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Spatial and temporal variation in respiration in a young ponderosa pine forest during a summer drought

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Abstract

Respiration rates of heterogeneous forest canopies arise from needles, stems, roots and soil microbes. To assess the temporal and spatial variation in respiration rates of these components in a heterogeneous ponderosa pine forest canopy, and the processes that control these fluxes, we conducted an intensive field study during the summer of 2000. We employed a combination of biological and micrometeorological measurements to assess carbon respiratory fluxes at the soil surface, within and above a 4-m-tall ponderosa pine forest. We also conducted manipulation studies to examine the carbon fluxes from the roots and heteorotrophs.

Spatial variation in soil CO_2 efflux was large, averaging 40% of the mean, which varied by nearly a factor of two between minima for bare soil to maxima beneath dense patches of understorey vegetation. The estimated vertical profile of respiration from chamber data, and the profile of nocturnal fluxes measured by the three eddy flux systems suggested that >70% of the ecosystem respiration was coming from below the 1.75-m measurement height of one of the flux systems, and 71% of photosynthetic carbon uptake in July was released by soil processes, thus there was a strong vertical gradient in respiration relatively close to the soil surface in this young forest. These results stress the importance of understanding spatial and temporal variation in soil processes when interpreting nocturnal eddy covariance data.

Keywords: Respiration; Eddy covariance; Soil CO_2 efflux; AmeriFlux; Soil chambers

1. Introduction

Respiration by a plant canopy represents about 50% of the carbon fixed by the vegetation (Waring et al., 1998; Gifford, 1994; Amthor and Baldocchi, 2001). At the ecosystem scale, we also have to consider carbon losses by soil respiration. Soil respiration, as referred to here, includes respiratory losses by heteortrophs, R_h and by roots, R_a. Soil respiration is by far the largest component of forest respiration (e.g. Law et al., 1999a; Janssens et al., 2000). Exact partitioning is difficult because of methodological differences in the measurements involved. For example, methods for partitioning include stable isotopes (Flanagan et al.,

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1999; Phillips and Gregg, 2001), radiocarbon dating (Trumbore et al., 1990), and physical separation of roots from soil (Hanson et al., 2000).

There is much need to assess respiration separately from conventional net CO_2 exchange measurements, NEE. Together, data on respiration and NEE can produce information on gross primary production, which in turn can be used to validate calculations produced by ecosystem models and satellite-based indices of GPP. Consequently, we use a physical separation method to estimate respiration loss from different plant components relative to gross ecosystem production (eddy covariance estimate of GEP $= |\mathrm{NEE_d}| + R_{\mathrm{ed}}$, where d is the daytime).

Micrometeorological systems have advanced our ability to spatially integrate and quantify net ecosystem CO_2 exchange (NEE) half-hourly above vegetation canopies, yet these studies require additional smaller scale information for understanding the factors regulating photosynthesis and respiration, which are the two large fluxes that determine NEE. At night, NEE is strictly ecosystem respiration (R_e), allowing closer examination of the respiration components and responses to environment.

Successfully capturing spatial and temporal variability using chamber measurements of respiration rates and then scaling them up to the stand level for comparison with eddy covariance measurements is not trivial. Nocturnal eddy covariance measurements are problematic under calm wind conditions, and often underestimate ecosystem respiration when compared with scaled-up chamber estimates from measurements on soils, foliage and woody tissue. In prior studies, nocturnal eddy covariance estimates of respiration averaged 23% lower than scaled-up chamber estimates in a tall ponderosa pine forest (Law et al., 1999b), 35% lower than chamber estimates in a mixed temperate forest (Goulden et al., 1996), and 27% lower than chamber estimates in six boreal coniferous forests (Lavigne et al., 1997). On the other hand, scaling-up has been done for evaporation from a 30-m-tall forest of complex architecture (Kelliher et al., 1992).

We also need to quantify how respiration responds to environmental drivers at the stand scale. For example, Högberg et al. (2001) recently reported a strong correlation between photosynthesis and soil respiration. Other studies report that respiration rate is very responsive to temperature under well-watered conditions (e.g. Lloyd and Taylor, 1994). Consequently, we expect much temporal variability in soil respiration, as there is a wide range of temperatures in a forest (e.g. Hollinger et al., 1994). Moreover, there is also controversy about nocturnal eddy covariance measurements over forests related to site terrain (Finnigan, 1999) and the measurement of soil CO_2 efflux using chambers (Le Dantec et al., 1999; Janssens et al., 2000; but also see Arneth et al., 1998 and Kelliher et al., 1999).

In this paper, our objectives are: (1) to assess spatial and temporal variation in respiration rates in a forest utilizing chamber and eddy covariance measurements; (2) evaluate the influence of different environmental conditions on nocturnal CO_2 flux profiles and (3) explore the response of respiration rates to key environmental variables. To make the exercise tractable and focus much of our attention on soil CO_2 efflux, we chose a relatively open 4-m-tall ponderosa pine forest with broadleaved shrub understorey in central Oregon, USA. Our interest in the young pine forest also reflects how it is regenerating following clearcutting of an old-growth forest. The tree canopy is heterogeneous and sparse with a significant shrub component typical of natural regeneration in ponderosa pine. Because of the presence of nitrogen fixing shrubs, clumping of vegetation, and exposed sandy soils with a large variation in surface temperature, we anticipate that the horizontal spatial variation in soil CO_2 effluxes and soil conditions is large. Likewise, we anticipate a strong vertical gradient in respiration rate because of the multi-layered canopy and large expected contribution of the soil. A comparison of the chamber estimates of the vertical profile of nocturnal CO_2 fluxes with eddy covariance measurements at several heights is conducted to examine controls on fluxes, and to determine how this might influence flux measurements under varying environmental conditions, such as low friction velocity.

2. Methods

2.1. Site description

Measurements were made in a young ponderosa pine forest (*Pinus ponderosa* Var. Laws) in central

Oregon, USA (44°26′N, 121°34′W, elevation 1188 m) during July 2000. The semi-arid climate is characterized by annual photosynthetically active irradiance, mean air temperature and precipitation of 2481 MJ m^{-2}, 7.5 °C and 552 mm, respectively (Law et al., 2001a). The site was previously an old-growth forest clearcut in 1978, and naturally regenerated. The average age of trees in 2000, 22 years after cutting, was 15 ± 1 years old. On average, they were 4 m tall (S.E. = 0.2 m). There were two size classes based on stem diameter at a height of 1.3 m, > or <0.05 m. The larger size class of 280 trees ha^{-1} had an average stem diameter of 0.1 m at a height of 1.3 m, while the others of density 975 trees ha^{-1} averaged 0.064 m at ground level. The broadleaved understorey, including the evergreen manzanita (*Arctostaphylos patula*) and deciduous bitterbrush (*Purshia tridentata*), accounts for about 40% of the stand leaf area. The understorey shrubs averaged 1 m tall. The soil is classified as Ultic haploxeralf, and the soil texture is sandy loam, with increasing silt and clay fraction with depth (69% sand, 26% silt, 5% clay in the top 0.2 m, and 54% sand, 35% silt, 11% clay for the 0.5–1-m depth). Thus, the soil is very porous and its relatively low bulk density (1.18 kg dry soil per liter at 0.0–0.2 m depth and 1.44 kg dry soil per liter at 0.2–0.5 m depths; Law et al., 2001a) implies that a predominance of large pores emptying with relatively little suction facilitating rapid drying by drainage and evaporation.

