Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer

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Summary We investigated key factors controlling mass and energy exchange by a young (6-year-old) ponderosa pine (*Pinus ponderosa* Laws.) plantation on the west side of the Sierra Nevada Mountains and an old-growth ponderosa pine forest (mix of 45- and 250-year-old trees) on the east side of the Cascade Mountains, from June through September 1997. At both sites, we operated eddy covariance systems above the canopy to measure net ecosystem exchange of carbon dioxide and water vapor, and made concurrent meteorological and ecophysiological measurements. Our objective was to understand and compare the controls on ecosystem processes in these two forests.

Precipitation is much higher in the young plantation than in the old-growth forest (1660 versus 550 mm year^{-1}), although both forests experienced decreasing soil water availability and increasing vapor pressure deficits (D) as the summer of 1997 progressed. As a result, drought stress increased at both sites during this period, and changes in D strongly influenced ecosystem conductance and net carbon uptake. Ecosystem conductance for a given D was higher in the young pine plantation than in the old-growth forest, but decreased dramatically following several days of high D in late summer, possibly because of xylem cavitation. Net CO_2 exchange generally decreased with conductance at both sites, although values were roughly twice as high at the young site. Simulations with the 3-PG model, which included the effect of tree age on fluxes, suggest that, during the fall through spring period, milder temperatures and ample water availability at the young site provide better conditions for photosynthesis than at the old pine site. Thus, over the long-term, the young site can carry more leaf area, and the climatic conditions between fall and spring offset the more severe limitations imposed by summer drought.

Keywords: canopy architecture, carbon exchange, energy exchange, leaf area, Pinus ponderosa, radiative transfer.

Introduction

Ponderosa pine (*Pinus ponderosa* Laws.) is a major forest type in the western United States, occupying approximately 20% of unreserved forest area (Powell et al. 1992). We compared mass and energy exchange of a young (6-year-old) ponderosa pine plantation in California and a mixed-age, old ponderosa pine forest in Oregon (mix of 45- and 250-year-old trees). Although both ecosystems occur in regions where soil water deficits are common during the summer growing season, annual precipitation differs between sites, averaging 1660 mm at the young plantation and 550 mm at the old site over the past 30 years. The old forest has never been logged, and exhibits a multi-layer canopy, whereas the young plantation is even-aged, and was planted at a high stocking density (1200 trees per hectare).

Understanding changes in physiology with forest developmental stage is important for predicting forest growth and response to stress, yet few studies have examined how physiological changes with tree size and age influence the ecosystem-scale energy balance, transpiration rates, and net carbon uptake. Our objective was to compare the factors controlling energy balance and net carbon uptake over the summer of 1997 in the two pine ecosystems using a combination of physiological, weather, and soils data, and energy and carbon fluxes measured by the eddy covariance method. Although the weather and climate differ between the ecosystems, our analyses focus on mechanistic relationships between physiological and physical variables that allow meaningful comparisons to be made.

Materials and methods

Study sites

Both sites are part of the AmeriFlux and Fluxnet networks of sites, where we seek to understand processes controlling carbon dioxide and water vapor exchange in a variety of terrestrial ecosystems, using a combination of eddy covariance and

ecophysiological measurements. Measurements at the old ponderosa pine site (O) began in spring 1996, and measurements at the young ponderosa pine plantation (Y) began in spring 1997. Most measurements used in this comparison were made between June and September 1997. The old ponderosa pine forest is located in a Research Natural Area (44°30′ N, 121°37′ W, 940 m) east of the Cascade Mountains in Oregon, and Y is located on Sierra Pacific Industries property adjacent to Blodgett Forest Research Station near Georgetown, CA (38°53.7′ N, 120°38′ W, 1315 m). Stand characteristics are listed in Table 1. Both forests grow in a region of wet, cool winters and warm, dry summers, with almost no rain in summer. The 30-year mean annual precipitation is about three times greater at Y than at O (1660 versus 550 mm).

At O, about 27% of the area supports stands of old trees (~250 years old, 34 m in height), 25% comprises patches of younger trees (~45 years old, 10 m in height), and 48% supports mixed young and old trees (Law et al. 1999*a*). The understory cover is sparse. Soil is a sandy loam derived from volcanic ash and classified as a light-colored andic inceptisol. Organic matter content is 2.9%, and total N is 0.15% in the top 30 cm (Table 1; S. Remillard, Oregon State University, Corvallis, OR, unpublished data).

The young pine plantation consists of 6-year-old trees with a mean height of 3 m (Goldstein et al. 2000). The plantation contains a homogeneous mixture of ponderosa pine, with other trees and shrubs making up less than 30% of the biomass. The soil is loam to clay-loam, and classified as a mesic ultic haploxeralf in the Cohasset series, with andesitic lahar parent material. Organic matter content in the top 30 cm (6.9%) is higher than at the O site, and total nitrogen is similar (0.17%).

Environmental measurements

At both sites, we made continuous eddy covariance measurements above the forest canopy to determine half-hourly fluxes of CO_2, water, and sensible heat. We limited this comparison to June 1 through September 10, 1997, the measurement period at Y. Wind velocity and virtual temperature were measured at 10 Hz with three-dimensional sonic anemometers (Y: ATI Electronics, Inc., O: Solent model 1012 R2, Gill Instruments, Lymington, England). The CO_2 and H_2O fluctuations were measured with an open-path infrared gas analyzer at O (Auble and Meyers 1992), and a closed-path analyzer at Y (IRGA Model 6262, Li-Cor, Inc., Lincoln, NE). Vertical flux densities of CO_2 (F_c), latent (λE) and sensible heat (H) between the forest and the atmosphere are proportional to the mean covariance between vertical velocity (w') and the respective scalar (c') fluctuations (e.g., CO_2, water vapor, temperature). We use the convention that positive flux densities represent mass and energy transfer into the atmosphere and away from the surface, and negative values denote the reverse.

