

Net Ecosystem Exchanges of Carbon, Water, and Energy in Young and Old-growth Douglas-Fir Forests

Jiquan Chen,^{1*} Kyaw Tha Paw U,² Susan L. Ustin,²
Thomas H. Suchanek,³ Barbara J. Bond,⁴ Kimberley D. Brosofske,¹ and
Matthias Falk²

¹Department of Earth, Ecological, and Environmental Sciences, University of Toledo, Toledo, Ohio 43606, USA; ²Department of Land, Air, and Water Resources, University of California, Davis, California 95616, USA; ³Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, California 95616, USA; ⁴Department of Forest Science, Oregon State University, Corvallis, Oregon 97331, USA

ABSTRACT

To be able to estimate the cumulative carbon budget at broader scales, it is essential to understand net ecosystem exchanges (NEE) of carbon and water in various ages and types of ecosystems. Using eddy-covariance (EC) in Douglas-fir dominated forests in the Wind River Valley, Washington, USA, we measured NEE of carbon, water, and energy from July through September in a 40-year-old stand (40YR) in 1998, a 20-year-old stand (20YR) in 1999, and a 450-year-old stand (450YR) during both years. All three stands were net carbon sinks during the dry, warm summers, with mean net daily accumulation of $-0.30 \text{ g C m}^{-2} \text{ d}^{-1}$, $-2.76 \text{ g C m}^{-2} \text{ d}^{-1}$, and $-0.38 \text{ g C m}^{-2} \text{ d}^{-1}$, respectively, in the 20YR, 40YR, and 450YR (average of 1998, 1999) stands; but for in-

dividual years, the 450YR stand was a carbon source in 1998 ($0.51 \text{ g C m}^{-2} \text{ d}^{-1}$) and a sink in 1999 ($-1.26 \text{ g C m}^{-2} \text{ d}^{-1}$). The interannual differences for the summer months were apparent for cumulative carbon exchange at the 450YR stand, which had 46.9 g C m^{-2} loss in 1998 and 115.9 g C m^{-2} gain in 1999. As predicted, the 40YR stand assimilated the most carbon and lost the least amount of water to the atmosphere through evapotranspiration.

Key words: net ecosystem exchange; carbon; water; energy; Douglas-fir; eddy-covariance; microclimate.

INTRODUCTION

In recent years, as scientific interest in determining the roles of ecosystems as carbon sinks or sources has intensified, direct measurements of net ecosystem exchange (NEE) of carbon and water between terrestrial vegetation and the atmosphere have increased (for example, see Falge and others 2002). For forested regions, it is essential to understand the carbon fluxes of various-aged stands so that we can

assess the impact of climate change and alternative land uses at landscape and regional scales (Turner and others 2000; Carey and others 2001). In terms of the major forces that drive changes in ecosystem productivity (Hansen and others 1991; Walker and Steffen 1997), there is a consensus among scientists that anthropogenic disturbances,—primarily land-use changes,—could have synergetic or even more severe impacts than climate change (Chen and others 1999; Dale and others 2002). In the western United States, for example, intensive human-induced land-use changes have led to the conversion of most of the virgin old-growth forests into younger stands, with consequent effects on the car-

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*Corresponding author; e-mail: jiquan.chen@utoledo.edu

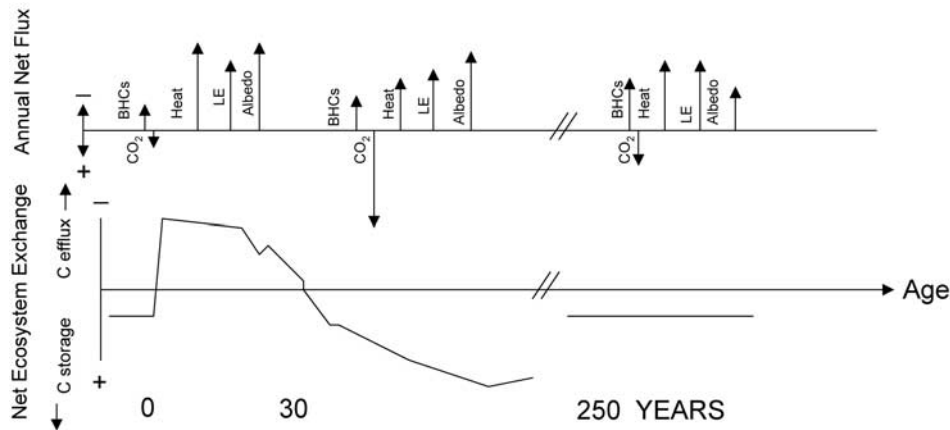


Figure 1. Upper panel: Hypothetical annual fluxes of biogenic hydrocarbons (BHCs), carbon dioxide (CO₂), sensible heat (H), latent heat (LE), and albedo for 20-year-old and 40-year-old stand and forests older than 250 years. Lower panel: Hypothetical net ecosystem exchange after a stand-replacing event.

bon fluxes and storage of the region (Harmon and others 1990). Indeed, Schimel and others (2000) have estimated that the effects of land conversion on carbon sequestration by US forests might be double that caused by the predicted global warming.

It has been hypothesized that terrestrial ecosystems in North America are sinks for atmospheric carbon (Tans and others 1990; Fan and others 1998); these systems could account for the missing carbon within the global carbon budget (Turner and others 1995), especially because many of them are young reforested stands. However, due to natural variability in carbon pools, fluxes in different terrestrial ecosystems (Sarmiento and Wofsy 1999), and problems with the precision and accuracy of measurements (Lee 1998) much uncertainty still exists in determining the location of the missing carbon sinks. Thus, it is becoming increasingly important to quantify NEE accurately at the broad spatial scales within which the contributions of individual ecosystems are understood. Currently, much of the available data are based on measurements at eddy flux towers, such as those obtained through the AmeriFlux and EuroFlux Networks, which are snapshots of larger land mosaics. Similarly, over longer temporal scales, it is well known that climatic variability (Wofsy and others 1993) and various disturbances (Dale and others 2002; Euskirchen and others 2002) drive the magnitudes and dynamics of carbon and water flux; however, drivers over shorter temporal periods are not as well understood. The work presented in this paper is one of the first attempts to quantify carbon flux at fine temporal scales within individual ecosystems of different ages within a landscape. Several projects within the CarboEurope Cluster program of the European Union have also been developed to ad-

dress similar space/time scale questions (<http://www.bgc.jena.mpg.de/public/carboeur/>).