2.2. Environmental measurements

Half-hourly measurements of air temperature, photosynthetically active radiation, and relative humidity were made at the 12-m height, and rainfall was measured in a clearing at 1 m above the ground with a tipping bucket (Campbell Scientific Inc., Logan, UT). At the automated soil chambers, ~100 m east of the sub-canopy flux systems, half-hourly measurements of soil water content were made at 0.1 and 0.3 m depths (horizontally placed CS615 sensors, Campbell Scientific, Logan, UT), soil temperature (T_{soil}) at 0.02, 0.08, and 0.15 m depths. We also measured soil temperature at 0.08 m depth with a temperature probe at 16 locations in conjunction with measurements using a portable soil chamber system (see Section 2.3).

2.3. Respiration from chamber measurements

Using the two portable infrared gas analyzers with a sampling area of 0.007 m^2, soil CO_2 effluxes were measured at 32 locations throughout a 300-m^2 area. The area was to the west and within 30 m of the 1.75 and 3.6-m height F_c measurement systems (Fig. 1). The LI6400 (LICOR, Lincoln, NE) measurements were made near four pine trees (*Pipo*), four bitterbrush shrubs (*Putr*), four manzanita shrubs (*Arpa*), and four were located in open areas devoid of plants, referred to here as bare soil. The PP Systems (coupled SRC-1 and EGM-1, Hitchin, Hertfordshire, England, UK) measurements were made nearby and at the same time at 08:00 and 14:00 h on 13 July but at 10 bare soil locations, and beneath six bitterbrush shrubs thereafter so that the combination of the 32 measurements was distributed approximately according to the fractional surface cover in shrubs, trees, and bare soil. The percentage cover was determined from line intercept measurements along two 40 m transects, one to the north and one to the west from the sub-canopy flux systems in a spoke pattern following the primary wind direction (W–SW; Fig. 1). Errors associated with disturbance of the soil and roots were minimized by placing soil collars ~0.3 m into the surface at least 24 h before measurements were initiated, and errors associated with pressure build-up within chambers were assumed to be minimized by making measurements within 3 min. The comparisons of the two portable systems at the same locations allowed us to assess differences in flux rates measured by the systems.

Soil surface CO_2 effluxes were also measured about 100 m to the east of the sub-canopy flux systems and 50 m to the northeast of the flux tower at three locations with an automated system with a continuous, sequential closed sampling cycle of 1.5 h. The sampling area of each chamber was 25 times larger at 0.21 m^2 and the three chambers were located within a 300-m^2 area. A closed-path infrared gas analyzer was used to measure headspace CO_2 concentration over a 10-min period (LI6262, LICOR, Lincoln, NE). Soil CO_2 effluxes from the three chambers were averaged over the 1.5-h cycle. A linear interpolation with time was used to obtain half-hourly estimates that would correspond with F_c data. Probability density functions were calculated for the spatial variation in soil CO_2

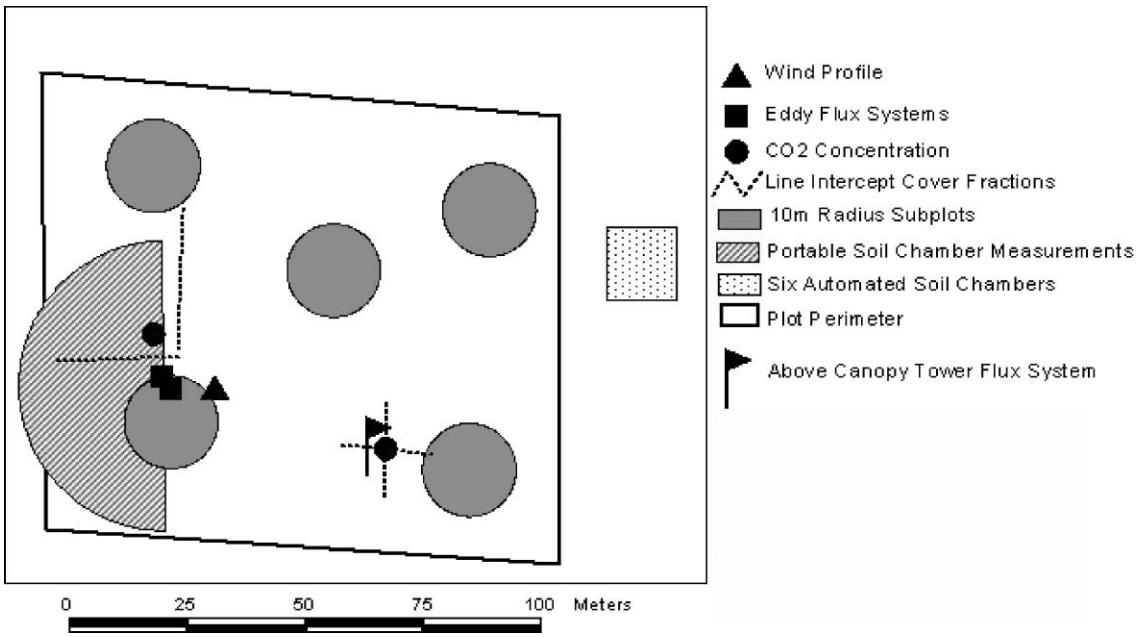

Fig. 1. Layout of the field intensive study at the young ponderosa pine site in July 2000.

effluxes measured by the automated and portable soil chamber systems.

We determined the fraction of total soil surface CO_2 effluxes that was from roots using measurements of total soil effluxes, root respiration, and litter respiration on Days 201 and 202. On Day 201, we first measured soil surface CO_2 effluxes at 10 locations using a LI6400 (LICOR, Lincoln, NE). We removed the litter and measured litter respiration in a modified soil chamber (LI6000-9, Lincoln, NE). We measured soil CO_2 concentration profiles with an LI6200 and a perforated brass tube that had been inserted in the soil, and determined that the ambient CO_2 concentration for fine roots in the top ~0.3 m of soil was ~500 ppm in the porous pumice soils. The next morning, we took 0.3 m deep soil cores from directly beneath the chamber collars, removed the roots by sifting, and then measured root respiration with the LI6400 at 500 ppm CO_2 concentration immediately so that roots would not dry out.

Foliage respiration of pine, bitterbrush, and manzanita was measured with a LI6400 and a modified chamber (similar to Hubbard et al., 1995) that allows us to produce response curves over a range of temperatures. Measurements of foliage respiration in response to temperature were made during the night on pine in June (Day 165) and July (Day 193), manzanita in June (Day 165) and July (Days 193 and 207), and bitterbrush in August (Days 215 and 218) 2000. Respiration rates were measured at descending temperatures (30, 25, 20, 15, and 10 °C). The pine respiration rates are expressed on a half-surface area of needles basis for purposes of scaling to site, and manzanita and bitterbrush were expressed on a projected leaf area basis. Exponential temperature response models were developed for each species. The measurements were scaled to site by the vertical profile of leaf area index (LAI, $m^2\,m^{-2}$ ground). To compare foliage respiration (R_f) by the three plant species at a common temperature, we normalized R_f to 10 °C (R_{f10}) using the temperature response function ($R_f = a\exp(bT_a)$), where T_a is air temperature, and 'a' and 'b' are empirical coefficients.

