

Biophysical controls of carbon flows in three successional Douglas-fir stands based on eddy-covariance measurements

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Summary We measured net carbon flux (F_{CO_2}) and net H₂O flux ($F_{\text{H}_2\text{O}}$) by the eddy-covariance method at three Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)—western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) sites located in the Wind River Valley of southern Washington State, USA. Stands were approximately 20, 40 and 450 years old and measurements were made between June 15 and October 15 of 1998 in the 40- and 450-year-old stands, and of 1999 in the 20- and 450-year-old stands. Our objectives were to determine if there were differences among the stands in: (1) patterns of daytime F_{CO_2} during summer and early autumn; (2) empirically modeled relationships between local climatic factors (e.g., light, vapor pressure deficit (VPD), soil water content, temperature and net radiation) and daytime F_{CO_2} ; and (3) water-use efficiency (WUE). We used the Landsberg equation, a logarithmic power function and linear regression to model relationships between F_{CO_2} and physical variables. Overall, given the same irradiance, F_{CO_2} was 1.0–3.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ higher ($P < 0.0001$ for both seasons) at the two young stands than at the old-growth stand. During summer and early autumn, F_{CO_2} averaged 4.2 and 6.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the 20- and 40-year-old stand, respectively. In contrast, the 450-year-old forest averaged 2.2 and 3.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in 1998 and 1999, respectively. Increases in VPD were associated with reduced F_{CO_2} at all three stands, with the greatest apparent constraints occurring at the old-growth stand. Correlations between F_{CO_2} and all other environmental variables differed among ecosystems, with soil temperature showing a negative correlation and net radiation showing a positive correlation. In the old-growth stand, WUE was significantly greater ($P < 0.0001$) in the drier summer of 1998 (2.7 mg g^{-1}) than in 1999 (1.0 mg g^{-1}). Although we did not use replicates in our study, the results indicate that there are large

differences in F_{CO_2} among Douglas-fir stands of different ages growing in the same general area, and that variations in age structure and site conditions need to be considered when scaling flux measurements from individual points to the landscape level.

Keywords: CO_2 flux, Pacific Northwest, succession, water-use efficiency.

Introduction

Long-term measurements of the exchanges of CO_2 between vegetation and the atmosphere are important in determining the role of terrestrial ecosystems in the global carbon budget. Most studies that employ the eddy-covariance technique (e.g., those participating in the AmeriFlux network, S.C. Wofsy, Harvard University and D.Y. Hollinger, USDA Forest Service 1998, <http://cdiac.esd.ornl.gov/programs/ameriflux/scif.htm>) have attempted to quantify ecosystem-level carbon fluxes based on measurements from forests at only one stage of development, and have not considered differences associated with developmental status. Few direct comparisons are available between mature forests and younger stands (Clark et al. 1999, Canadell et al. 2000, Schimel et al. 2000). However, an estimated 45% of the potential forest cover of the continental United States has been converted to other land uses (Turner et al. 1993, Nemani and Running 1995), with the remaining forest cover dominated by mixed-aged stands and plantations. In the United States Pacific Northwest (PNW), more than 90% of the forested landscape is estimated to be dominated by young conifer plantations (Cohen et al. 1995). An accurate assessment of the contribution of terrestrial ecosystems to the global

carbon budget should consider the diversity of site conditions and developmental stages within the landscape mosaic.

Predictable changes in stand structure, composition and microclimate occur throughout the developmental stages of coniferous forests in the PNW (Chen et al. 1993, Franklin et al. 2001). For example, old-growth forests are characterized by a multi-layered forest canopy with many canopy gaps that alter patterns of light penetration (Spies and Franklin 1991, Parker et al. 2002). Changes in foliage distribution and function as conifers mature have also been observed (Yoder et al. 1994, Bond 2000, Phillips et al. 2002, N.G. McDowell, Oregon State University, Corvallis, OR, unpublished data). In addition, the pool of dead woody material changes dramatically with forest age (Janisch and Harmon 2002) and contributes, through decomposition, to considerable variation in net fluxes of CO_2 (F_{CO_2}). Thus, we might expect to see clear distinctions in F_{CO_2} among coniferous forest stands of different ages.

Variations in net ecosystem fluxes of materials and energy exist across landscapes because of the diversity of vegetation types, microclimates, soils and disturbance regimes (Baldocchi et al. 1996, Chen et al. 1999, Valentini et al. 2000). In the PNW, forest stands as old as 500 years can still serve as appreciable net carbon sinks, although older stands may assimilate less carbon than much younger stands (> 20 years old; Black et al. 1996, Waring and McDowell 2002). Few previous studies, however, have measured F_{CO_2} directly at different developmental stages, and there has been little effort to examine possible changes in environmental controls on net ecosystem carbon exchange in stands at different developmental stages.

Our goal was to determine whether the biophysical driving forces for F_{CO_2} differed significantly among three Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)–western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands of different ages. Specifically, we determined whether there were significant differences among the stands in: (1) patterns of daytime F_{CO_2} during summer and early autumn (June 15–October 15); (2) empirically modeled relationships between local climatic factors (e.g., light, vapor pressure deficit, soil water content, temperature and net radiation) and daytime F_{CO_2} ; and (3) water-use efficiency (WUE).