Our study objective was to compare the NEE of carbon and water in the summer season (July–September) among different-aged stands of Douglas-fir dominated forests. Franklin and others (2002) proposed that Douglas-fir/western hemlock forests at approximately 20–30 years should reach canopy closure and initiate the stage of rapid biomass accumulation, whereas mature forests (over 300 years old) should increase vertical and horizontal diversification due to mortality of the canopy dominants. When Janisch and Harmon (2002) modeled net ecosystem production (NEP) for these forests, they found that young stands shift from being a carbon source to a sink between 0 and 57 years. Thus, the transition between a forest acting as a source or a sink occurs near the 20–30-year period.

Figure 1 illustrates the hypothetical net annual ecosystem fluxes for energy budgets and carbon for forests of different ages. We chose to study 20-, 40-, and 450-year-old stands based on these probable functional transitions. The summer study period was selected based on the timing of onset of seasonal drought and the fact that drought has a major impact on the annual carbon budget (see Chen and others 2002; Unsworth and others 2004; Paw U and others 2004). The precipitation regime in the US Pacific Northwest is strongly seasonal, with little precipitation in summer months (Shaw and others 2004; Paw U and others 2004). The 3-month period between 1 July and 1 October encompasses the seasonal transition from high to low carbon sequestration (Waring and Franklin 1979; Paw U and others 2004).

We developed and installed mobile eddy-covariance (EC) systems in two Douglas-fir (*Pseudotsuga*

Table 1. Monthly Air Temperature (°C) between June and October of 1998 and 1999 at the Wind River Canopy Crane Research Facility

	1998				1999			
	Mean	Max	Min	SD	Mean	Max	Min	SD
June	14.81	30.73	5.06	5.19	13.85	31.95	1.86	5.51
July	19.97	39.70	7.98	6.21	16.61	33.18	3.52	6.81
August	19.07	36.60	5.20	7.19	18.64	33.90	7.72	6.10
September	15.86	36.37	2.28	7.24	14.91	28.71	3.03	7.03

menziesii) stands (20- and 40-year-old, abbreviated as 20YR and 40YR hereafter) to directly measure net exchange of carbon, water, and energy between the forest and the atmosphere and thereby test the hypothesis that both the 20-year-old stand and the 40-year-old stand should be near the zero-net exchange point for carbon and that the highest net flux would occur in the 40-year-old stand. Data collected from a more permanent EC system in a 450-year-old stand (450YR hereafter) (see Paw U and others 2004) were used for comparison. Specifically, we (a) compared carbon, water, and energy fluxes at hourly, daily, and monthly scales; and (b) examined possible biophysical controls of carbon and water fluxes along Douglas-fir chronosequences to assess the potential implications for forest management.

METHODS

Our measurements were made at the Wind River Canopy Crane Research Facility (WRCCRF) in the T. T. Munger Research Natural Area and in the Trout Creek Hill Experimental Forest in the Gifford Pinchot National Forest, located in southwestern Washington, USA. (see Shaw and others 2004; Paw U and others 2004). The prevailing wind was from 270°, as determined by measurements between 1995 and 1998 at 70-m height on the canopy crane. The long-term average precipitation at the Wind River site is 2,467 mm y⁻¹, with only 5% occurring in June, July, and August (Paw U and others 2004; Shaw and others 2004). The summer of 1998 was extremely dry, as indicated by persistent drought until late September and record low soil moisture levels and high vapor pressure deficits (Unsworth and others 2004). Climate records show that these months were in the lowest quartile of monthly precipitation for the period from 1931 to 1997. In contrast, May 1999 was in the highest quartile for monthly precipitation, and June and July 1999

were near the long-term mean. The measured summer temperatures were significantly higher in the summer of 1998 than 1999 (Table 1).

Scaffolding towers for the younger tree canopies were constructed in spring 1998 near the east end of each stand to maximize the fetch of 30 tree heights in directions between 200° and 310°. The 36-m tower was placed in the 40YR stand in June 1998 and moved to the 20YR stand in June 1999.

The 20YR stand is located at 565 m a.s.l. It was clear-cut in 1976 and planted in 1978 with Douglas-fir seedlings at 2.7 m × 2.7 m spacing as part of a plantation experiment. The 33-ha stand was located 3.5 km west of the WRCCRF crane and was dominated in 1999 by Douglas-fir and western hemlock (*Tsuga heterophylla*) at a density of 1,529 trees ha⁻¹. Average tree height was 16 m, and average diameter at breast height (dbh) was 11.3 cm (Table 2). A 19.5-m scaffolding tower was installed with micrometeorological sensors at about 18.5 m above the ground.

The 40YR stand is located at 561 m a.s.l. It was clear-cut in 1958 and planted in 1960 with 3-year-old Douglas-fir at 1.8 m × 1.8 m spacing. The 33-ha stand was located about 6 km west of the WRCCRF and dominated by Douglas-fir (67.8%), with a mean density of 710 trees ha⁻¹. Average tree height was 31 m, with a closed canopy and a dbh of 19.3 cm (Table 2). A 36-m scaffolding tower was installed with micrometeorological sensors at about 36.2 m above the ground. The stand is located in the southwestern part of the Trout Creek Hill Experimental Forest on the residual lava flow.