The leaf area density profile was estimated from optical measurements every 10 m on a 100 m × 100 m plot, measurements around individual shrubs, and tree and shrub canopy dimension measurements on five 10-m radius subplots (LAI2000, LICOR, Lincoln,

NE). We used these data in a model that we developed, CANLAD, which distributes leaf area in the canopy volume in 0.1 m layers. Details of the model and correction of optical data for clumping within shoot and at scales larger than shoot are provided in Law et al. (2001b,c) and Treuhaft et al. (2001).

Photosynthetic response to CO_2 response (A–c_i curves) was also measured on trees and shrubs in the morning hours before vapor pressure deficits were large to determine if species differences in foliage respiration were associated with maximum carboxylation efficiency (V_{cmax}).

Woody tissue respiration of stems and branches was calculated from an exponential temperature response function that we developed in an earlier study (Law et al., 1999a). The measurements were scaled to site using tree dimension data from the five 10-m radius subplots, and wood core estimates of total sapwood volume per square meter ground (trees and shrubs), as in Law et al. (2001a). We harvested five shrubs of each species to determine wood biomass for a range of shrub canopy volumes, and we combined this information with shrub canopy volume on the subplots to determine shrub woody tissue per square meter ground. Air temperature was used in the equations, assuming that sapwood temperature of the vegetation followed air temperature. The ponderosa pine woody tissue respiration equation was used for shrubs, assuming similar respiration rates for sapwood. We do not believe that this will result in a large error in the estimate of woody tissue respiration, because in an earlier study on ponderosa pine with a much larger amount of sapwood present, we found that woody tissue contributed less than 10% of total ecosystem respiration. Data from the portable chamber measurements of soil effluxes, and modeled foliage and woody tissue respiration were used to estimate ecosystem respiration for comparison with nocturnal fluxes measured at the three heights.

2.4. Micrometeorological measurement of respiration

The eddy covariance method was used to determine half-hourly fluxes of sensible heat (F_H) and CO_2 (F_c) at heights 1.75, 3.6, and 12 m. The two lower measurements are hereafter known as sub-canopy eddy flux systems. Vertical flux densities of CO_2 (F_c), latent (λE) and sensible heat (H) between vegetation 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, and temperature). Positive flux densities represent mass and energy transfer into the atmosphere and away from the surface and negative values denote the reverse; ecologist use an opposite sign convention where the uptake of carbon by the biosphere is positive. Turbulent fluctuations were computed as the difference between instantaneous and mean scalar quantities.

A sampling rate of 10 Hz ensured complete sampling of the high frequency portion of the flux co-spectrum. The sampling duration (30 min) was long enough to capture low frequency contributions to flux covariances, but was not too long to be affected by diurnal changes in temperature, humidity and CO_2. Coordinate rotation calculations of the orthogonal wind vectors (w, u, v) are performed to correct for instrument misalignment and non-level terrain. The vertical velocity, w, is rotated to 0, allowing flux covariances to be computed orthogonal to the mean streamlines. Open-path infrared gas analyzers were used to measure CO_2 concentrations (LAI7500, LICOR Inc., Lincoln, NE). Wind speed and temperature were measured with three-dimensional sonic anemometers (Solent Windmaster, Gill instruments, Lymington, England, UK; CSAT-3 Campbell Scientific, Inc., UT). Corrections for cross-wind contamination of virtual temperature (Schotanus et al., 1983) and air density fluctuations (Webb et al., 1980) were applied. The latter correction was minimal at night when F_H is near zero. The data were screened for possible instrumentation and sampling problems following Anthoni et al. (1999).

A closed-path infrared gas analyzer, tubing and switching system determined half-hourly CO_2 concentration profiles at 1, 3, and 12 m heights to estimate rates of storage (F_{stor}) and NEE ($F_c + F_{stor}$) at 12 m height. Details on the instrumentation, flux correction methods and calculations are reported in Anthoni et al. (1999), and Baldocchi et al. (1997a, 2001). We summarize methods here to briefly explain processing of the flux data.

Calibration of the CO_2 sensors was referenced to standards produced by NOAA/CMDL, with accuracies of ± 0.1 ppm. Water vapor sensors were calibrated against a dewpoint generator (LICOR, Lincoln, NE).

3. Results and discussion

3.1. Vegetation properties

The young forest has an open-canopy with a significant shrub understorey, and large areas of soil with no vegetation cover. The cover estimates from the line intercept transects in the vicinity of the sub-canopy eddy flux systems showed that 6% of the surface cover was ponderosa pine (*Pipo*), 31% bitterbrush (*Putr*), 3% manzanita (*Arpa*), and 60% soil. The one-sided LAI at the site was $1.0\,m^2\,m^{-2}$, and 60% of it was pine. *Pipo* LAI was 0.6, *Putr* was $0.3\,m^2\,m^{-2}$, and *Arpa* was $0.1\,m^2\,m^{-2}$. The mismatch between percentage cover and leaf area is due to the height and thus vertical distribution of leaf area in the pine trees (Fig. 2). Bitterbrush, a deciduous shrub, was in full leaf in July, and the tree canopy reached maximum leaf area in mid-August.

3.2. Litter and soil properties

The litter cover was scant, averaging 0.01 m in depth. On Day 207 (25 July), the litter was very dry, acidic and comprised of intact, relatively indecomposable material with a total carbon to nitrogen ratio (C:N) of 57. Fine litter carbon (<10 mm diameter) was low ($708\,g\,C\,m^{-2}$) compared with that of our old pine site nearby ($1233\,g\,C\,m^{-2}$), which has had many years to accumulate litter since major disturbance. The soil was also very dry through most of the study, and water content averaged $0.1\,m^3\,m^{-3}$.

3.3. Chamber measurements of respiration

3.3.1. Foliage respiration

The relation between foliage respiration rate (R_f, expressed on a one-sided leaf area basis) and air temperature (T_a) was exponential for ponderosa pine, bitterbrush, and manzanita (Fig. 3). Normalized to 10 °C, R_{f10} of *Putr* ($1.1\,\mu mol\,m^{-2}\,s^{-1}$) was four times that of *Pipo*, and twice that of *Arpa* (Table 1). Maximum carboxylation efficiency (V_{cmax}) of *Pipo* foliage was 30% lower than that of *Putr*.

Foliar nitrogen content can be a regulating variable of R_f (Reich et al., 1998; Ryan et al., 1996), and it is correlated with photosynthetic capacity (Schulze et al., 1994) that supplies carbohydrates for respiration. Foliar nitrogen content of bitterbrush was twice that of ponderosa pine, but those of manzanita and ponderosa pine were not significantly different (11.0 ± 0.3 and $11.5 \pm 0.5\,mg\,g^{-1}$, respectively). Bitterbrush has been

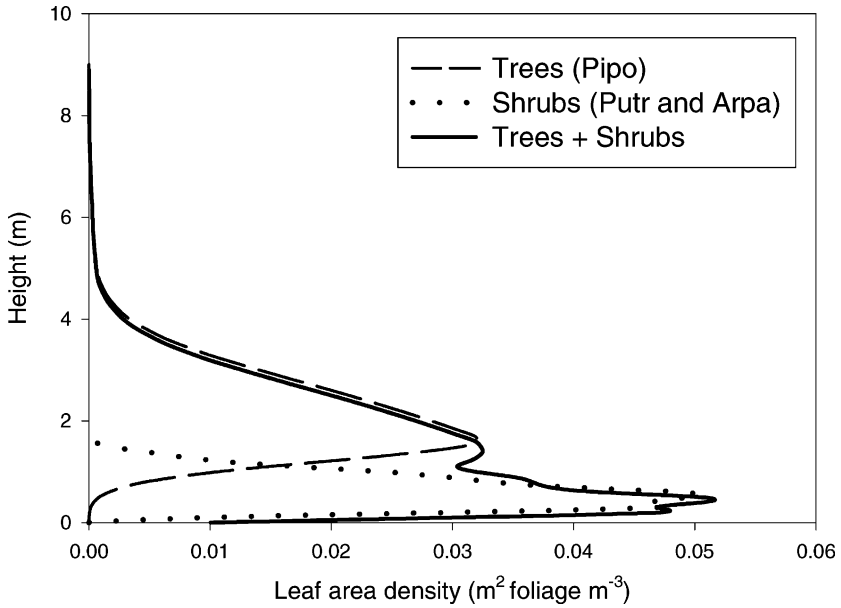

Fig. 2. Vertical distribution of leaf area density (m^2 half-surface area foliage m^{-3}) for trees (*Pipo*), shrubs (*Putr*, *Arpa*), and both combined.