Materials and methods

Study area

Field data were collected at three Douglas-fir–western hemlock forest stands in the Wind River Valley of southwestern Washington (Figure 1). The forests were approximately 20, 40 and 450 years old at the time of measurement (Bond and Franklin 2002) and are hereafter referred to as the 20-, 40- and 450-year-old (or old-growth) stands, respectively. The 450-year-old stand was located at the Wind River Canopy Crane Research Facility (WRCCRF) at 371 m elevation. The younger stands were located due west of the WRCCRF (3.4 and 6.1 km for the 20- and 40-year-old stands, respectively) at the same latitude and at elevations of 561 and 565 m for the 20- and 40-year-old stands, respectively. The prevailing wind di-

rection, measured from 1995 to 1998, was from the west. Scaffold towers, 19.5 m tall in the 20-year-old stand and 36 m tall in the 40-year-old stand, were constructed near the east end of the sites to maximize fetch from the prevailing wind direction.

The 33-ha, 40-year-old stand averaged 710 trees ha^{-1} and is located in a residual lava flow. The stand was clear-cut in 1958 and planted in 1960 with 3-year-old Douglas-fir at a spacing of 0.2×0.2 m. In 1998, the closed-canopy stand was 31 m in height, and dominated by Douglas-fir (68%) with a mean diameter at breast height (DBH) of 19.3 cm. The 33-ha, 20-year-old stand had a mean density of 1529 trees ha^{-1} . This stand was clear-cut in 1976 and planted in 1978 with Douglas-fir seedlings at a spacing of 0.3×0.3 m as part of a plantation experiment of the Trout Creek Hill Experimental Forest. In 1999, the stand was dominated by Douglas-fir and western hemlock. Mean tree height was 16 m, and mean DBH was 11.3 cm.

The old-growth stand surrounded the WRCCRF within the T.T. Munger Research Natural Area in the Gifford Pinchot National Forest. The forest was approximately 450 years old with a mean of 437 trees ha^{-1} and 664 Mg ha^{-1} of aboveground biomass. Mean tree height was 62 m and mean basal area was 72 m^2 . The overstory of Douglas-fir was being replaced by western hemlock, western red cedar (*Thuja plicata* Donn ex D. Don), Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), grand fir (*Abies grandis* Dougl. ex D. Don), noble fir (*Abies procera* Rehd) and western white pine (*Pinus monticola* Dougl. ex D. Don).

Instruments and measurements

We did not have enough equipment to measure the two younger stands simultaneously. Eddy flux sensors and a microclimate station were used in the 40-year-old stand in 1998 and moved to the 20-year-old stand on June 10, 1999. The old-growth stand was instrumented in both years. The microclimate station used in the younger stands continuously measured the following microclimatic variables every 15 s and stored 30-min means in data loggers (CR10 and 21X, Campbell Scientific (CS), Logan, UT): air temperature (T_a) at 2 m above ground and above the canopy (HMP45C temperature and RH probe, CS); relative humidity (h) (HMP45C probe, CS); soil temperature (T_s) at 5 and 10 cm depth (107 temperature probes, CS); soil water content (M) (257 Watermark soil moisture block, CS); three soil heat fluxes (G) at the mineral soil surface (HFT3 soil heat flux plate, Radiation and Energy Balance Systems (REBS), Seattle, WA); net radiation (R_n) (Q7.1 net radiometers, REBS); and photosynthetically active radiation (PAR) above the canopy (190SB quantum sensor, CS).

A three-dimensional sonic anemometer (CSAT3, CS) was mounted at 18.5 and 36.0 m, in the 20- and 40-year-old stands, respectively, beginning in mid-June of 1998 and 1999, facing 255 and 265°, toward the “good” fetch directions (i.e., homogeneous structure for at least 30 tree heights). A CR23X data logger (CS) was programmed to measure sonic temperature and 10-Hz wind speeds in three orthogonal directions (i.e., u, v

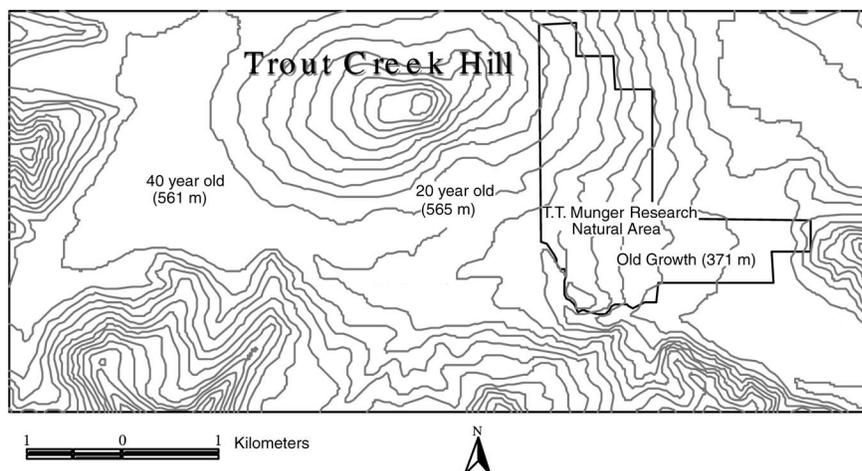


Figure 1. Locations of the three study sites on an elevation map in the Wind River valley in southern Washington. All three stands were relatively flat ($< 10^\circ$ slope) and located at the same latitude ($210\text{--}310^\circ\text{N}$) with prevailing westerly winds.

