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Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA)

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Abstract

Fluxes of CO₂, water vapor, and sensible heat were measured by the eddy covariance method above a young ponderosa pine plantation in the Sierra Nevada Mountains (CA) over two growing seasons (1 June–10 September 1997 and 1 May–30 October 1998). The Mediterranean-type climate of California is characterized by a protracted summer drought, with precipitation occurring mainly from October through May. While drought stress increased continuously over both summer growing seasons, 1998 was wetter and cooler than average due to El Niño climate patterns and 1997 was hotter and drier than average. One extreme 3-day heat wave in 1997 (Days 218–221) caused a step change in the relationship between H₂O flux and vapor pressure deficit, resulting in a change in canopy conductance, possibly due to cavitation of the tree xylem. This step change was also correlated with decreased rates of C sequestration and evapotranspiration; we estimate that this extreme climatic event decreased gross ecosystem production (GEP) by roughly 20% ($4 \mu\text{mol C m}^{-2} \text{ s}^{-1}$) for the rest of the growing season. In contrast, a cooler, wetter spring in 1998 delayed the onset of photosynthesis by about 3 weeks, resulting in roughly 20% lower GEP relative to the spring of 1997. We conclude that the net C balance of Mediterranean-climate pine ecosystems is sensitive to extreme events under low soil moisture conditions and could be altered by slight changes in the climate or hydrologic regime. ©2000 Elsevier Science B.V. All rights reserved.

Keywords: Net ecosystem exchange; Climate variability; Ponderosa pine; Eddy covariance

1. Introduction

Forests play an important role in the exchange of carbon, water and energy between the land and the atmosphere. As a major store of mobilizable carbon, they can strongly influence the global carbon cycle and thus climate (Musselman and Fox, 1991). Understanding the dynamics of carbon exchange between

the atmosphere and the forested biosphere has been the goal of recent ecosystem-scale projects, many of which are now part of the Ameriflux or Euroflux networks. These projects study biomes that are representative of large areas of the terrestrial biosphere, such as boreal forest (BOREAS, e.g. Margolis and Ryan, 1997), temperate broad-leaved deciduous forest (Wofsy et al., 1993; Baldocchi, 1997), southeast coniferous forest (Clark et al., 1999), and tropical forest (Grace et al., 1995). The carbon sequestration rate for most of these ecosystems is controlled by light availability and timing of new leaf development

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(e.g. Goulden et al., 1996), among other factors; a limited number of canopy-scale eddy covariance studies have shown that drought stress can also play a significant role in net ecosystem exchange (e.g. Baldocchi, 1997). While the Mediterranean zonobiome (including California) is a significant biome globally, little attention has been given to canopy-scale forest responses to this climate. Furthermore, although ponderosa pine (*Pinus ponderosa* Doug. ex. Laws) is the most common conifer species in North America, this forest type has only recently been investigated by such canopy scale studies (Anthoni et al., 1999; Baldocchi et al., 2000; Law et al., 1999a, b, 2000a). Finally, recent forest management in many parts of the US has resulted in millions of acres of young, growing forest. Of the US Forest Service land in the Sierra Nevada, 380,000 acres (4%) is in plantation, and 34% of that is ponderosa pine plantation (Landram, 1996). These even-aged stands provide an excellent opportunity to investigate the capacity of a young, managed forest to sequester carbon under drought-stressed conditions.

Winter precipitation (October–May) and summer drought characterize the Mediterranean-type climate of California. Freezing temperatures limit growth in the early spring, and low soil moisture and high vapor pressure deficits (VPD) limit growth in the late summer. This climate thus imposes hydrologic and temperature limitations to ecosystem gas and energy exchange during summer months.

To examine the effects of interannual climate variability on canopy-scale carbon, water, and energy fluxes, we established a measurement site in a young ponderosa pine plantation in the Sierra Nevada Mountains of California and observed forest response during natural variations of climatic conditions. We present data acquired continuously over two climatically different growing seasons: 1997 was drier than the climatic mean, and 1998 was cooler and wetter than the climatic mean (influenced by El Niño).

2. Materials and methods

2.1. Site description

The field site was established in May 1997 in a ponderosa pine plantation, owned and operated by

Sierra Pacific Industries. The plantation is located (38°53'42.9"N, 120°37'57.9"W, 1315 m) adjacent to Blodgett Forest Research Station, a research forest of the University of California, Berkeley (Fig. 1).

The forest constituting the sampled daytime 'footprint' of the tower was a 4 m homogenous canopy of 6–7-year-old trees dominated by ponderosa pine. The canopy also included individuals of Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), giant sequoia (*Sequoiadendron giganteum*), incense-cedar (*Calocedrus decurrens*) and California black oak (*Quercus kelloggii*). The major understory shrubs were manzanita (*Arctostaphylos* spp.) and *Ceanothus* spp. In 1997, about 25% of the ground area was covered by shrubs, 30% by conifer trees, 2% by deciduous trees, 7% by forbs, 3% by grass and 3% by stumps. Two separate model estimates of the tower footprint agreed that roughly 90% of the footprint was within the young plantation (200 m of the tower) during the daytime (lagrangian stochastic dispersion model by Hsieh et al., 1997, results provided by Hsieh; eulerian advection-diffusion model by Horst and Weil, 1994, results reported in Baker et al., 1999). This footprint area was in a stage of rapid growth, as exhibited by the large (30–35%) increase in leaf area index (LAI) between the 1997 and 1998 growing seasons (Table 1). Two hundred meters upwind (daytime) of the measurement site, the canopy foliar density increased sharply; the transition reflected the borderline between the 6–7-year-old plantation and a 12–13-year-old plantation southwest of the measurement site. The predominant daytime air mass trajectory at the site is directed upslope from the Sacramento Valley (from the southwest, 210–240°). At night, air flows downslope from the Sierra Nevada Mountains (from the northeast, ~30°). The site was relatively flat. The slope of terrain within

Table 1
Ecosystem total LAI (m² leaf per m² ground area)^a

	Initial	Maximum	Final
1997 LAI	3.9	6.6	5.3
1998 LAI	5.3	9.0	7.1
Ratio	1.4	1.4	1.3

^a LAI includes tree and shrub leaf area. Initial indicates LAI before budbreak, and final indicates LAI after loss of third year needles. Two age classes of needles were typically retained through the winter. Uncertainty in LAI estimates is approximately 20%.

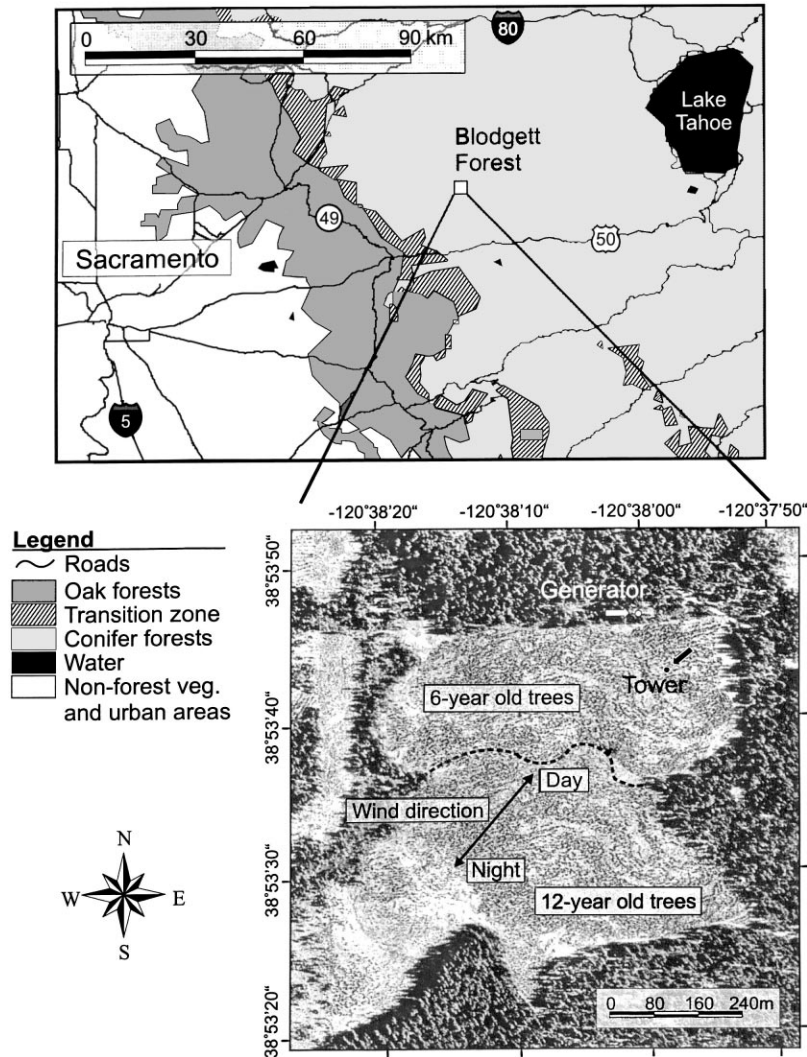


Fig. 1. Index map showing the regional setting and details of the Blodgett Forest tower site. The upper image shows regional vegetation. It is derived from the USGS Seasonal Land Cover Regions classification, which is based on 1 km pixel AVHRR data. The 'Oak Forests' category shown here comprises both oak forest and woodland areas. The lower image shows details of the tower site and is based on a USGS 3.75 min digital orthophoto quadrangle with 1 m pixels.