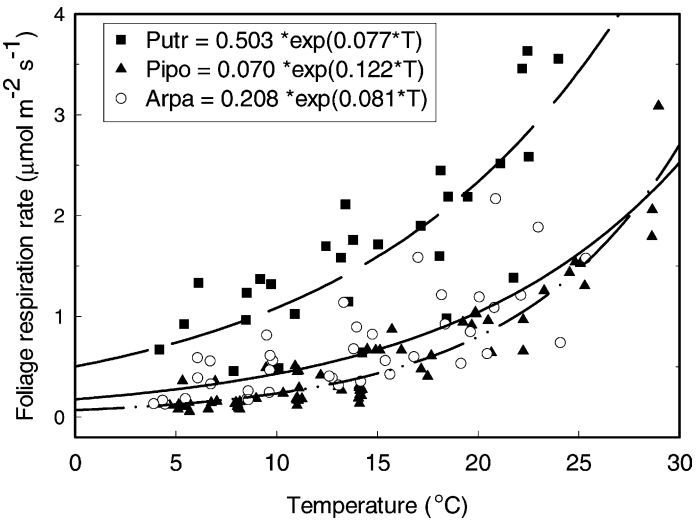

Fig. 3. Foliage respiration temperature responses for *Purshia tridentata* (*Putr*), *Pinus ponderosa* (*Pipo*) and *Arctostaphylos patula* (*Arpa*).

identified as a nitrogen fixing plant (Virginia and Delwiche, 1982; Farnsworth, 1975), and this could explain the higher foliar N, V_{cmax}, and respiration rates per unit leaf area. Although ponderosa pine accounted for 60% of the stand leaf area, it contributed only 45% of the canopy respiration rate. Bitterbrush contributed most of the other half (48%), and manzanita foliage respiration was minimal (7%).

In a closed canopy forest, leaf nitrogen content and R_f are often well correlated with height, suggesting a connection with the vertical distribution of irradiance (Reich et al., 1998). However, for this open-canopied ponderosa pine stand, there was no relation between leaf nitrogen content and height, as all needles are highly illuminated. This was also the case for an open-canopied old-growth ponderosa pine forest nearby (LAI 2.0; Law et al., 2000), a 26-m-tall pine forest (LAI 2.6) during summer in central Siberia (Leuning, personal comminication, 2001), and boreal black spruce (Rayment and Jarvis, 1997). In another study, there was no correspondence between intercepted radiation and leaf nitrogen content of shoot tips on all branches of a 6-m-tall, open grown pine tree in New Zealand (Livingston et al., 1998). The

Table 1
Structural properties and foliage characteristics for *Pinus ponderosa* (*Pipo*), *Purshia tridentata* (*Putr*), and *Arctostaphylos patula* (*Arpa*)[a]

Variable	*Pipo*	*Putr*	*Arpa*
Mean height (m)	4.3 (0.2)	1.1 (0.2)	0.9 (0.2)
Density (plants ha^{-1})	974	1299	382
Percentage ground cover (%)	6	31	3
Leaf area index (m^2 half surface area m^{-2} ground)	0.8	0.3	0.1
Foliar mass ($g\,m^{-2}$ ground)	181	21	22
Foliar N ($mg\,g^{-1}$)	11.5 (0.5), Days 178–186 ($n = 23$)	27.8 (1.1), Day 163 ($n = 6$); 23.5 (1.2), Day 205 ($n = 8$)	11.0 (0.33), Day 163 ($n = 5$)
Foliage respiration at 10 °C ($\mu mol\,m^{-2}\,s^{-1}$)	0.24, Days 165 and 194	1.08, Days 165, 193 and 207	0.47, Days 215 and 218

[a] Measurement dates are provided. For height and foliar N, 1 S.E. of the mean is shown in parenthesis.

positive linear correlation between leaf nitrogen content and height was interpreted to reflect the influence of strong apical control on nutrient concentration and photosynthesis (i.e. proximity to the tree top).

3.3.2. Soil CO_2 efflux

During the morning (a.m.) and afternoon (p.m.) of Day 195 (13 July), soil CO_2 efflux rate was measured at 16 locations in a side-by-side comparison of the two portable chamber systems to determine whether or not it was appropriate to combine measurements from the two portable systems for further analyses. Other studies have shown that the fluxes were overestimated by the PP-Systems compared with other portable infrared gas analyzers (e.g. Le Dantec et al., 1999). There was no significant difference between the two sets of measurements including locations near pine, bitterbrush, and manzanita, and bare soil (mean ± S.E. in $\mu mol\,m^{-2}\,s^{-1}$ were LI6400: 1.8 ± 0.1 a.m., 2.0 ± 0.2 p.m.; PP-Systems: 1.9 ± 0.2 a.m., 2.1 ± 0.2 p.m.). There was also a similar ranking and consistency of the data for the two systems at individual locations. Thus, we combined measurements from the two portable systems in further analyses.

We could not statistically distinguish between morning and afternoon soil CO_2 efflux measurements made with the portable infrared gas analyzers, despite a $\sim 10\,^{\circ}C$ difference in mean soil temperature at the measurement depth of 0.08 m (Table 2). This probably reflected the constant limitation of soil water deficit on a daily basis.

For the nine occasions that we measured soil CO_2 efflux rates with the portable chambers, including five early morning and four afternoon sets of measurements, the overall mean rate was $2.0\,\mu mol\,m^{-2}\,s^{-1}$ ($n = 256$) and the coefficient of variation was 40% (Table 2). Because of the large sample size ($n = 32$), we believe this relatively large coefficient of variation is a property of the forest indicative of significant spatial variation at a length scale less than 0.5 m, based on an exponential decline in soil CO_2 efflux from 0.5 to 1, 2 and 4 m from the stems of isolated trees at the site. Mean tree crown and shrub diameter is also 0.5 m. A 0.1-m length scale was determined for the exponential decline in soil CO_2 efflux with radial distance from the stem of an isolated 4-m-tall pine tree grown in New Zealand for 2 years in otherwise carbon-free sand (Cook et al., 1998). With larger spatial averaging, we found no significant difference in average soil respiration rates between the $30\,m \times 30\,m$ study area and two 25 m long transects 70 m North of the tower.