and w). An infrared gas analyzer (Model LI-6262 IRGA, Li-Cor, Lincoln, NE) was used to measure CO_2 , H_2O , temperature and chamber pressure at the same frequency. Heated Li-Cor Bev-A-Line tubing (4–5 m long) was used to draw in ambient air at about 10 l min^{-1} . The Li-Cor 6262 was calibrated before installation and recalibrated in the laboratory every 2–3 weeks during the sampling period, following the AmeriFlux standard (D.Y. Hollinger, personal communication). The 10-Hz data were processed to calculate 30-min fluxes of CO_2 , H_2O and energy. Lag times for CO_2 and H_2O fluxes, pressure and temperature corrections (Leuning and Moncrieff 1990, Leuning and Judd 1996) and tilt corrections were included in the computations.

Because of limitations in equipment and power supplies, we were unable to measure the canopy storage and advective terms of CO_2 , H_2O and energy fluxes in the young stands (Lee 1998). Advective terms are expected to be relatively low during the day, but storage could be important in the early morning and late afternoon when the carbon and water vapor concentrations may be changing rapidly. Therefore, we did not attempt to calculate total daily net fluxes, but limited our objectives to an examination of biophysical controls over daytime F_{CO_2} . We analyzed data collected between 0500 and 2000 h from the fetch directions between 200 and 310° . Furthermore, we excluded data obtained during rain events, low wind speed conditions, and when $\text{PAR} = 0$.

Data were collected continuously over the 2-year measurement period in the old-growth stand and results are designated as OG98 and OG99 for 1998 and 1999, respectively. The data sets collected at the 20-year-old stand in 1999 and the 40-year-old stand in 1998 are identified as 20Y99 and 40Y98, respectively. Differences between the data sets were compared with a two-sided *t*-test.

Empirical modeling

Numerous models have been proposed to describe the relationship between CO_2 uptake and photosynthetically active radiation (PAR) (e.g., Berry and Raison 1981, Hollinger et al.

1998). For this study, we used the Landsberg equation (Landsberg 1977):

$$F_{\text{CO}_2} = P_{\text{max}} (1 - e^{-\alpha(\text{PAR} - I_{\text{comp}})}), \quad (1)$$

where P_{max} is maximum F_{CO_2} , α is the slope of the F_{CO_2} increase with PAR (i.e., a shape factor) and I_{comp} is the light compensation point (i.e., $F_{\text{CO}_2} = 0$). The equations provided by Landsberg (1977) were designed for leaf-level photosynthesis and also include interactions with other environmental variables (e.g., fertility through quantum efficiency, vapor pressure deficit (VPD), suboptimal temperatures and drought). This model has been used previously to examine ecosystem-level CO_2 fluxes as a function of irradiance (Hollinger et al. 1994). We used the nonlinear regression procedure within the SAS statistical analysis software package (SAS Institute, Cary, NC) to estimate the parameters related to each set of F_{CO_2} and PAR measurements.

We analyzed the residuals (i.e., measured F_{CO_2} – predicted F_{CO_2}) after fitting the Landsberg equation (Equation 1) to explore potential relationships between F_{CO_2} and other physical variables, including air and soil water content, air and soil temperature, wind direction, VPD and time of day. In all cases, VPD explained the most variation in F_{CO_2} after PAR. Although multivariate techniques (e.g., principal component analysis) can provide a synthesized analysis that considers all the variables, residual analysis allows us to decompose the direct influence of each forcing variable, which is more applicable to our study objectives. We examined several mathematical models (e.g., linear, power and logarithmic power functions) to determine the best empirical model of the residuals from Equation 1 as a function of VPD. The logarithmic power model was selected based on its overall goodness of fit:

$$F_{\text{CO}_2} \text{ residuals} = a + b \log(\text{VPD}) + c \log^2(\text{VPD}), \quad (2)$$

where a , b and c are parameters to be estimated through nonlinear regression analysis for each stand. After applying Equa-

tion 2, the subsequent residuals were further explored with other physical variables.

We defined ecosystem water-use efficiency (WUE) as:

$$\text{WUE} = \frac{F_C}{F_{\text{H}_2\text{O}}}, \quad (3)$$

where the fluxes are based on the masses of carbon (F_C) and H_2O vapor. This definition differs from that of traditional micrometeorology and physiological expression where $\text{WUE} = \text{CO}_2$ uptake/transpiration loss by vegetation alone (Rosenberg et al. 1983). Smaller WUE values indicate low net carbon uptake for a given amount of water lost from the system. Our analysis was restricted to times when both F_{CO_2} and $F_{\text{H}_2\text{O}}$ were greater than 0.