200 m of the tower varied less than 2° in the north, east, and south but was $0\text{--}15^\circ$ to the west where a creek flows from south to north. The slopes beyond 200 m but within 1000 m of the site were larger and varied from $0\text{--}15$, $0\text{--}10$, $0\text{--}5$, and $0\text{--}30^\circ$ in the north, east, south, and west, respectively.

The site is characterized by a Mediterranean climate (Table 2). Since 1961, annual precipitation has averaged 163 cm (254 cm snow), with the majority of

precipitation falling between September and May, and almost no rain in the summer. Summer temperature averages range from $14\text{--}27^\circ\text{C}$ (daily low to daily high) and winter temperatures from $0\text{--}9^\circ\text{C}$ (data from Blodgett Forest archives, F. Schurr). Trees generally break bud in May and set bud in late July to early August; 1998 was an exception, with the start of needle elongation delayed until late June. Predawn water potential in ponderosa pine can be expected to drop as low as

Table 2
Rainfall and climate comparison^a

	1997	1998
February–May rainfall	18 cm	117 cm
% of normal February–May rainfall	27%	176%
Last subzero day	Day 121	Day 146
Bud break	Day 145	Day 180

^a The 1997 February–May rainfall was 27% of normal (average since 1961); in 1998 the rainfall was 176% of normal. The last frost and bud break were delayed by approximately 1 month in 1998.

–1.0 MPa by the end of the growing season (based on observations of 12-year-old ponderosa pine at a site 2 km upwind of the tower throughout the 1997 growing season).

The soil is a fine-loamy, mixed, mesic, ultic haploxeralf in the Cohasset series whose parent material was andesitic lahar. It is relatively uniform, comprised predominantly of loam or clay-loam. Cohasset soils are inherently very porous (up to 65% by volume) primarily due to the high proportion of fine particles (L. Paz, personal communication). The top 30 cm of soil in 1998 contained 6.9% organic matter and 0.17% nitrogen.

Infrastructure for the canopy scale flux measurements included a 10 m measurement tower (Upright Inc.), a temperature-controlled instrument building, and an electrical generation system powered by a 30 kW diesel generator (Kohler). The measurement tower was placed towards the eastern end of the stand to maximize the ponderosa pine plantation fetch during the day. The generator was located 130 m northwest of the tower, as far outside of the major airflow paths as possible. Hydrocarbon measurements at the site indicated that exhaust from the generator affected our measurements less than 5% of the time, and contamination occurred only at night (Lamanna and Goldstein, 1999).

2.2. Measurements and calculations

From 1 June to 10 September 1997 and from 1 May to 30 October 1998, fluxes of CO₂, H₂O, and sensible heat were measured by the eddy covariance method. Environmental parameters such as wind direction and speed, air temperature and humidity, net and photosynthetically active radiation (R_n and PAR, respectively),

soil temperature, soil moisture, soil heat flux, rain, and atmospheric pressure were also monitored. Additional continuous measurements at the site included O₃ concentration and flux, and concentrations of a wide variety of volatile organic compounds (Lamanna and Goldstein, 1999). A system to measure the vertical profiles of CO₂ and H₂O was added in 1998. The data acquisition system was separated in two parts: (1) a fast response system which monitored data at high frequency (up to 10 Hz) used to calculate eddy covariance, with raw data stored in 30 min data sets; and (2) a slow response system which monitored environmental parameters and stored 30 min averaged data.

2.2.1. Eddy covariance measurements

Wind velocity and virtual temperature fluctuations were measured at 10 Hz with a three-dimensional sonic anemometer (ATI Electronics Inc., Boulder, CO) mounted on a horizontal beam at 9 m above the ground (~5 m above the trees), 3 m upwind (daytime) of the tower. CO₂ and H₂O mixing ratios were measured with an infrared gas analyzer (IRGA, LICOR model 6262, Lincoln, NE). The Licor A-D converter was used in 1997 providing response times of 5 Hz for CO₂ and 3 Hz for H₂O. The raw analog data was used in 1998 providing response times of 10 Hz for both gases. CO₂ was calibrated every other day in 1997 and three times per day in 1998 with two standards (In 1997: Scott Marrin, Riverside, CA, 364 and 421 ppm CO₂ in N₂, ±1%, NIST traceable. In 1998: Scott Marrin, 351.9 and 413.0 ppm CO₂ in air, ±.05%, calibrated against SIO scale (R. Weiss)). H₂O concentration was calibrated using relative humidity, temperature and pressure measured simultaneously by other sensors. Ambient air was sampled 10 cm downwind from the sonic anemometer at 71 min⁻¹ through 2 μm (Zefluor, Gelman Sci., Ann Arbor, MI) and 1 μm (Acro 50, Gelman Sci., Ann Arbor, MI) filters. In 1997, the IRGA was mounted on the tower, requiring sample air to travel through 4 m of 1/4" Teflon tubing; this length increased to 13 m in 1998 as the IRGA was placed in the temperature-controlled structure at ground level. Dry N₂ gas (UHP, Puritan Bennett, St. Louis, MO) was passed through the reference cell of the IRGA.

Fluxes of CO₂, H₂O, and sensible heat between the forest and the atmosphere were determined by the

eddy covariance method. This method quantifies vertical fluxes of scalars between the forest and the atmosphere from the covariance between vertical wind velocity (w') and scalar (c') fluctuations averaged over 30 min periods (e.g. Shuttleworth et al., 1984; Baldocchi et al., 1988; Wofsy et al., 1993; Moncrieff et al., 1996). Turbulent fluctuations are determined from the difference between instantaneous and mean scalar quantities. Positive fluxes indicate mass and energy transfer from the surface to the atmosphere. Fluxes were calculated using RAMF 8.1 (*Routinen zur Auswertung Meteorologischer Forschungsflüge*, Routines for the Processing of Meteorological Research Flights) data processing software coded in FORTRAN (Chambers et al., 1997). RAMF was originally developed by Jörg Hacker (Flinders Institute for Atmospheric and Marine Sciences, Flinders University of South Australia), and was provided to us by Scott Chambers.

Systematic errors associated with the eddy covariance method include time lags between wind and scalar data due to travel through sampling tube and instrument response time, damping of high frequency fluctuations by the closed-path IRGA and travel through the sampling tube, sensor separation between wind and scalar measurements (Rissman and Tetzlaff, 1994), and inability of the sonic anemometer to resolve fine-scale eddies in light winds (Goulden et al., 1996; Moncrieff et al., 1996). Generally, these type of errors result in the underestimation of flux (Leuning and King, 1992). The inability of the sonic anemometer to resolve the vertical wind occurs mainly at night as the fluctuations become dominated by small, high-frequency eddies (Goulden et al., 1996 use $u^* < 0.17 \text{ m s}^{-1}$ as the threshold for reliable measurements).

The sonic anemometer data set was rotated to force the mean vertical wind speed to zero, and to align the horizontal wind speed onto a single horizontal axis. The calculated vertical rotation angle was typically 0.6° and did not vary by more than a few degrees, suggesting that local topography distortions to the airflow were minor. The small angle of rotation also suggests that the terrain at the site is relatively level. The time lag for sampling and instrument response was determined by maximizing the covariance between w' and c' . Typical values were 2.2 s in 1997 and 5 s in 1998 and were extremely consistent throughout the mea-

surement period. Errors due to sensor separation and damping of high frequency eddies were corrected using spectral analysis techniques as outlined by Rissman and Tetzlaff (1994). Under ideal conditions the shapes of the power spectra for $w'T'$ (sensible heat flux), $w'c'$ (CO_2 flux), and $w'H_2O'$ (water vapor flux) should be similar. Sensible heat flux (using fast response air temperature data from the sonic anemometer) does not have errors due to sensor separation or damping of high frequency eddies; by comparing the power spectra of the sensible heat flux to those of the gas fluxes, errors in the gas fluxes based on loss of high-frequency eddies can be assessed. Spectral analysis revealed an underestimation of gas fluxes of roughly 9% for CO_2 and 12% for H_2O . Correction factors for each half hour were calculated for each gas and applied to the fluxes during the times when the sensible heat flux data were reliable.