To determine if the micro-scale spatial variability was associated with cover type, we conducted analysis of variance for pooled data (eight measurements per cover type) from the morning and afternoon of Day 195. This showed that cover types had significantly different ($P < 0.01$) soil surface CO_2 effluxes, with bare soils (mean 1.4 ± 0.04) < *Pipo* (1.8 ± 0.1) < *Putr* (2.1 ± 0.2) < *Arpa* (mean 2.5 ± 0.2) (Table 3). Thus, soil surface CO_2 effluxes were lowest for bare soil, reflecting the likely paucity of roots, and highest near the shrubs, some of which are nitrogen fixers that have higher photosynthesis rates, and consequently, may provide more photosynthate to roots and microbes.

Table 2
Variation in soil surface CO_2 effluxes (F_s) measured with portable soil chamber systems, and soil temperature measured at 0.08 m depth with the analyzer temperature probes (T_{soil}) over 1 h on several occasions within 30 m of the sub-canopy flux systems[a]

Day	Standard time (h)	Mean F_s	S.E.	n	T_{soil} (0.08 m depth)	S.E.	n
193	08:00	1.9	0.12	16	13.6	0.8	16
193	15:00	2.1	0.14	16	38.4	3.3	16
195	07:30	1.86	0.02	32	15.18	0.28	16
195	13:50	2.04	0.09	32	23.95	1.11	16
199	13:15	1.78	0.11	32	21.37	0.66	16
200	08:30	3.02	0.14	32	15.86	0.39	16
200	16:00	1.95	0.14	32	24.65	1.03	16
207	08:30	1.61	0.11	32	16.86	0.32	16
208	08:30	1.71	0.12	32	16.01	0.31	16

[a] It rained 1.8 mm on Day 189 at 16:00–17:00 h, and 1.5 mm on Day 199 at 15:30–17:30 h.

Table 3
Comparison of soil surface CO_2 effluxes near ponderosa pine (*Pipo*), bitterbrush (*Putr*), manzanita (*Arpa*), and in open areas of bare soil (open) on Day 195 (07:22 h)

Cover	Mean CO_2 efflux ($\mu mol\,m^{-2}\,s^{-1}$)	S.E.	*n*
Open	1.36	0.04	16
Pipo	1.82	0.19	16
Putr	2.10	0.19	16
Arpa	2.53	0.20	16

Spatial variation in soil CO_2 efflux was similar before and after 1.5 mm of rain in terms of shapes of the probability density functions, and the ranges of values were $\sim$3.5 $\mu mol\,m^{-2}\,s^{-1}$ (Fig. 4a). The mean soil CO_2 efflux increased by about 70% 14 h after rain on Day 200, but 24 h after rain, it had returned to the lower level with a similar distribution as the pooled remaining data obtained when there was no rain. Soil evaporation, measured with small weighing lysimeters, was 1.0 mm from 11 to 18 h on Day 200, so all

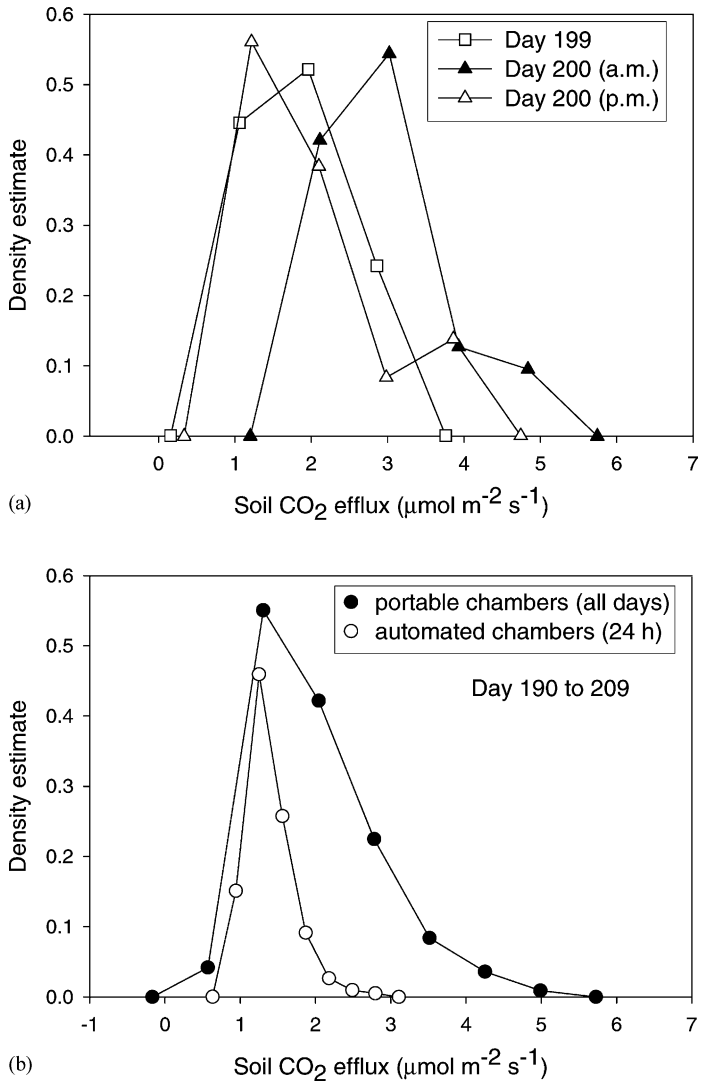

Fig. 4. (a) Probability density functions of soil CO_2 efflux measurements with the portable soil chamber systems 10 days after rain (Day 199), 14 h after rain (Day 200 in the morning), and 24 h after rain (Day 200 in the afternoon); (b) probability density functions for the portable soil chamber systems on days without rain, and for the automated soil chamber system over 24 h from Days 190 to 209.

of the rain had evaporated within a day. Kelliher et al. (1999) also report only a 24-h effect of rain increasing soil CO_2 efflux by 52% for a sandy soil beneath a central Siberian pine forest (Kelliher et al., 2001). These data from semi-arid climates suggest rainfall frequency may be more important that quantity in affecting soil CO_2 efflux in pine forests. Moreover, the short duration of the effect means frequent measurements or monitoring with automated systems is needed to capture it.

For three operational automated soil chambers, using the 1.5-h means (for Days 189–207), the probability distribution is narrow (range: 0.9–2.8; mean: 1.4, median: 1.3 $\mu mol\,m^{-2}\,s^{-1}$; $n = 295$) compared with that of the portable chamber data (Days 193–208, Fig. 4b, range: 0.6–5.0; mean: 2.0; median: 1.8 $\mu mol\,m^{-2}\,s^{-1}$). The coefficient of variation for the automated chamber measurements of soil CO_2 efflux was 22% of the mean, about half that of spatial variation determined with the portable chamber systems. This supports our findings that except when there was rainfall, morning and afternoon measurements by the portable soil chamber systems were statistically indistinguishable.

A *t*-test showed that automated chamber soil CO_2 effluxes were significantly lower than for the portable chamber data ($P < 0.01$, 95% CI). Part of the reason is that the automated chambers were located in a relatively open area of the forest ~100 m to the east of the portable chamber sampling area, and the lowest soil CO_2 effluxes were obtained for bare soil.

We assumed that the soil surface CO_2 efflux measured at the 32 locations in the early morning of Day 207 (only 4 h after sunrise) was a good approximation of the mean nocturnal soil efflux. For example, mean nocturnal soil CO_2 efflux from the six automated chambers was only 8% less than during the timing of the portable gas analyzer measurements on Day 207. For the scaled-up chamber data, on the night of Days 206 and 207, soil, foliage and stem and branch wood accounted for 67, 33 and 1%, respectively, of nocturnal ecosystem respiration rate (Table 4).