The 450YR stand surrounds the canopy crane and is located within the T. T. Munger Research Natural Area. The Wind River Experimental forest is located at 371 m a.s.l. and is 4,208 ha in extent. The forest, which was approximately 450–550 years old, originated after a fire or a series of fires and continues to be dominated by Douglas-fir, although the stand is undergoing natural succession and is being gradu-

Table 2. Stand Structure and Site Information for Three Douglas-Fir Forests of Different Ages (20-year-old, 40-year-old, and old-growth 450-year-old) Used for Measurements of Microclimate and Fluxes of Carbon, Water, and Energy Obtained Using Eddy-Covariance Methods

	20YR	40YR	450YR
Latitude (°)	45°49'23.64"N	45°49'13.76"N	45°49'13.8"N
Longitude (°)	122°1'34.85"W	122°57'6.88"W	121°49'6.9"W
Elevation (m)	565	561	371
Age (y)	21	40	450
Last known disturbance (y)	1977	1959	500–600 bp
Stand density (tree ha ⁻¹)	1529	710	443
Mean tree height (m) ± SD	15.1 ± 1.77	31.4 ± 1.047	62 ± 12.5
Average dbh (cm)	11.3	19.3	33.8
Basal area (m ²)	19.30	44.77	71.93
LAI	6.8	8.6	8.9
Sampling period	7/15/99–10/15/99	6/18/98–1/15/98	5/98–10/99

dbh, diameter at breast height; LAI, leaf area index; bp, before present

ally replaced by western hemlock, western red cedar (*Thuja plicata*), Pacific silver fir (*Abies amabilis*), grand fir (*A. grandis*), noble fir (*A. procera*), and western white pine (*Pinus monticola*). It contains a tree density of 443 trees ha⁻¹ and an aboveground biomass of 669 Mg ha⁻¹; it has an average height of 62 m, a dbh of 33.8 cm, and a basal area of 71.93 m² (Table 2). A 75-m construction tower was installed with micrometeorological sensors at about 70 m above the ground.

Tree heights in the 20YR and 40YR stands were measured on the tallest 20 trees using Ishii's equation (2000). All trees in the 12 ha around the WRC-CRF were measured; the mean heights of the tallest trees in the 4 ha immediately surrounding the crane are shown in Table 2.

Beginning in mid-June of their respective sampling years, measurements were taken in the young stands. Limited equipment and personnel prevented continuous measurements at all three sites simultaneously. A 3-D sonic anemometer (CSAT3; Campbell Scientific Instruments, Logan, UT, USA) was mounted in the 20YR and 40YR stands at 18.5 m and 36.0 m, respectively, facing 265° and 255°, toward the good fetch directions. A data logger (CR23X; Campbell Scientific Instruments) was programmed to measure sonic temperature and 10-Hz wind speeds in three orthogonal directions (that is, x, y, z). An infrared gas analyzer (Li-Cor 6262 IRGA; Li-Cor, Lincoln, NE, USA) was used to measure carbon dioxide (CO₂), water (H₂O), temperature, and chamber pressure at the same frequency. Heated Li-Cor Bev-A-Line tubing (4–5 m long) was used to draw ambient air at about 10 L min⁻¹. The IRGA was calibrated prior to installation

and brought back to the laboratory every 2–3 weeks during the sampling period for recalibration and cross-calibration using the same gas and dew point generators as for the old-growth stand (Paw U and others 2004). Because of equipment and power supply limitations, we did not measure the canopy storage and advective terms at the young stands (Lee 1998; Paw U and others 2000). A net radiometer (Q7.1; Radiation Energy and Balance Systems, Seattle, WA, USA) was mounted more than 2 m above the canopy, and three soil heat flux plates (HFT3; Radiation Energy and Balance Systems) were buried near the soil surface (1 cm) to record continuous 30-min means of net radiation (R_n) and soil heat flux (G) based on 20-s scans. The instrumentation and measurements at the 450YR stand are described by Paw U and others (2004).

RESULTS

Clear diurnal patterns in CO₂ exchanges (F_{CO2}) were observed (Figures 2 and 3), with CO₂ uptake (that is, C sink) dominating daylight hours and respiration (C source) dominating the night. Complex temporal patterns in F_{CO2} seemed to occur among the 3 sampling months and between the 2 sampling years. For example, the F_{CO2} of the old-growth forest in 1998 and 1999 was clearly different in both its average diurnal change (Figures 2 and 3) and daily cumulative values (Table 3). The 450YR stand was a net source in both July and September of 1998 (Table 3), but whereas high nocturnal respiration rates contributed to this in July, low daytime CO₂ uptakes were more significant in September (Figure 3). In addition, in 1998,

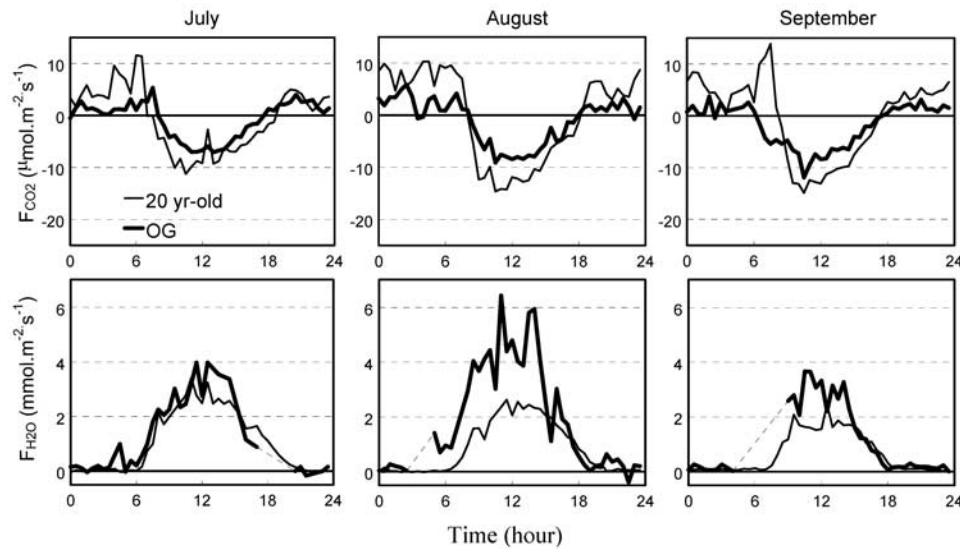


Figure 2. Average diurnal fluxes of carbon dioxide (CO_2) and water (H_2O) in July, August, and September 1999 in a 20- and a 450-year-old Douglas-fir forest in southern Washington, USA. Only data from good fetch directions ($200\text{--}310^\circ$) were used. Negative values indicate uptake (that is, sink); positive values indicate loss (that is, source). Dashed lines indicate missing values.