The inability of the sonic anemometer to resolve fine-scale eddies in light winds (e.g. during night) produces systematic errors in the sensible heat flux, which precludes the use of sensible heat flux to correct the CO_2 and H_2O fluxes. Thus, although daytime turbulence was strong enough to produce reliable measurements, the calmer conditions during night rendered the nighttime flux measurements less reliable. In general, nighttime sensible heat fluxes were close to zero, so appropriate correction factors based on spectral analysis were difficult to determine. Therefore, the daytime gas fluxes were corrected using spectral techniques, but the correction based on spectral analysis was not applied to the nighttime data.

In some studies of CO_2 fluxes over canopies (e.g. Grace et al., 1995), a short burst of positive CO_2 flux can be seen in the early morning due to the 'flush out' of CO_2 as the nighttime inversion layer breaks down. This ecosystem exhibited no such 'flush out'; furthermore, measurements of intracopy CO_2 storage in 1998 (Fig. 2) confirm that nocturnal CO_2 storage was small in this ecosystem: for most times, the change in intracopy storage (and therefore the error in top-of-canopy C flux measurements) is near zero. Only during times of low winds (09:00 and 20:00 h) did the storage change, and then only for a short period representing about 10% of the maximum flux. Since the canopy storage term was measured only in 1998, we have neglected this correction for the comparisons presented in this paper.

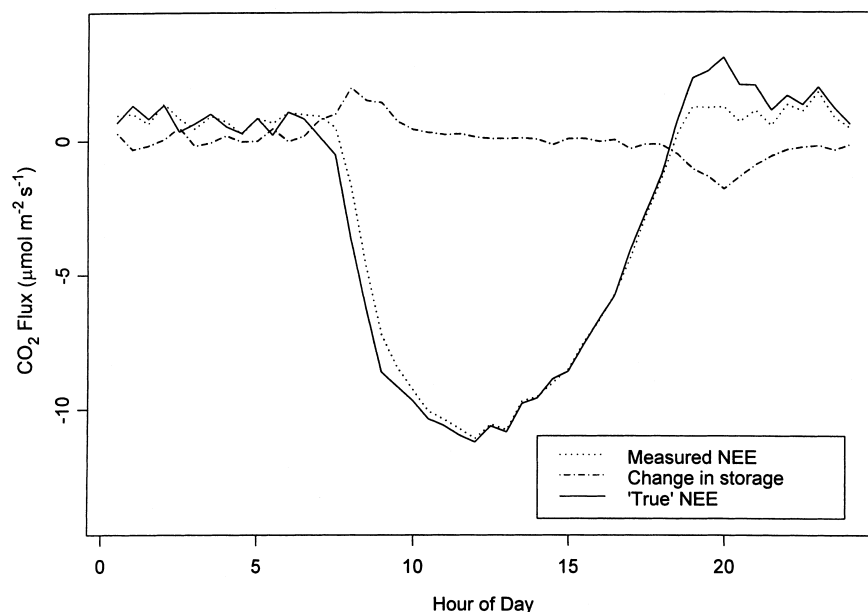


Fig. 2. Average diurnal pattern of C storage from May to October 1998. Changes in intracanopy CO_2 storage are limited to two brief periods of low wind in the morning and evening.

2.2.2. Environmental measurements

Environmental parameters were recorded on a CR10X datalogger (Campbell Scientific Inc., Logan, UT). In 1997, the wind monitor (R.M. Young, Traverse City, MI), relative humidity (Vaisala Inc., Woburn, MA) and temperature probe (Fenwal Electronics Inc.), net radiation (REBS, Seattle, WA) and PAR (Li-Cor Inc., Lincoln, NE) sensors were located on a beam at the top of the tower. Three soil temperature thermistors (Campbell Scientific Inc.) were placed 5, 10, and 15 cm below the surface, 6 m from the tower and were in partial shade during the day. A heat flux plate (REBS, Seattle, WA) was placed at 10 cm depth next to the middle thermistor. Two soil moisture probes (Campbell Scientific Inc., Logan, UT) were buried horizontally at 10 and 20 cm depth; rain gauge and barometric pressure devices (Campbell Scientific Inc., Logan, UT) were located one mile away on a tower belonging to the Blodgett Forest Research Station. This sensor configuration was enhanced in 1998 with the addition of four relative humidity and temperature probes (Vaisala Inc., Woburn, MA) in aspirated radiation shields (Campbell Scientific Inc., Logan, UT), three cup anemometers (Met-one, Inc., Grants Pass, OR), an on-site rain gauge (TMI) and

pressure sensor (Vaisala Inc., Woburn, MA), seven soil thermistors (Campbell Scientific Inc., Logan, UT) in two new, deeper (to 50 cm) soil columns, two heat flux plates (REBS, Seattle, WA), and one soil moisture probe (Campbell Scientific Inc., Logan, UT) at 50 cm. Vertical profile measurements of CO_2 and H_2O were also initiated in 1998 using a Li-Cor 6262 IRGA (Li-Cor Inc., Lincoln, NE) which sampled at five heights sequentially for 6 min each. The old soil sensors were moved before the 1998 measurements in order to consolidate with the new sensors. VPD was calculated as the difference between the saturated and the actual vapor pressure of the air. Table 3 summarizes the relevant measurements and sensors at the site for the two field seasons.

In addition to these measurements taken at the tower, measurements of leaf, bole, and soil respiration were carried out in the surrounding ecosystem. Leaf level respiration measurements (Li-Cor 6400) were used to calibrate the leaf respiration model detailed in Section 3. Measurements were made on S-facing foliage of three trees between 21:00 and 04:00 h in June 1999. Temperatures were manipulated to $+5$ and -5°C of ambient to determine the relationship between respiration and temperature. Daytime respi-

Table 3
Environmental measurements and sensors at Blodgett Forest tower site

Parameter	Sensor	N '97	N '98	Model	Manufacturer
Wind velocity	Sonic anemometer	1	1		ATI
H ₂ O/CO ₂ concentration	Infrared gas analyzer	1	1	6262	Li-Cor
H ₂ O/CO ₂ profile	Infrared gas analyzer	0	1	6262	Li-Cor
Air temp/humidity	RH/T sensor, shielded and aspirated	1	4	HMP-45C	Vaisala
Barometric pressure	Capacitive pressure sensor	0	1	CS105	Vaisala
Net radiation	Net radiometer	1	2	Q7.1	REBS
PAR	Quantum sensor	1	2	LI190SB	Li-Cor
Rainfall	Tipping bucket	0	1	TR-525T	TMI
Soil heat flux	Heat flow transducer	1	3	HFT-3.1	REBS
Soil moisture	Time-domain reflectometer	2	3	CS615	Campbell Scientific, Inc.
Soil temperature	Thermistor	3	10	107	Campbell Scientific, Inc.
Wind speed/direction	Wind vane and rotor anemometer	1	1	5103	R. M. Young, Inc.
Wind speed	Cup anemometer	0	3	014A	Met-one

ration values were extrapolated from nighttime values using this relationship.

Soil CO₂ efflux was measured (Li-Cor 6400 Soil CO₂ Flux System, Li-Cor Inc., Lincoln, NE) at 18 points within two 20 m×20 m plots within the tower footprint (Qi et al., 2000). Soil respiration was sampled approximately every 2 weeks for the whole year except in winter when snow covered the ground. Data from June to November 1998 were used to establish the relationships between soil respiration, soil temperature, and soil moisture. The function of the soil respiration chamber was extended to measure bole respiration by gluing PVC collars on stem surfaces (Xu et al., 2000a, submitted for publication). The PVC collars had inner diameters of 10 cm and heights of 3–5 cm (depending on tree diameter). Since the trees in the plantation were relatively small and the stem surfaces were curved, PVC collars were cut to fit the bole and glued on using silicon II (CO₂ emissions from the PVC collars were not detectable). Measurements were made on seven trees with DBH ranging from 8.7–15.0 cm and height ranging from 3.8–5.6 m. Bole respiration was measured on the north sides at 1.3 m height. Branch respiration was not measured directly but was estimated using the relationship between bole respiration and bole diameter. DBH, height, and crown width of all the trees (DBH>3 cm) in the two 20 m×20 m plots were measured, and this data was used to scale respiration for the ecosystem model (detailed in Section 3).

