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USING NOCTURNAL COLD AIR DRAINAGE FLOW TO MONITOR ECOSYSTEM PROCESSES IN COMPLEX TERRAIN

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Abstract. This paper presents initial investigations of a new approach to monitor ecosystem processes in complex terrain on large scales. Metabolic processes in mountainous ecosystems are poorly represented in current ecosystem monitoring campaigns because the methods used for monitoring metabolism at the ecosystem scale (e.g., eddy covariance) require flat study sites. Our goal was to investigate the potential for using nocturnal down-valley winds (cold air drainage) for monitoring ecosystem processes in mountainous terrain from two perspectives: measurements of the isotopic composition of ecosystem-respired CO_2 ($\delta^{13}C_{ER}$) and estimates of fluxes of CO_2 transported in the drainage flow. To test if this approach is plausible, we monitored the wind patterns, CO_2 concentrations, and the carbon isotopic composition of the air as it exited the base of a young (~40 yr-old) and an old (>450 yr-old) steeply sided Douglas-fir watershed.

Nocturnal cold air drainage within these watersheds was strong, deep, and occurred on more than 80% of summer nights. The depth of cold air drainage rapidly increased to tower height or greater when the net radiation at the top of the tower approached zero. The carbon isotope composition of CO_2 in the drainage system holds promise as an indicator of variation in basin-scale physiological processes. Although there was little vertical variation in CO_2 concentration at any point in time, we found that the range of CO_2 concentration over a single evening was sufficient to estimate $\delta^{13}C_{ER}$ from Keeling plot analyses. The seasonal variation in $\delta^{13}C_{ER}$ followed expected trends: during the summer dry season $\delta^{13}C_{ER}$ became less negative (more enriched in ^{13}C), but once rain returned in the fall, $\delta^{13}C_{ER}$ decreased. However, we found no correlation between recent weather (e.g., vapor pressure deficit) and $\delta^{13}C_{ER}$ either concurrently or with up to a one-week lag. Preliminary estimates suggest that the nocturnal CO_2 flux advecting past the 28-m tower is a rather small fraction (<20%) of the watershed-scale respiration. This study demonstrates that monitoring the isotopic composition and CO_2 concentration of cold air drainage at the base of a watershed provides a new tool for quantifying ecosystem metabolism in mountainous ecosystems on the basin scale.

Key words: advection; carbon isotopic discrimination; Cascade Mountains; CO_2 flux; Douglas-fir; ecosystem respiration; old growth.

INTRODUCTION

Consider a large area of flat land. A variety of tools and measurement approaches could be used to characterize metabolic processes of the ecosystem(s) associated with this land, including micrometeorology, remote sensing, flask sampling of air above the surface, and process-level modeling (Baldocchi 1997, Canadell et al. 2000). However, many of the earth's ecosystems are regions with complex terrain. Most of the tools used to measure and monitor ecosystem metabolism, most notably conventional micrometeorology, are difficult or impossible to use in this complex terrain because nighttime advection of CO_2 in cold air drainages increases the uncertainty in the estimates (e.g., Black et al. 1996, Lavigne et al. 1997, Aubinet et al. 2003, Paw U et al. 2004, Staebler and Fitzjarrald 2004). Many ecosystems in mountainous terrain are carbon rich (Harmon et al. 2004) and may be sensitive to climate change (Paw U et al. 2004), but due to topographic considerations, these ecosystems are poorly represented in current research networks to characterize climate–ecosystem interactions. Understanding how mountain ecosystems function and developing new ways to investigate interactions between ecosystem metabolism and environmental conditions in mountain ecosystems are among today's most important ecological problems (Schimel et al. 2002).