At O, instruments were positioned on a tower 47 m above ground (14 m above the canopy), and 2 m above the soil surface. Full details of the instrumentation and flux corrections are reported in Law et al. (1999*a*, 1999*b*) and Anthoni et al. (1999). The CO_2 and water vapor fluxes were corrected for density fluctuations arising from variations in temperature and humidity (Webb et al. 1980) and for influences of horizontal wind speed on virtual temperature (Schotanus et al. 1983). The data were screened to remove possible eddy covariance instrumentation and sampling problems (Law et al. 1999*a*). Fluxes were also rejected when inconsistently large CO_2 values were observed. After screening, about 75% of the above-canopy carbon flux and 85% of the water vapor fluxes remained available for further analysis. Although we had profile measurements of CO_2 in the canopy airspace for O, we only compared daytime CO_2 fluxes because the storage term, which is critical for estimates of nocturnal net ecosystem exchange of CO_2 (NEE), was not measured at Y.

At Y, the instruments were positioned 9 m above the soil surface (6 m above the canopy). Data were corrected for the time lag associated with sample tube length, and errors caused by sensor separation and damping of high frequency eddies were corrected by spectral analysis techniques (Kaimal and Finnigan 1994). Details of measurements and flux calculation methods have been described by Goldstein et al. (2000).

We calculated ecosystem resistance to water vapor transfer (r_c), boundary layer resistance (r_b), and aerodynamic resistance (r_a) following Shuttleworth (1984). Ecosystem conductance (G_c), the inverse of r_c, therefore describes canopy transpiration and evaporation from all surfaces. We did not use values during or immediately following rain because evaporation dominated the water flux, causing anomalous small values of r_c. Atmospheric and boundary layer conductances were large relative to canopy conductance during the day. The Bowen ratio (β) was calculated from the ratio of H to λE. The decoupling coefficient between the forest and the atmosphere, Ω, was calculated following Kelliher et al. (1990).

Fluxes calculated by the eddy covariance method show much variability. Baldocchi et al. (2000) showed that bin-averaging many days resulted in good agreement between turbulent energy fluxes and available energy (or model calculations). Therefore, we use 10-day means of mass and energy exchange in this paper.

Table 1. Characteristics of a mixed-age, old-growth, ponderosa pine stand in Oregon and a 6-year-old, ponderosa pine plantation in California (Young). Site means are provided for leaf area index (LAI), soil organic matter (SOM), and nitrogen. Standard errors are in parenthesis.

	Old-growth		Young
	Diameter class		
	0–30 cm	> 30 cm	
Age (years)	45	250	6
Trees per hectare	555	72	1200
Average canopy height (m)	10 (0.2)	34 (0.8)	3
Diameter at breast height (cm)	12 (0.2)	63 (2.7)	6.6
LAI	1.6		3.2
SOM (%, top 30 cm)	2.9		6.9
Soil nitrogen (%)	0.15		0.17

Meteorological variables were calculated as half-hourly means from measurements of air temperature, humidity, precipitation, photosynthetically active radiation (PAR), soil temperature, soil water content, soil heat flux, and rainfall. Soil temperature was measured at several depths at both sites. Soil water content (θ) was measured at O (0–30 cm and 0–100 cm depths) in several locations by automated and manual time domain reflectometry (Campbell Scientific, Logan, UT; Tektronix, Beaverton, OR), and similar automated instruments were placed horizontally at 10- and 20-cm depths at Y. Because of the differences in depths, absolute values of θ are not directly comparable between sites; however, we include this information to indicate relative changes in soil water content, which are critical at both sites.

Ecological measurements

Leaf area index (LAI, calculated on the basis of half the total leaf area) for O was estimated from optical measurements at 5-m intervals over a 10,000 m^2 plot with a Li-Cor LAI-2000 instrument. The effective leaf area estimate (L_e) from the LAI-2000 program was corrected for needle clumping within the shoot ($\gamma_E = 1.29$), clumping at scales larger than the shoot ($\Omega_E = 0.83$), and wood interception ($W = 0.33$, Law et al. 2001):

$$LAI = (L_e \gamma_E / \Omega_E) - W.$$

At Y, LAI was estimated in 1998 from LAI-2000 measurements every 5 m on two 20 × 20 m plots. The L_e was corrected based on γ_E (1.25) and W (0.01) from a young ponderosa pine site in Oregon (B.E. Law, unpublished data), and Ω_E from a red pine plantation (0.91; Chen 1996). The LAI was scaled to 1997 values based on sap wood area increments (M. Xu, University of California, Berkeley, unpublished data) that indicate that LAI increased about 30% from 1997 to 1998 (Goldstein et al. 2000).

We made several physiological and soil measurements periodically throughout the year for model input parameters, and to evaluate whole-ecosystem fluxes. At both sites, we repeatedly measured assimilation rates in relation to leaf internal CO₂ (A–C_i curves) with a Li-Cor LI-6400 (Law et al. 1999a). Maximum carboxylation rates (V_{cmax}) were calculated from the A–C_i curves based on the Farquhar model fitted with parameters in De Pury and Farquhar (1997). The activation energies $E_V = 68,000$ J mol^{-1} and $E_J = 199,000$ J mol^{-1} and relations between V_{cmax} and leaf temperatures were used for normalization to 25 °C (D. Ellsworth, Brookhaven National Laboratory/Duke University, unpublished data).

Other periodic gas exchange measurements included foliage and stem respiration, and soil surface CO₂ fluxes for estimating hourly ecosystem respiration (R_e) from meteorological data (Law et al. 1999a, Goldstein et al. 2000). Site-specific temperature response equations were developed for each component (e.g., foliage respiration as a function of air temperature, bole respiration as a function of bole temperature, and soil surface CO₂ flux as a function of soil temperature at 15 cm depth at O and 5 cm depth at Y).

At Y, foliage respiration was measured only in summer at ± 5 °C from ambient, and scaled up:

$$R_{leaf} = LAI\, a \exp(b(T_{leaf} - T_{ref})),$$

where T is temperature, and a and b are empirical coefficients. Bole respiration (R_{bole}) at the Y site was measured periodically throughout 1998 (M. Xu et al., unpublished data), and was computed for 1997 based on an exponential fit to soil temperature. Soil surface CO₂ flux (R_{soil}) was measured periodically throughout 1998 (Qi et al., University of California, Berkeley, unpublished data) and computed for 1997 as a function of soil temperature and soil water content (Goldstein et al. 2000).

