:GPP (gross primary production), for regional and global carbon balance modelling to circumvent uncertainties associated with calculating respiration. Some studies suggest that the ratio R_a:GPP is fairly conservative at 0.53 ± 0.04 across forest ecosystems (Waring *et al.* 1998), yet data from other sites suggest it ranges between 0.50 and 0.70 (Amthor & Baldocchi 1998), and Ryan *et al.* (1997) estimated the ratio for boreal forests

at 0.71 ± 0.02 . Some of the variation is likely due to uncertainty of the stand-level estimates of respiration and GPP.

Robust estimates of respiration are necessary to estimate carbon losses at night, and also to estimate photosynthesis during the day from eddy covariance measurements of NEE. Eddy covariance measurements, F_{ca} above the canopy at night, may not be reliable, because of poor mixing (Wofsy *et al.* 1993; Hollinger *et al.* 1994; Grace *et al.* 1995; Black *et al.* 1996; Goulden *et al.* 1996b; Baldocchi *et al.* 1997). When mixing is poor, changes in CO₂ concentration within the air layer below the tower flux instruments (F_{stor}) combined with eddy flux measurements (F_{ca} + F_{stor}) improves estimation of ecosystem respiration (Wofsy *et al.* 1993; Jarvis 1994; Ruimy *et al.* 1995; Black *et al.* 1996; Goulden *et al.* 1996a; Baldocchi *et al.* 1997), but this approach may still underestimate fluxes at some sites compared with chamber estimates (Goulden *et al.* 1996b; Lavigne *et al.* 1997). Chamber measurements of respiration provide an alternative estimate of ecosystem respiration, and identify the environmental and biological controls on component fluxes.

In this study, we measured respiration by foliage (F_f), wood (sapwood and cambial activity of living trees; F_w), and CO₂ efflux from soil surface (root respiration and respiration by soil heterotrophs; F_s). We developed empirical models of F_s, F_f, and F_w from measurements of these components throughout the year, and compared scaled up chamber measurements to estimates of respiration made from nocturnal eddy flux and CO₂ storage. Next, we extrapolated our chamber measurements to an annual budget using half-hourly soil, air, and sapwood temperature, and assessed the contribution of these components to the annual carbon budget for a ponderosa pine forest (*Pinus ponderosa*). Finally, we compared our results with

Table 1 Characteristics of the dominant old trees and patches of young trees at the ponderosa pine site [mean (SE)]

	Young stands	Old stands
Age of trees	45	250
Leaf area index (m ² leaf m ⁻² ground)	1.5 (0.10)	1.5 (0.10)
Trees per hectare	555	72
Tree height (m)	10 (0.2)	34 (0.8)
Diameter breast height (cm)	12 (0.2)	63 (2.7)
Sapwood volume (m ³ sapwood ha ⁻¹)	37 (0.1)	293 (3)
Soil Nitrogen (%)	0.149 (0.021)	0.098 (0.022)
Humus Nitrogen (%)	0.974 (0.185)	0.592 (0.109)
Soil carbon content of top 1 m (kg m ⁻²)	5.90 (0.9)	3.52 (1.17)
Annual litterfall biomass (g m ⁻² ground)	500 (75)	310 (43)

those from studies on other forest ecosystems with different climatic constraints.

Methods

Study site

The Metolius site is a ponderosa pine (*Pinus ponderosa*) forest, located in a Research Natural Area in the Metolius River valley (44°30' N, 121°37' W, elevation 940 m) near Sisters, Oregon. The terrain of the site has a slope between 2 and 6%. The pine forest extends at least 12 km in all directions. The forest consists of old (≥ 250 years), young (≈ 45 years) and mixed old and young patches of ponderosa pine. It has never been logged. The young trees appear to have been the first successful regeneration following initial fire suppression in the area (S. Greene, pers. comm.). Based on data from 45 plots (8 m radius), about 48% of the area is mixed young and old trees, 27% is old, open stands, and 25% is denser patches of younger trees. The canopy of the old and mixed stands is very open. The understorey is sparse with patches of bitterbrush (*Purshia tridentata*) and bracken fern (*Pteridium aquilinum*), and groundcover of strawberry (*Fragaria vesca*).

Soil at the site is a sandy loam and is classified as a light-coloured andic (high in ash content) inceptisol that is low in nutrients. Soil texture analysis from four stands (0–15 cm depth) showed the soil is 73% sand, 21% silt, and 6% clay. Surface litter is scant in the old stands (310 g m⁻²; Table 1) and the young stands (500 g m⁻²).

The site experiences warm, dry summers and wet, cool winters. Total precipitation in 1996 was 600 mm, a wetter than normal year. At a nearby weather station (Sisters, OR) the 1996 total precipitation was about 162% of the

normal annual total for the years 1961–90. The mean precipitation for July and August is about 21 mm and the mean temperature at this time is ≈ 17 °C (Oregon Climate Service, pers. comm.). At our site in July and August 1996, air temperatures at 1 m height ranged from a minimum of -1 °C at night to a maximum of 37 °C in the day, and there was no rain over the two months. Winter snow cover was intermittent, reaching a maximum depth of about 50 cm.

Soil surface CO₂ efflux

We measured soil surface CO₂ efflux (F_s) on 23 days over the year in old, young and mixed-age stands, with a LI-COR 6200 infrared gas analyser (IRGA) in a closed circuit and a LI-COR 6000–09 chamber (chamber volume of 1152 cm³; LI-COR, Inc., Lincoln, NE). Soil temperature was measured concurrently with an attached temperature probe (15 cm depth). Before we began this study, we compared soil collar depths and chamber sizes to determine the best approach to sampling effluxes from pine forest soils with chambers. We found no significant difference between collar depths of 3 and 9 cm ($P = 0.41$), and no significant difference between the LI-COR chamber (71.5 cm² soil surface area) and a larger chamber (299 cm² surface area; $P = 0.62$). Soil collars were placed in the soil at least 24 h before measurements to avoid influences of soil disturbance and root injury on the measurements. Living vegetation was clipped at the soil surface inside the soil collar at the time of placement. Prior to each measurement, the CO₂ level in the chamber was drawn down to below ambient CO₂ concentration, and the measurement taken as [CO₂] increased through ambient. The flow rate was maintained at ≈ 800 $\mu\text{mol s}^{-1}$. Five observations were recorded per measurement, and each measurement took less than five minutes. There were five young, five old, and five mixed stands (3 collars per stand) where we measured F_s during the growing season. We continued measurements at two stands of each type through the winter, when there was no snow on the plots. To determine if F_s differed between old and young stands, we used an analysis of variance test with repeated measures.

Foliage respiration and photosynthesis

We measured nocturnal foliage respiration rates (F_f) of the overstorey pine on four days through the year (February, April, June, July). On Day 208, F_f was sampled on three age classes at three heights in the canopy (ponderosa pine normally carries foliage for four years). We found that respiration rates of age class 1 (previous year growth) averaged 10% higher than rates of foliage formed three years prior to measurement (class 3), and

that rates for expanding foliage (class 0) averaged 10% higher than for age class 1. Foliage expansion occurred from mid-May to mid-August. Because expanding foliage was a small fraction of total foliage biomass (25% maximum), and F_f for expanding foliage of conifers showed little seasonal difference that could be attributed to construction respiration (Ryan *et al.* 1997), we did not estimate respiration of expanding foliage separately. Because our initial sample showed little difference among canopy positions and foliage age classes (not surprising since ponderosa pine is very intolerant of shade), we assumed that age class 1 represented the mean for all classes. We made measurements on four to six samples of age class one at mid-canopy on two trees on the other dates.

Foliage respiration was measured with a LI-COR 6400 open system (LI-COR, Inc., Lincoln, NB) at night (21.00–02.00 hours) on all dates, but most of the data for Day 208 was from an ADC LCA3 open system (Analytical Development Company, Hoddeston, Herts, UK). The LI-COR and ADC were compared after the measurements on Day 208, and the measurements were within 10%. We used 9 needles (3 fascicles) in all of the LI-COR measurements, and several fascicles in the ADC measurements. We evaluated the temperature response of F_f by using the cuvette temperature in the relationship.