In mountainous regions, disproportionate heating and cooling between air in the valley slopes and the surrounding area results in up-valley airflows during the day and down-valley flow at night (cold air drainage;

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Fleagle 1950, Manins and Sawford 1979, Mahrt and Larsen 1982, Doran et al. 1990, Whiteman 1990). At night, the surface of the valley cools radiatively (long wave radiation is lost to the night sky). This cooling is greatest on cloudless nights because greater losses of long wave radiation occur (Stull 1988, Monteith and Unsworth 1990). Because air becomes denser as it cools, the cooler air "slides" (advects) downhill along gravity-driven pathways, often mimicking the pathways of stream systems (for more details see Whiteman 1990). Thus, the airsheds defined by cold air drainage are often superimposed on watersheds.

If the canopy interacts with the atmosphere in any way, such as by release or absorption of gases, cold air drainage flows will carry "signals" of these interactions. Several studies have shown that the isotopic composition of ecosystem-respired CO_2 ($\delta^{13}C_{ER}$) changes with respect to environmental conditions (e.g., vapor pressure deficit or temperature; e.g., Ekblad and Högberg 2001, Bowling et al. 2002, Barbour et al. 2005), ecosystem type (Bowling et al. 2002), or stand age (Fessenden and Ehleringer 2002). The isotopic composition of respired CO_2 varies because C_3 plants discriminate against the heavy stable isotope of carbon (^{13}C; Farquhar et al. 1980, 1989, Ehleringer et al. 1992); thus, CO_2 respired from plants and soils is depleted in ^{13}C (Pataki et al. 2003). Thus, monitoring the carbon isotopic composition of CO_2 in cold air drainage flows may provide a tool to estimate $\delta^{13}C_{ER}$ of all or part of a watershed. However, to accurately estimate the $\delta^{13}C_{ER}$, the characteristics of the cold air drainage must be understood.

The characteristics of a cold air drainage flow will vary with vegetation cover. Cold air drainage flows have been observed on slopes as small as 1% (Soler et al. 2002), and this flow is usually laminar (i.e., stratified or poorly mixed) because of the strong stability in the flow. If the land surface is sparsely vegetated, most of the radiative cooling occurs close to the ground, and the flow travels below the canopies of any trees that may be present. The flow may become nonlaminar (i.e., turbulent and mixed) if individual turbulent wakes formed in the lee of each tree branch or stem merge (Mahrt 1986). If the slope is heavily vegetated, the radiating surface to the night sky is the top of the canopy rather than the ground, and a drainage flow may occur above the canopy (Komatsu et al. 2003). In heavily vegetated terrain, the drainage may extend below the canopy, creating regions of high windspeeds above the canopy and near the ground (s-shaped vertical wind profile; e.g., Fons 1940, Allen 1968, Landsberg and James 1971, Shaw 1977, Turnipseed et al. 2003). The vertical gradient in CO_2 concentration will depend on whether the drainage is stratified (laminar) or well mixed (turbulent). Therefore, the characteristics of the cold air drainage must be understood because the precision of the method used to determine $\delta^{13}C_{ER}$ hinges on sampling a sufficient range of CO_2 concentration (Pataki et al. 2003).

To date, virtually all studies of $\delta^{13}C_{ER}$ have been conducted in relatively flat terrain. This is because measurements of $\delta^{13}C_{ER}$ require collecting air samples with a relatively wide range of CO_2 concentrations from a single location; the set of samples is then analyzed using a graphical approach known as a "Keeling plot" (Keeling 1958, 1961, Buchmann and Ehleringer 1998, Flanagan and Ehleringer 1998). In previous studies, the requisite range in CO_2 concentration has been obtained by sampling air at different heights over relatively flat terrain where a vertical stratification of CO_2 develops at night (e.g., Flanagan et al. 1996, Buchmann et al. 1997, Bowling et al. 2002). In mountainous terrain it may not be possible to collect an adequate range of CO_2 concentration because the vertical stratification may be disrupted by turbulence caused by flow around stems and boles (Mahrt 1986). However, we reasoned that in steeply sided watersheds with very well-developed nocturnal air drainage, the concentration of CO_2 may vary sufficiently over the course of an evening, even though it may not vary vertically; thus, it might be possible to obtain a sufficient range of CO_2 concentration for Keeling plot analysis from samples collected over time rather than over a height gradient if the cold air drainage is not stratified. An appeal of using cold air drainages is that the ground area ("footprint") contributing to respired CO_2 of samples collected in the cold air drainage system likely represents a much larger area than that contributing to samples collected over flat terrain, and it would also provide a new way to monitor variations in ecosystem metabolic processes in mountainous ecosystems.