At O, respiration by all components was measured periodically throughout the year, normalized to a common temperature, interpolated between measurement dates, and then applied in the following generic equation to estimate hourly fluxes (Law et al. 1999a):

$$R_i = M_i F_b \exp(\beta(T - T_b)),$$

where R_i is the respiration for component i (foliage, wood, soil), F_b is the flux at base temperature, β is the exponential coefficient from the component temperature response equations (ln(Q_{10})/10), T_b is base temperature (10 °C), T is the half-hourly temperature (air temperature for F_f, bole temperature for F_w, and soil temperature at 15 cm for F_s), and M_i is mean sapwood volume (m^3 sapwood m^{-2} ground) or leaf area (m^2 m^{-2} ground). Parameter M_i is not included in the soil equation because F_s was measured per m^2 ground. Gross ecosystem productivity (GEP) was calculated from the sum of respiration (bole, foliage, soil surface CO₂ flux) and F_c.

To identify the onset of water stress, we measured predawn leaf water potential bi-weekly to monthly throughout the growing season. We scaled data to the ground level to normalize for differences in measurement height (0.1 MPa per 10 m of height above ground), and assumed that the scaled value was representative of soil water potential (Ψ_s).

Results

Environmental variables

In 1997, the greatest climatic difference between sites was in annual precipitation, which was 3.5 times greater at Y than at O (2210 versus 488 mm; Table 2). Precipitation was slightly less than normal at O in 1997. Although annual rainfall was higher than normal at Y, rainfall from February through June was only 34% of normal, leading to lower than normal soil water content in spring 1997. In July and August, environmental conditions were similar at the two sites (Figure 1). In September, incident PAR, D, and air and soil temperatures were significantly higher at Y than at O ($P < 0.01$; Figure 1). Between June and September, the rate of change in soil water content at Y (20 cm depth, 0.025 m^3 m^{-3} day^{-1}) was greater than at O (0–30 cm depth, 0.016 m^3 m^{-3} day^{-1}).

Table 2. Climatic characteristics of the old growth (O) and young plantation (Y) ponderosa pine sites. Standard deviations are given in parenthesis.

	Old-growth	Young[1]
Latitude	44°30′ N	38°53.7′ N
Longitude	121°37′ W	120°38′ W
Elevation (m)	941	1315
1997 Annual incident PAR (MJ m^{-2})	2313	2900
30-Year mean annual precipitation (mm)	550	1660
1997 Annual precipitation (mm)	488	2210
Mean daytime D (kPa; July through Sept 1997)	1.31 (0.55)	1.46 (0.55)
Mean annual temperature (°C)	8.5	10.4
Mean daytime air temperature (°C; July through Sept 1997)	16.6 (3.5)	18.5 (3.2)

[1] Climate data for the young plantation was supplied by F. Schurr, Blodgett Forest Research Station.

Controls on evapotranspiration

Predawn water potentials (Ψ_p) scaled to the tops of the trees were similar between the 6- and 45-year-old trees (4 and 10 m height), but more negative for the taller (34 m) old-growth trees (Figure 2). Soil water potential, Ψ_s, estimated from predawn leaf water potential, was similar among age classes until
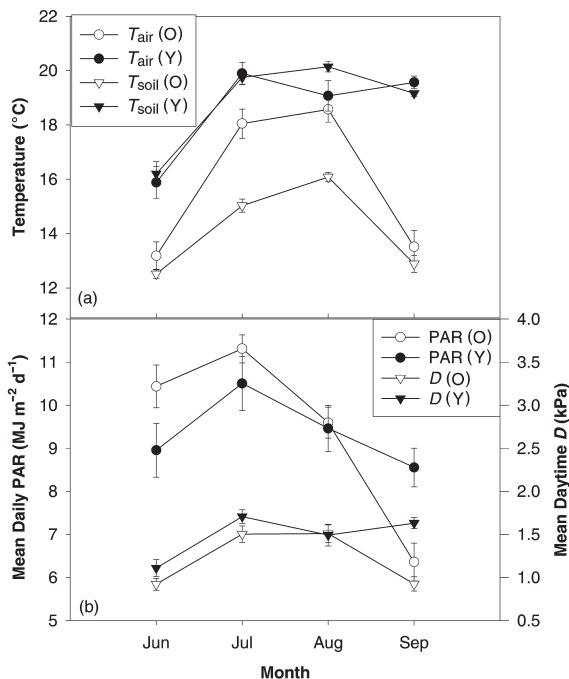

Figure 1. (a) Monthly mean air temperature (T_{air}) and soil temperature (T_{soil}) at 15-cm depth at the old-growth site (O) and the young plantation (Y). (b) Monthly mean daytime vapor pressure deficit (D, sunrise to sunset), and monthly mean of daily sum of incident photosynthetically active radiation (PAR).
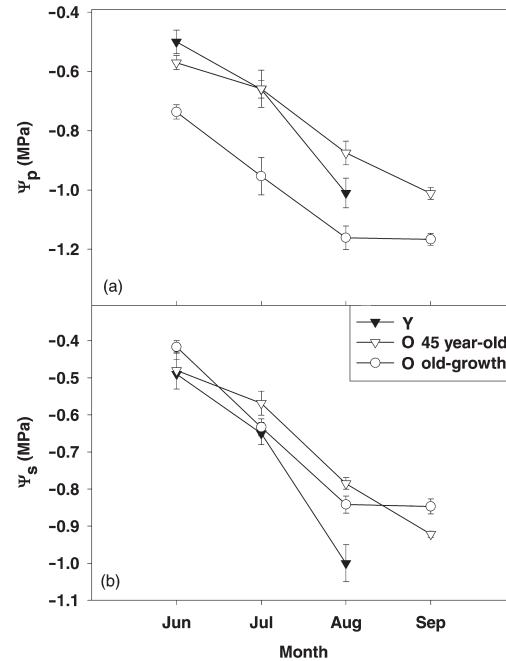

Figure 2. (a) Monthly mean predawn leaf water potential (Ψ_p) scaled to the top of the tree at the old-growth site (O) and the young plantation (Y), and (b) monthly mean soil water potential (predawn water potential scaled to the ground, accounting for gravitational effects of 0.01 (Ψ_s)).