Foliage was removed from branches after sampling and the leaf area that was in the cuvette was measured with calipers. We converted projected leaf area to total surface area with a conversion factor (2.36) developed for ponderosa pine (B. Bond, pers. comm.), then divided by two to get hemi-surface area (HSA; one-half the total surface area) (Chen *et al.* 1997). Foliage samples were stored at < 5 °C prior to analysis of nitrogen. Flux rates per unit leaf area were calculated per m^2 HSA, and half-hourly estimates per m^2 ground.

To determine whether foliage respiration by *P. ponderosa* increased seasonally as maximum photosynthesis increased, we measured photosynthetic light response from about 10.00–12.00 hours on five days through the year with a LI-COR 6400 open system (LI-COR, Inc., Lincoln, NB). We sampled foliage age class 1 from the mid-to upper-canopy. The light level in the cuvette was incrementally reduced from a maximum of 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while maintaining temperature and relative humidity at ambient conditions.

Wood respiration

Wood respiration rates (F_w) were measured on five days in 1996 from January to October (days 9, 156, 184, 213, and 284). We sampled 10 young trees (< 27 cm dbh, 45 years) and 10 old trees (33–87 cm dbh, about 250 years). The measurements were made on the north side of each

tree with an ADC LCA3 open system using methods similar to Ryan (1990). The chambers were a clear acrylic with a fan, and enclosed part of the stem circumference 1.5 m above the ground. Ponderosa pine bark is thick and furrowed. The stems were prepared by carving a groove through the loose bark, and attaching a permanent frame in the groove with putty. We ensured that there was a good seal between the chamber and stem. Sapwood temperature was measured next to the chamber (2 cm depth) during each of the measurements, using thermocouple wire and a digital thermometer. Sapwood temperature was also recorded with thermocouples continuously (half-hourly) on three young and three old trees through much of the year. We used analysis of variance to test for differences between F_w and sapwood temperature of young and old trees on all sample days.

Annual estimates for the site

The chamber measurements of respiration throughout the year were used to estimate annual respiration for the site (March 1996 to March 1997). Temperature response equations were developed for each respiration component. We then normalized F_f , F_s and F_w using component-specific temperature equations. Fluxes were normalized with:

$$F_b = F_i \cdot \exp[\beta (T_b - T)], \quad (1)$$

where F_b is the flux rate at base temperature, F_i is the measured flux rate from component i (foliage, wood, soil), β is the exponential coefficient from the component temperature response equations, T_b is the base temperature (10 °C for all three components), and T is temperature measured at the time and location of the flux measurement (°C air temperature for F_f , bole temperature for F_w and soil temperature at 15 cm for F_s). The β coefficient is based on flux measurements made through the year and likely includes the effects of influences other than temperature (e.g. tissue repair). To estimate rates between sample dates, we used linear interpolation of the normalized rates. Half-hourly respiration rates were then calculated from the continuous temperature data using a generic equation:

$$R_i = M_i \cdot F_b \cdot \exp[\beta (T - T_b)], \quad (2)$$

where R_i is the respiration for component i (foliage, wood, soil), and T is the half-hourly temperature (air temperature for F_f , estimated bole temperature for F_w and soil temperature at 15 cm for F_s). M_i is the mean sapwood volume (m^3 sapwood m^{-2} ground) or leaf area ($m^2 m^{-2}$ ground). M_i is not in the soil equation because F_s was measured per m^2 ground. The same methods for estimating half-hourly respiration rates throughout the year were applied by Ryan *et al.* (1998).

Table 2 Temperature response equations used to estimate half-hourly respiratory flux of carbon from foliage, wood, and soils, where T_s is soil temperature (15 cm depth), T_a is air temperature at 45 m, and T_w is sapwood temperature at 2 cm depth in °C. Flux rates for soil (F_s) are expressed in $\mu\text{mol m}^{-2}$ ground s^{-1} , foliage (F_f) per m^2 leaf hemi-surface area, and wood (F_w) per m^3 sapwood under the chamber. The number of soil samples reflects the mean of three subplots per stand in 1 young, 1 old and 1 mixed stand on 23 days through the year, F_f is from 8 to 9 individual foliage samples on four days through the year, and F_w is from 20 trees on five days through the year (15 of the F_w data points were missing due to rain or instrument failure)

Component	Equation	R^2	N	Q_{10}
Soils (F_s)	$1.216 \exp(0.059 T_s)$	0.61	69	1.8
Foliage (F_f)	$0.104 \exp(0.073 T_a)$	0.76	34	2.1
Wood (F_w)	$2.894 \exp(0.077 T_w)$	0.49	85	2.2

Soils

In Law *et al.* (1998), we evaluated empirical models for estimating F_s from soil moisture at 0–30 cm and 0–100 cm, soil temperature at various depths, carbon and nitrogen in mineral soil, humus and litter layers, and litterfall biomass at the ponderosa pine site. The model with the best fit included soil temperature (measured at 15 cm), the C:N ratio of litter, and soil water content at 0–100 cm (RSE = 0.539). To calculate half-hourly F_s and sum over the year, we applied the soil temperature model (RSE = 0.544) because the more complex model required more soil moisture data than we had available, and the RSEs were not much different. The model we used in the present study is:

$$F_s = 1.216 \cdot \exp(0.059 \cdot T_s) \quad (R^2 = 0.61, \text{RSE} = 0.544), \quad (3)$$

where T_s is soil temperature at 15 cm depth ($Q_{10} = 1.8$; Table 2). We estimated F_s from soil temperature measurements recorded over a year at half-hourly intervals at 15 cm depth in young, old and mixed stands and took the mean to represent the site.

Foliage

We scaled foliage respiration to the site with leaf area index (LAI), which, because of the open nature of the canopy, was estimated by two methods. First, we made concurrent measurements of canopy light transmittance (Q_t) and ambient photosynthetically active radiation (ambient PAR = Q_o) with Decagon ceptometers (Decagon Devices, Pullman, Washington), at mid-day with clear skies following methods described by Law & Waring (1994). Ambient direct and diffuse PAR were recorded continuously at the top of the flux tower above the forest canopy and transmitted PAR measurements were made 200 m apart at plots along four 2000 m transects. Trans-

mitted PAR was measured at the plot centre ($n = 45$ plots), and in four orthogonal directions 8 m from plot centre, for a total of 225 sample stations. LAI was calculated from the equation:

$$\text{LAI} = \ln(Q_t/Q_o) \cdot ((1-0.5/K) \cdot f_b - 1) / (0.86 \cdot (1-0.47 \cdot f_b)) \quad (4)$$

where f_b is fraction direct beam (0.97 from diffuse and direct PAR measurements), K ($= 0.5/\cos \theta$) is the extinction coefficient, and θ is the zenith angle calculated from latitude (44.5°N), day, and hour of day (Rosenberg *et al.* 1983). We also made measurements with a LI-COR LAI-2000 plant canopy analyser (PCA; LI-COR, Lincoln, Nebraska) on an overcast morning. A second PCA at the top of the 45 m tower recorded readings every 30 s during the time of the below-canopy measurements. The diffuse nonintercepted measurements (DIFN) were made on a 100 m \times 100 m plot at five m grid points for a total of 242 sample points.

We estimated leaf area of the understory vegetation using the line intercept method within a 1 m \times 1 m frame. Thirteen plots were established along two transects 180 m in length. Because most of the understory was *Fragaria vesca* (flat, planophile leaves), LAI and HSA were estimated to be the same as the percentage cover.