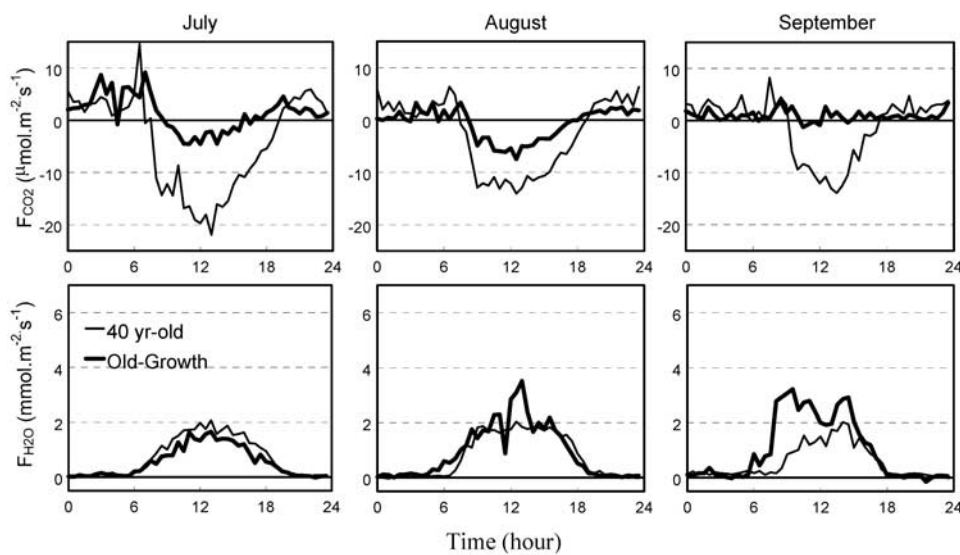


Figure 3. Average diurnal fluxes of carbon dioxide (CO_2) and water (H_2O) in July, August, and September 1998 in a 40- and a 450-year-old Douglas-fir forest in southern Washington, USA. Only data from good fetch directions ($200\text{--}310^\circ$) were used. Negative values indicate uptake (that is, sink); positive values indicate loss (that is, source).

the 450YR stand lost an average of $0.51 \text{ g C m}^{-2} \text{ d}^{-1}$ (or 46.92 g C m^{-2} over the 3-month sampling period) to the atmosphere, but in 1999 it assimilated $1.26 \text{ g C m}^{-2} \text{ d}^{-1}$ (or $115.92 \text{ g C m}^{-2}$ in 3 months) from the atmosphere (Table 3).

At the younger stands, F_{CO_2} was higher than at the old-growth stand during the night, with largest values at the 20YR stand (Figure 2). Although daytime F_{CO_2} at both of the young stands was larger (that is, more negative values at the old-growth stand), very small differences in daytime F_{CO_2} were found between the 20YR and the 450YR stands in July 1999. Because of the high respiratory loss, the daily average F_{CO_2} of the 20YR stand in 1999 ($-0.30 \text{ g C m}^{-2} \text{ d}^{-1}$) was 23.8% that of the 450YR stand ($-1.26 \text{ g C m}^{-2} \text{ d}^{-1}$) (Table 3). In comparing F_{CO_2} between the 40YR and the 450YR in 1998, we

found that nighttime F_{CO_2} was slightly higher at the 40YR stand, but daytime F_{CO_2} was also much higher (up to $-20 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in July) (Figure 3). Over the 3-month sampling period, the daily average F_{CO_2} was $-2.76 \text{ g C m}^{-2} \text{ d}^{-1}$ at the 40YR stand but $+0.51 \text{ g C m}^{-2} \text{ d}^{-1}$ (that is, a carbon source) at the 450YR stand (Table 3). In summary, the two younger stands were net carbon sinks from July through September, but the old-growth stand appeared to be a source in summer 1998 and a sink in summer 1999 (Table 3).

The F_{CO_2} of the three coniferous stands showed clear relationships with the biophysical environment, with photosynthetically active radiation (PAR) and vapor pressure deficit (VPD) as the most important variables. The F_{CO_2} -PAR relationship—a typical sigmoid increase with elevated PAR—was

Table 3. Average Daily Net Exchange of Carbon and Water in July, August, and September of 1998 and 1999 at Three Douglas-Fir Forests of Different Ages (20, 40, and 450 years old) in Southern Washington, USA

		1998		1999	
		40YR	450YR	20YR	450YR
Carbon ($\text{g C m}^{-2} \text{d}^{-1}$)	July	-4.27	1.39	-0.56	-0.79
	August	-2.69	-0.79	-1.10	
	September	-1.21	0.93	-1.97	
	Overall	-2.76	0.51	-1.26	
Water (mm d^{-1})	July	1.15	0.87	1.67	2.09
	August	1.20	1.43	2.98	
	September	0.87	1.58	1.74	
	Overall	1.15	1.29	2.30	
CWR (g kg^{-1} /mmol mol^{-1})	July	3.71/5.57	-1.59/-2.35	0.34/0.51	0.38/0.57
	August	2.24/3.36	0.55/0.83	0.07/0.010	0.37/0.56
	September	1.39/2.09	-0.59/-0.89	0.32/0.48	1.13/1.70
	Overall	2.40/3.60	-0.40/-0.60	0.22/0.33	0.55/0.83

CWR, carbon dioxide–water vapor flux ratio.

For carbon, negative values indicate uptake (that is, sink), whereas positive values indicate loss (that is, source). For CWR, negative values indicate a carbon source associated with water loss.