August, when Ψ_s of the 6-year-old trees at the Y site reached significantly lower values than at the O site (–1.0 versus –0.8 MPa).

Mean net radiation above the canopy (sunrise to sunset) was similar at both sites throughout summer ($P > 0.01$), but 10-day mean Bowen ratios were much higher at O until Day 240 (Figure 3), when soil water content at Y had reached a minimum of 0.10 m^3 m^{-3}, and Ψ_p had reached –1.0 MPa. Midday ecosystem conductance, G_c, decreased at Y as soil water content at 20-cm depth decreased from 0.13 to 0.10 m^3 m^{-3} from June to September (Figure 4a). Ecosystem conductance appeared to follow a similar trend at O as soil water content (integrated over 0–30 cm depth) decreased from 0.14 to 0.09 m^3 m^{-3} from June through August; after rain in September, soil water content increased to 0.11 m^3 m^{-3}. From June through August, monthly mean G_c was significantly higher at Y than at O ($P < 0.01$), but values were similar at both sites in September. Ecosystem conductance was initially much higher for a given D (1000 to 1400 h) at Y than at O (Figure 4b). After predawn and soil water potentials reached a low of –1.0 MPa at Y in August, following prolonged drought and a period of high D (Days 218–220), the relationship between G_c and D was similar at the two sites.

The 10-day mean λE at O (λE(O)) was 30 to 55% less than λE at Y (λE(Y)) over the measurement period, with the greatest differences occurring in early summer (Figure 3b; $P < 0.01$). Mean maximum λE per day (third quartile, excluding up to 3 days following rain) was 3.6 mm day^{-1} at the Y site and 1.9 mm day^{-1} at the O site. Mean maximum transpiration was
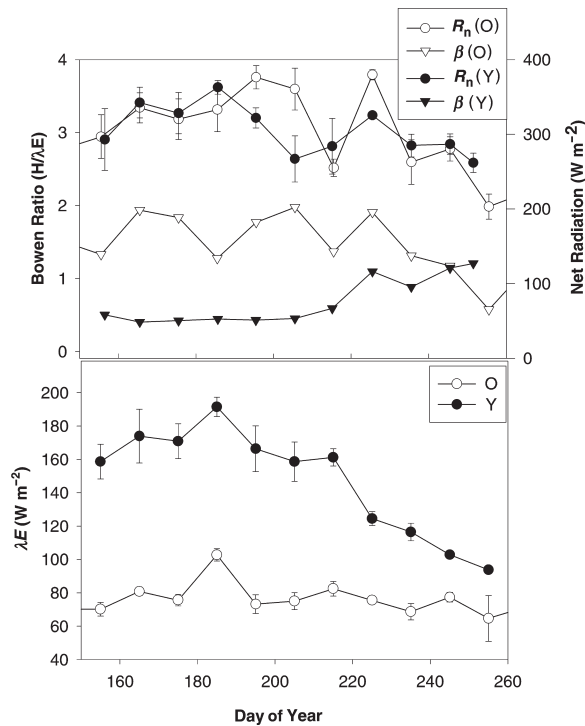
Figure 3. Ten-day mean of (a) daytime net radiation (R_n, sunrise to sunset) measured above the old-growth forest (O) and young plantation (Y), and Bowen ratios (β, sensible/latent heat flux, or $H/\lambda E$), and (b) 10-day mean λE. Although R_n was generally similar at both sites, β was higher at O until after Day 220, when possible cavitation at Y limited transpiration and thus more available energy was partitioned to sensible heat.

1.5 mm day^{-1} at the O site (0.9 mm day^{-1} unit leaf area^{-1}), calculated from above-canopy minus below-canopy flux during this period; thus, soil + understory evaporation was ~20% of total λE.

Carbon and water linkages

Maximum carboxylation rate, V_{cmax}, was higher at Y than at O during both measurement periods, and values were not significantly different between the two measurement periods (70.1 ± 3.8 in June, 68.0 ± 9.0 μmol m^{-2} (projected leaf area) s^{-1} in August, normalized to 25 °C). The V_{cmax} at O (V_{cmax}(O)) increased slightly but not significantly from June to August (59.7 ± 8.5 in June, 63.7 ± 4.3 in August, normalized to 25 °C). Measurements at O were made during bud break in June, and retranslocation probably limited carboxylation rates more than the high temperatures and drought in August.

Mean daytime net carbon uptake (sunrise to sunset) was significantly greater (F_c more negative) at Y than at O in July and August ($P < 0.01$), when F_c above the old-growth forest approached zero (Figure 5). Daytime F_c averaged −7.5 (SE 0.21) and −5.8 (SE 0.18) μmol m^{-2} s^{-1} in July and August, respectively, at Y, and the corresponding values at O were −1.9 (SE 0.51) and −2.6 (SE 0.34) μmol m^{-2} s^{-1}. Values of F_c were similar at both sites in early June, and daytime net carbon uptake was greater (F_c more negative) at O than at Y in September.
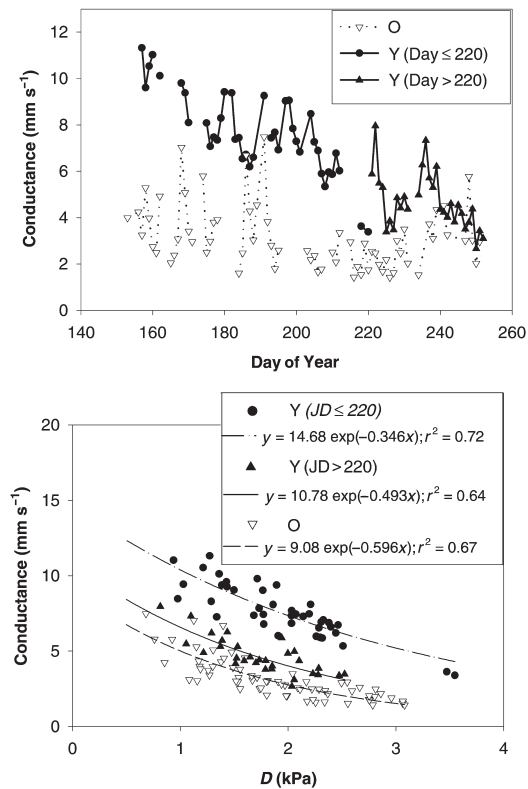

Figure 4. Mean midday (1000–1400 h) ecosystem conductance for water vapor transfer (a) on a daily basis, where conductance decreased at the young plantation (Y) as summer progressed, and (b) in relation to midday vapor pressure deficit (D). Following prolonged drought and a period of extremely high D (Days 218–220) at Y, the relationship between G_c and D was similar at the two sites.