The goal of this study was to investigate the potential for using nocturnal cold air drainage flows for monitoring ecosystem processes in mountainous terrain from two perspectives: measurements of the carbon isotope composition of nocturnal ecosystem respiration and estimates of the fraction of the respired CO_2 flux in the watershed that is advected in the drainage flow. Our specific objectives were to (1) examine nocturnal air flow patterns within two steep-sided watersheds to determine the characteristics of the cold air drainage, (2) determine whether $\delta^{13}C_{ER}$ can be determined by applying the "Keeling plot" approach to air sampled from cold air draining out of the base of the watersheds, and (3) estimate the CO_2 flux advected from one of the watersheds and identify uncertainties and additional measurements necessary for quantifying respired CO_2 fluxes at the watershed scale.

Methods

Study site

Towers were constructed near the bases of two adjacent small watersheds located in the H. J. Andrews Experimental Forest in the western Cascades of central Oregon, USA (44.2° N, 122.2° W). One of the

TABLE 1. Instrument positions on 28-m and 10-m towers at the base of the young and old-growth watersheds, respectively.

Height (m)	Young forest	Old-growth forest
1		thermistor
1.5	thermistor, two-dimensional sonic anemometer	
3	thermistor, two-dimensional sonic anemometer	thermistor, cup anemometer
6	thermistor, cup anemometer	
10	thermistor, two-dimensional sonic anemometer	thermistor, cup anemometer
15	thermistor, cup anemometer, wind vane	
20	thermistor, two-dimensional sonic anemometer	
25	thermistor, cup anemometer	
28	thermistor, net radiometer	
29	propeller anemometer with wind vane	

watersheds (WS1) covers 96 ha and was harvested in the late 1960s. It is now populated by a relatively young, closed-canopied forest (~25 m) that consists primarily of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) with a smaller component of bigleaf maple (*Acer macrophyllum* Pursh.), red alder (*Alnus rubra* Bong.), and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.; Moore et al. 2004). The other watershed (WS2) covers 60 ha, has not had a major disturbance for more than 450 years, and has a mix Douglas-fir and western hemlock that accounts for ~90% of the sapwood basal area (Moore et al. 2004). This old-growth forest is >60 m tall and has large canopy gaps that are typical of old-growth Douglas-fir/western hemlock forests in the Pacific Northwest (Gray and Spies 1996, Franklin et al. 2002). The site has wet, mild winters and warm, dry summers with a mean annual precipitation of 2300 mm. The soil is described as gravelly clay loam (Swanson and James 1975).

Tower measurements

Towers, initially 10 m tall, were constructed in the late spring of 2002 at the base of the young and old-growth watersheds because past research suggested that the air drainage flows may be shallow (Mahrt 1986). However, it quickly became apparent that the drainage was substantially deeper in our ecosystems, and the tower in the young watershed was extended to 28 m (close to the canopy top) and furnished with more instruments in the spring of 2003 (Table 1). The tower in the old-growth watershed was not extended for budgetary reasons. Wind speed and wind direction were measured on the towers using a combination of cup anemometers (010C, Met One Instruments, Grants Pass, Oregon, USA and Ultralight, Thornthwaite, Centerton, New Jersey, USA), wind vanes (020C, Met One Instruments), propeller anemometers (Model 05103, R. M. Young, Traverse City, Michigan, USA), and sonic anemometers (WS425, Vaisala, Helsinki, Finland). Air temperature was measured at several heights using shielded thermistors (107, Campbell-Scientific, Logan, Utah, USA) and net radiation was measured at the top of the tower with a net radiometer (Q7, Campbell-Scientific). Signals were measured by a data logger (CR10x, Campbell-Scientific) every second and were averaged over either 1 minute (sonic anemometers) or 15 minute intervals (all other meteorological instruments). Continuous measurements of these instruments began in May 2003.