Results

In all three stands, the light response curve for F_{CO_2} saturated at 4.8–9.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ when PAR reached 700–800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 2). Overall, for a given PAR, both F_{CO_2} and the variability of F_{CO_2} were significantly higher ($P < 0.0001$ for both seasons) in the young stands than in the old-growth stand. The mean F_{CO_2} values for the measurement periods were 2.17, 3.19, 6.07 and 4.22 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for OG98, OG99, 40Y98 and 20Y99, respectively. In saturating sunlight, F_{CO_2} peaked at 5.0, 5.1, 9.3 and 9.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for OG98, OG99, 40Y98 and 20Y99, respectively (i.e., P_{max}). The high mean F_{CO_2} for 40Y98 was influenced by a large number of very high F_{CO_2} values (i.e., $> 25 \mu\text{mol m}^{-2} \text{s}^{-1}$), whereas such high F_{CO_2} values were rare for the other stands. Values of F_{CO_2} were significantly lower ($P = 0.0002$) for OG98 than for OG99, probably because of lower rainfall and drier soil conditions in 1998 than in 1999 (K.T. Paw U, unpublished data). The differences in F_{CO_2} between 1998 and 1999 in the old-growth stand were most pronounced at low PAR (e.g., $< 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, Fig-

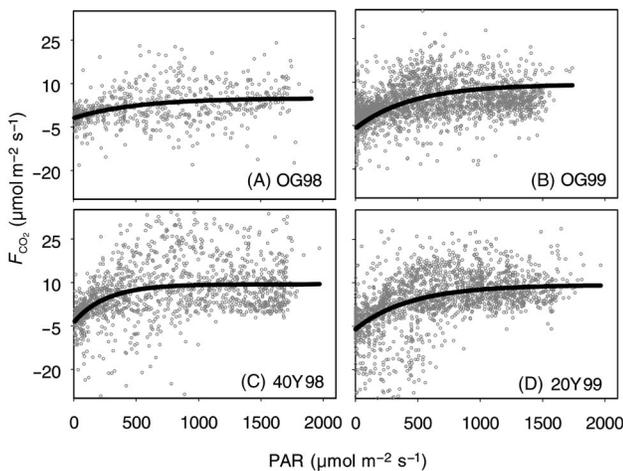


Figure 2. Relationship between F_{CO_2} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) for the old-growth stand (A and B) and two young Douglas-fir stands (C and D) between June 15 and October 15 of 1998 and 1999.

ures 2A and 2B). At all three stands, F_{CO_2} was extremely variable at all irradiances, ranging from a net carbon loss of 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to a gain of nearly 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Ecosystem respiration, indicated by negative F_{CO_2} values at low PAR, appeared to be greatest in 20Y99 (Figure 2D). The y-intercept of the light-response curve indicated that the youngest stand had the highest rates of respiration (Figure 3A), averaging $-6.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ as PAR approached zero. The compensation point (I_{comp}) was lowest in 20Y99, suggesting a larger respiration contribution to net ecosystem carbon flux in 20Y99 than in the other stands (Table 1).

There was great variation in α values among age classes (Table 1), an indication of the rate of change of F_{CO_2} per unit PAR, suggesting that F_{CO_2} differences among the stands were most pronounced at intermediate PAR (200–300 $\mu\text{mol m}^{-2} \text{s}^{-1}$). There were insignificant differences ($P = 0.3132$) between the young stands and between the measurements in 1998 and 1999 in the old-growth stand ($P = 0.4772$) at high PAR ($> 1600 \mu\text{mol m}^{-2} \text{s}^{-1}$, Figure 3). These findings were consistent with the similarity of the saturation coefficients at the three sites (P_{max} , Table 1). However, significant differences were measured between the young stands ($P < 0.0001$) and between OG99 and OG98 ($P < 0.0001$) when PAR ranged between 200 and 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Residuals remaining after accounting for the light response generally showed a negative relationship between F_{CO_2} and VPD (Figure 4) at all three stands, suggesting that the Landsberg equation underestimated F_{CO_2} (i.e., produced positive residuals) when VPD was low, but overestimated F_{CO_2} when VPD was high. Based on the predictions from the logarithmic power function with VPD = 3.5 kPa (Equation 2), the light response curves overestimated F_{CO_2} by 5.3, 4.1, 4.3 and 9.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for OG98, OG99, 20Y99 and 40Y98, respectively. After accounting for the light response, the minimum threshold VPD value that negatively impacted F_{CO_2} was 1.31, 0.91, 1.30 and 1.25 kPa for OG98, OG99, 20Y99 and 40Y98, respectively (Figure 5). Below these thresholds, relationships between VPD and F_{CO_2} varied; however, they appeared generally positive for 1998 and neutral for 1999.