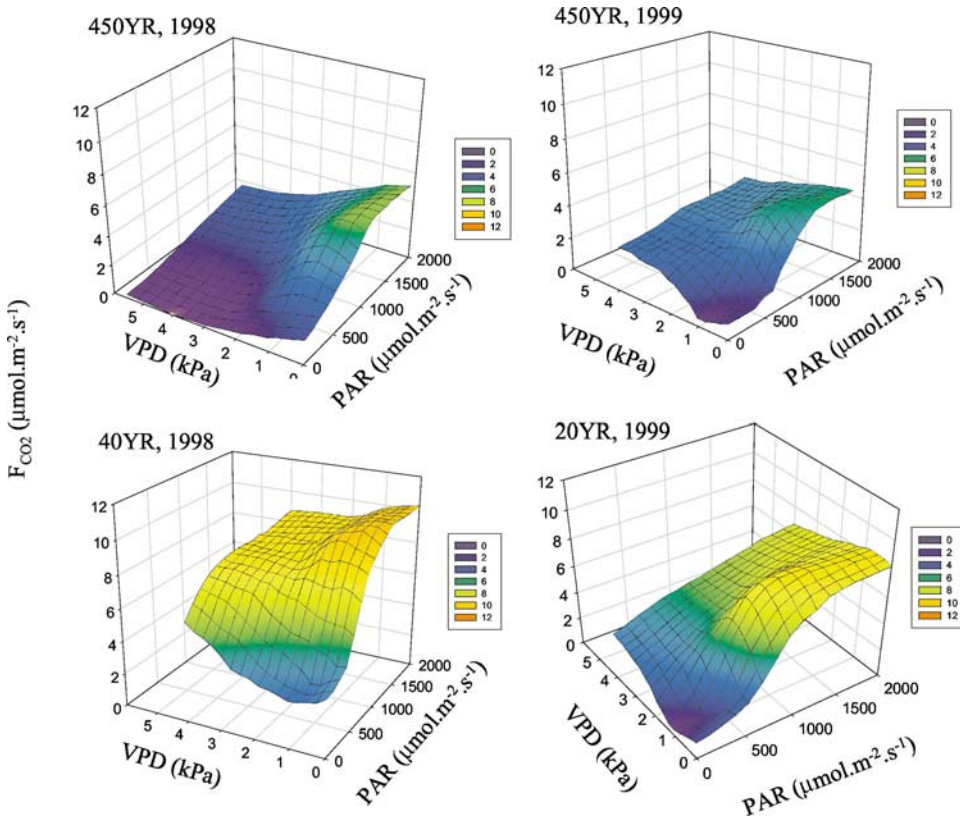


Figure 4. Effects of photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) and vapor pressure deficit (VPD, kPa) on mean carbon dioxide (CO_2) flux (F_{CO_2} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) during summer and fall (15 June and 15 October) in 1998 and 1999.

dependent of VPD at all three stands (Figure 4), with the 450YR in 1998 showing a clearly different response from the others. In the 450YR stand in 1999 and the two young stands, F_{CO_2} decreased

with increasing VPD at high PAR levels, but it increased at low PAR levels, suggesting stronger negative influences of VPD when photosynthesis reached high levels (that is, at high PAR) than that

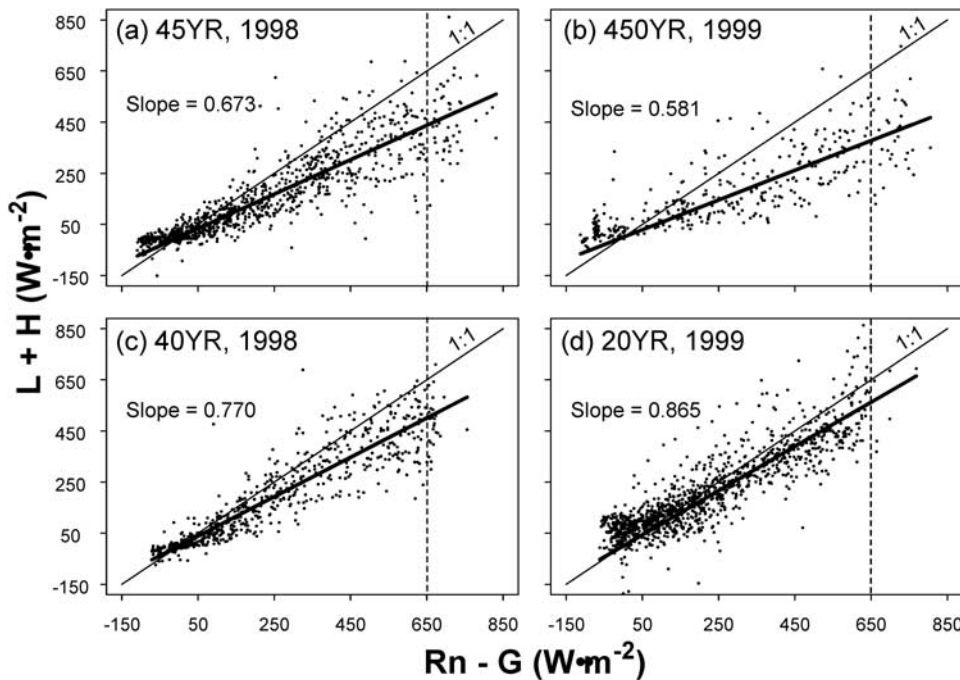


Figure 5. Energy budget closures of three stands as measured by 30-min means of net radiation (R_n), sensible heat (H), latent heat (L), and soil heat flux (G) between June and October in 1998 and 1999. Only data from good fetch directions ($200\text{--}310^\circ$) were used.

at low PAR levels. However, a decreasing trend of F_{CO_2} with VPD was observed at all PAR levels in the 450YR stand in the summer of 1998, when moisture was extremely low (Table 1). The effect of VPD on F_{CO_2} at the old-growth forest seemed stronger than those at the young stands.

Water flux (F_{H_2O}) also showed diurnal, seasonal, and interannual differences. The amount of H_2O lost from the 450YR stand in 1998 (1.29 mm d^{-1}) was much less than in 1999 (2.30 mm day^{-1}) from July through September (Table 3). With the exception of July 1998, daily average F_{H_2O} was higher at the old-growth stand than at the two young stands (Figures 2 and 3, Table 3). These differences were associated with large F_{H_2O} before midafternoon (around 14:00 h), when F_{H_2O} dropped very quickly to levels similar to or lower than the younger stands. Decreases in F_{H_2O} at the two younger stands were less dramatic (Figures 2 and 3). Over the sampling periods, daily average F_{H_2O} (loss) of the 450YR stand was 70.4% and 12.2% higher than the 20YR and 40YR stands, respectively. The energy budget closure was closer to 100% for the young stands than for the old-growth forest (Figure 5). In 1998, the closure was 77% at the 40YR stand and 67% at the 450YR stand; whereas in 1999, the closure was 87% at the 20YR stand and 58% at the 450YR forest (Figure 5b and d). Nevertheless, on some days, energy budget closure was greater than 90% even in the old-growth stand. The available energy ($R_n - G$) in the old-growth stand seemed to be

higher than in the younger stands, with values frequently greater than 650 W m^{-2} (Figure 5a and b). We found that the average Bowen ratios (based on 30-min mean sensible to latent heat ratio between 09:00 and 16:00 h) and standard deviations in 1998 were 3.7 ± 4.1 and 2.6 ± 2.7 , respectively, for the 40YR and 450YR stands; they were 2.9 ± 2.9 and 1.6 ± 1.8 , respectively, for the 20YR and 450YR stands in 1999. The missing energy was negatively correlated with the Bowen ratio ($r^2 = -0.95$) and positively correlated with canopy height ($r^2 = 0.94$).