Total (all-sided) LAI was estimated using two techniques which resulted in similar estimates, (1) the LI-2000 (Li-Cor Inc., Lincoln, NE), and (2) scaling

from leaf-level determination using the measured geometry of trees. The LAI-2000 measurements were made every 5 m on two 20 m×20 m plots in 1998. The effective leaf area estimate, L_e , from the LI-2000 program (c2000.exe; Li-Cor Inc., Lincoln, NE) was corrected for needle clumping within shoot, γ_E , clumping at scales larger than shoot, Ω_E , and wood interception, W , (Law et al., 2000a) to yield an estimate of total LAI:

$$\text{LAI} = 2 \left\{ \frac{L_e \gamma_E}{\Omega_E} - W \right\} \quad (1)$$

Values of γ_E (1.25) and W (0.01) were taken from a young ponderosa pine site in Oregon (Law, unpublished data), and Ω_E from a red pine plantation (0.91; Chen and Cihlar, 1996). This method introduces some error as the LAI-2000 measures whole ecosystem LAI (including shrubs) while the final values are corrected using coefficients based on pine leaf clumping. LAI was scaled to the end of the 1997 and 1996 growing seasons using sapwood area ratios. The end-of-season LAI was then extended to seasonal time series using leaf-level measurements of needle length made at four points during the growing season. The resulting LAI estimates are consistent with estimates of ponderosa pine LAI based on scaling up from observed tree allometry. Maximum ponderosa pine total (all-sided) LAI for 1998 was 7.0. Maximum ecosystem LAI, based on LI-2000 measurements, was 9.0, which implies a shrub LAI of approximately 2.0. The high total LAI for this young plantation results from its high stocking density of approximately 1200

trees ha^{-1} and will decline significantly in the future due to pre-commercial thinning.

2.3. Carbon respiration model and gross ecosystem productivity

Measuring net ecosystem C exchange at the top of the canopy yields no independent information on photosynthetic versus respiration C fluxes; only with sufficient knowledge of respiration rates can the effects of climate on gross ecosystem productivity (GEP) be deduced. Furthermore, the nighttime flux measurement limitations mentioned earlier, complicate attempts to determine respiration fluxes based on nighttime eddy covariance measurements. Accordingly, we modeled the total ecosystem respiration flux from scaled field measurements of leaf, bole, and soil respiration.

The leaf respiration model was based on measurements of dark respiration which should exhibit exponential temperature dependence (e.g. Law et al., 1999b):

$$R_{\text{leaf}} = \text{LAI} a \exp\{b(T_{\text{leaf}} - T_{\text{ref}})\} \quad (2)$$

where R_{leaf} is the ecosystem scale leaf respiration, LAI is the Leaf area index, T_{ref} is the reference temperature (10°C), and T_{leaf} is the leaf temperature. The parameters a and b are empirically fit to the dark respiration measurements for both old ($a=0.17$, $b=0.047$) and new ($a=0.17$, $b=0.090$) needles. Scaling the leaf level respiration model with LAI yielded an estimate of ecosystem leaf respiration.

Bole CO_2 efflux was modeled as a function of soil temperature at 5 cm depth, which most closely matched the measured bole temperature (bole temperature was not measured in 1997). The average bole respiration can be estimated by (Xu and Qi, 2000b, submitted for publication):

$$R_{\text{bole}} = c \exp(d T_{\text{soil}} + e) \quad (3)$$

where c is 0.85, d is 0.057, e is 0.17 (empirically fit parameters), and T_{soil} is the soil temperature at 5 cm depth.

Soil CO_2 efflux was modeled as a function of temperature and soil moisture using the equation defined by Mischerlich (1919). Soil CO_2 efflux measurements at all 18 points of both measurement plots, together with corresponding measurements of soil moisture in

top 20 cm and temperature at 10 cm depth were used to fit the model (Qi et al., 2000):

$$R_{\text{soil}} = R_{\text{max}}(1 - \exp(-fM))(1 - \exp(-g T_{\text{soil}})) \quad (4)$$

where R_{soil} is soil respiration, R_{max} is $9.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ (maximum soil respiration), f is 0.96 and g is 0.71 (empirically fit parameters), M is the soil moisture in the top 20 cm, and T_{soil} is the soil temperature at 10 cm depth. The total ecosystem respiration is the sum of the bole, soil, and leaf respiration:

$$R_e = R_{\text{bole}} + R_{\text{soil}} + R_{\text{leaf}} \quad (5)$$

The GEP was then estimated by subtracting total ecosystem respiration from measured net ecosystem exchange (NEE):

$$\text{GEP} = \text{NEE} - R_e \quad (6)$$

These GEP estimates can then be compared with changes in climatic variables to assess climatic impact on GEP.

3. Results

3.1. Energy budget

The energy budget for this ecosystem (R_n = sensible+latent+soil heat fluxes, Fig. 3) is closed by our measurements to 11–12% in both years, suggesting that our measurements are consistent within that range. Soil heat fluxes were measured at 5 cm, then extrapolated to the soil surface. Extrapolation was based on calculations of soil heat conductivity (from soil heat flux divided by vertical temperature gradients) and scaling flux to the surface using vertical temperature profiles. Contributions from aboveground heat storage and energy storage through photosynthesis were estimated to be insignificant. The small imbalance in the heat flux is likely due to one of three factors: underestimate of the soil heat flux due to open spots in the canopy where the soil is heated directly by the sun, differences in the footprint between measurements of R_n (at the tower) and the scalar fluxes (90% of footprint estimated to be within 200 m upwind of tower), or systematic errors in the energy flux measurements or calculations. In any case, these errors are likely to be small given the near closure

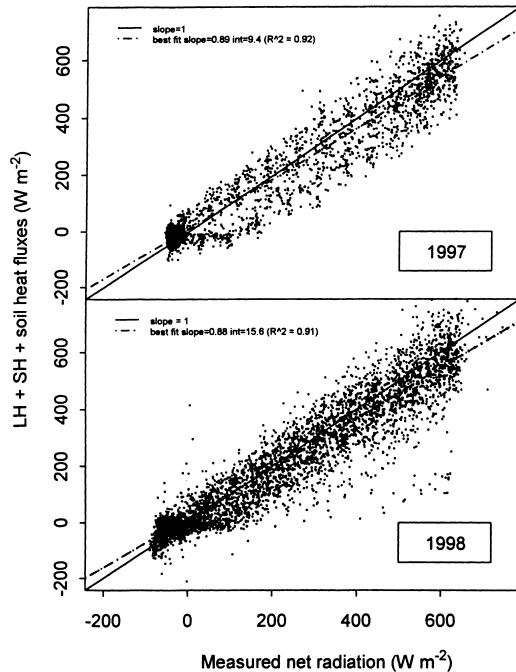


Fig. 3. Energy balance measurements of net radiation vs the sum of latent, sensible, and soil heat fluxes for the entire 1997 and 1998 measurement periods. The solid line represents the ideal case with a slope equal to 1.0; the dashed line indicates the best fit, which has slope of approximately 0.9 for both years.

of the energy budget and will not affect any of the conclusions drawn in this paper.

3.2. Time period averages

The impact of the interannual differences in climate on CO_2 , H_2O , and sensible heat fluxes can be assessed through changes in their midday mean values over the growing season and in their mean diurnal cycles for both years. To compare diurnal cycles of fluxes under different conditions, four time periods were chosen to divide the growing season into differing soil moisture and VPD regimes. These time periods are 25 days long and begin on Day 153 of each year.

In 1997, the first period (Days 153–178) represents the period of highest soil moisture and lowest VPD; the second period (Days 178–203) was a period of decreasing soil moisture and moderate VPD; the third period (Days 203–228) was similar, except it included a short event of extremely high VPD; and the fourth

period (Days 228–253) was a period of low soil moisture with a minor rain event, and moderate to low VPD. These trends are similar in the 1998 data, except that soil moisture was higher, needle development occurred later, and high VPD events were more frequent.

3.3. Environmental variables

Values for the environmental variables that most strongly influence CO_2 and energy fluxes are shown in Fig. 4 as time series for 1997 and 1998. These variables are soil moisture, PAR, air temperature, and daytime mean (09:00–15:00 h PST) VPD. Vertical lines in these figures indicate the starting and ending points for the four averaging periods defined in Section 3.2. Soil moisture (Fig. 4a) decreased over both seasons, although it was much higher throughout the 1998 measurement period. Photosynthetically active radiation (Fig. 4b) was similar for both years, remaining approximately constant over the comparison periods with slight variations due to cloud cover and the expected seasonal progression of sun angle and day length. Air temperature (Fig. 4c) varied, with coldest temperatures in the first period and extreme warm temperature events in the third period in 1997 and in the third and fourth periods in 1998. Additionally, the first period was significantly colder in 1998, delaying bud break and needle elongation. The short-term (2–5 days) oscillations in air temperature were associated with passing weather fronts. VPD (Fig. 4d) varied with season and passing weather fronts in a manner similar to air temperature.