To obtain estimates of foliage respiration through the year, we used the air temperature data (°C) recorded at 45 m height on the flux tower. Ideally, we would have used air temperature measured within the canopy, but there was little difference between air temperature at 8 m height and 45 m. The canopy is quite open, and data in the old stand showed that air temperature at 8 m height was only 6% lower than temperature at 45 m at night and 4% higher in the day. Because foliage respiration was not measured at night on *F. vesca*, we estimated F_f of this species from seasonal changes in the fraction of daytime respiration (photosynthetic light response at 0 PAR) by *F. vesca* vs. *P. ponderosa*. We applied this fraction to the temperature response equation for *P. ponderosa*. Foliage respiration rates were converted from m^2 HSA to m^2 ground in (2).

Wood

To estimate half-hourly wood respiration for the year, we developed a regression relationship between measured CO_2 efflux ($\mu\text{mol m}^{-3}$ sapwood under the chamber s^{-1}) and sapwood temperature. The equation incorporates both the response of instantaneous respiration to temperature and seasonal changes in respiration in response to changes in phenology (primarily growth).

Sapwood volume for the site was estimated by sampling 45 8-m-radius plots throughout the site (the same plots that we used for PAR measurements). At each plot,

we measured tree height and diameter at breast height (dbh = diameter at 1.4 m height) on all trees, and determined sapwood radius and mean annual growth in the past five years from wood cores taken on the first and fifth tree. The data were divided into two diameter classes of trees (≤ 30 cm dbh, and > 30 cm). Stem biomass was calculated from an allometric equation developed at the site using optical dendrometry (S. Acker, pers. comm.; Means *et al.* 1994), and branch biomass was calculated from an allometric equation for ponderosa pine (Gholz 1982). Sapwood volume per tree was calculated as the outer cylinder of the stem (less bark), using sapwood radius, bark radius and biomass data. Branches were assumed to be 100% sapwood. Sapwood volume ($\text{m}^3 \text{m}^{-2}$ ground) was determined from sapwood volume per tree and number of trees per unit ground area in each class.

Because sapwood temperature was not recorded for the whole year, we developed a lag correlation between sapwood temperature and air temperature at 45 m to estimate F_w half-hourly.

Annual net and gross primary production

Annual above-and below-ground net primary production (NPP) was calculated to determine the ratio of NPP to gross primary production ($\text{GPP} = \text{NPP} + R_a$). Above-ground stemwood production was calculated as the difference between current biomass and biomass of the previous year, which was determined from the allometric equations and mean annual growth increment of the wood cores. The same procedure was used for branch production. These calculations were made on the young and old classes separately, scaled to site by the trees per m^2 in each class and then summed. Foliage biomass was determined from measurements of specific leaf area ($\text{m}^2 \text{leaf g}^{-1}$ dry weight) and the mean leaf area. Foliage production was calculated from the fraction of total foliage biomass that was newly expanded foliage, which was determined from a subsample of branches from at least 12 trees. Wood and foliage production were summed to estimate above-ground net primary production (ANPP).

We estimated below-ground carbon allocation (B_{p+c+m} = sum of root production, construction and maintenance respiration) from our measurements of soil respiration and litterfall and from the Raich & Nadelhoffer (1989) equation:

$$B_{p+c+m} = 130 + 1.92 \cdot L_f \quad (5)$$

where L_f is annual litterfall carbon ($\text{g C dry weight m}^{-2} \text{y}^{-1}$). Litterfall was collected monthly from 45 traps located near the soil chamber collars. Litter, root and soil carbon can be assumed to be in equilibrium with one another, because this is an older forest that has not been logged,

and the most recent disturbance was an underburn in some stands 3–7 years previously (S. Greene, pers. comm.). In a study on *P. ponderosa* stands near the site, Monleon *et al.* (1997) showed that in the top 5 cm of soil, carbon decreased up to five years after a burn, but there was no significant difference in carbon in the 5–15 cm depth soil layer. Assuming no net change in the soil carbon pool of this ecosystem, and that F_s equals autotrophic respiration (root respiration) plus heterotrophic decomposition of above-and below-ground inputs, then the annual F_s minus the annual input of above-ground litterfall carbon approximates below-ground carbon allocation to roots. We compared estimates made by this method with the model in (5), which is based on the same principles and calculated from data across a variety of sites. Gross primary production was calculated from the sum of below-ground carbon allocation, 24-h F_f , F_w and above-ground NPP.

Nocturnal eddy covariance measurements

Above-canopy wind speed and temperature were measured with a three-dimensional sonic anemometer (Solent model 1012 R2, Gill instruments, Lymington, England). The carbon dioxide and water vapour fluctuations were measured simultaneously with an open-path infrared gas analyser (NOAA ATDD, Oak Ridge, TN; Auble & Meyers 1992). The water vapour and CO_2 sensor responds to frequencies up to 15 Hz, and has a low noise-to-signal ratio. The instruments were positioned at 47 m height, 13 m above the canopy. The CO_2 eddy covariance flux (F_{ca}) between the ecosystem and the atmosphere is proportional to the mean covariance of the vertical wind speed and the co-occurring fluctuations in carbon dioxide concentration. Trends in the wind speed and scalars (e.g. CO_2) were removed with a digital recursive filter following McMillen (1988). Baldocchi & Vogel (1996) suggest that a detrending time constant of 400 s is adequate for flux density calculations, but we tested several time constants (e.g. 50, 200 and 400 s). The flux covariances 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 eddy flux CO_2 data were screened for validity by removal of time periods with (i) high kurtosis in the raw data, (ii) IRGA analogue signal outside the specified range of the sonic, (iii) wind attack angle to the horizontal $> 15^\circ$, (iv) excessive spikes in the sonic and IRGA data (due to moisture on the sensors), and (v) incomplete sampling over the entire half-hour. After screening, about 90% of the nocturnal above-canopy eddy fluxes were available for further analysis.

The CO_2 profile measurements were made with a

closed-path infrared gas analyser (Li-6262; LiCor, Lincoln, NE) and a computer-controlled solenoid-switching system. Half-hourly mean CO₂ concentration profile measurements were made at four heights (1, 8, 31, and 46 m). Air was ducted sequentially from each level for 30 s and the CO₂ concentration was measured during the last 15 s, to allow for purging of the tubing and gas analyser sample cell. The zero offset and gain of the gas analyser was checked with two calibration gases every day at midnight and periodically during maintenance visits. The change in carbon dioxide storage in the canopy (F_{stor}) was estimated by integrating changes in the trend of half-hour CO₂ concentration from the ground to 46 m (Anthoni *et al.* in prep.).

Nocturnal CO₂ flux (F_{ne} ; sunset to sunrise) from eddy covariance measurements was calculated for two different turbulence conditions, when air was not well-mixed (friction velocity $u^* < 0.25 \text{ m s}^{-1}$) and when $u^* > 0.25 \text{ m s}^{-1}$. We calculated F_{ne} for both conditions from F_{stor} alone, and from:

$$F_{\text{ne}} = F_{\text{ca}} + F_{\text{stor}} + F_{\text{adv}} \quad (6)$$

Lateral advection (F_{adv}) was not quantified; it is generally assumed to be negligible. This approach was used in a similar study at Harvard Forest (Wofsy *et al.* 1993) and on boreal forests (Lavigne *et al.* 1997).

We compared chamber estimates of ecosystem respiration (F_{nc}) with F_{ne} during the growing season. Linear regression analysis was used to determine model parameters ($F_i = b F_{\text{nc}}$, where F_i is F_{stor} or $F_{\text{stor}} + F_{\text{ca}}$) for 141 nights in 1996 (when data were collected between days 146 and 294) and differences in means were tested with a paired *t*-test.

Results

Soil surface CO₂ efflux

Daily mean F_s ranged from 0.5 to 3.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (yearly mean = 2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 23 measurement dates). The Q_{10} for the seasonal temperature response was 1.8 (Table 2, $\beta = 0.059$). F_s normalized to 10 °C varied substantially with season, with the lowest rates in winter, and the highest rates in late May (Fig. 1). Soil surface CO₂ efflux was consistently higher in the young stands (2.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$) than in the old stands (2.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $P = 0.08$).