Although we detected strong relationships between F_{CO_2} and both PAR and VPD, some residuals remained high after accounting for these factors (in this case, residuals = F_{CO_2} – Equation 1 – Equation 2). Correlations between the residuals and all other physical variables (i.e., soil temperature, air temperature, soil water content, net radiation and available energy) varied among stand ages and between years of measurement (Figure 5). Except for OG98, increases in soil temperature were negatively related ($P < 0.017$) to the F_{CO_2} residuals, with the most pronounced relationship at 40Y98 (i.e., lowest b values, Figure 5A). A significant inverse relationship ($P < 0.001$) between air temperature and the F_{CO_2} residuals was only seen for 40Y98 (Figure 5B). In contrast, net radiation (i.e., approximately equal to available energy because of low soil heat flux in these densely foliated systems) was positively related ($P > 0.004$) to F_{CO_2} residuals at all sites (Figure 5C). Finally, sensible heat also showed a positive relationship with the residuals at the old-growth stand in

Table 1. Parameters estimated for the Landsberg and logarithmic equations for predicting F_{CO_2} fluxes ($\mu\text{mol}^{-2} \text{s}^{-1}$) by photosynthetically active radiation (PAR, $\mu\text{mol} \text{m}^{-2} \text{s}^{-1}$) and vapor pressure deficit (VPD, kPa) on CO_2 flux (F_{CO_2} , $\mu\text{mol} \text{m}^{-2} \text{s}^{-1}$) in two growing seasons (June 15 and October 15) in 1998 and 1999.

Model	Parameter	OG98	OG99	40Y98	20Y99
Landsberg equation	P_{\max}	4.986	5.126	9.255	9.457
	α	1.998×10^{-3}	4.439×10^{-3}	2.225×10^{-3}	3.812×10^{-3}
	I_{comp}	166.449	103.606	223.244	87.377
Logarithmic equation	a	1.0931	-0.2202	1.3181	0.7237
	b	-3.5470	-2.3634	-5.2633	-2.4917
	c	-1.2001	-0.5858	-2.5598	-1.1941

both 1998 ($P < 0.001$) and 1999 ($P = 0.0116$), but a negative relationship at 40Y98 ($P < 0.001$) and an insignificant relationship ($P = 0.168$) at 20Y99 (Figure 5D). The F_{CO_2} residuals were not significantly ($P > 0.05$) related to other biophysical variables.

There were changes over time in F_{CO_2} residuals after accounting for PAR, VPD and soil temperature at the two young stands (Figure 6). The residuals were less than zero before 0900–1100 h (i.e., the models overestimated F_{CO_2}), but were generally greater than zero from mid-morning to early after-

noon (i.e., the models underestimated F_{CO_2}). During mid-afternoon, the residuals were close to zero. The trend then reversed to slightly lower residuals around 1600–1700 h.

Ecosystem-level WUE during the daytime hours differed among the three stands and between measurement years in the old-growth stand (Figure 7). The old-growth stand was more water-use efficient in the dry summer of 1998 (season-average \pm SD WUE = $2.7 \pm 4.4 \text{ mg g}^{-1}$) than in 1999 ($1.0 \pm 2.3 \text{ mg g}^{-1}$; $P < 0.0001$). The 40Y98 stand had significantly lower WUE (season-average WUE = $2.5 \pm 3.2 \text{ mg g}^{-1}$) than the old-growth stand in 1998 ($P < 0.0001$), and the 20Y99 stand had higher WUE ($1.7 \pm 2.7 \text{ mg g}^{-1}$) than the old-growth stand in 1999 ($P = 0.001$). All three stands showed higher WUE during early morning (before 0900 h) and somewhat higher WUE in the late afternoon (1700 h) compared with the middle of the day.

Discussion

Net ecosystem carbon exchange (F_{CO_2}) in daylight hours is de-

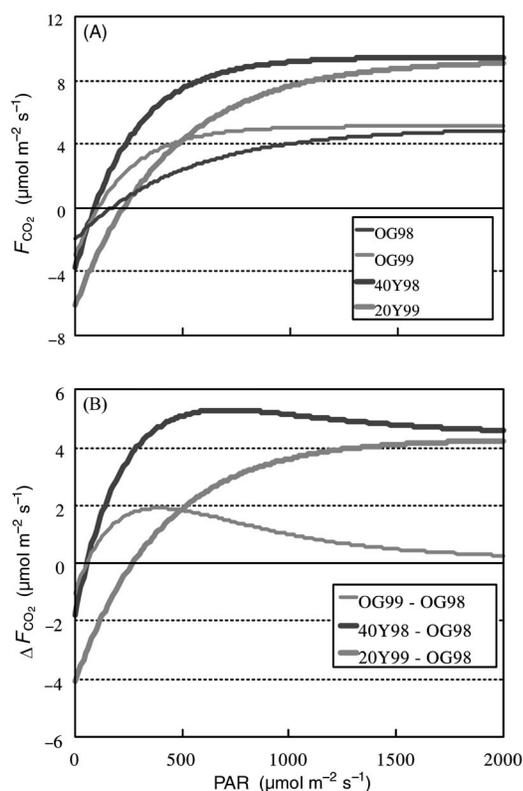


Figure 3. (A) Changes in F_{CO_2} ($\mu\text{mol} \text{m}^{-2} \text{s}^{-1}$) with photosynthetically active radiation (PAR, $\mu\text{mol} \text{m}^{-2} \text{s}^{-1}$) as predicted by the Landsberg equation for three Douglas-fir forests during the growing seasons of 1998 and 1999; and (B) difference from predicted F_{CO_2} at OG98. See Table 1 for stand-associated parameters obtained in nonlinear regressions.