To put our summertime values of soil and ecosystem respiration into a seasonal perspective, we combined the 12-m height eddy covariance data and mean values of the portable chambers using measurements made before 08:00 h PST for the nights in July, and found that soil contributed 63% of the nocturnal ecosystem respiration rate. On an annual basis, we found that soil accounted for ~75% of ecosystem respiration rate (Law et al., 1999a, 2001a).

3.3.3. Root contribution to soil CO_2 effluxes

Because soil CO_2 efflux was significantly greater near plants than in open areas where there was bare soil, we examined the contributions of roots. The mean fine root density was 5 $kg\,m^{-3}$ (S.E. = 0.7, $n = 10$), surprisingly similar to that of an old-growth pine forest nearby (4.23 $kg\,m^{-3}$, S.E. = 0.95, $n = 9$). Fine roots occupied the 0.05–0.20-m zone of the 0.30-m deep cores taken from the soil. Respiration rate of the sifted roots was 53% (S.E. = 0.08, $n = 10$)

Table 4
Mean fluxes on a windy night in July (night of Days 206 and 207), from 19:30 to 04:30 h standard time[a]

Flux	Mean nocturnal flux ($\mu mol\,m^{-2}\,s^{-1}$)	Friction velocity ($m\,s^{-1}$)
Soil CO_2 efflux	1.61 (0.11)	
Foliage respiration	0.79 (0.06)	
Woody tissue respiration	0.01 (0.004)	
R_e chamber (sum)	2.41 (0.17) a	
Eddy flux (F_c) 1.75 m	2.09 (0.10) b	0.31 (0.01)
Eddy flux (F_c) 3.6 m	2.64 (0.14) ac	0.43 (0.02)
Eddy flux (F_c) 12 m	2.85 (0.15) c	0.48 (0.02)
NEE ($F_c + F_{stor}$) 12 m	3.04 (0.16) c	0.48 (0.02)

[a] Ecosystem respiration calculated from chamber data (R_e chamber) is compared with ecosystem respiration from nocturnal fluxes (eddy flux, NEE). T_a is air temperature. One standard error is shown in parenthesis. The error associated with soil CO_2 effluxes is attributed to spatial variation, and the remaining errors indicate temporal variation. The letters a, b and c denote statistical differences between the mean nocturnal fluxes measured.

of the total soil CO_2 effluxes. The litter was dry, and its contribution was nil using our measurement system. Thus, by difference, microbes in the bulk soil accounted for ~47% of soil CO_2 efflux.

3.3.4. Autotrophic respiration and GEP

We used our estimate of root respiration rate to examine autotrophic respiration in relation to GEP. This included the 12-m height eddy flux measurements (for Days 190–209, $|NEE_d| = 3.8\,\mu mol\,m^{-2}\,s^{-1}$) plus the sum of the foliage respiration ($1.3\,\mu mol\,m^{-2}\,s^{-1}$), wood respiration ($0.02\,\mu mol\,m^{-2}\,s^{-1}$), and soil CO_2 effluxes measured with the portable soil chamber systems ($2.0\,\mu mol\,m^{-2}\,s^{-1}$). By this calculation, GEP was $7.1\,\mu mol\,m^{-2}\,s^{-1}$.

The ratio R_a:GEP is commonly used in simple forest process models, and is believed to be fairly conservative at 0.53 ± 0.04 across forest ecosystems (Waring et al., 1998). Autotrophic respiration, the sum of foliage, wood and root respiration, was $2.4\,\mu mol\,m^{-2}\,s^{-1}$ or 34% of GEP. This percentage during summer drought was significantly less than our annual estimate of 55%, calculated from $R_a/(NPP + R_a)$, where NPP is annual net primary production, and R_a was estimated in a similar manner using our site-specific temperature response equations (Law et al., 2001a).

Drought effects included reduced photosynthesis, soil CO_2 efflux, and root respiration, in agreement with the Högberg et al. (2001) assertion that current photosynthate is used for root respiration, although foliage respiration normalized to 10 °C increased 36% from May to July, similar to results in old-growth pine (Law et al., 1999a). Foliage was still expanding until mid-August, during drought, so perhaps growth respiration became a larger fraction of total foliage respiration during this period (Amthor and Baldocchi, 2001). Foliage respiration was high relative to photosynthesis, as found for trees on a dry site compared with a wet site (Turnbull et al., 2001). Consequently, the ratio R_a:GEP changes seasonally due to above- and below-ground phenology of the trees and shrubs (e.g. carbon allocation and growth respiration during cell division; Kramer, 1995; Lyr and Hoffmann, 1967; Ryan et al., 1997), as suggested by the relative changes in maximum ecosystem respiration and GEP from eddy flux measurements at a suite of FLUXNET sites (Falge et al., 2001). Calculation of root R_a from soil CO_2 efflux measurements, thus should be conducted several times during the year to produce annual estimates of R_a and GEP. This information is needed to convert NEE to GEP for testing models and remotely sensed estimates of fluxes.

3.4. Micrometeorological measurements of respiration

We examined the eddy fluxes measured at 12 m height and CO_2 storage rates over the range of wind speed to ensure there were no lateral fluxes involved at our measurement site (Grace et al., 1996). Fluxes were bin-averaged by u_* and compared at the different measurement heights to detect potential biases in the data. We confine our analysis to 361 rain-free half-hourly periods with a W–SW wind direction so that our nearby portable chamber locations were upwind. For $u_* > 0.1\,m\,s^{-1}$, bin-averaged eddy fluxes did not vary systematically between 2.5 and $3.0\,\mu mol\,m^{-2}\,s^{-1}$ (Fig. 5), and the associated standard deviations were relatively small, so that these data were generally conservative as would be expected in the absence of lateral fluxes. However, when u_* was $0.1\,m\,s^{-1}$, the bin-averaged eddy flux (F_c) declined sharply to $2\,\mu mol\,m^{-2}\,s^{-1}$ and variability in the data increased significantly (Fig. 5). A similar trend was noted in the sub-canopy flux measurements at 2.56 m measurement height. Including the relatively large storage rate in the above-canopy estimates of net ecosystem exchange ($F_c + F_{stor}$), then eliminated the apparent change in the mean ecosystem respiration rate, but we exclude these data ($u_* \leq 0.1\,m\,s^{-1}$) hereafter because of concern about the variability. The summed respiration components should be similar to the nocturnal NEE values.

3.5. Comparison of chamber and micrometeorological estimates of respiration

On the windy night of Days 206 and 207 (mean $u_* > 0.5\,m\,s^{-1}$ at 12 m height, 20:30–04:30 h), scaled-up chamber estimates of respiration rates indicate that 61% of the foliage respiration occurred below the 1-m height in accordance with the vertical distribution of leaf area density for the understorey species, despite the pine having only 12% of its leaf area there. With respect to the measurement heights of the two

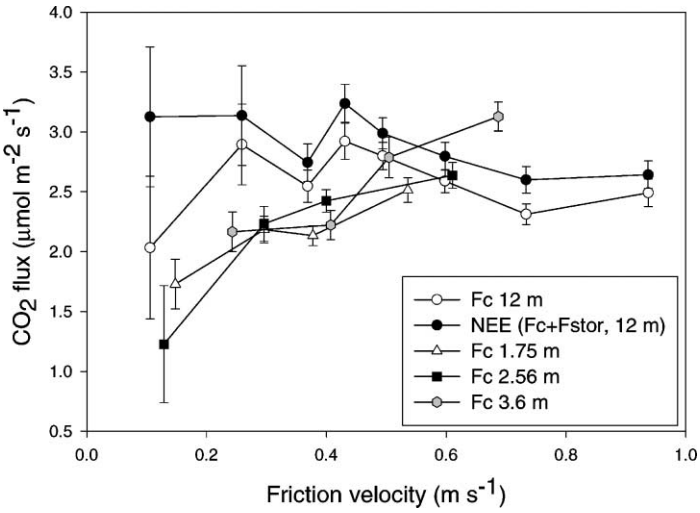

Fig. 5. The relation between nocturnal CO_2 flux measured at several heights (F_c), NEE (F_c + change in storage of CO_2 in the canopy air space, F_{stor}), and friction velocity for Days 190–209, excluding two nights of Days 189, 190 and 199, 200 due to rain, and only using data for the wind direction of 180–300° (south to west). Data were bin-averaged by friction velocity, and error bars indicate variation about the mean rate over the measurement period.