Foliage respiration

The mean nocturnal foliage respiration was 0.27 $\mu\text{mol m}^{-2}$ (leaf hemi-surface area) s^{-1} for the four measurement dates (days 49–208). Measured nocturnal F_f varied seasonally, with the lowest rate in spring (Day 49, 0.08 $\mu\text{mol m}^{-2}$ (HSA) s^{-1}), and the highest rate in July (day 208,

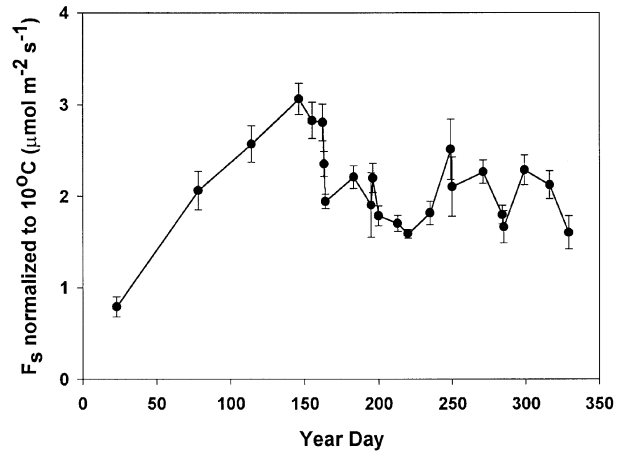


Fig. 1 Soil surface CO₂ flux (F_s) normalized to 10 °C, using the temperature response equation developed from soil temperature and F_s . Rates are expressed per m^2 ground. Error bars show SE.

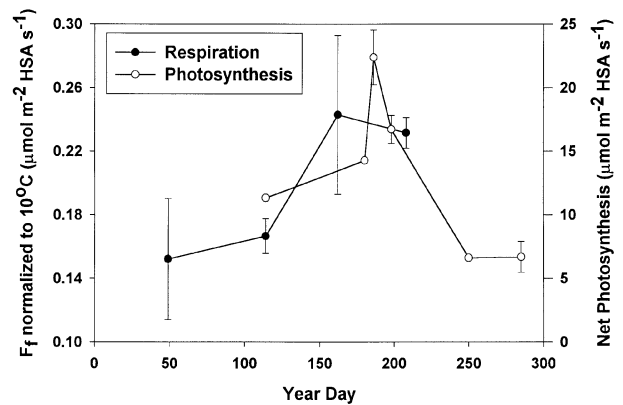


Fig. 2 Foliage respiration (F_f) normalized to 10 °C, using the temperature response equation developed from air temperature at 45 m and F_f . Net photosynthesis (\ominus) measured on same trees, canopy position, and foliage age class. Rates are expressed per m^2 leaf hemi-surface area. Error bars show SE.

0.33 $\mu\text{mol m}^{-2}$ (HSA) s^{-1}). Q_{10} for the temperature response (all samples for the year) was 2.1 (Table 2, $\beta = 0.073$). F_f normalized to 10 °C also showed seasonal variation (Fig. 2). Foliage nitrogen concentration ranged from 2.8 to 5.3 g N m^{-2} leaf (1.1–1.6%), but it explained only 22% of the variation in F_f normalized to 10 °C. In Fig. 2, we show the maximum photosynthetic rate by *P. ponderosa* from light response curves during the year (PAR $\approx 2000 \mu\text{mol m}^{-2} \text{s}^{-1}$). Both photosynthesis and normalized respiration appear to have increased in summer. Maximum photosynthetic rate (vapor pressure deficit $< 1 \text{ kPa}$) was 22.0 $\mu\text{mol m}^{-2}$ (HSA) s^{-1} on day 188; foliage respiration estimated for the same time was 1.1 (5% of net photosynthesis).

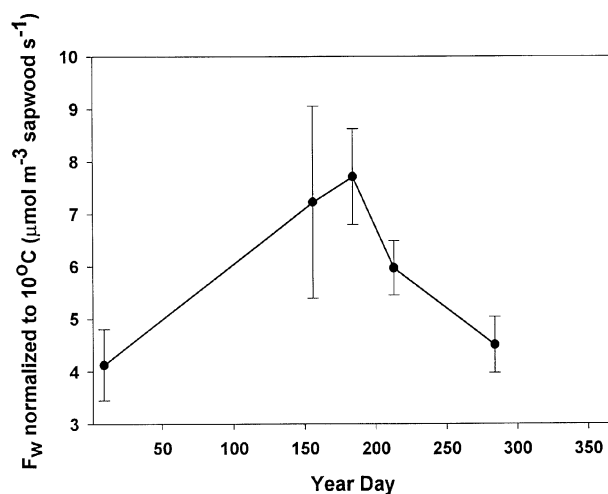


Fig. 3 Wood respiration (F_w) normalized to 10 °C, using the temperature response equation developed from sapwood temperature and F_w . Rates are expressed per m³ sapwood. Error bars show SE.

Wood respiration

Daily mean F_w ranged from 2.5 to 19.5 $\mu\text{mol m}^{-3}$ sapwood s^{-1} (annual mean = 5.9 for five measurement days); sapwood radius averaged 7 cm for the young trees, and 10 cm for the old trees. F_w did not differ between young and old trees ($P > 0.30$), except on Day 213 when F_w for young trees was 50% higher ($P = 0.03$). Sapwood temperature was 0.4–4.2 °C higher for the young trees than for the old trees on four of the five measurement days ($P < 0.10$; range 1–24 °C among days). Q_{10} for seasonal temperature response of F_w was 2.2 (Table 2). F_w normalized to 10 °C varied seasonally, with maximum rates (7–8 $\mu\text{mol m}^{-3}$ sapwood s^{-1}) obtained between days 156 and 184, and minimum rates (4–4.5 $\mu\text{mol m}^{-3}$ sapwood s^{-1}) on days 9 and 284 (Fig. 3).

Annual site estimates

The ceptometer and PCA gave similar estimates of 1-sided projected LAI (1.5 and 1.6, respectively), and we used 1.5 m² leaf m⁻² ground to scale the *P. ponderosa* F_f measurements to m² ground area. Understorey LAI was 0.16. Mean daily estimated F_f (24-h) ranged from 0.1 to 1.6 $\mu\text{mol m}^{-2}$ (ground) s^{-1} throughout the year (annual mean = 0.41). The diurnal amplitude in F_f was larger than that in fluxes from wood and soil. The annual sum of F_f in units of carbon was 157 g C m⁻² y⁻¹ (Table 3).

The old open stands average 72 trees ha⁻¹, 63 cm mean diameter at breast height (dbh), and 34 m height (Table 1). The young trees average 555 trees ha⁻¹, 12 cm dbh and 10 m height. The mean sapwood volume per unit ground area (m³ sapwood m⁻² ground) was 0.0037 for the young trees and 0.0293 for the old trees.

Table 3 Biomass (g C m⁻² ground), respiration (g C m⁻² y⁻¹), and annual net primary production (NPP; g C m⁻² y⁻¹) by component (mean (SE))

Component	g C m ⁻² ground
Biomass:	
Foliage biomass	236
Wood biomass (stem and branch)	9591 (120)
Above-ground biomass total	9826
Annual litterfall carbon	129 (11)
Respiration:	
Annual foliage respiration (F_f)	157
Annual wood respiration (F_w)	54
Annual soil surface CO ₂ flux (F_s)	683
Annual ecosystem respiration (total)	894
Production:	
Annual foliage production	59
Annual above-ground wood production	77 (1)
Annual ANPP (total)	136
Annual below-ground carbon allocation (F_s - litterfall carbon)	554
Annual below-ground carbon allocation (Raich & Nadelhoffer 1989 eqn)	379
Below-ground carbon allocation/GPP	0.61
Below-ground carbon allocation/ F_s	0.81
Below-ground NPP/NPP	0.67
Above-ground NPP/above-ground carbon allocation	0.39
NPP/GPP	0.45

The relationship between sapwood temperature (T_{sw}) and air temperature (T_{air}) was:

$$T_{\text{sw}} = 0.84 \cdot T_{\text{air} - 2 \text{ h}} + 1.167 \quad (R^2 = 0.93), \quad (7)$$

where $T_{\text{air} - 2 \text{ h}}$ is air temperature measured half-hourly at 45 m height two hours before sapwood temperature was measured (Sapwood temperature lagged air temperature by two hours). Daily mean F_w ranged from 0.04 to 0.42 $\mu\text{mol m}^{-2}$ (ground) s^{-1} throughout the year (mean = 0.14), and reached a maximum on Day 196. The annual sum of F_w in units of carbon was 54 g C m⁻² y⁻¹.