Definition of cold air drainage

For the wind patterns within this valley to be considered nocturnal cold air drainage, we required the flow measured at the tower to meet three criteria: (1) the wind direction must be within between 90° and 135° (down valley); (2) the wind-speed profile measured on the 28-m tower must have a local maximum near the ground (Stull 1988); and (3) because we were only interested in *nocturnal* cold air drainage, the net radiation measured above the tower was required be negative (indicating a surface cooling; Whiteman 1989). We focused exclusively on nocturnal drainage flow because our interest was in nocturnally collected samples of air for Keeling plot analyses. However, it should be noted that under the right conditions, cold air drainage can continue all day below the canopy while uphill flow occurs above the canopy (Hawkes 1947, Whiteman 1986, 1990). The prevailing wind direction measured on the ridge at the head of these valleys was typically up valley, between 240° and 360° (data not shown). Hence, down-valley winds near the surface usually indicated cold air drainage in the valley.

Measurement of CO_2 concentration

We measured the CO_2 concentration of the air in the nocturnal cold air drainage in the young and old-growth watersheds on six and three nights, respectively, between June and September 2003 using a vertical profile system. In the younger watershed, a switching system was used to sample air sequentially from six heights on the tower (3, 6, 10, 15, 20, and 28 m). Because the tower was smaller in the old-growth watershed, the profile system only monitored CO_2 concentration at 3, 6, and 10 m. In both watersheds, the air from each height was pumped (pump model UNMP30KNDC, KNF Neuberger, Trenton, New Jersey, USA) at 1.5 L/min for 2 minutes to an infrared gas analyzer (LI6262, Li-Cor, Lincoln, Nebraska, USA). The infrared gas analyzer was calibrated in the field using a nitrogen tank (no CO_2) and a second tank of known CO_2 concentration. To ensure that the measurements only represented the current interval, the last 30 seconds for each 2 minute interval were averaged and stored on a data logger (CR10x, Campbell-Scientific). Each sample height had its own 6.4 mm diameter tubing that connected to a switching mechanism placed near the infrared gas analyzer.

Isotope Sampling and Analysis

Air samples for isotope analysis were collected by hand in the field at multiple heights in the young (3, 6, 10, 15, 20, and 28 m) and old-growth forests (1, 3, and 10 m). Air was pumped at $\sim$1.5 L min^{-1} (Model number UNMP30KNDC, KNF Neuberger) from one of the heights through an infrared gas analyzer (IRGA; LI-6252, Li-Cor) and then discharged out of a tygon tube inserted into a 15-mL septum-sealed vial, which was flushed with gas for approximately one minute. As the sample was collected, the CO_2 concentration from the IRGA was noted and a cap was quickly placed onto the vial as the tygon tube was simultaneously withdrawn. To smooth out higher frequency variations transition in the gas compositions, the air was passed through a small buffer volume (2 L) before it was routed to the IRGA. For each sample period 16–40 sets of vials were collected and analyzed.

For $\delta^{13}C$ analysis, we used a Finnigan/MAT Delta-Plus XL isotope ratio mass spectrometer (San Jose, California, USA) interfaced to a GasBench II automated headspace sampler (Finnigan) at the College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, Oregon, USA. The GasBench-II is a continuous flow interface that allows injections of several aliquots of a single gas sample into a mass spectrometer for automated isotope determinations of small gas samples. A typical analysis consists of three gas standards (tank CO_2–He mixtures), six sample replicates, and an additional two gas standards.