Throughout the season, daytime ecosystem respiration (R_e; foliage + wood + soil) was greater by 30 to 47% at Y than at O (Figure 5). This indicates that, compared with O, gross carbon uptake (GEP = daytime $F_c - R_e$) was 58% greater at Y in July, and only 12% greater in September.

Figure 6 shows the variation of net CO$_2$ flux (F_c) with D when PAR > 900 μmol m^{-2} s^{-1} (i.e., when radiation was unlikely to limit F_c; data were bin-averaged with an equal number of points per bin of D). At Y, F_c showed a more complex response to D compared with O. After 3 days of high D at Y (mean daytime D ~3 kPa on Days 218–220), xylem cavitation may have occurred because soil water potential decreased significantly to −1.0 MPa, and F_c was significantly more positive at a given D than previously. Mean daily F_c generally became increasingly negative as G_c increased at both sites (i.e., net carbon uptake increased as ecosystem conductance increased; Figure 7).

The dependence of canopy CO$_2$ flux on incident PAR is shown in Figure 8. The response was strikingly different between sites: a rectangular hyperbola model (Michaelis-Menten model: $F_c = R_d - A_{max}$ PAR$/(K + PAR)$) calculated A_{max} at the ecosystem level to be ~5.7 and 22.6 μmol m^{-2} s^{-1} at O and Y, respectively. Light saturation occurred at lower PAR at O than at Y. Apparent quantum yield (α), calculated from the
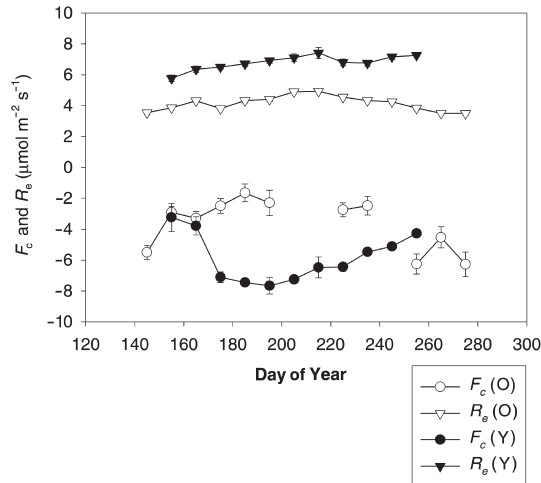
Figure 5. Ten-day mean of daytime (sunrise to sunset) ecosystem respiration (R_e; foliage + woody tissue + soil surface CO_2 flux), and CO_2 flux (F_c). Ecosystem respiration was consistently higher in the young plantation (Y), and net carbon gain by the old-growth site (O) was much less than that of Y in the middle of summer.

Figure 7. Relationship between midday (1000–1400 h) net CO_2 flux (F_c) and ecosystem conductance (G_c); F_c generally decreased with increasing G_c, except for periods of high conductance early in the season at the young plantation (Y) as a result of evaporation of rain. The symbol O signifies the old-growth site.

slope of F_c versus PAR at PAR < 250 µmol m^{-2} s^{-1}, was not significantly different between sites ($\alpha = 0.01$ mol CO_2 mol^{-1} photon). The canopy α values are low compared with leaf-level values, where α averaged 0.04 and 0.047 mol CO_2 mol^{-1} photon at the O and Y site, respectively (projected leaf area basis; Law et al. 2000, Panek and Goldstein 2001). The value of α for the Y site is comparable with ponderosa pine measurements across the San Bernardino mountains in California where nitrogen deposition was low (N. Grulke, University of California, Berkeley, unpublished data).

We applied a generalized model, 3-PG, with data from both sites to investigate monthly variation in carbon uptake and water use over the year (details of the model in Law et al. 2001). First, we ran the model for the Y site, assuming soil water holding capacity of 160 mm, quantum yield of 0.047 mol CO_2
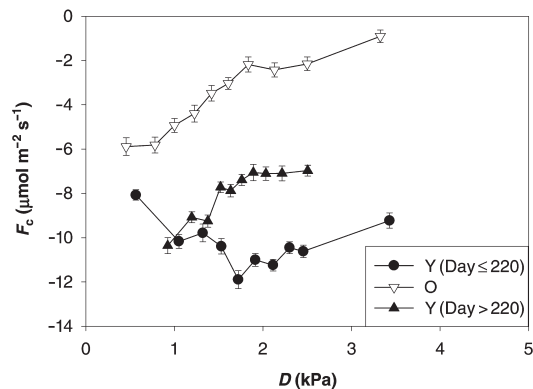
mol^{-1} photon, and site fertility 13% higher than at the O site (based on soil N for each location, Table 1). We used local volume tables for Blodgett Forest to develop the stem and foliage allometrics for the model (Meyers 1938, Oliver and Powers 1978). Simulated LAI and number of stems per unit area approximately matched the measured values. Results from the model indicated that, with this parameterization, air temperature (T_{air}) was optimal for growth during 5 months of the year, and only limited carbon uptake in winter by ~55%, resulting in an LAI of 5.6 and an annual GEP of 2100 g C m^{-2} year^{-1} at Age 60 (LAI 4.2 and GEP 2200 g C m^{-2} year^{-1} at Age 6). Then we ran the model for Y using the Metolius climate data (colder winters, lower annual precipitation) to assess how growth of the young forest would be influenced by the changed climate. In this case, the model indicated that temperature was optimal for photosynthesis only 3 months of the year, carbon uptake was limited by 90% in winter, and maximum LAI and GEP at Age 60 decreased to 3.9 and 1600 g C m^{-2} year^{-1}, respectively. When the model was run with allometrics, parameters,