F_s estimated from soil temperature averaged 1.8 $\mu\text{mol m}^{-2}$ (ground) s^{-1} over 24-h periods, and ranged from 0.4 in winter to 3.6 in June (Day 159). The daily amplitude of F_s was fairly low due to buffering of soil temperature at 15 cm depth, which typically differed from air temperature by 7 °C during the day and 5 °C at night in summer, and lagged air temperature by 4–6 hs. The annual sum of F_s was 683 g C m⁻² y⁻¹.

Above-ground R_a (foliage plus wood) averaged 0.6 $\mu\text{mol m}^{-2}$ (ground) s^{-1} over 24 h. Annual foliage and wood respiration consumed 211 g C m⁻², more than above-ground net primary production (136 g C m⁻² y⁻¹). Fluxes from soil dominated contributions to ecosystem

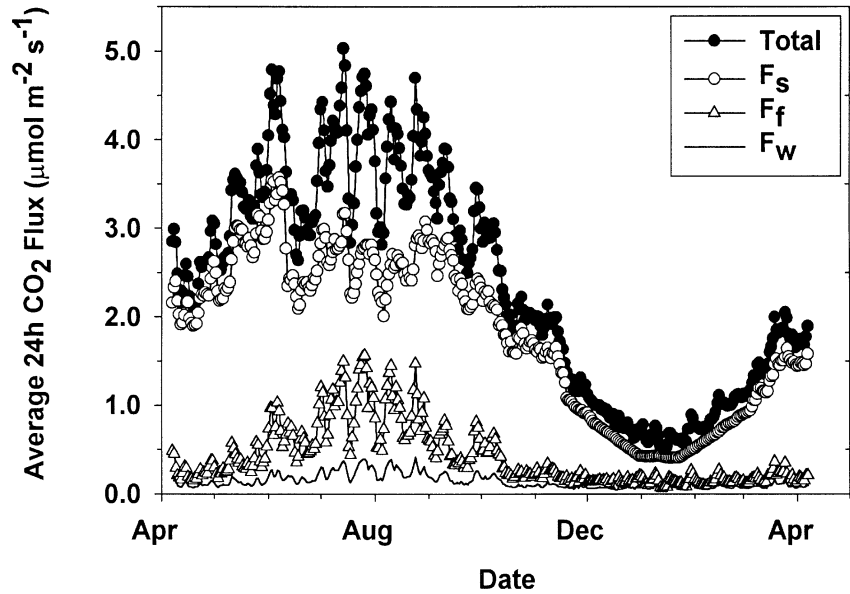


Fig. 4 Average 24-h CO_2 flux, by soils (F_s), foliage (F_f), and wood (F_w). The components are summed (total). F_s accounts for 76% of the total ecosystem respiration, F_f 18%, and F_w 6%.

respiration (Fig. 4), as the fraction of annual respiration from F_s , foliage, and wood was 76%, 18%, and 6%. The 24-h mean ecosystem respiration averaged over the year was $2.4 \mu\text{mol m}^{-2} (\text{ground}) \text{ s}^{-1}$ (range for 24 h means = 0.6–5.0); the annual total was $894 \text{ g C m}^{-2} \text{ years}^{-1}$. An estimated 21% of the annual total occurred outside the growing season (mid-October to mid-March).

Total soil carbon content, obtained from 15 samples (five young stands, five old stands and five mixed stands) to 1 m depth averaged $4.6 \pm 0.5 \text{ kg m}^{-2}$, and was higher in young stands than in old stands (Table 1).

Below-ground carbon allocation estimated from annual F_s and litterfall was $554 \text{ g C m}^{-2} \text{ y}^{-1}$ ($683\text{--}129 \text{ g C m}^{-2} \text{ y}^{-1}$), 32% higher than estimated with the Raich and Nadelhoffer equation (Table 3). The ratio of below-ground carbon allocation to F_s was 0.81. If root production was $\approx 50\%$ of the below-ground carbon allocation, then root respiration (F_r) would have been $277 \text{ g C m}^{-2} \text{ y}^{-1}$ or 41% of F_s , and about 31% of ecosystem respiration.

Gross primary production (GPP), estimated from the sum of above-ground NPP, below-ground carbon allocation, 24-h F_f , and F_w was $901 \text{ g C m}^{-2} \text{ y}^{-1}$. The summed respiratory fluxes from foliage, wood and roots was $488 \text{ g C m}^{-2} \text{ y}^{-1}$. The efficiency of converting gross photosynthesis to biomass (NPP:GPP) was 0.45 ($R_a\text{:GPP} = 0.54$). The ratio of below-ground carbon allocation to GPP was 0.61, and the ratio of F_s to GPP was 0.76.

The uncertainty associated with scaling chamber measurements to the site and over time has been addressed in Ryan *et al.* (1997). Using the same approach, our sources of error are: (i) Uncertainty in respiration measurements – standard errors averaged 8% of the mean for F_s (range 2–33%) and 9–22% for foliage; (ii) Distribution of samples in space – we selected foliage, wood and soil samples

to be representative of the site; (iii) Extrapolation of respiration rates through the year – we assumed phenological differences were captured in the temperature response; (iv) Uncertainty in biomass estimates for scaling respiration – (SE = 1.5–4% of mean). We could not estimate the error associated with #2 and #3 above, but we estimated the combined error for #1 and #4 by recalculating half-hourly respiration rates with the upper and lower confidence intervals (95%) for respiration rates, biomass and LAI. Using this approach, the uncertainty estimate was 18–22% of the mean for the flux estimates.

Chamber-eddy flux comparison

On calm nights ($u^* < 0.25 \text{ m s}^{-1}$), chamber estimates of half-hourly nocturnal ecosystem respiration (F_{nc}) closely agreed with F_{ne} estimated as the change in CO_2 storage (F_{stor}) in the canopy (Table 4). On more turbulent nights ($u^* > 0.25 \text{ m s}^{-1}$), F_{ne} , estimated as the sum of above-canopy nocturnal flux (F_{ca400} , calculated with the 400 s detrending time constant) and F_{stor} was lower than F_{nc} by 50%, and the correlation was weak (Table 4). Decreasing the detrending time constant of the eddy flux data from 400 to 50 s increased F_{ne} , but the correlation with F_{nc} was still weak; $F_{ca50} + F_{stor}$ was lower than F_{nc} by 51 and 9% for $u^* > 0.25$, and $u^* < 0.25 \text{ m s}^{-1}$, respectively.