The tank CO_2 was calibrated both on a MAT-252 (dual inlet) mass spectrometer (Finnigan), by comparison to NIST-8544 (also known as NBS-19) limestone prepared using a Kiel-III online acid digestion device (Finnigan), which yields isotopic values of −2.19‰ ± 0.06‰ for $\delta^{18}O$ and 1.94‰ ± 0.02‰ for $\delta^{13}C$ ($n = 25$), which compares with certified values of −2.20‰ and 1.95‰ for $\delta^{18}O$ and $\delta^{13}C$, respectively (no precision estimate; NIST 1992*a*). The reference gas was also calibrated on the DELTAplus-XL (Finnigan) by analysis of NIST-8541 (also known as USGS-24 Graphite, certified value of $\delta^{13}C = -15.90 \pm 0.25‰$) and NIST-8542 (also known as ANU Sucrose, certified value of $\delta^{13}C = -10.47 \pm 0.13‰$), which were prepared by online combustion using a Carlo-Erba NA-1500 elemental analyzer (Milan, Italy), and CONFLO-III inlet system (Thermo Finnigan, San Jose, California, USA). Repeated analyses of a single gas sample (tank CO_2–He mixtures of 1% CO_2) by the GasBench-II yields external precision for $\delta^{13}C$ in multiple vials of this continuous flow device to ±0.03‰, which is close to the level typical of dual-inlet mass spectrometry (typically ±0.02‰ on our Finnigan/MAT-252).

We conducted extensive tests of procedures for collecting and storing air samples. We found no measurable change in isotope ratios of air samples stored in 15-mL vials sealed with non-punctured butyl or Kel-F septa for up to one week or moved across an altitude range of >500 m. However, if the septa were punctured, the isotope values changed significantly during transport and storage, and unlike Tu et al. (2001), we were not able to adjust for the change with punctured and non-punctured standards. Therefore, we collected field samples in glass vials, capping them by hand with non-punctured septa. Between early June and late September of 2003, we conducted thirteen measurements of $\delta^{13}C_{ER}$: seven in WS1 and six in WS2.

The $\delta^{13}C_{ER}$ was estimated using a two-end member-mixing model or "Keeling plot" (Keeling 1958, 1961, Buchmann and Ehleringer 1998, Flanagan and Ehleringer 1998). The $\delta^{13}C$ of the air samples in the vials was plotted against $1/CO_2$ concentration. Because there are measurement errors in both the x and y axes (Pataki et al. 2003), a geometric mean regression approach (Sokol and Rohlf 1995) was used to estimate the value of the y-intercept, or $\delta^{13}C_{ER}$. The use of geometric mean regression for calculating Keeling plot intercepts has recently been challenged (Zobitz et al. 2006). However, the use of geometric mean regression instead of ordinary least squares regression will have little effect on conclusions drawn in this paper. Because collecting samples by hand has a high probability of operator error (e.g., recording the CO_2 concentration off the IRGA that represents the CO_2 concentration collected in the file), outliers in each data set were systematically removed. Using a procedure outlined by Bowling (2002), we selected outliers by first performing a geometric mean (GM) regression on all the data points. Any data point with a residual greater than two standard deviation was removed and the GM regression was performed on the remaining data points. This procedure was repeated until all the residuals were within two standard deviations. The data were continuously refit until all the points were within this limit. This method may remove some valuable biological information; however, the error associated with our sampling technique (hand samples) required an unbiased method for removing outliers. Future work with an automated sampler will hopefully negate the need to remove outliers in this manner.

Pre-dawn water potential

Pre-dawn water potential of trees was measured on most of the nights that air samples were taken for isotope analysis. Water potential of small twigs was measured one hour prior to sunrise using a field portable pressure chamber (PMS systems, Corvallis, Oregon, USA). In the young watershed, between 5 and 10