DISCUSSION

Our field measurements suggest that the younger stands (20YR and 40YR) were net carbon sinks during the summer months (Table 3, Figures 2 and 3), with average carbon fluxes of -0.30 and $-2.76\text{ g C m}^{-2}\text{ d}^{-1}$, or 27.60 and 253.92 g C m^{-2} , respectively, over the 3-month sampling period. Although they are within the ranges reported for a young, coastal Douglas-fir forest in British Columbia ($5\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ at PAR greater than $1,000\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$) (Wilson and others 2002), they are much smaller than values reported for other temperate forests during the growing season (Black and others 1996; Greco and Baldocchi 1996; Wofsy and others 1993; Wilson and others 2002). The values are higher than those reported in boreal coniferous forests (Hollinger and others 1998; Law and others

2001) and lower than those in tropical and southern deciduous forests (Greco and Baldocchi 1996; Clark and others 1999) and a Mediterranean beech forest in Italy (Valentini and others 1996).

Surprisingly, the 450YR stand was a carbon source in 1998 ($0.51 \text{ g C m}^{-2} \text{ d}^{-1}$, or 46.9 g C m^{-2} total for the study period), but it was a significant sink for the same period in 1999 ($-1.26 \text{ g C m}^{-2} \text{ d}^{-1}$, or 115.9 g C m^{-2} total). These values constitute about 24.6% of the loss and 61.0% of the annual net carbon accumulation between July 1998 and June 1999 of the total net $1.9 \pm 0.2 \text{ Mg C ha}^{-1}$ measured in the 450 YR forest (Paw U and others 2004). Thus, the role of the old-growth stand as either source or sink appears to be markedly dependent on the local climate conditions (Wofsy and others 1993; Paw U and others 2004).

Because the study area is characterized by a warm, dry summer climate, photosynthetic uptake in this period is typically limited by moisture (Waring and Running 1998). The 1998 year was an unusually dry summer with almost no measurable precipitation, compared with an average precipitation (around 120 mm) during the same period in 1999; this may explain why there was a carbon loss in the old-growth forest in 1998 and a carbon gain in 1999.

Waring and Franklin (1979) hypothesized that a large proportion of ecosystem productivity occurs during winter and spring in these evergreen forests, when net photosynthetic gain is combined with low respiration. Our eddy flux measurements at the old-growth stand confirm that summer carbon assimilation is lower than maximum rates recorded in March (Paw U and others 2004), but that net assimilation can continue into late summer during years with more spring precipitation. Clearly, continuous direct measurements of carbon flux are needed (especially for young stands) during winter and spring to quantify the annual carbon budget and to gain a fuller understanding of the controls on carbon flux.

The 24-h water-use efficiency, as indicated by using the carbon dioxide–water vapor flux ratio (CWFR), was higher for the 40YR stand (2.4 g kg^{-1}) than the 450YR stand (-0.40 g kg^{-1}) in the summer of 1998, but the 450YR stand had a higher CWFR (0.55 g kg^{-1}) than the 20YR stand (0.22 g kg^{-1}) in the summer of 1999 (Table 3). It is generally thought that the CWFR increases when the stomatal or surface resistance increases (Rosenberg and others 1983), at least for individual leaves and daytime CWFR. Our results are therefore consistent with the sap flow–derived resistances and direct gas exchange measurements (McDowell and others

2002) for these forests, which were higher for the 40YR stand than the 450YR stand in 1999 and higher for the 450YR stand than the 20YR stand in 1998 and 1999 (Phillips and others 2002). Our results also support the leaf/branch level gas exchange measurements of Thomas and Winner (2000) for this 450YR stand and a 5–10-year-old stand, which found higher CWFR for the 450YR stand, if it is inferred that the CWFR for the 5–10-year-old stand is similar to that of the 20YR. Isotopic studies also imply a higher stomatal or surface resistance for the 450YR stand than younger stands (Fessenden and Ehleringer 2002), which supports our CWFR estimates for the 1999 data but not the 1998 data. However, isotopic data for plant tissue and other carbon stocks are subject to multiple interpretations because several factors may create isotopic ratio variations (Bowling and others 2003).

The marked difference of CWFR for the 450YR stand between years implies that there is a potential for great interannual variation between summers. In 1998, the negative value of CWFR indicated a carbon source while water was still being lost from the ecosystem; whereas in 1999, the CWFR was not only positive but greater than CWFR in a younger ecosystem. One caution that must be noted in comparing the 24-h CWFR and the CWFR derived from daytime-based measurements and measurements on particular plant elements is that nocturnal respiration and other element respiration (including soil, large woody debris, and understory carbon exchange) are included in the EC-based 24-h CWFR.

Differences in available energy (that is, $R_n - G$) (Baldocchi and Meyers 1991) among the three sites may be an important factor for the higher $F_{\text{H}_2\text{O}}$ measured at the old-growth site. For example, Eugster and others (1997) found that $F_{\text{H}_2\text{O}}$ was linearly correlated with R_n across landscapes. In our study, it was common for the old-growth forest to reach R_n greater than 650 W m^{-2} (Figure 5a and b) but rare for R_n at the either younger stands to reach these levels (Figure 5c and d), suggesting that $F_{\text{H}_2\text{O}}$ should be higher at the older stand to maintain leaf temperatures. The old-growth forest has exceptionally low albedo (Mariscal and others 2004) in contrast to younger stands (Roberts and others 2004), which explains the higher net radiation at this site. The lack of energy budget closure at the old-growth forest for both years (Figure 5 a and b) additionally suggests that we probably underestimated $F_{\text{H}_2\text{O}}$, proportional to the difference in net energy at the sites, that was likely underestimated in the calculation of $F_{\text{H}_2\text{O}}$.