Errors associated with the eddy covariance method include those introduced by nonstationarity (mean rate of change in mass density with time is different from zero) and instrument limitations (Moncrieff *et al.* 1996). Selective systematic errors (e.g. inadequate sensor response to night-time fluxes) do not cancel and could be the most important type of error, yet they can be difficult to detect. Random errors in estimated mean

Table 4 Comparison of the nocturnal half-hourly sums of soil CO₂ efflux, foliage respiration, and wood respiration from chambers (F_{nc}) with change in nocturnal CO₂ storage (F_{stor}) and nocturnal CO₂ flux measured above the canopy (F_{ca}). The comparison is made on half-hourly data over the year, when tower flux data were available. The model fit was $F_i = b F_{nc}$, where F_i is F_{stor} or F_{stor} + F_{ca}. F_{ca400} is the above-canopy eddy CO₂ flux calculated with a 400 s detrending time constant and F_{ca50} with a 50 s detrending time constant. Results are shown of a paired *t*-test comparison of nocturnal eddy covariance fluxes and chamber estimates of ecosystem respiration

Model	u* constraint	F _{stor} (mean (SE))	F _{ca} + F _{stor} (mean (SE))	F _{nc} (mean (SE))	P	n	R ²
F _{stor} + F _{ca400} = 0.50 F _{nc}	> 0.25	–	1.59 (0.17)	3.50 (0.03)	0	719	0.14
F _{stor} + F _{ca50} = 0.49 F _{nc}	> 0.25	–	1.55 (0.12)	3.50 (0.03)	0	719	0.23
F _{stor} = 0.39 F _{nc}	> 0.25	1.30 (0.09)	–	3.50 (0.03)	0	719	0.28
F _{stor} + F _{ca400} = 0.59 F _{nc}	< 0.25	–	1.91 (0.11)	3.38 (0.02)	0	1872	0.17
F _{stor} + F _{ca50} = 0.91 F _{nc}	< 0.25	–	3.07 (0.07)	3.38 (0.02)	0	1872	0.51
F _{stor} = 0.97 F _{nc}	< 0.25	3.29 (0.06)	–	3.38 (0.02)	0.249	1872	0.60

fluxes decrease with increasing number of data points. The random error for each half-hour F_{ca} was estimated as the standard error of fluxes from six five-minute subintervals per half-hour for all nights ($\sigma/n^{1/2}$, where *n* is 6 subintervals). The mean random error for different turbulence conditions was calculated from the half-hour random errors. Assuming there was a tendency to underestimate the actual flux by 30% as in Moncrieff *et al.* (1996) and Businger (1986), we calculated the selective systematic error by adding 30% to each half-hour flux. The mean nocturnal F_{ca400} would be -1.38 ± 2.25 (random error) + 0.78 (systematic error) $\mu\text{mol m}^{-2} \text{s}^{-1}$ during calm periods ($u^* < 0.25 \text{ m s}^{-1}$), and $0.29 \pm 2.24 + 0.67 \mu\text{mol m}^{-2} \text{s}^{-1}$ during more turbulent conditions ($u^* > 0.25$). For nocturnal F_{ca50}, the mean estimate for calm and more turbulent conditions would be $-0.22 \pm 0.63 + 0.28 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $0.25 \pm 0.95 + 0.39 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Errors in F_{stor} are primarily associated with instrument and calibration gas accuracy (about $\pm 10\%$). For the same time period and wind conditions as the F_{ca} calculations, F_{stor} would be $1.30 \pm 0.13 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $3.29 \pm 0.33 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively.

Discussion

Soil surface CO₂ efflux

Soil surface CO₂ efflux is derived from metabolic activities of plant roots, and those of mycorrhizae, decomposers and other soil organisms that consume shed plant material. At this ponderosa pine site, F_s was likely closely related to the activity of roots, because total below-ground allocation (root production, root respiration, and mycorrhizae) was $> 80\%$ of F_s, and soil carbon content was low (4.6 kg m⁻² compared with 13.4 for temperate forests in general; Raich & Schlesinger 1992). Fine root growth may explain the seasonal pattern we observed in normalized F_s. At our site, F_s reached a maximum in late May, and

again in September. Using ¹⁴C labelling, Smith & Paul (1988) found that carbon allocation to *P. ponderosa* roots peaked in spring and fall, coinciding with root growth. During periods of rapid shoot growth on trees (June and July at the pine site), there is typically little root growth (Eissenstat & Van Rees 1994).

On the global scale, F_s has been estimated as 1.24 times annual total net primary productivity across terrestrial vegetation biomes (Raich & Schlesinger 1992). In our study, we found that the annual soil surface CO₂ efflux was 1.65 times total NPP. Annual F_s (683 g C m⁻² y⁻¹) is similar to soil fluxes for other temperate coniferous forests in the north-western U.S. (flux for *Tsuga heterophylla* and *Abies amabilis* ecosystems was 650 and 620 g C m⁻² y⁻¹ (Vogt *et al.* 1986). The comparable rates are somewhat surprising, given that these sites receive considerably more annual precipitation than the ponderosa pine site in this study. Raich & Schlesinger (1992) reported mean rates for temperate coniferous forests of $681 \pm 95 \text{ g C m}^{-2} \text{ y}^{-1}$. Further work is necessary to improve annual estimates and to understand the contribution of roots and decomposers to F_s, because F_s is such a large component of the annual carbon balance.

Foliage respiration

Foliage respiration has been shown to be an exponential function of temperature and a linear function of foliage nitrogen (Kajimoto 1990; Reich *et al.* 1996). Perhaps because foliage N varied little for our samples, we did not observe a strong linear relationship with foliage N. Foliage N and chlorophyll concentrations were lower in the fall, which may have depressed F_f. Low normalized F_f in winter suggests that factors other than air temperature reduced respiration rates. Reduced photosynthesis and growth will decrease respiration (Amthor 1993), and tissue repair will result in an increase in respiration (e.g. in the spring following winter temperature damage). The

highest rates of normalized F_f were in June and July, when new foliage was expanding. Perhaps respiration rates on the 1-year foliage increase to support transport of photosynthate to the newly expanding foliage (Chabot & Hicks 1982).

Wood respiration

Wood respiration normalized to 10 °C for young and old trees on Day 284 ($4.5 \mu\text{mol m}^{-3}$ sapwood s^{-1}) was lower than estimates of F_w in the autumn for *P. ponderosa* in Montana, *P. resinosa*, and *P. elliotii* (8.0, 7.1, and 8.3, respectively; Ryan *et al.* 1995). If we estimate construction respiration as 26% of F_w in the summer (cf. Ryan *et al.* 1997), maintenance respiration normalized to 10 °C could be as low as 5.7 in July. F_w may have been higher at the *P. ponderosa* in Montana because the site was a relatively young stand (51 years), the LAI was 44% higher than at the Oregon site (2.7 vs. 1.5 in Oregon), trees may not have been water stressed, or nutrient contents may have differed. For young trees, F_w normalized to 10 °C was $5.0\text{--}6.9 \mu\text{mol m}^{-3}$ sapwood s^{-1} in October and July, respectively — low compared with the Montana data.

The increase in normalized wood respiration in June and July is consistent with observations in a temperate forest of 20-year-old *P. sylvestris* (Linder & Troeng 1981), and coincides with wood growth in the summer. Normalized F_w decreased, however, in early August (Day 213), when water stress was at its peak. Predawn water potentials were -0.9 MPa on Day 213, and reached a minimum of -1.0 MPa on days 235, 271 and 285, indicating water stress into October (Law *et al.* 1998). Reduced photosynthesis caused by water stress may reduce the amount of carbohydrates available in the stem for respiration (Negisi 1975; Linder & Troeng 1981; Teskey *et al.* 1995).

Annual estimates for the site

Gross primary production estimated for this site ($901 \text{ g C m}^{-2} \text{ y}^{-1}$) is comparable to estimates for old *P. banksiana* and *Picea mariana* and ($772\text{--}1090 \text{ g C m}^{-2} \text{ y}^{-1}$, respectively) at four coniferous sites of the BOREAS study (Ryan *et al.* 1997). The greatest uncertainty in our calculations of NPP:GPP and R_a :GPP is in our estimate of the fraction of below-ground carbon allocation that is root production vs. respiration, although our estimates are similar to findings in other carbon budget studies (Raich & Schlesinger 1992). For example, Ryan *et al.* (1997) estimated that autotrophic respiration for several boreal conifer sites was $> 50\%$ of GPP.

The difference between our estimate of below-ground carbon allocation and the estimate from the Raich and Nadelhoffer equation confirms an analysis across sites by Gower *et al.* (1996), who showed a poor correlation

between estimates made on site using measured F_s and litterfall and those derived from the Raich and Nadelhoffer model. They suggested that the model is not an acceptable substitute for measuring soil carbon fluxes of individual stands because of species differences in allocation patterns, variation in allocation associated with water and nutrient availability, and violation of certain assumptions (e.g. soil carbon storage is near steady state).