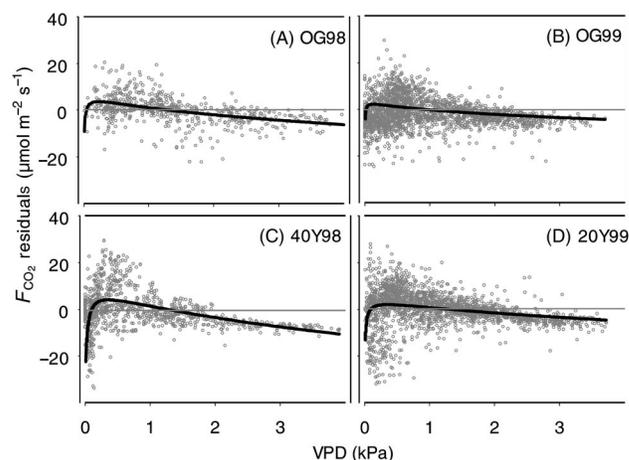


Figure 4. Changes in F_{CO_2} residuals ($\mu\text{mol} \text{m}^{-2} \text{s}^{-1}$) after applying the Landsberg equation to determine the relationship between F_{CO_2} and vapor pressure deficit (VPD, kPa) at three Douglas-fir forests during summer and fall (June 15 and October 15) in 1998 and 1999. The curves were fitted with a logarithmic power function. Negative values indicate overestimation of F_{CO_2} by the Landsberg equation. See Table 1 for stand-associated parameter values obtained in nonlinear regressions.

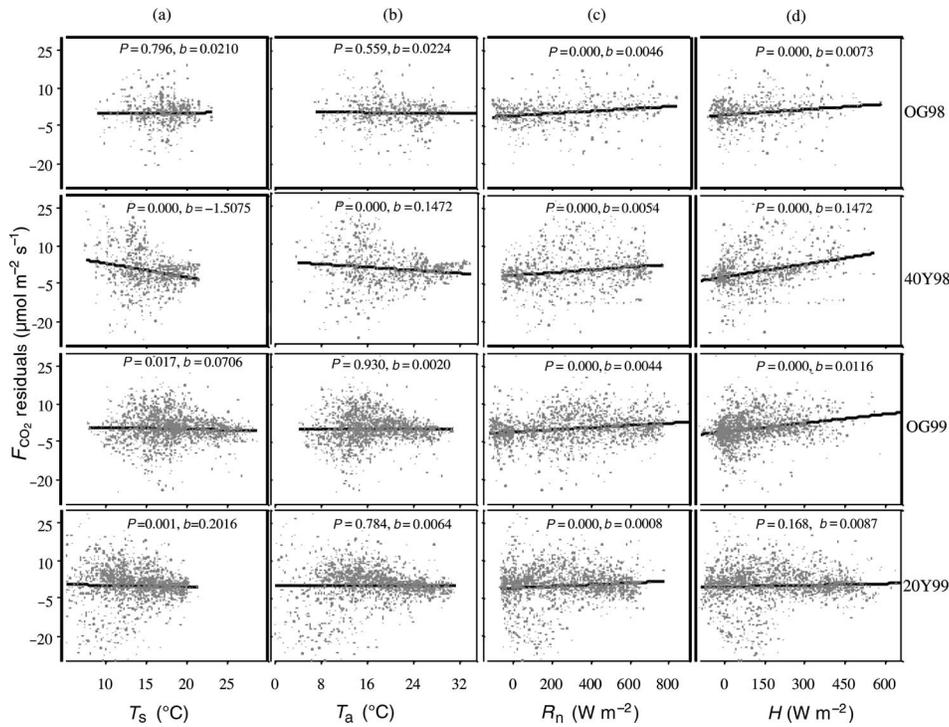


Figure 5. Relationships between residual F_{CO_2} (after the Landsberg and logarithmic equations) and other biophysical variables, including soil temperature (T_s), air temperature (T_a), net radiation (R_n) and sensible heat (H), at three Douglas-fir forests. The solid line represents the best fit linear regression with a coefficient (b) and its significant deviation (t -test, $P = 0.05$) from zero.

terminated by ecosystem respiration and photosynthesis. Respiration is largely influenced by soil and plant tissue temperature, soil water content, substrate quality and biomass, whereas photosynthesis is controlled by PAR, leaf chemistry (e.g., nitrogen content), VPD, available water and temperature. However, recent studies suggest that soil respiration may be strongly influenced by recent photosynthesis (Högberg et al. 2001). Following disturbance, ecosystem respiration tends to be high because of increased decay of roots, large sources of woody debris, and leaf litter (Harmon et al. 1990), whereas

carbon uptake by young plants is low because of the low leaf area; this may result in young stands being a net carbon source to the atmosphere for some years (Janisch and Harmon 2002). As succession proceeds, F_{CO_2} becomes balanced, eventually peaks, and finally returns to a relatively stable value greater than zero (Arneeth et al. 1999, Schulze et al. 2000). However, relative rates of photosynthesis and respiration vary with age and species composition (Buchmann and Schulze 1999, Clark et al. 1999). Thus, different ecosystem types and successional stages are likely to have different F_{CO_2} values.