3.4. Ecosystem response to environmental variables

Fluxes of sensible heat, H_2O , and CO_2 are presented as mean diurnal cycles during the four averaging periods (Fig. 5).

3.4.1. Heat flux

The seasonal pattern in sensible heat flux F_{sh} (Fig. 5a) varied between 1997 and 1998. In 1997, F_{sh} was consistent during the first and second averaging periods. During the third and fourth periods (including the high temperature event and afterwards), sensible heat flux increased by roughly 30%, with a slight shift of the maximum flux earlier in the day.

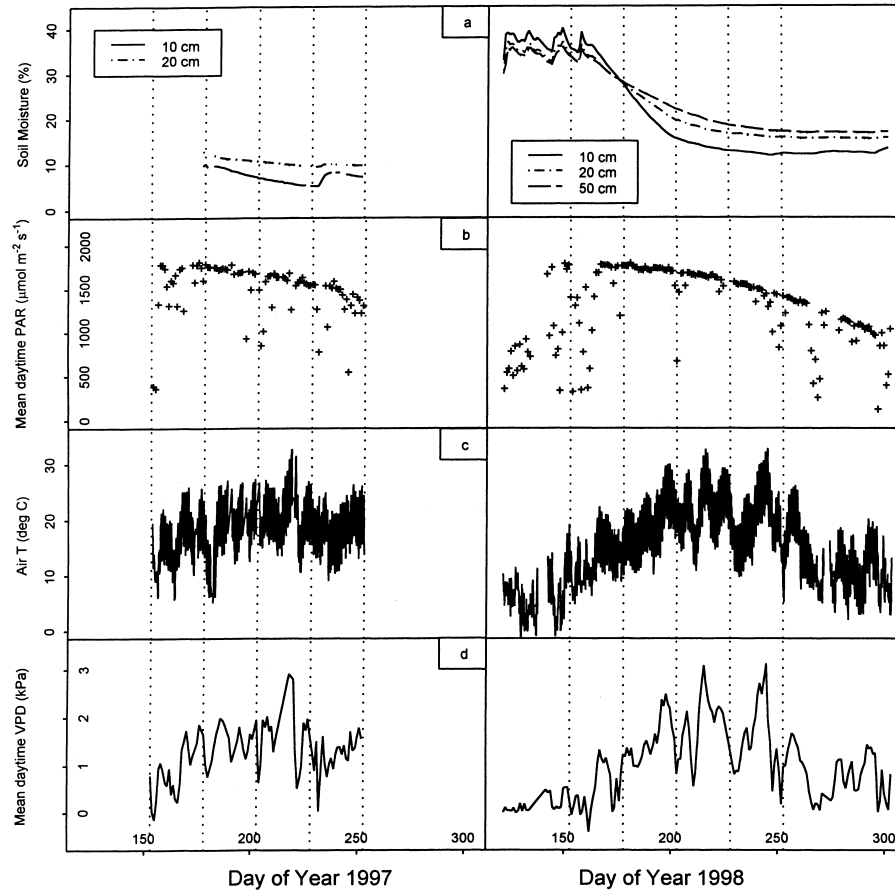


Fig. 4. Time series of environmental variables that most strongly influence CO_2 and energy fluxes including (a) soil moisture, (b) daily maximum photosynthetically active radiation measured at the top of the tower, (c) air temperature measured at the top of the tower, and (d) vapor pressure deficit presented as midday (09:00–15:00 h PST) mean values. Vertical lines separate the averaging periods presented in Figs. 5 and 8.

In 1998, F_{sh} decreased steadily from its peak values during the first period, reaching a minimum in Period 3 and then increasing somewhat during Period 4.

3.4.2. H_2O flux

Mean daytime H_2O flux (Fig. 5b) was not statistically different over the first three periods in 1997. During the heat spell of the third period, the water flux increased rapidly to extremely high values in the morning, decreased until 12:00 h then remained relatively steady until sunset (data not shown separately). During this period of high temperatures, VPD rose to its highest observed values and early afternoon H_2O fluxes were depressed by approximately 25% com-

pared to the previous periods. The diurnal cycle of this period was distinct from the rest of the summer. After this event (Period 4), H_2O flux was significantly lower for the remainder of the 1997 measurement period. In contrast, H_2O fluxes in 1998 followed a more symmetrical pattern of starting out low, becoming higher during midseason, and then decreasing again during late season; in 1998 they did not show sensitivity to similarly high VPD and temperature events.

3.4.3. Bowen ratio

After the high temperature event in 1997 (Period 3), the maximum ecosystem Bowen ratio increased abruptly from less than 1 to greater than 1 (Fig. 6).

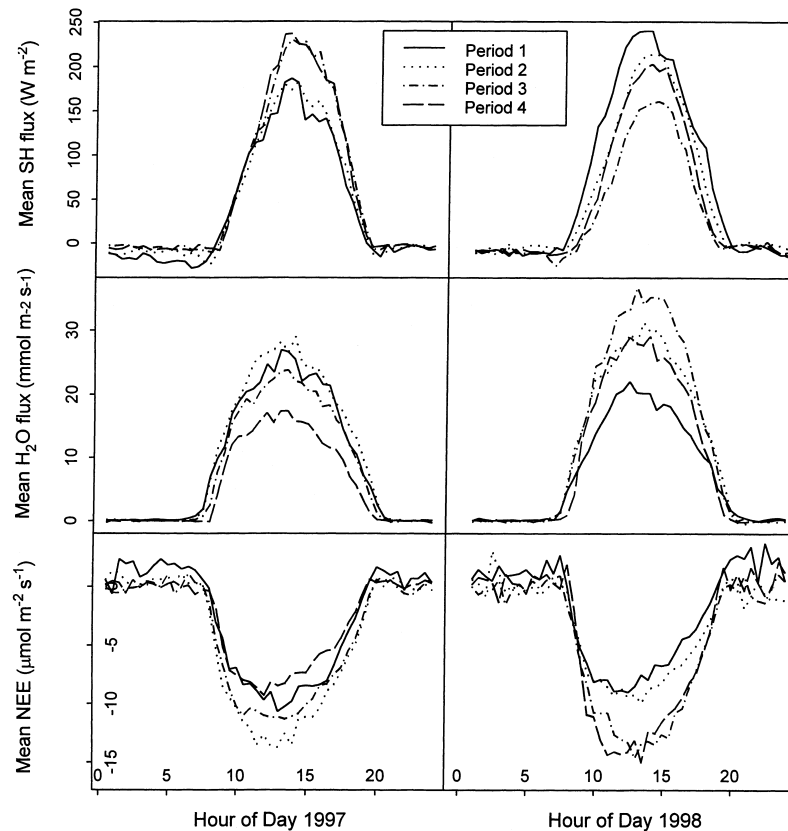


Fig. 5. Average diurnal cycles for (a) sensible heat flux, (b) H₂O flux, and (c) CO₂ flux, over four 25-day time periods (Periods 1–4 include Days 153–178, 178–203, 203–228, and 228–253, respectively). Sensible heat flux maxima were approximately equal for the 2 years, despite showing differences in seasonality. Maximum fluxes of H₂O and CO₂ were higher by about 30% in 1998, likely in response to increased leaf area. The seasonality is similarly delayed in 1998.

This shift indicates the increasing ratio of heat lost as sensible versus latent heat as the water flux from the ecosystem abruptly decreased. The seasonal change in the Bowen ratio reflects a decrease in evapotranspiration through the growing season due to the decrease of soil moisture and maintenance of the energy balance through changes in the sensible heat flux. Yet the abruptness of the transition at the extreme event indicates that it induced a non-elastic change in the physiological functioning of the plants. The year 1998 did not show a similar transition in the Bowen ratio until nearly a month later.