Fluxes from soil are clearly the largest source of ecosystem respiration. Lavigne *et al.* (1997) found soils contributed 48–71%, foliage 25–43% and wood 5–15% in young and old coniferous boreal forests with LAI ranging from 1 to 5.7. At Harvard Forest, a deciduous forest with an LAI of 3.2 in the north-eastern United States, chamber measurements of respiration from ecosystem components showed that soils contributed 68% of the fluxes, foliage 27%, and wood 5% (Goulden *et al.* 1996b). Our estimates for *P. ponderosa* (76%, 18%, and 6%) agreed closely with their estimates. The small difference in the partitioning of respiration at the two sites may be explained by the differences in LAI. Our high ratio of below-ground carbon allocation to GPP (0.61) is typical of sites subject to more water constraints (Raich & Nadelhoffer 1989).

The ratio of NPP to GPP is the efficiency of conversion of photosynthetic carbon fixation to the production of plant tissues. NPP:GPP for *P. ponderosa* (0.45) is within the range of estimates for conifer sites along the Oregon transect (0.40–0.50), from the coast to the pine and juniper forests on the east side of the Cascade Mountains (Williams *et al.* 1997), and *P. radiata* plantations in Australia (Ryan *et al.* 1996). It is higher than values reported for boreal coniferous forests (0.23–0.36; Ryan *et al.* 1997). The ratio of above-ground NPP to above-ground carbon allocation (0.39) is slightly lower than *P. radiata* plantations (0.43–0.50; Ryan *et al.* 1996), but much greater than that for boreal conifers (0.18–0.24; Ryan *et al.* 1997). In general, however, the ratio NPP:GPP is within the range of 0.30–0.70 reported for temperate forests with a wide variety of annual temperatures and above-ground biomass (Amthor & Baldocchi 1998; Ryan *et al.* 1997; Waring *et al.* 1998).

Chamber-eddy flux comparison

Nocturnal ecosystem respiration, estimated by micrometeorological methods ($F_{ca} + F_{stor}$), is dominated by F_{ca} under more turbulent conditions, and by F_{stor} under calm conditions (Grace *et al.* 1996; Goulden *et al.* 1997). Calm nocturnal conditions (defined here as $u^* < 0.25 \text{ m s}^{-1}$) occurred at least 70% of the time at the ponderosa pine site and 55–90% of the time at the boreal conifer sites (Lavigne *et al.* 1997). The low-turbulence observations are usually excluded from further analysis. Although there was a good correlation between F_{stor} and chamber

estimates of nocturnal ecosystem respiration at our site when there was little turbulence ($u^* < 0.25 \text{ m s}^{-1}$), the correlation was poor at Harvard Forest and the boreal sites (Goulden *et al.* 1996b; M.G. Ryan, unpubl. data). Goulden *et al.* (1996b) suggested that air escaped by an undetected route at Harvard Forest. At one of the boreal sites, Sun *et al.* (1997) showed evidence of nocturnal horizontal advection of CO_2 from the forest canopy air space and venting over a lake. They suggested that, when there are weak winds even in the absence of lakes, local convergence of drainage flows or other meandering nocturnal circulations could lead to vertical venting in events that would not be observed by tower instruments.

Under more turbulent conditions ($u^* > 0.25 \text{ m s}^{-1}$), $F_{\text{ca}} + F_{\text{stor}}$ was lower than chamber estimates by about 25% in a deciduous hardwood forest (Goulden *et al.* 1996b), and 6–42% lower at the six boreal coniferous sites examined by Lavigne *et al.* (1997), with larger discrepancies at the sites with more complex terrain. The apparent underestimation of nocturnal fluxes by eddy covariance could be due to observational problems associated with stable conditions that generally occur at night (e.g. failure of instrument to resolve small-scale eddies), and analysis-related issues (e.g. intermittent turbulence; Goulden *et al.* 1996b; Moncrieff *et al.* 1996; Mahrt, pers. comm.).

An analysis of the influence of the detrending time on our flux estimates showed that shortening the detrending time constant and thereby excluding all flux contributions on a scale greater than 50 s improved the comparison of $F_{\text{ca}} + F_{\text{stor}}$ with F_{nc} during poorly mixed conditions. This suggests that much of the discrepancy between the nocturnal $F_{\text{ca}} + F_{\text{stor}}$ and F_{nc} is associated with a few large-scale events occurring during the 30-min averaging period. An averaging period that includes an inadequate number of observed main transporting eddies will result in a large uncertainty in flux estimates. Increasing the record length by increasing the averaging window may solve this problem, but it can lead to problems of non-stationarity. Non-stationarity (e.g. wind speed increasing during the averaging window) generally occurs with weak large-scale flow and mesoscale variability, and is more frequent over heterogeneous terrain (Vickers & Mahrt 1997). Using eddy covariance methods for nocturnal measurements at our site and others with similar features may therefore be limited by forest heterogeneity and complex topography. Improvements in measurement and analytical methods are warranted.

Nocturnal measurements of net ecosystem exchange (NEE) by the eddy covariance method can be used to provide time- and area-integrated estimates of ecosystem respiration. This approach has an advantage over chamber measurements in that it eliminates the uncertainty of aggregating chamber data over time and space. However,

given the general lack of agreement between scaled-up chamber measurements and $F_{\text{ca}} + F_{\text{stor}}$ estimates of respiration and NEE with either technique remain uncertain (see Lavigne *et al.* 1997 for further discussion of the problem). If the chamber estimates are correct, then the common technique of estimating ecosystem respiration from the relationship between nocturnal NEE (during turbulent periods) and soil temperature (Waring *et al.* 1995; Goulden *et al.* 1996b) will likely underestimate ecosystem respiration and GPP, and overestimate annual NEE.

Conclusions

Soil surface CO_2 efflux contributes a major portion of ecosystem respiration in a *P. ponderosa* ecosystem, accounting for 76% of the total. Foliage (18%) and wood (6%) respiration are less important. The study showed that about 61% of gross primary production was allocated below-ground, and 76% of GPP was lost through soil surface efflux. Soil processes are clearly a dominant factor in this ecosystem. The site provides a challenge to carbon balance modelling in that it is subject to summer droughts and high vapour pressure deficits, and it has a relatively low leaf area index. Thus, it is important to focus efforts on better characterization of below-ground processes in carbon balance modelling. In particular, good estimates of below-ground NPP, R_a and R_h are critically needed to improve models.

Most of the carbon lost from the ecosystem through respiration occurs in summer when temperatures are high, but dormant season respiration (21% of the annual total in this study) is large enough to determine whether NEE is positive or negative for the year. Understanding why nocturnal eddy flux estimates consistently differ from measurements extrapolated from chambers is an important challenge, because respiration measurements determine both NEE and GPP. As demonstrated in this study, respiration is important to the carbon balance of ecosystems and it can respond to environmental change. Quantification of global change effects on the terrestrial ecosystem carbon balance and atmosphere–vegetation interactions requires a better understanding of respiration responses.

Acknowledgements

This study was funded by NASA (grant #NAGW-4436). We are grateful to Steve Van Tuyl, Rob Hubbard and Will Hutchinson for their field assistance, and to Magda Oplustilova and Vitezslav Dvorak for assistance with sampling woody respiration. Steve Acker provided stem biomass equations for the site. Larry Mahrt and Mike Unsworth provided helpful comments on the eddy flux measurements and analysis. We gratefully acknowledge the assistance of the Sisters Ranger District of the US Forest Service

in site selection, and Sarah Greene for aid in establishing the study site. The study site is located in a Research Natural Area—areas selected to represent vegetation types in a natural condition.