Figure 6. Net CO_2 flux (F_c) and vapor pressure deficit (D), bin-averaged with an equal number of data points per bin of D. Ecosystem function changed at the young plantation (Y) after an extreme temperature and D event. After the event, the slopes of the relationship were similar at Y and the old-growth site (O).
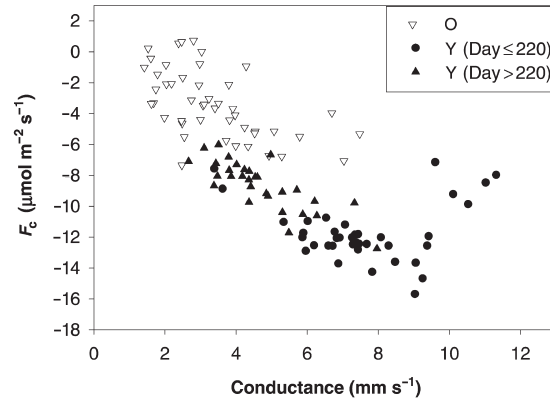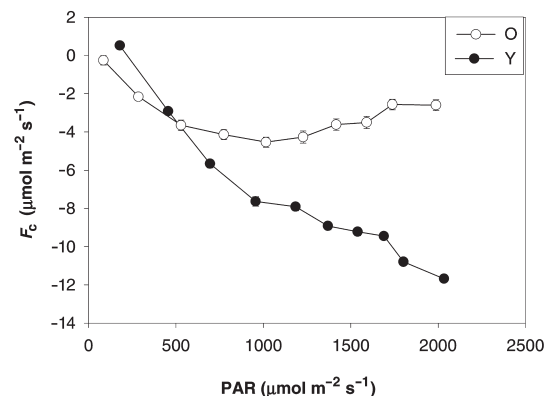

Figure 8. The dependence of hourly CO_2 flux (F_c) of the old-growth forest (O) and the young plantation (Y) on incident photosynthetically active radiation (PAR), averaged over the measurement period.

and climate data for O, it predicted a maximum LAI of 1.8, an annual GEP of 965 g C m^{-2}, and a slower rate of depletion of soil water. At Y, the model indicated that the soil water content reached 8% of maximum soil water by August, whereas it reached this point in September at O. This modeling exercise suggests that mild temperatures, higher annual rainfall, and slightly higher soil fertility at Y lead to a higher maximum LAI and GEP than at O, more than offsetting the drought constraints in summer.

Discussion

Controls on evapotranspiration

Although net radiation (R_n) and atmospheric saturation deficit (D), the principal driving terms for evapotranspiration, were similar at the two sites (Figures 1 and 3a), daily evapotranspiration at Y ($\lambda E(Y)$), was about twice as large as daily evaporation at O ($\lambda E(O)$) until about Day 220 (Figure 3b). Values of $\lambda E(O)$ were remarkably constant, both within averaging periods (as shown by the small standard errors in Figure 3b) and throughout the season. Values of $\lambda E(Y)$ were also rather constant until about Day 220, although there was more variation within averaging periods (Figure 3b). After Day 220, $\lambda E(Y)$ declined by about 40%, whereas $\lambda E(O)$ remained constant.

The mean maximum $\lambda E(Y)$ (3.6 mm day^{-1}, LAI 3.2) before Day 220 was similar to maximum values reported by Kelliher et al. (1993) for coniferous forests with leaf area indices ranging from 1.6 to 9.8 (median maximum λE 4.0 mm day^{-1}). The maximum λE at O (LAI 1.6) was only 1.9 mm day^{-1}. Kelliher et al. (1993) concluded that maximum λE was remarkably similar among the forest ecosystems they reviewed despite a fivefold range of LAI. They and others (Jarvis 1981, Lloyd et al. 1995, Law et al. 2001) attributed this to plasticity in the partitioning of λE between the canopy and the understory + soil surface, noting that (i) additional units of LAI above a value of about 3.0 do not enhance canopy transpiration, and (ii) understory and soil evapotranspiration tend to be inversely proportional to LAI (Black and Kelliher 1989).

At our sites, where LAI was lower than ~3, the ratio R of maximum $\lambda E(O)/\lambda E(Y)$ was influenced by both transpiration and soil evaporation. Suppose that the maximum transpiration rate (λE_t) was proportional to LAI, that maximum understory + soil evaporation (λE_u) was inversely proportional to LAI, and that the coefficients of proportionality were the same at both sites. At O, we found that λE_u was about 20% of mean maximum $\lambda E(O)$ in August (determined from above-canopy λE – below-canopy λE). Then, because the ratio LAI(O)/LAI(Y) was 0.50, algebraic manipulation shows that $R = 0.48$, and $\lambda E_u(Y) = 0.05\lambda E(Y)$. For the full period of comparison between sites, the eddy flux evapotranspiration data above the canopies yielded $R = 0.53$. Differences between these two estimates of R are probably related to the different time periods of the observations. A *caveat* to our simple ratio analysis of the influence of LAI on site differences in maximum λE concerns the influence of tree height on transpiration. Predawn leaf water potential at O, scaled to tops of trees, was

more negative for old trees (34 m tall) than for young trees (10 m tall) because of the gravitational effect (0.10 MPa per 10 m in height) and possible differences in physiology with tree age and size (Ryan et al. 2001). At a heavily thinned ponderosa pine stand near O, Ryan et al. (2001) estimated that transpiration by 10-m trees was 31% greater than by 34-m trees from June through August. So, in addition to the influence of differences in LAI between O and Y, maximum $\lambda E(O)$ may be less than maximum $\lambda E(Y)$ because of canopy height and age influences. However, because ~50% of the area at O is covered by tall (34 m) trees and ~50% by shorter (10 m) trees, and there is mutual shading in the dense patches of young trees, we expect the influence of height and branch hydraulics on transpiration rates at O to be less than that found by Ryan et al. (2001). We conclude that LAI differences are the most likely factor influencing the ratio of maximum λE between Y and O.