3.4.4. CO₂ flux

As leaf area increased in the spring of 1997, the magnitude of daily net CO₂ uptake (Fig. 5c) in-

creased until around Day 185. After approximately Day 210, the magnitude of the CO₂ flux began to decrease and the timing of daily maximum uptake shifted progressively earlier in the day, from around 13:00 to 11:00 h. During the extreme temperature event, when air temperature and VPD were extremely high, CO₂ uptake reached a maximum at 10:00 h and then started decreasing quickly towards the lowest daylight values of the summer. After this event, daily CO₂ uptake decreased significantly for the rest of the growing season, suggesting that the physiology of the ecosystem had changed. The decreasing magnitude of net CO₂ uptake and the shifted diurnal pattern of CO₂ flux toward morning were coincident with similar changes in the H₂O flux. CO₂ fluxes were much higher in 1998 (in Periods 3 and 4)

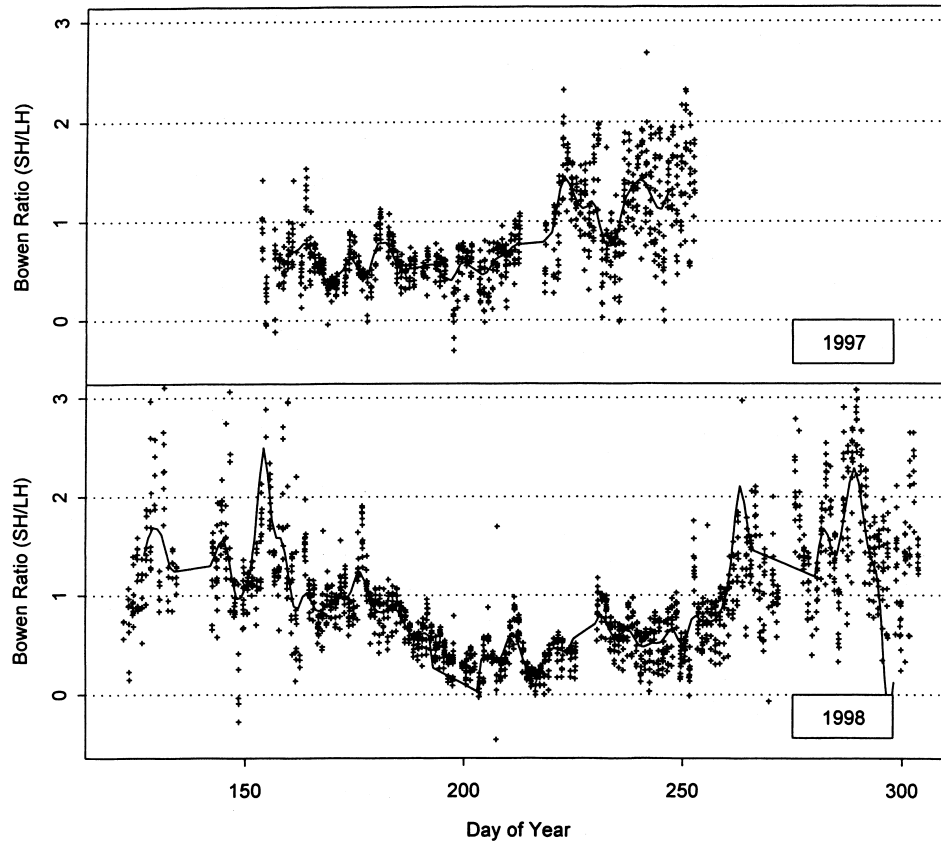


Fig. 6. Bowen ratio (sensible/latent heat fluxes) presented as midday mean values (09:00–15:00 h PST) over the whole measurement period, showing a steady decrease as the ecosystem became drier over the course of the summer. Values were excluded for standard errors greater than 1.

but also exhibited earlier maxima for Periods 1, 2, and 4.

3.4.5. Gross ecosystem productivity

Measured NEE, modeled ecosystem respiration R_e , and resultant ecosystem productivity GEP for both years are presented in Fig. 7 as midday mean values. Years 1997 and 1998 had noticeably different CO_2 exchange characteristics. The modeled daytime mean ecosystem respiration was approximately 25% higher during 1998, primarily as a result of wetter conditions increasing the soil respiration component and the increase of respiring leaf and bole area due to tree growth. The maximum measured NEE was also slightly larger in 1998. The differences between the years are most pronounced for GEP. The primary

difference in the GEP pattern lies in the timing of the maximum value: in 1997, maximum GEP occurred around Days 190–220, while 1998 had its maxima nearly a month later (Days 210–240). Furthermore, whereas the 1998 GEP exhibited a gradual decrease from peak values, the 1997 GEP values exhibit a much sharper decrease following their peak values. Maximum daytime mean GEP was approximately 25% greater in 1998 (with a change from -20 to $-25 \mu\text{mol m}^{-2} \text{s}^{-1}$), a difference that is consistent with the 30–35% increase in maximum LAI over 1997.

4. Discussion

The close correlation of the high temperature/VPD event in 1997 and the step change in Bowen ratio and

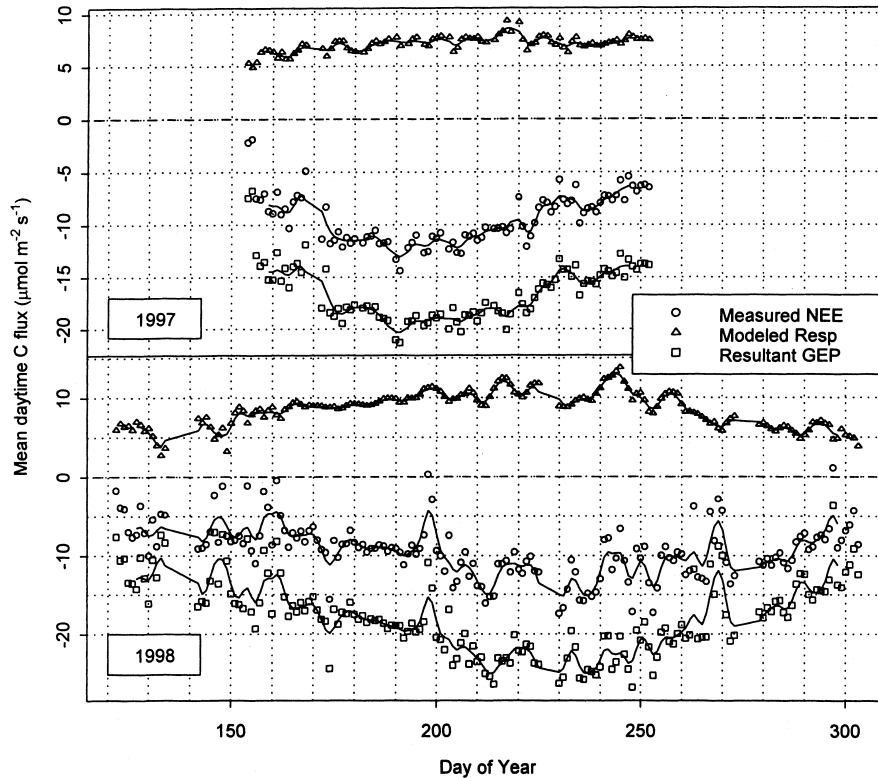


Fig. 7. Daytime mean measured NEE (circles) plotted with modeled respiration (triangles) and resultant GEP (squares) for 1997 and 1998. Note the difference in timing of maximum GEP, with 1998 peaking much later due to delayed leaf development. Note also the 1997 change in GEP from -19 to $-15 \mu\text{mol m}^{-2} \text{s}^{-1}$ after the extreme VPD event at Day 220.

carbon sequestration suggests that the productivity of the study ecosystem can undergo sharp changes in response to extreme weather events. Furthermore, the presence of equally high extreme temperature/VPD events in 1998 without associated abrupt changes in water and carbon fluxes indicates that the sensitivity of the system also depends on other climatic factors. These factors, which may involve longer-timescale events like the timing of snowmelt or the frequency and distribution of rainfall events, also influence the timing of phenological changes in spring and therefore the length of time during which the plants can photosynthesize.

Seasonal variations in leaf area, incident sunlight, temperature, VPD, and soil moisture are expected to exert control on the net transfer of CO_2 , H_2O , and sensible heat between vegetation and the atmosphere because these variables control photosynthesis, respiration, and transpiration. Leaf area determines the

amount of available photosynthetic and transpiring material and the amount of light intercepted by the forest. Temperature affects rates of enzyme kinetics associated with photosynthesis and respiration, and soil moisture and VPD affect the hydraulic status of plants and leaves, and therefore stomatal conductance.