References

- Amthor JS (1993) Higher plant respiration and its relationships to photosynthesis. *Ecological Studies: Analysis and Synthesis*, **100**, 71–102.
- Amthor JS, Baldocchi DD (1998) Terrestrial higher-plant respiration and net primary production. In: *Terrestrial Global Productivity: past, present and future* (eds Roy J, Mooney HA, Saugier B). Academic Press, San Diego, CA in press.
- Auble DL, Meyers TP (1992) An open path, fast response infrared absorption gas analyzer for H₂O and CO₂. *Boundary Layer Meteorology*, **59**, 243–256.
- 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, Vogel CA, Hall B (1997) Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. *Agricultural and Forest Meteorology*, **83**, 147–170.
- Black TA, Den Hartog G, Neumann HH *et al.* (1996) Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Global Change Biology*, **2**, 219–229.
- Businger JA (1986) Evaluation of the accuracy with which dry deposition can be measured with current micrometeorological techniques. *Journal of Climate and Applied Meteorology*, **25**, 1100–1124.
- Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. *Annual Review of Ecology and Systematics*, **13**, 229–259.
- Chen JM, Rich PM, Gower ST, Norman JM, Plummer S (1997) Leaf area index of boreal forests: theory, techniques and measurements. *Journal of Geophysical Research*, **102**, 29,429–29,443.
- Eissenstat DM, Van Rees KCJ (1994) The growth and function of pine roots. *Ecological Bulletins*, **43**, 76–91.
- Gholz H (1982) Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology*, **63**, 469–481.
- Goulden ML, Daube BC, Fan S-M, Sutton DJ, Bazzaz A, Munger JW, Wofsy SC (1997) Gross CO₂ uptake by a black spruce forest. *Journal of Geophysical Research*, **102**, 28,987–28,996.
- Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsy SC (1996a) Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science*, **271**, 1576–1578.
- Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsy SC (1996b) Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biology*, **2**, 169–182.
- Gower ST, Pongracic S, Landsberg JJ (1996) A global trend in belowground carbon allocation: can we use the relationship at smaller scales? *Ecology*, **77**, 1750–1755.
- Grace J, Lloyd J, McIntyre J *et al.* (1995) Fluxes of carbon dioxide and water vapour over an undisturbed tropical forest in south-west Amazonia. *Global Change Biology*, **1**, 1–12.
- Grace J, Malhi Y, Lloyd J, McIntyre J, Miranda A, Meir P, Miranda H (1996) The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. *Global Change Biology*, **2**, 209–217.
- 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.
- IPCC (1995) *Climate Change 1995: The Science of Climate Change, the IPCC Scientific Assessment* (eds Houghton JT, Meiro Filho LG, Callander A, Harris N, Kattenburg A, Maskell K). Cambridge University Press, Cambridge.
- Jarvis PG (1994) Capture of carbon dioxide by a coniferous forest. In: *Resource Capture by Crops* (eds Monteith JL, Scott RK, Unsworth MH), pp. 351–374. Nottingham University Press, UK.
- Jarvis PG (1995) The role of temperate trees and forests in CO₂ fixation. *Vegetatio*, **121**, 157–174.
- Kajimoto T (1990) Photosynthesis and respiration of *Pinus pumila* needles in relation to needle age and season. *Ecological Research*, **5**, 333.
- Lavigne MB, Ryan MG, Anderson DE *et al.* (1997) Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements. *Journal of Geophysical Research*, **102**, 28,977–28,985.
- Law BE, Baldocchi DD, Anthoni PM (1998) Below-canopy and soil CO₂ fluxes in a ponderosa pine forest. *Agricultural and Forest Meteorology* (in press).
- Law BE, Waring RH (1994) Combining remote sensing and climatic data to estimate net primary production across Oregon. *Ecological Applications*, **4**, 717–728.
- Linder S, Troeng E (1981) The seasonal variation in stem and coarse root respiration of a 20-year-old Scots pine (*Pinus sylvestris* L.). *Mitt. Forst. Bundesvers.*, **142**, 125–139.
- McMillen RT (1988) An eddy correlation technique with extended applicability to non-simple terrain. *Boundary-Layer Meteorology*, **43**, 231–245.
- Means JE, Hansen HA, Koerper GJ, Alaback PB, Klopsch MW (1994) Software for computing plant biomass – Biopak users guide. *General Technical Report PNW-GTR-340*, USDA Pacific Northwest Research Station, Portland, Oregon, 184 pp.
- Moncrieff JB, Malhi Y, Leuning R (1996) The propagation of errors in long-term measurements of land atmosphere fluxes of carbon and water. *Global Change Biology*, **2**, 231–240.
- Monleon VJ, Cromack K, Landsberg JD (1997) Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Canadian Journal of Forest Research*, **27**, 369–378.
- Negisi K (1975) Diurnal fluctuation of CO₂ released from the stem bark of standing young *Pinus densiflora* trees. *Journal of the Japanese Forestry Society*, **57**, 375–383.
- Raich JW, Nadelhoffer KJ (1989) Belowground carbon allocation in forest ecosystems: global trends. *Ecology*, **70**, 1346–1354.
- Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, **44B**, 81–99.
- Reich PB, Oleksyn J, Tjoelker MG (1996) Needle respiration and nitrogen concentration in Scots Pine populations from a broad latitudinal range: a common garden test with field-grown trees. *Functional Ecology*, **10**, 768–776.

- Rosenberg NJ, Blad BL, Verma SB (1983) *Microclimate and the Biological Environment*, 2nd edn. John Wiley, New York, 495 pp.
- Ruimy A, Jarvis PG, Baldocchi DD, Saugier B (1995) CO₂ fluxes over plant canopies and solar radiation: a review. *Advances in Ecological Research*, **26**, 1–68.
- Ryan MG (1990) Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. *Canadian Journal of Forest Research*, **20**, 48–57.
- Ryan MG, Gower ST, Hubbard RM, Waring RH, Gholz HL, Cropper WP, Running SW (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia*, **101**, 133–140.
- Ryan MG, Hubbard RM, Pongracic S, Raison RJ, McMurtrie RE (1996) Autotrophic respiration in *Pinus radiata* in relation to nutrient status. *Tree Physiology*, **16**, 333–343.
- Ryan MG, Lavigne M, Gower ST (1997) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal of Geophysical Research*, **102**, 28,871–28,884.
- 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.
- Sellers PJ, Dickinson RE, Randall DA *et al.* (1997) Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science*, **275**, 502–509.
- Smith JL, Paul EA (1988) Use of an *in situ* labeling technique for the determination of seasonal ¹⁴C distribution in Ponderosa pine. *Plant and Soil*, **106**, 221–229.
- Sun J, Lenschow DH, Mahr L *et al.* (1997) Lake-induced atmospheric circulations during BOREAS. *Journal of Geophysical Research*, **102**, 29,155–29,166.
- Tans PP, Fung IY, Takahashi T (1990) Observational constraints on the global atmospheric CO₂ budget. *Science*, **247**, 1431–1438.
- Teskey RO, Sheriff DW, Hollinger DY, Thomas RB (1995) External and internal factors regulating photosynthesis. In: *Resource Physiology of Conifers* (eds Smith WK, Hinckley TM), pp. 105–142. Academic Press, San Diego, CA.
- Vickers D, Mahr L (1997) Quality control and flux sampling problems for tower and aircraft data. *Journal of Atmospheric and Oceanic Technology*, **14**, 512–526.
- Vogt KA, Grier CC, Vogt DJ (1986) Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Advances in Ecological Research*, **15**, 303–377.
- Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology*, **18**, 129–134.
- Waring RH, Law BE, Goulden ML, Bassow S, McCreight RW, Wofsy SC, Bazzaz FA (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.
- 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, Rastetter EB, Fernandes DN, Goulden ML, Shaver GR, Johnson LC (1997) Predicting gross primary productivity in terrestrial ecosystems. *Ecological Applications*, **7**, 882–894.
- Wofsy SC, Goulden ML, Munger JW, Fan S-M, Bakwin PS, Daube BC, Bassow SL, Bazzaz FA (1993) Net exchange of CO₂ in a mid-latitude forest. *Science*, **260**, 1314–1317.