Why was LAI (and consequently maximum λE) so small at O? Baldocchi and Vogel (1996) reported daily λE between 0.5 and 2.5 mm day^{-1} for a boreal jack pine forest with LAI of about 2. Other low daily λE values (< 3.0 mm day^{-1}) have been reported for jack pine in central Canada (Amiro and Wuschke 1987, Baldocchi et al. 2001), and for a boreal spruce–lichen canopy (Fitzjarrald and Moore 1994). Baldocchi and Vogel concluded that, although in the short term, low values of λE could be explained by chronic effects of limited soil water or humidity deficits, there were underlying biogeochemical factors that linked the carbon and water cycles at their site and ultimately limited canopy transpiration. We discuss carbon– water linkages at our sites later, but first compare conductances between sites to assess the influences of soil water and atmospheric humidity.

For the two forests compared in this study, atmospheric conductances, g_a, were large (56.7 ± 1.3 mm s^{-1} for Blodgett Forest and 57.3 ± 2.6 mm s^{-1} for Metolius), so the Penman-Monteith (P-M) equation can be used to show that D was normally more important than R_n in driving λE, and measured values of D are a good approximation for D_o, the saturation deficit at the needle surface that is the appropriate term to use for analysis of stomatal conductance. Because mean values of R_n, D, and T_{air} (which influences the temperature-dependent coefficients in the P-M equation) were similar between sites for much of the season, observed differences in λE between sites can be attributed to differences in canopy (mainly stomatal) conductance.

At both sites, ecosystem conductances (G_c) around noon were much smaller than maximum values noted by Kelliher et al. (1993), who concluded that maximum G_c was largely invariant among forests and grasslands, typically about 20 mm s^{-1}. Values of G_c at O ($G_c(O)$) were usually in the range 2–4 mm s^{-1}, with occasional increases to 6–8 mm s^{-1} (Figure 4a), and declined only slightly with time. The soil water potential decreased substantially over the summer (Figure 2), and is likely to have caused the slow seasonal decline in $G_c(O)$. On a day-to-day basis, there was a strong relationship between $G_c(O)$ and D (Figure 4b). We interpret the constant and low value of $\lambda E(O)$ as indicating that this ecosystem is limited by

water availability, and that, in the short term, the trees adjust G_c in response to D so that λE does not exceed the maximum rate at which the roots can extract water. If this maximum rate were exceeded, cavitation would be likely (Tyree and Sperry 1989). The lack of a strong influence of soil water in the top 30 cm on $G_c(O)$ may indicate that roots are extracting water from deeper layers, or that this old-growth ecosystem has developed only sufficient leaf area to match its transpiration to the water extraction rate that can be achieved in the driest conditions. Thus, we conclude that in the short term, G_c at O is principally controlled by D, and in the long term, G_c is restricted to a low value by the small leaf area of the ecosystem, and declines slightly through summer as the soil dries.

At Y, $G_c(Y)$ and $\lambda E(Y)$ decreased by a factor of about 2 from Day 160 to 220. Why was G_c at Y ($G_c(Y)$) less than half the typical maximum values reported by Kelliher et al.(1993)? The most likely factors are: the relatively small leaf area of the canopy; the dry soil surface; and the soil water potential that declined over the summer more rapidly than at O. Until about Day 220, conductances at Y and O responded rather similarly, although their magnitudes were different. They both declined by a factor of about two as soil water potential decreased, and both were similarly sensitive to day-to-day variations in D (Figure 4). Around Day 220, $G_c(Y)$ decreased sharply, and thereafter the absolute magnitude of G_c and the variation of G_c with D were more similar to the relationships at O (Figure 4b). It seems likely that a 3-day period of high D (> 3.5 kPa around noon) combined with low soil water potential (Figure 2) caused sufficiently prolonged water stress to generate irreversible xylem cavitation. The consequent reduction in hydraulic conductivity requires a decline in stomatal conductance to protect the plant from further decreases in leaf water potential and catastrophic xylem failure (Jones 1992). After Day 220, $G_c(Y)$ was typically about 45% of earlier values.

Because the canopies had different conductances (until about Day 220), energy partitioning differed at the two sites although net radiation was similar (Figure 3a). Daytime mean Bowen ratios at Y were unusually small, around 0.5, whereas values at O, ~1.8, were similar to those reported for other dry forest canopies (Baldocchi and Vogel 1996, Jarvis et al 1997). The Bowen ratios at Y and O correspond to evaporation ratios (mm s^{-1} $\lambda E/R_n$) of 0.66 and 0.36, respectively. Thus at Y, much of the available energy was used in evaporating water, but at O, more of the energy was partitioned to sensible heating of the atmosphere. As a consequence, air temperature and saturation deficit at O attained values comparable to those at Y. After Day 220, when Bowen ratios at both sites became similar, air temperatures and saturation deficits at the sites diverged, indicating the strong feedback of heat from the water stressed Y canopy to the atmosphere. Incident PAR was also higher at Y than at O during this period, and likely contributed to the differences in temperatures and D.

Another way of contrasting the interactions of the old and young forests with the atmosphere is by comparing the decoupling coefficients Ω (Jarvis and McNaughton 1986). The mean value of Ω was 0.20 (SE 0.01) at O and 0.32 (SE 0.01) at

Y ($P = 0$) over the full measurement period, indicating stronger coupling for the more open, taller old-growth canopy. The Ω values were similar over the 4 months at O, but they steadily decreased at Y from 0.41 in June to 0.21 in September, indicating better coupling as ecosystem conductance declined, and evaporation was imposed more by D (McNaughton and Jarvis 1991) and controlled by the rate at which roots could extract water (Monteith and Unsworth 1990).