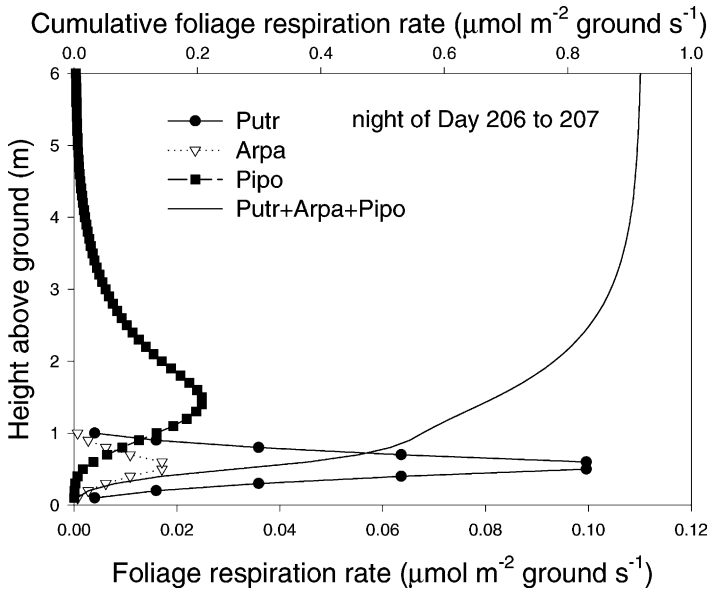

Fig. 6. Vertical profile of foliage respiration, estimated from the temperature response equations and the leaf area density profile modeled for the site from canopy dimension and optical data. Bitterbrush accounts for most of the foliage respiration below 1 m height, and the total foliage respiration changes little above the 3-m measurement height of one of the flux systems.

sub-canopy eddy flux systems, the scaled-up chamber estimates indicate that 79 and 97% of foliage respiration occurred below the 1.75 and 3.6 m heights on the night of Days 206 and 207 (Fig. 6). Thus, chamber data suggested that ∼90% of ecosystem respiration came from below 1.75 m (Table 4). On this night, the two sub-canopy CO_2 flux measurements were significantly different from each other with the 1.75-m height mean being 79% of that at 3.6 m (2.6 μmol m^{-2} s^{-1}). There was no significant difference between the measurements made at 3.6 and 12 m ($P > 0.05$). Because it was windy, the storage rate was minimal, and its inclusion led to only a 7% increase in the mean flux at 12 m that was not statistically significant.

At night, an eddy covariance measurement of respiration rate includes temporal and spatial integration. A flux footprint defines the upwind source area and hence length scale involved in the

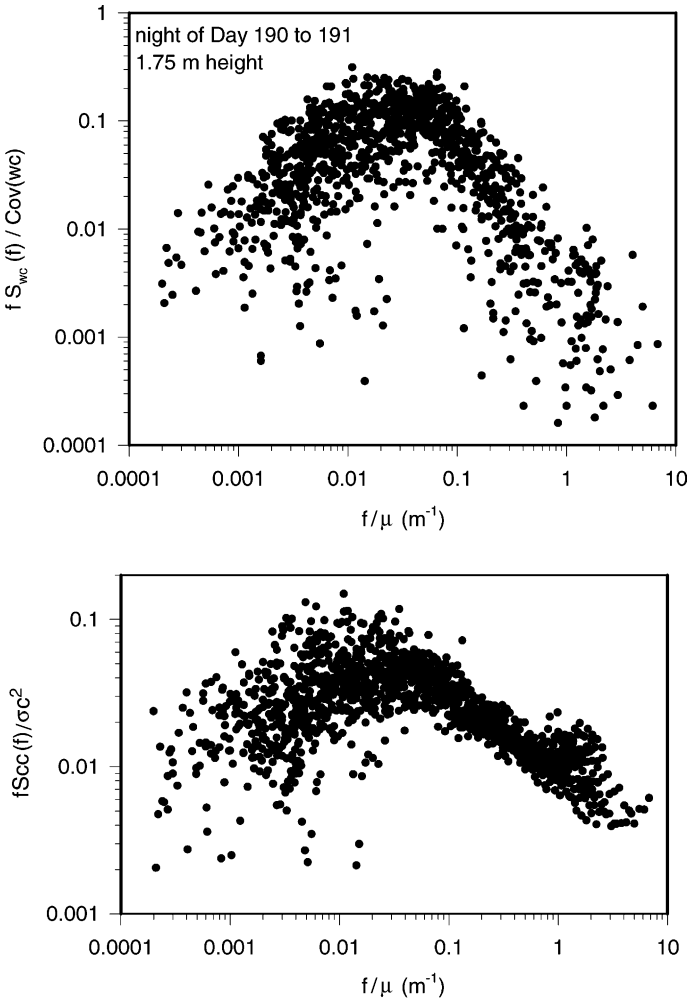

Fig. 7. (a) Co-spectrum between the vertical wind speed (w) and CO_2 concentration (c). The measurements were made at 1.75 m height for the night of Days 190 and 191. The x-axis represents the wavenumber (natural frequency divided by wind velocity). The y-axis normalizes the co-spectrum by the covariance and multiplies this ratio by natural frequency. With this normalization, the integral under the curve sums to 1. (b) The power spectrum of CO_2. The measurements were made at 1.75 m height for the night of Days 190 and 191. The x-axis represents the wavenumber (natural frequency divided by wind velocity). The y-axis normalizes the power spectrum by the variance and multiplies this ratio by natural frequency. With this normalization, the integral under the curve sums to 1.

measurements. Assuming neutral atmospheric conditions, a two-dimensional Lagrangian random walk model (Baldocchi, 1997b) was used to estimate the flux footprint by determining the probability that air parcels, released at various distances upwind, cross the flux measurement plane. For the two sub-canopy systems, 90% of the parcels or flux originated 1–12 and 1–32 m upwind for the 1.75 and 3.6 m measurement heights, respectively. For measurements made at the 12-m height, 90% of the flux emanated from 1 to 200 m upwind. The calculations thus suggest that the sub-canopy flux footprints are much contracted compared with that above the canopy, reflecting the higher wind speed and different turbulence there. Hence, noise in the sub-canopy flux measurements likely reflects the variation in source air from bare patches and vegetation.