The contribution of understory vegetation offers

yet another potential explanation for the relatively high F_{H_2O} at the old-growth site. Abundant understory vegetation typically contributes 5%–10% of total ecosystem F_{H_2O} (Price and others 1986), but this may increase significantly when stands are patchy or open, or when soils are dry. For example, Tan and others (1978) found that the percentage of total ecosystem transpiration accounted for by the understory (salal) of a thinned Douglas-fir stand increased from 45% to 70% over a 4-week drying period. In our study, there was almost no understory at either younger stands, whereas it was abundant in the old-growth stand, suggesting that classical water-use efficiency theory may need to be adjusted when applied at the ecosystem level.

Our results for F_{H_2O} are similar to those observed in a ponderosa pine (*Pinus ponderosa*) forest in the eastern Cascades of Oregon (Law and others 2001; Irvine and others 2002), where both F_{H_2O} and F_{CO_2} were lower in young stands than in older ones. However, in the pine ecosystems, there was evidence that the old-growth trees were able to access deeper sources of water than the younger trees (Irvine and others 2002). Ongoing studies of root distribution and water uptake with depth at the Wind River sites have shown no indication that roots in the old-growth stand had access to water at depths unavailable to younger stands (B. J. Bond and others unpublished; Brooks and others 2002), although total fine-root biomass was significantly greater in the old stand than the two younger stands (Klopatek 2002). Despite the greater overall F_{H_2O} at the old-growth stand compared with the younger stands, differences in the diurnal behavior of F_{H_2O} at the three stands indicated that there was greater midday stomatal regulation of transpiration in the old stand (Yoder and others 1994).

CONCLUSIONS

One of the most significant findings of this study concerns the large variation in NEE of CO_2 , H_2O , and energy among differently aged forest stands of the same type within the same landscape that results from differences in species composition, tree age and structure, microclimates, soils, and disturbance regimes (Chen and others 1999). This suggests that flux measurements obtained at single locations are not representative of the overall landscape, thus limiting the applicability of these results at broader spatial scales. More work is needed to understand the scaling mechanisms in complex forest landscapes. If EC systems are used to establish a regional carbon budget, it is clear that they must be established at multiple sites across the landscape

instead of taking measurements only at a single point, or they must be placed at sufficient heights to measure flux footprints that include other landscape types (although horizontal advection below the sensors must then be addressed). Finally, serious attention should be given to developing a more complete understanding of the coupled effects of climate change and land use on terrestrial ecosystems.

Caution should be used in interpreting our findings that indicate higher carbon sequestration in young stands than in old-growth stands, because our results strongly suggest that the old-growth forest may be a stronger carbon sink than previously believed. However, given its shift between a carbon source and sink in these two summers, the potential for long-term net carbon accumulation in the old-growth stand is uncertain. The 2 years of data for the summer season examined imply that these forests are sensitive to interannual weather conditions and thus will be sensitive to any directional climate change.

The conversion of long-lived forests into young stands may change the system from a sink to a source of carbon for several decades because the lower leaf area in regenerating forests limits photosynthesis while the residual carbon in soils and woody debris contributes to respiration, whereas old-growth forests may continue to function as a net carbon sink, in addition to their many other important ecosystem functions (for example, critical habitat, aesthetic values, watershed protection). Stands younger than 20 years old are expected to be carbon sources because of low photosynthetic potential and substantial respiratory losses (Janisch and Harmon 2002), but no such stands were examined in this study. Our sites are not perfect chronological sequences due to many physical and ecological differences—for example, elevation, soil nutrients, climate, and historical silvicultural treatments (Chen and others 2002; Klopatek 2002)—but this study does demonstrate the importance of age structure in determining the carbon budget. Further investigation of carbon and water fluxes in multiple ecosystems along chronological stages of development are needed because we know very little about the mechanisms or timing that switch forest ecosystems from carbon sources to sinks following a disturbance.