Light response

Canopy photosynthesis models can be used to show that, when the canopy is sparse, canopy photosynthesis is strongly curvilinear and saturates at relatively low irradiance (Baldocchi and Meyers 1997). When the canopy is closed, however, and a larger fraction of leaves are shaded, photosynthesis increases approximately linearly with irradiance (e.g., Valentini et al. 1999). This can partly explain the linearity of the photosynthetic-light response curve at Y, where the canopy is closed (Figure 8). Limitations to photosynthesis other than light are likely to have caused the photosynthetic light-response curve at O to saturate.

Carbon and water linkages

Mean daytime net carbon gain at Y ($F_c(Y)$) (Figure 5) was similar to mean summer values reported by Hollinger et al. (1999) for a boreal forest in Maine, but later in summer $F_c(Y)$ declined more (i.e., values became more positive) than Hollinger et al. observed. Seasonal changes in ecosystem respiration account for a minor portion of the decline in F_c (Figure 5). It seems likely that the reduction was caused by decreasing soil water availability and increasing evaporative demand, which influenced both canopy conductance and photosynthetic capacity. Although leaf-level measurements at Y showed no significant difference in V_{cmax} and quantum efficiency through the summer, net photosynthesis and stomatal conductance decreased during this period (Panek and Goldstein 2001). At O, net carbon gain ($F_c(O)$) declined rapidly after Day 140 but increased late in the season so that $F_c(O)$ was numerically larger than $F_c(Y)$ by Day 255 (Figure 5). The small LAI at the O site imposes inherent limitations on F_c throughout the year. The increase in $F_c(O)$ in September corresponded to an increase in $G_c(O)$ (Figure 4a), probably because of lower temperatures and smaller D (Figure 1b). In contrast, by September, $G_c(Y)$ was at its lowest point of the season, and D, T_{air} and T_{soil} were large (Figures 1a and 1b).

We think that differences in tree height between sites account for only a small fraction of the differences in F_c. At a heavily thinned pine stand near O, at typical midday D (2.5–3.0 kPa), Hubbard et al. (1999) found that mean photosynthesis and stomatal conductance were 21 and 32% lower at the tops of 34 m tall trees compared with 10 m tall trees. Thus, height had a smaller effect on photosynthesis than on stomatal conductance. In their study, leaf nitrogen and photosynthetic capacity were similar between the tall and short trees, suggesting that differences in photosynthesis and stomatal conductance were unrelated to these factors. Assuming a linear

scaling of the reduction in photosynthesis with height between 4 and 34 m, weighted by the fraction of trees in each size class at O, differences in height between trees at Y and O can explain only about 15% of the difference in F_c.

Although $F_c(O)$ decreased almost linearly as saturation deficit increased (Figure 6), $F_c(Y)$ seemed relatively independent of D up to Day 220. After Day 220, when cavitation appears to have occurred, $F_c(Y)$ showed similar sensitivity to D as we observed at O. Our finding that net carbon uptake decreased with decreasing ecosystem water vapor conductance (Figure 7) supports Valentini's assertion that this relationship occurs in a range of vegetation types (Valentini et al. 1999). In addition, data from our 14-year-old ponderosa pine flux site near O overlap both data sets in Figure 7 (unpublished data). Why was $F_c(Y)$ apparently not influenced by D early in the season (Figure 6)? Perhaps because G_c was sufficiently large that it was not a limiting factor in photosynthesis. After Day 220, $G_c(Y)$ became comparable to $G_c(O)$, and seemed to severely constrain F_c.

The link between the carbon and water cycles is strong in both of the ecosystems studied. Exploratory analysis with the 3-PG model indicates that the higher fertility, milder temperatures and greater fall through spring precipitation at Y give rise to a larger LAI at Y than at O. Although carboxylation rates and quantum efficiencies were higher at Y than at O, they were not significantly so. Over the summer during which this study was conducted, the denser canopy at Y used water more rapidly than the canopy at O, resulting in substantially greater water stress by August, which caused a large reduction in canopy conductance. The reduction prevented further cavitation, at the expense of substantially reducing net carbon uptake. However, the model suggests that the mild temperatures and soil water recharge over the fall–spring period, would allow photosynthesis to occur over a long period, more than offsetting the late summer inhibition of photosynthesis due to water stress. Thus, long-term climatic and soil fertility effects on LAI at Y likely account for much of the variation between sites in GEP, F_c, and λE, because D and available energy during much of the summer were similar between sites.

The smaller LAI at O relative to Y allows the forest at O to survive the summer drought without the extremes of water stress experienced by the forest at Y, but net carbon gain is much less than at Y. However, in the colder, cloudier climate in fall through spring at O, a greater leaf area would not enhance annual productivity, but would incur the risk of damaging water stress in summer. It is interesting to speculate on the changes in carbon and water relations in recent decades that must have occurred in the old growth forest as fire protection has allowed a younger tree cohort to become established.

Conclusions

The old-growth ponderosa pine forest differed from the young plantation in several respects, including lower stand density (~50%), LAI (50%), soil nitrogen (13%), soil organic matter content (42%), and tree age (45–250 years). In addition, the old-growth site experienced lower soil and air temperatures (by about 2 and 4 °C, respectively) and precipitation through the year (~67% lower) than the young plantation during a typical year. These differences led to a substantially higher Bowen ratio (30–55% lower λE) in summer, slower soil water depletion (~50%), lower respiration (30–47%), lower GEP (12–58%), and stronger coupling between the ecosystem and the atmosphere (60%) in the old-growth forest. In addition, trees in the young plantation displayed high sensitivity to several days of high D in late summer, which likely caused cavitation, and led to similar conductances at both sites in relation to D. Comparison of these two ecosystems shows that ponderosa pine forests retain similar general relationships between physiological activity, ecosystem conductance, and carbon flux in response to changing climatic conditions, although there may be offsets in the relations due to long-term effects of climate and fertility on potential LAI. Our results suggest that it should be possible to model and predict the impacts of climate variability and forest management practices on GEP for this type of ecosystem, if relationships between conductance, evaporative demand, and moisture availability can be modeled accurately. Measurements of whole ecosystem fluxes and ecophysiological responses in a range of forest age classes and management regimes within a forest type can be valuable for testing such models, and evaluating how processes controlling carbon and water vapor exchange vary with climate, stand age and management.

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