In 1997, leaf area increased during the first averaging period then remained fairly constant over the last three; thus, the initial increase in net CO_2 uptake could be attributed to increasing leaf area, but this parameter would seem not to exert a strong influence on C fluxes after this time. However, as noted earlier, the timing of leaf elongation was offset by approximately 1 month in 1998, and this delay was also reflected in a delay in the timing of maximum NEE. As Fig. 5 indicates, NEE peaked in Period 2 in 1997 but not until Periods 3 and 4 in 1998. The amount of available PAR establishes an upper limit for canopy photosynthesis, so the gradual decrease (by about 15%) of day-

time maximum PAR over the four periods likely led to a small decrease of net CO₂ uptake but had similar timing for both years. The remaining parameters (air temperature, VPD, and soil moisture content) varied more markedly over the measurement periods and thus likely influenced the different patterns of fluxes observed in the 2 years.

The magnitudes of observed NEE and GEP in this ecosystem reflect the rapid growth rates characteristic of a young, even-aged forest. Anthony et al. (1999) report significantly lower maximum daytime NEE values for an older drought-stressed ponderosa pine forest in Oregon with total LAI of 3.2 ($\sim 7 \mu\text{mol m}^{-2} \text{s}^{-1}$, compared with $\sim 15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for this site in 1997). A more thorough comparison of these two ecosystems is presented in Law et al. (2000b, submitted for publication).

4.1. Controls on H₂O flux

Stomata provide the primary pathways for plant H₂O loss. Increasing VPD can cause the H₂O flux to increase if the stomatal conductance remains constant, but could also cause a reduction in stomatal conductance, thus reducing H₂O flux. Fig. 8 compares mean midday H₂O flux with VPD for the different periods: before (Periods 1 and 2), during (Period 3), and after (Period 4) the extreme temperature event in 1997. Note that the mean midday H₂O flux was significantly reduced (by over 30%) after this event. The change in relationship between H₂O flux and VPD after the extreme temperature event could be due to crossing a critical threshold of soil moisture (approximately 10% at 20 cm on Day 221), but this seems unlikely given that the soil moisture was steadily decreasing by 0.04% per day during this period. Thus, the shift in relationship between H₂O flux and VPD is more likely due to a physiological change in the plants during the event that persisted for the remainder of the growing season.

One possible change is cavitation in the water conducting system of the plants. Because trees and other plants maximize their carbon uptake per unit water lost, stomata may remain open until tension in the xylem reaches a critical threshold just prior to catastrophic cavitation. Thus, trees function very near the cavitation point (Tyree and Sperry, 1988). While it is

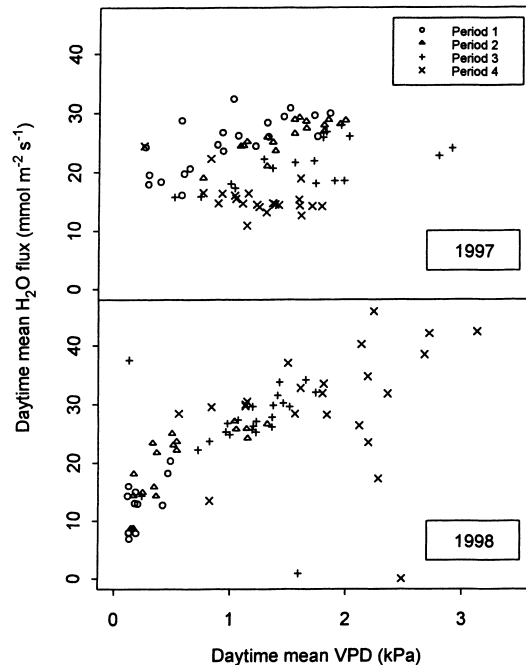


Fig. 8. Relationship between vapor pressure deficit and H₂O flux (Periods 1–4 include Days 153–178, 178–203, 203–228, and 228–253, respectively). After the extreme event in 1997 (which can be seen in the two outlier points for Period 3), H₂O fluxes decreased significantly. No similar patterns were seen in 1998 as a result of similar extreme events in Period 3, although there is some evidence that the two extreme VPD events in Period 4 may have begun a similar shift.

deleterious for trees to cavitate during the growing season because they lose important water conducting vessels, it is not unusual to observe the phenomenon (Zimmermann, 1963; Tyree and Sperry, 1989). Therefore, the unusually high H₂O flux early in the morning during the extreme event could result from extra water release from cavitating tracheids. After this event, mean conductance was lower than pre-heat spell levels, a state consistent with the loss of conducting area in the xylem of the plants (Tyree and Ewers, 1991; Panek and Waring, 1995).

No similar event-driven changes in the relationship between VPD and H₂O flux were observed in 1998 (Fig. 8). Although higher VPD events did occur in 1998, the soil moisture was also higher than in 1997, suggesting the ecosystem is sensitive to extreme heat events only when soil moisture is low.

4.2. Controls on the Bowen ratio

Because the Bowen ratio reflects the ecosystem's partitioning of incoming energy between water flux (largely dominated by plant transpiration during the summer) and sensible heat flux (that does not directly reflect plant physiology), it provides a good indicator of the relative physiological activity of the ecosystem. Thus, Fig. 6 demonstrates not only the abruptness in ecosystem change after the 1997 extreme event but also provides a rough indication of the timing of seasonal ecosystem shifts. That the ecosystem in 1998 experienced a similar low Bowen-ratio regime for nearly 40 days after the time of the extreme 1997 event suggests that the ecosystem does not have an inherent physiological limitation that begins at Day 220 but rather responds to extant environmental conditions.

4.3. Controls on CO_2 flux and GEP

Major ecosystem C fluxes (NEE, R , GEP) for both measurement seasons are presented in Fig. 7. The ex-

treme event of 1997, which considerably influenced the water vapor flux, had a similar effect on GEP (and thus NEE). Less than a week after the event, daytime mean GEP had decreased by approximately 20%. Since 1998 did not show a similar decrease in GEP during the same period (despite several high VPD events), the low soil moisture seems to have combined with the extreme VPD event in 1997 to produce this step change in ecosystem C cycling rate. This result is consistent with the hypothesis that the ecosystem experienced a step change in the ability of *P. ponderosa* to photosynthesize as the result of an extremely high temperature and VPD event at Day 220. A similar decrease was not observed in 1998 until nearly 30 days later, indicating that the extreme event initiated an early decrease in the ecosystem's carbon sequestration potential in 1997. In cumulative terms, this reduction of 20% of GEP over 30 days results in a decreased sequestration of over 90 g C m^{-2} land area. If we assume that the seasonality in productivity changes in 1998 represents an ideal maximum, this decreased sequestration accounts for a roughly 5–10% reduction in the total 1997 growing season sequestration.

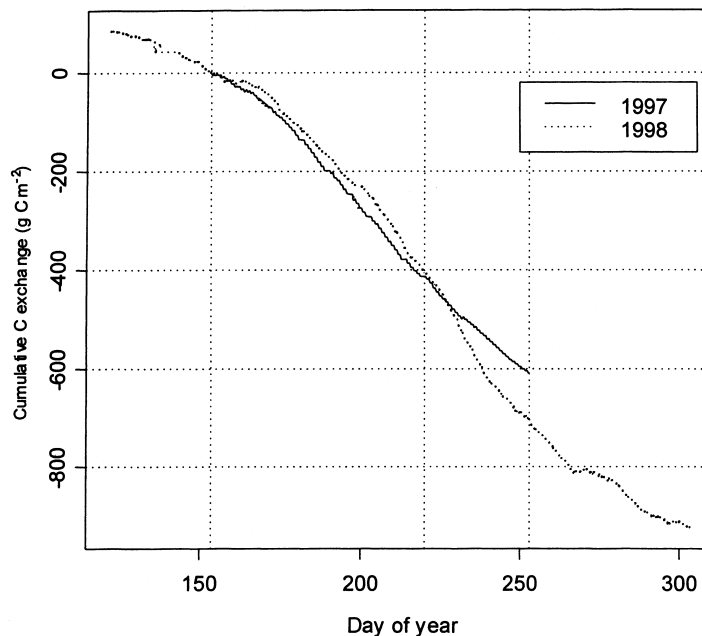


Fig. 9. Cumulative NEE for 1997 and 1998. Gaps in the data were filled by modeling NEE as a function of T , PAR, and M based on available data. If these data were missing, gaps were filled by interpolating the average diurnal cycles from 3 days before and after the missing time period. Nighttime data were replaced using the respiration model when $u^* < 0.17$ and when the wind was not coming from the main tower fetch direction.

Cumulative NEE curves (Fig. 9) also provide an overview of differences in carbon uptake between 1997 and 1998. The earlier onset of photosynthesis is evident as the 1997 curve shows higher cumulative sequestration (relative to Day 153) in the first half of the growing season. Later, the larger 1998 LAI and decreased 1997 uptake due to the extreme event led to the much larger ultimate 1998 sequestration. By Day 200, 1997 cumulative NEE was 19% higher than in 1998, but by Day 253, this balance shifted such that the 1998 cumulative NEE for Days 153–253 was 18% higher than in 1997.