Examination of the normalized co-spectra of vertical wind speed and CO_2 concentration indicates that the 1.75-m sub-canopy flux system captured most of the CO_2 fluxes at night (Fig. 7), so the ability of the flux system to measure small eddies does not appear to explain the discrepancy. A mean vertical profile of CO_2 fluxes at night for $u_* = 0.5\,\mathrm{m\,s^{-1}}$ during the length of the study period, estimated from a regression between eddy covariance CO_2 flux and u_* at the various sub-canopy measurement heights, indicates similar variation with height as on Day 206/207 (Fig. 8), with higher fluxes at 3.6 m measurement height. Spatial variation in respiration contributing to the 12, 32 and 200-m long upwind footprints involved in the eddy flux system measurements may have led to their determination of a different vertical profile, but it is likely within the error of measurement.

For well-mixed nights during the entire study period, there was no significant difference between NEE at 12, 3.6 m, and the scaled up chamber estimates of respiration ($P > 0.05$). Fig. 9 shows the hourly CO_2 fluxes at the various heights and NEE bin-averaged by hour for all nights during the measurement period except during rain (nights of Days 189, 190 and 199, 200). The CO_2 flux rates measured at 1.75 m height were generally 75% of the rates measured at 3.6 m height, suggesting a strong vertical gradient of respiration loss close to the ground. There was no distinct temporal trend in the respiration rate during the night (Fig. 9). The primary abiotic variables regulating respiration, soil water content and temperature, were relatively constant throughout the night. Consequently, at a given height, variation in the eddy flux at night reflects the measurement itself and associated atmospheric transport processes (Hollinger

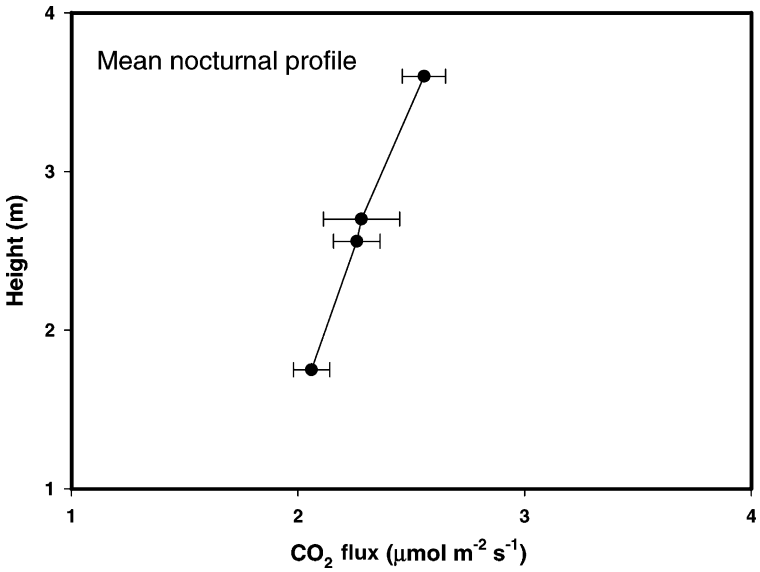

Fig. 8. The mean nocturnal CO_2 flux profile for Days 190–209, estimated from eddy covariance measurements made at various heights above the surface at $u_* = 0.5\,\mathrm{m\,s^{-1}}$. Error bars indicate variation in CO_2 fluxes over the measurement period.

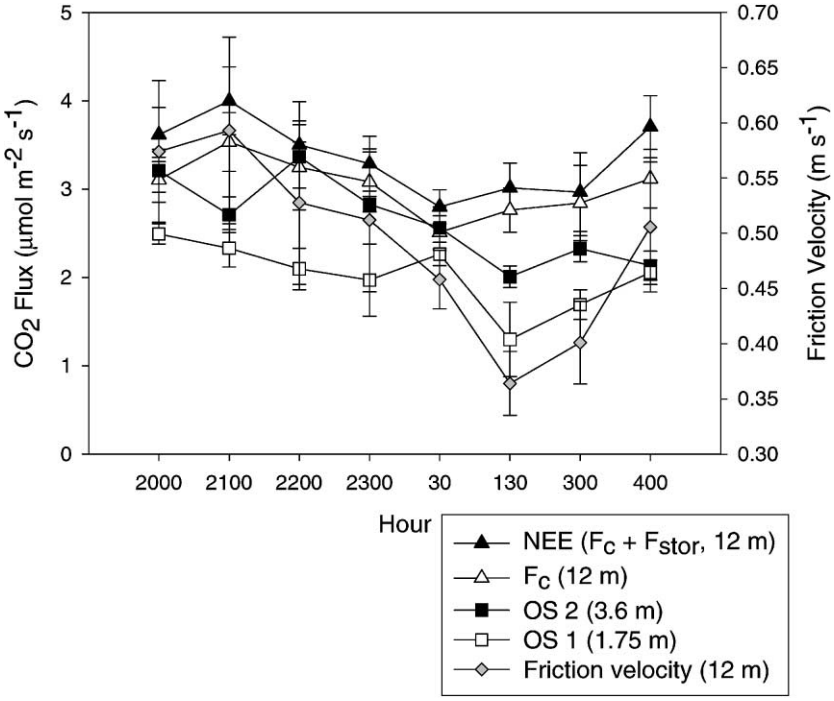

Fig. 9. Nocturnal fluxes averaged by time for all nights in July, except the nights of Days 189, 190 and 199, 200 due to rain. Data are limited to friction velocity >0.1 m s^{-1} at 12 m.

et al., 1994). Time averaging significantly reduced nighttime eddy flux variability because it was mostly stochastic reflecting the generally Gaussian nature of turbulence and open canopy architecture of our forest. It also appears that the sub-canopy eddy fluxes increased with increases in the 12-m u_*, which is expected based on Monin–Obukhov similarity theory for very stable air (Massman and Lee, 2001).

4. Conclusions

For 8–27 July 2000, during a summer drought when soil (0–0.1 m depth) water content and temperature at 0.08 m depth averaged 0.1 m^3 m^{-3} and 19 °C, soil CO_2 efflux rate averaged 2.0 μmol m^{-2} s^{-1} in a 4-m-tall, central Oregon, USA, *Pinus ponderosa* forest of LAI 1.2. Rainfall of 1.8 mm during the late-afternoon of 17 July (Day 199) corresponded with a 70% increase in average soil CO_2 efflux rate measured 15 h later, but the rate had returned to the lower level 24 h after rainfall as had the soil water content by evaporation. Diurnal variation in soil CO_2 effluxes was less than the spatial variation, averaging 22% of the mean during July. We found no significant difference in average soil respiration rates between a 30 m × 30 m area about 70 m West and two 25 m long transects 70 m North of the tower as measured by a portable chamber system. However, micro-scale variation of soil efflux was large (coefficient of variation of R_s was 40% of the mean) and related to the vicinity of the efflux measurement to dense patches of vegetation and areas of bare soil. The means for individual locations varied by nearly a factor of 2, between minima at locations with bare soil to maxima beneath dense patches of understorey vegetation. Although pine comprised 60% of the forest's leaf area, its foliar respiration was only 45% of the total foliage respiration. This corresponded with leaf nitrogen content that was half that of the broadleaved, deciduous and nitrogen-fixing understorey species, *Purshia tridentata*. Consistent eddy covariance measurement of forest respiration rates was limited to windy nights (friction velocity > 0.1 m s^{-1}) when the atmosphere was regularly mixed by turbulence. Based

on eddy covariance measurements made at three heights and chamber measurements of respiration rates, most of the fluxes coming from within <2 m of the ground, with soil surface CO_2 flux dominating respiration in this relatively short, open canopy forest.

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