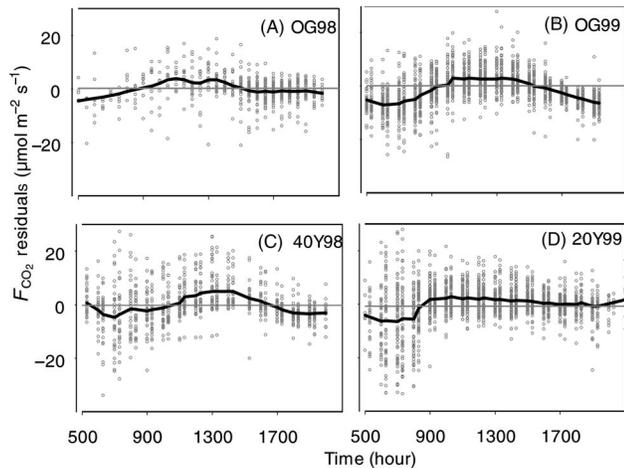


Figure 6. Changes in F_{CO_2} residuals ($\mu\text{mol m}^{-2}\ \text{s}^{-1}$), after accounting for PAR, VPD and soil temperature, with daytime hours at three Douglas-fir forests during summer and fall (June 15 through October 15) in 1998 and 1999. Negative values indicate overestimation of F_{CO_2} by the models.

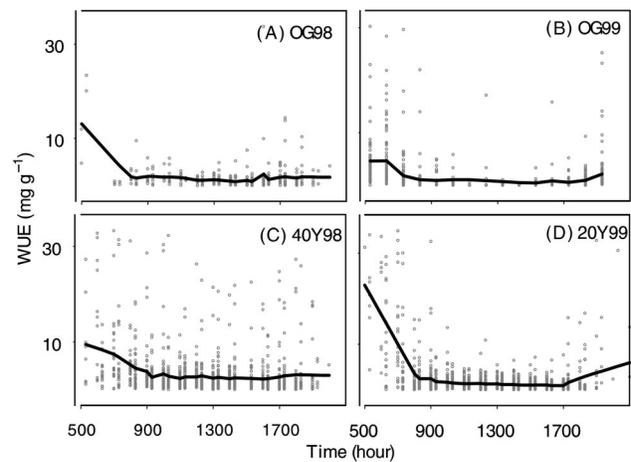


Figure 7. Diurnal changes in water-use efficiency (WUE) at three Douglas-fir forests during summer and fall (June 15 through October 15) in 1998 and 1999. The trends over the measurement periods are presented using Friedman smoothing, a technique that selects an appropriate degree of smoothness based on cross-validation.

In our study, F_{CO_2} of the 20-year-old Douglas-fir stand was strongly influenced by high respiration, as indicated by the large number of observations of negative F_{CO_2} at low PAR ($< 600 \mu\text{mol m}^{-2} \text{s}^{-1}$, Figure 2) and the high I_{comp} (Table 1). Based on the high respiration in the 20-year-old stand and the relatively high F_{CO_2} at high PAR, we conclude that the stand had high photosynthetic capacity (also highest P_{max} , Table 1). This is consistent with the relatively high photosynthetic rates measured for this stand (N.G. McDowell, unpublished data). The photosynthetic capacity of the old-growth stand appeared to be lower than that of the young stands, as indicated by its low y -intercept in the light-response curve (Figure 3) and low P_{max} values (Table 1).

In previous studies, several simple models have been proposed to investigate relationships between environmental variables and F_{CO_2} (e.g., Collatz et al. 1991, Hollinger et al. 1994, Waring et al. 1995, Aber et al. 1996, Goulden et al. 1996). It is generally accepted that variable interactions cannot be ignored; that is, a statistical relationship based on a limited number of variables is unlikely to be applicable when values of other variables change. As expected, we found that multiple environmental variables jointly controlled F_{CO_2} of the ecosystems, and there were strong interactions among these variables, resulting in some difficulty in discerning their individual effects. For example, PAR and VPD played significant roles in controlling F_{CO_2} ; however, they also interacted with each other, because the relationship between F_{CO_2} residuals and VPD varied with PAR at all the stands (Figure 4). Despite a general inverse relationship between VPD and F_{CO_2} residuals (Figure 4), there was a tendency for the Landsberg equation to underestimate F_{CO_2} at low VPD (i.e., ecosystem respiration was underestimated in the morning when the VPD was low), but to overestimate F_{CO_2} at high VPD. In all analyses, both PAR and VPD exhibited significant effects on F_{CO_2} . Furthermore, the interactions between VPD and PAR differed among stands; after accounting for responses to PAR, F_{CO_2} was more sensitive to variation in VPD (above a 1.0–1.5 kPa threshold) in the old-growth stand than in the younger stands. Similarly, Hubbard et al. (1999) found that light-saturated leaf-level photosynthesis of old-growth ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) was more sensitive to VPD than that of co-occurring younger trees. However, N.G. McDowell, unpublished data, found no differences in leaf-level responses of photosynthesis to VPD for Douglas-fir trees measured at our study sites.