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REFERENCES

- Baldocchi DD, Meyers TP. 1991. Trace gas exchange above the floor of a deciduous forest. 1. Evaporation and CO₂ efflux. *J Geophys Res* 96:7271–85.
- Black TA, Denhartog G, Neumann HH, Blanken PD, Yang PC, Russel G, Nestic Z, and others. 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Global Change Biol* 2:219–29.
- Bowling DR, Pataki DE, Ehleringer JR. 2003. Critical evaluation of micrometeorological methods for measuring ecosystem-atmosphere isotopic exchange of CO₂. *Agric For Meteorol* 116:159–79.
- Brooks JR, Meiner FC, Coulombe R, Gregg J. 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiol* 22:1107–17.
- Carey EV, Sala A, Kean R, Callaway RM. 2001. Are old-forests underestimated as carbon sinks. *Global Change Biol* 7:339–44.
- Chen J, Saunders S, Crow T, Naiman R, Brososke K, Mroz G, Brookshire B, and others. 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49:288–97.
- Chen J, Falk M, Paw U KT, Suchanek T, Ustin S, Bond B, Brososke K, and others. 2002. Biophysical controls of carbon flows in three successional Douglas-fir stands based upon eddy-covariance measurements. *Tree Physiol* 22:171–80.
- Clark KL, Gholz HL, Moncrieff JB, Cropley F, Loescher HW. 1999. Environmental controls over net exchanges of carbon dioxide from contrasting Florida ecosystems. *Ecol Appl* 9:936–48.
- Dale VH, Joyce LA, McNulty S, Neilson RR, Ayres MP, Flannigan MD, Hanson PJ, and others. 2002. Climate change and forest disturbances. *BioScience* 51(9):723–34.
- Eugster W, McFadden JP, Chapin FS III. 1997. A comparative approach to regional variation in surface fluxes using mobile eddy correlation towers. *Boundary-Layer Meteorol* 85:293–307.
- Euskirchen E, Chen J, Li H, Gustafson EJ, Crow TR. 2002. Modeling net carbon flows under alternative management regimes at a landscape level. *Ecol Model* 154:75–91.
- Falge E, Tenhunen J, Baldocchi D, Aubinet M, Bakwin P, Bernbigier P, Bernhofer C, and others. 2002. Phase and amplitude of ecosystem carbon release and uptake potentials as derived from FLUXNET measurements. *Agric For Meteorol* 113:75–95.
- Fan S, Gloor M, Mahlman J, Pacala S, Sarmiento J, Takahashi T, Tans P. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* 282:442–6.
- Fessenden JE, Ehleringer JR. 2002. Age-related variations in d¹³C of ecosystem respiration across a coniferous forest chronosequence in the Pacific Northwest. *Tree Physiol* 22:159–67.
- Franklin JF, Spies TA, Van Pelt R, Carey AB, Thornburgh DA, Berg DR, Lindenmayer DB, and others. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For Ecol Manage* 155:399–423.
- Greco S, Baldocchi DD. 1996. Seasonal variation of CO₂ and water vapour exchange rates over a temperate deciduous forest. *Global Change Biol* 2:183–97.
- Hansen AJ, Spies TA, Swanson FJ, Ohmann JL. 1991. Conserving biodiversity in managed forests: lessons from natural forests. *BioScience* 41:382–92.
- Harmon ME, Ferrell WK, Franklin JF. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247:699–702.
- Hollinger DY, Kelliher FM, Schulze E-D, Bauer G, Arneith A, Byers JN, Hunt JE, and others. 1998. Forest-atmosphere carbon dioxide exchange in eastern Siberia. *Agric For Meteorol* 90:291–306.
- Irvine J, Law BE, Anthoni PM, Meinzer FC. 2002. Water limitations to carbon exchange in old-growth and young ponderosa pine stands. *Tree Physiol* 22:189–96.
- Ishii H, Reynolds JH, Ford ED, Shaw DC. 2000. Height growth and vertical development of an old-growth *Pseudotsuga-Tsuga* forest in southwestern Washington State, U.S.A. *Can J For Res* 30:17–24.
- Janisch E, Harmon ME. 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Physiol* 22:77–89.
- Klopatek JM. 2002. Belowground carbon pools and processes in different age stands of Douglas-fir. *Tree Physiol* 22:197–204.
- Law BE, Thornton PE, Irvine J, Anthoni PM, Van Tuyl S. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biol* 7:755–77.
- Lee X. 1998. On micrometeorological observation of surface-air exchange over tall vegetation. *Agric For Meteorol* 91:39–45.
- Mariscal MJ, Martens SN, Chen, J, Roberts D, Ustin SL (2004) "Spatial variability of PAR within canopy gaps in an old-growth Douglas-fir/western hemlock forest". *Ecosystems* 7: 454–67.
- McDowell N, Phillips N, Lunch C, Bond BJ, Ryan MG. 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiol* 22:763–74.
- Paw U KT, Baldocchi DD, Meyers TP, Wilson KB. 2000. Correction of eddy-covariance measurements incorporating both advective effects and density fluxes. *Boundary-Layer Meteorol* 97:487–511.
- Paw U KT, Suchanek TH, Ustin SL, Chen J, Park Y-S, Winner W, and others. (2004) Carbon dioxide exchange between an old-growth forest and the atmosphere. *Ecosystems* 7:513–24.
- Phillips N, Bond BJ, McDowell NG, Ryan MG. 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. *Tree Physiol* 22:205–11.
- Price DT, Black TA, Kelliher FM. 1986. Effects of salal understory

- removal on photosynthetic rate and stomatal conductance in young Douglas-fir trees. *Can J For Res* 16:90–7.
- Roberts DA, Ustin SL, Ogunjemiyo S, Chen J, Hinkley TM. 2004. Spectral and structural measures of Northwest forest vegetation at leaf to landscape scales. *Ecosystems* 7:545–62.
- Rosenberg NJ, Blad BL, Verma SB. 1983. *Microclimate: the biological environment*. New York: Wiley.
- Sarmiento JL, Wofsy SC. (1999) A U.S. carbon cycle science plan. Report of the Carbon and Climate Working Group, Washington D.C.
- Schimel DJ, Melillo J, Tian H, McGuire AD, Kicklighter D, Kittel T, Rosenbloom N, and others. 2000. The contribution of increasing CO₂ and climate to carbon storage by natural and agricultural ecosystems of the US 1980–1993. *Science* 287: 2004–6.
- Shaw DC, Franklin JF, Bible K, Klopatek J, Freeman E, Greene S, Parker GG (2004) "Ecological setting of the Wind River old-growth forest". *Ecosystems* 7:427–39.
- Tan CS, Black TA, Nnyamah JU. 1978. A simple diffusion model of transpiration applied to a thinned Douglas-fir stand. *Ecology* 59(6):1221–9.
- Tans PP, Fung IY, Takahashi T. 1990. Observational constraints on the global atmospheric CO₂ budget. *Science* 247:1431–8.
- Thomas SC, Winner WE. 2000. Leaf area index of an old-growth Douglas-fir forest estimated from direct structural measurements. *Can J For Res* 30:1922–30.
- Turner DP, Koerper GJ, Harmon ME, Lee JJ. 1995. A carbon budget for forests of the conterminous United States. *Ecol Appl* 5:421–36.
- Turner DP, Cohen WB, Kennedy RE. 2000. Alternative spatial resolutions and estimation of carbon flux over a managed forest landscape in western Oregon. *Landscape Ecol* 15(5): 441–52.
- Unsworth MH, Phillips N, Link T, Bond B, Falk M, Harmon M, Hinkley T, and others. 2004. Components and controls of water flux in an old-growth Douglas-fir/western hemlock ecosystem. *Ecosystems* (7):468–81.
- Valentini R, De Angelis P, Matteucci G, Monaco R, Dore S, Mugnozza GES. 1996. Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biol* 2:199–207.
- Walker B, Steffen W. 1997. An overview of the implications of global change for natural and managed terrestrial ecosystems. *Conserv Ecol*. Available online at <http://www.consecol.org/vol1/iss2/art2>.
- Waring R, Franklin JF. 1979. Evergreen coniferous forests of the Pacific Northwest. *Science* 204:1380–6.
- Waring R, Running SW. 1998. *Forest ecosystems: analysis at multiple scales*. San Diego: Academic Press.
- Wilson K, Goldstein AH, Falge E, Aubinet M, Baldocchi D, Aubinet M, Berbigier P, and others. 2002. Energy balance closure at FLUXNET sites. *Agric For Meteorol* 113:223–43.
- Wofsy SC, Goulden ML, Munger JW, Fan S-M, Bakwin PS, Daube BC, Bassow SL, and others. 1993. Net exchange of CO₂ in a mid-latitude forest. *Science* 260:1314–7.
- Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR. 1994. Evidence of reduced photosynthesis rates in old trees. *For Sci* 40(3):513–27.