5. Conclusions

The ponderosa pine ecosystems of the western US function differently from many other ecosystems monitored by eddy correlation due to the annual summertime drought stress. The ponderosa pines are well adapted to this climate, but our results suggest that their carbon uptake rates will respond in unique and important ways to changes in climate and hydrologic regime.

Our data set provides distinct periods under which the separate influences of environmental variables can be observed. By investigating the effects of different combinations of variables during different periods, we were able to determine that the system exhibits some modes that are prone to change abruptly after an extreme climatic perturbation. Specifically, we observed that the relationship between soil moisture, VPD, and conductance is complex and can respond nonlinearly to an extreme VPD event when the soil moisture is already low. Correctly modeling the changes in physiological activity after extreme drought stress events requires appropriate representation of event-driven physiological changes (such as cavitation) in the ecosystem's capacity for photosynthesis and respiration, in addition to their direct response to soil moisture and VPD.

Based on our measurements, the major factors that affected carbon uptake in this ecosystem were (a) the timing of new leaf development, (b) the severity of seasonal drought conditions (soil moisture), and (c) the timing and severity of extreme events with high VPD which can affect the physiological function of the ecosystem for the remainder of the growing sea-

son. Variability in climate and hydrology should have significant impacts on carbon uptake and physiological function of Mediterranean-type drought-stressed ecosystems. If an extremely high VPD event occurs early in the season in a dry year, and causes physiological damage to the plants, annual carbon uptake rates could be severely reduced. If no high VPD events occur and/or soil moisture is higher, annual carbon uptake rates could be significantly enhanced. Therefore, climate change in this type of ecosystem can cause large interannual variability in carbon storage.

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References

- Anthoni, P.M., Law, B.E., Unsworth, M.H., 1999. Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. *Agric. For. Meteorol.* 95, 151–168.
- Baker, B., Guenther, A., Greenberg, J., Goldstein, A., Fall, R., 1999. Canopy fluxes of 2-methyl-3-buten-2-ol over a ponderosa pine forest: field data and model comparison. *J. Geophys. Res.* 104, 26107–26114.
- Baldocchi, D., Hicks, B., Meyers, T., 1988. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology* 69, 1331.
- Baldocchi, D., 1997. Measuring and modelling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant, Cell and Environ.* 20, 1108.
- Baldocchi, D.D., Law, B.E., Anthoni, P.M., 2000. On measuring and modeling energy fluxes above the floor of a homogeneous and heterogeneous conifer forest. *Agric. For. Meteorol.*, in press.

- Chambers, S.D., Hacker, J.M., Williams, A.G., 1997. RAMF Version 8.1 User's Manual, 2nd Edition. FIAMS Technical Report 14, 150 pp.
- Chen, J.M., Cihlar, 1996. Optically-based methods for measuring seasonal variation of leaf area index in boreal conifer stands. *Agric. For. Meteorol.* 80, 135–163.
- Clark, K.L., Gholz, H.L., Moncrieff, J.B., Cropley, F., Loescher, H.W., 1999. Environmental controls over net exchanges of carbon dioxide from contrasting Florida ecosystems. *Ecol. Applications* 9 (3), 936–948.
- Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biol.* 2, 169.
- Grace, J., Lloyd, J., McIntyre, J., Miranda, A., Meir, P., Miranda, H., Moncrieff, J.B., Massheder, J.M., Wright, I., Gash, J., 1995. Fluxes of carbon dioxide and water vapor over an undisturbed tropical forest in South-West Amazonia. *Global Change Biol.* 1, 1.
- Horst, T.W., Weil, J.C., 1994. How far is far enough? The fetch requirements for micrometeorological measurement of surface fluxes. *J. Atmos. Oceanic Technol.* 11, 1018–1025.
- Hsieh, C.I., Katul, G.G., Schiedge, J., Sigmon, J.T., Knoerr, K.R., 1997. The Lagrangian stochastic model for fetch and latent heat flux estimation above uniform and non-uniform terrain. *Water Resources Res.* 33, 427–438.
- Lamanna, M.S., Goldstein, A.H., 1999. In-situ measurements of C2-C10 VOCs above a Sierra Nevada ponderosa pine plantation. *J. Geophys. Res.* 104, 21247–21262.
- Landram, M., 1996. Sierra Nevada Ecosystem Project Final Report to Congress, III. Wildland Resources Center Report No. 38, University of California, Davis, pp. 513–542.
- Law, B.E., Ryan, M.G., Anthoni, P.M., 1999a. Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biol.* 5, 169–182.
- Law, B.E., Baldocchi, D.D., Anthoni, P.M., 1999b. Below-canopy and soil CO₂ fluxes in a ponderosa pine forest. *Agric. For. Meteorol.* 94, 13–30.
- Law, B.E., Waring, R.H., Anthoni, P.M., Aber, J.D., 2000a. Measurements of gross and net ecosystem productivity and water vapor exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models, and an evaluation of two generalized models. *Global Change Biol.* 6, 155–168.
- Law, B.E., Goldstein, A.H., Anthoni, P.M., Unsworth, M.H., Panek, J.A., Bauer, M.R., Fracheboud, J.M., Hultman, N., 2000b. CO₂ and water vapor exchange by young and old ponderosa pine ecosystems during a drought year. *Tree Physiol.*, submitted for publication.
- Leuning, R., King, K.M., 1992. Comparison of eddy-covariance measurements of CO₂ fluxes by open-path and closed-path CO₂ analysers. *Boundary-Layer Meteorol.* 59 (3), 297–311.
- Margolis, H.A., Ryan, M.G., 1997. A physiological basis for biosphere-atmosphere interactions in the boreal forest: an overview. *Tree Physiol.* 17, 8–9.
- Mischerlich, J.L., 1919. The law of plant growth. In: Lieth, H.F. (Ed.), *Patterns of Primary Productivity in the Biosphere*. Benchmark Papers in Ecology, 8. Dowden, Hutchinson and Ross, Inc., Strausbourg, Penn, 1978, 239 pp.
- Moncrieff, J.B., Malhi, Y., Leuning, R., 1996. The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. *Global Change Biol.* 2, 231.
- Musselman, R.C., Fox, D.G., 1991. A review of the role of temperate forests in the global CO₂ balance. *J. Air Waste Manage. Assoc.* 41, 798.
- Panek, J.A., Waring, R.H., 1995. Carbon-isotope variation in Douglas-fir foliage: improving the δ¹³C-climate relationship. *Tree Physiol.* 15, 657–663.
- Qi, Y., Xu, M., Goldstein, A.H., 2000. Modeling joint effect of temperature and moisture on soil CO₂ efflux: a non-Q10 approach. American Geophysical Union Fall Meeting, supplement to EOS, Transactions, Vol. 80, H52A–12.
- Rissmann, J., Tetzlaff, G., 1994. Application of a spectral correction method for measurements of covariances with fast-response sensors in the atmospheric boundary layer up to a height of 130 m and testing of the corrections. *Boundary-Layer Meteorol.* 70 (3), 293–305.
- Shuttleworth, W.J., Gash, J.H., Lloyd, C.R., Moore, C.J., Roberts, J., Filho, A.O.M., Fisch, G., Filho, V.P.S., Ribeiro, M.N.G., Molion, L.C.B., Sa, L.D.A., Nobre, J.C.A., Cabral, O.M.R., Patel, S.R., De Moraes, J.C., 1984. Eddy Correlation Measurements of Energy Partition for Amazonian Forest. *Q. J. R. Meteorol. Soc.* 110, 1143–1162.
- Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody plants (Tansley Review No. 34). *New Phytol.* 119, 345–360.
- Tyree, M.T., Sperry, J.S., 1989. Vulnerability of xylem to cavitation and embolism. *Annu. Rev. Plant Physiol. Mol. Biol.* 40, 19–38.
- Tyree, M.T., Sperry, J.S., 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiol.* 88, 574–580.
- Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Net exchange of CO₂ in a mid-latitude forest. *Science* 260 (5112), 1314–1317.
- Xu, M., DeBiase, T.A., Qi, Y.A., 2000a. A simple technique to measure stem respiration using horizontally-oriented soil chamber. *C. J. For. Res.*, submitted for publication.
- Xu, M., Qi, Y., 2000b. Stem respiration in a young ponderosa pine plantation in Sierra Nevada Mountains, California. *For. Ecol. Manage.*, submitted for publication.
- Zimmermann, M.H., 1963. How sap moves in trees. *Sci. Am.* 154, 3–10.