Temperature had no significant influence on F_{CO_2} at the old-growth stand but it significantly affected F_{CO_2} at the younger stands (Figure 5), and the most pronounced effect of soil temperature was for 40Y98. Net radiation and sensible heat (H) partially represent how energy is partitioned in an ecosystem (especially if we assume a constant Bowen ratio; Black et al. 1996) and are also closely linked to leaf temperature. We found that both latent heat (λE) and H were significantly and positively correlated to F_{CO_2} , except for H at the 20Y99 (Figure 5), supporting the concept of an effect of leaf temperature

on photosynthetic rates. Overall, it seemed that the controls of PAR and VPD over F_{CO_2} remained similar over time, but other biophysical controls varied among ecosystems and sampling periods (i.e., 1998 versus 1999).

Differences in biophysical controls on F_{CO_2} among the stands can have significant consequences for spatial variation in F_{CO_2} at broader scales for an ecosystem that has been significantly impacted by changing land use over the past 150 years. Regardless of community composition and structural differences among ecosystems (Spies and Franklin 1991) or changes in individual tree function over time (N.G. McDowell, unpublished data, Phillips et al. 2002), our previous studies in the same forest showed that microclimatic conditions differed significantly in temperature, soil water content, VPD, vertical light distribution and energy balance (Chen et al. 1999, Parker et al. 2002). For example, mean daily soil temperatures for young (15–20-year-old) Douglas-fir stands and a 500-year-old forest during the growing season were 18.3 and 13.9 °C, respectively (Chen et al. 1993). Multi-layer differences in vertical LAI between the young and the old-growth stands may have varied the amounts of radiation at the soil surface at these sites (Parker et al. 2002). Chen et al. (1993) also reported a significantly higher VPD, lower soil water content and lower available energy at the young stands than at the old-growth forest. If we assume solar irradiance is relatively constant among ecosystems throughout the region (e.g., within 20 km), our results suggest that VPD, temperature and available energy are the key environmental variables that determine differences in F_{CO_2} of each ecosystem. A combination of modeling, remote sensing and extensive field measurements of ecosystem structure and biophysical environment are needed to predict regional patterns when multiple ecosystems are included in a landscape-level synthesis.

Mean daily net accumulations of carbon were estimated to be 68.05, 628.10, 115.71 and 286.41 g C ha⁻² day⁻¹ in the 20Y99, 40Y98, OG98 and OG99, respectively. However, these estimates ignore the possibility that maximum carbon uptake at the different sites occurs at different times as a result of differences in the phenology of the vegetation and other site characteristics. For example, differences in the timing of leaf expansion and spring wood growth may greatly alter F_{CO_2} in response to differences in maintenance respiration. The old-growth stand showed maximum carbon uptake in the early spring (March and April), several months before our measurements were made (K.T. Paw U, unpublished data). Because of elevation differences between the sites (200 m between the younger stands and the old-growth stand), it is possible that later snow melt and differences in precipitation resulted in greater water availability at rooting depth later in the season for the younger stands than for the old-growth stand. This would result in higher carbon assimilation rates for the younger stands during the summer months, but possibly lower rates in the early spring, which could tend to even out the site differences. Lack of data for the younger stands during the early spring precluded a careful analysis of phenology. Although this study has provided some insight into the differences in

biophysical controls from PAR, VPD, temperature and available energy among the three stands, the high residuals indicate that much of the total variance in F_{CO_2} remains unexplained (Figures 5 and 7).

Although all three stands, as well as nearby locations, were dominated by Douglas-fir and western hemlock (Figure 1), the study stands may not represent mean regional conditions (e.g., composition, structure, microclimate and soil) of forest succession following harvesting (Franklin et al. 2001). As determined by disturbance history, amount of debris left after harvesting, site index, leaf chemistry (e.g., nitrogen), elevation and management differed among the sites. For example, leaf area indices were about 6.8, 8.6 and 8.9 (Thomas and Winner 2000, Phillips et al. 2002) and the nitrogen concentrations of the soils were 1.8, 3.9 and 1.65 g kg⁻¹ for the 20-, 40- and 450-year-old stands, respectively (Klopatek 2002). Finally, our analysis focused on F_{CO_2} in daytime hours, and field measurements for the two younger stands were collected from only one sampling season each. In addition, storage and advective terms, which can be significant, were ignored when calculating net CO₂ flux. Long-term, direct measurements of F_{CO_2} in other seasons (including storage and advective terms), through diurnal cycles, and for additional ecosystems of different developmental stages are necessary to fully understand successional differences in the carbon budget and possible differences in environmental controls. Further research is needed to determine the importance of photosynthesis and respiration, including nocturnal components, in overall F_{CO_2} as succession proceeds through forest development following a major disturbance.

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