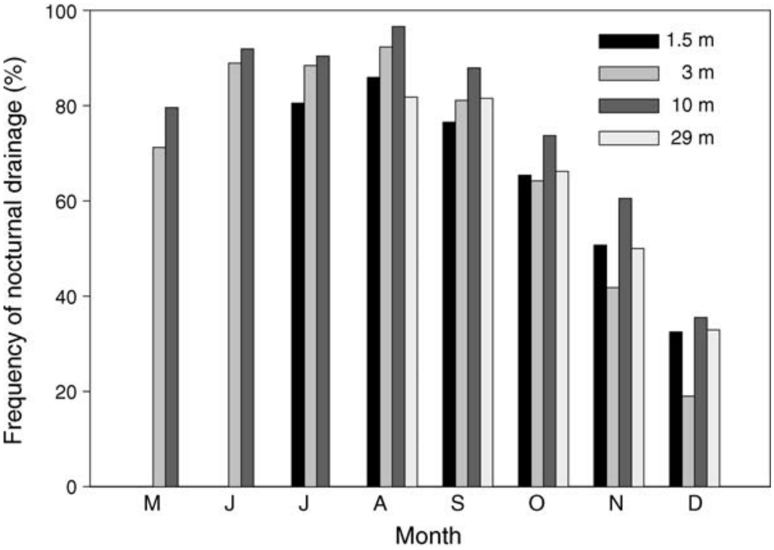

FIG. 1. Percentage of 15-min intervals where nocturnal cold air drainage occurred in the young Douglas-fir watershed from May to December 2003 at four different heights. For the wind to be considered nocturnal cold air drainage, the wind measured at the tower was required to meet three criteria: (1) the wind direction must be within between 90° and 135° (down valley); (2) the wind speed profile measured on the 28-m tower must have a local maximum near the ground; and (3) the net radiation measured above the tower must be negative.

Douglas-fir trees were randomly selected within a 100-m radius of the tower, and one branchlet from each tree was removed to determine water potential. In the old-growth forest, five Douglas-fir and five western hemlock trees were randomly selected and water potential determined on shoots from the lower-canopy.

Pre-dawn twig water potentials for sampling nights where pre-dawn measurements were not made were estimated by linear interpolation from the other data points. In the Pacific Northwest there is a pronounced summer dry season and the soil water continuously decreases as the summer progresses (Parsons et al. 2001). During the summer of 2003 there were only two rainfall events in July and August, totaling <5.75 mm of rain (Pypker et al. 2006). Given that young and old-growth Douglas-fir forests lose approximately 20% of gross precipitation to evaporation during a storm event and have a canopy water storage of 1–2 mm and 3 mm respectively (e.g., Klaassen et al. 1998, Pypker et al. 2005), only a very small fraction of this rainfall would reach the forest floor. Therefore, interpolating pre-dawn water potential between measurements is not unreasonable in this ecosystem.

RESULTS

Characteristics of the cold air drainage

Nocturnal down-valley winds (20:00–05:00) were observed at all heights to 28 m from May to December 2003 (DOY 121–365; Fig. 1). The proportion of down-valley flow was calculated for each measurement height. The cold air drainage in the old-growth watershed followed a similar pattern for periods when the winds (>0.45 m/s) were sufficient to move the wind vane (data not shown). The drainage was most common at the lower heights and during the summer months when the days were warm and the nights were clear. Cloudless nights allowed for greater losses of long-wave radiation from the surface to the atmosphere at night.

The shapes of the vertical wind profiles during cold air drainage were similar from May to December. Beneath the canopy, the wind speed was maximum at 5 m/s, with increasing drag causing decreased wind speeds near the ground surface (1.5 m/s) and within the canopy air space (18 m/s to 25 m/s; Fig. 2). The drainage flow appeared to extend above the canopy to an unknown depth greater than the tower height (Fig. 2), and its velocity typically decreased from 21:00 to 04:00 (Fig. 3a).

The depth of cold air drainage rapidly increased to tower height or greater when the net radiation at the top of the tower approached zero and the vertical gradient of potential temperature approached zero (Fig. 4). Potential temperature represents the temperature an air mass would attain if it expanded or compressed adiabatically from its current elevation to sea level (for more information see Wallace and Hobbs 1977). Hence, it allows for direct comparison between temperature measurements from different elevations.

At all the heights, the down-valley wind speeds were greatest in the early evening, when the thermally caused pressure gradient (greater air density near the slope) between the air adjacent to the slope and the ambient air at the same elevation over the valley was presumably the greatest (Whiteman 1990). The wind speeds typically decreased as the evening progressed.

The vertical potential temperature profile followed a well-defined pattern in summer. By day, the air

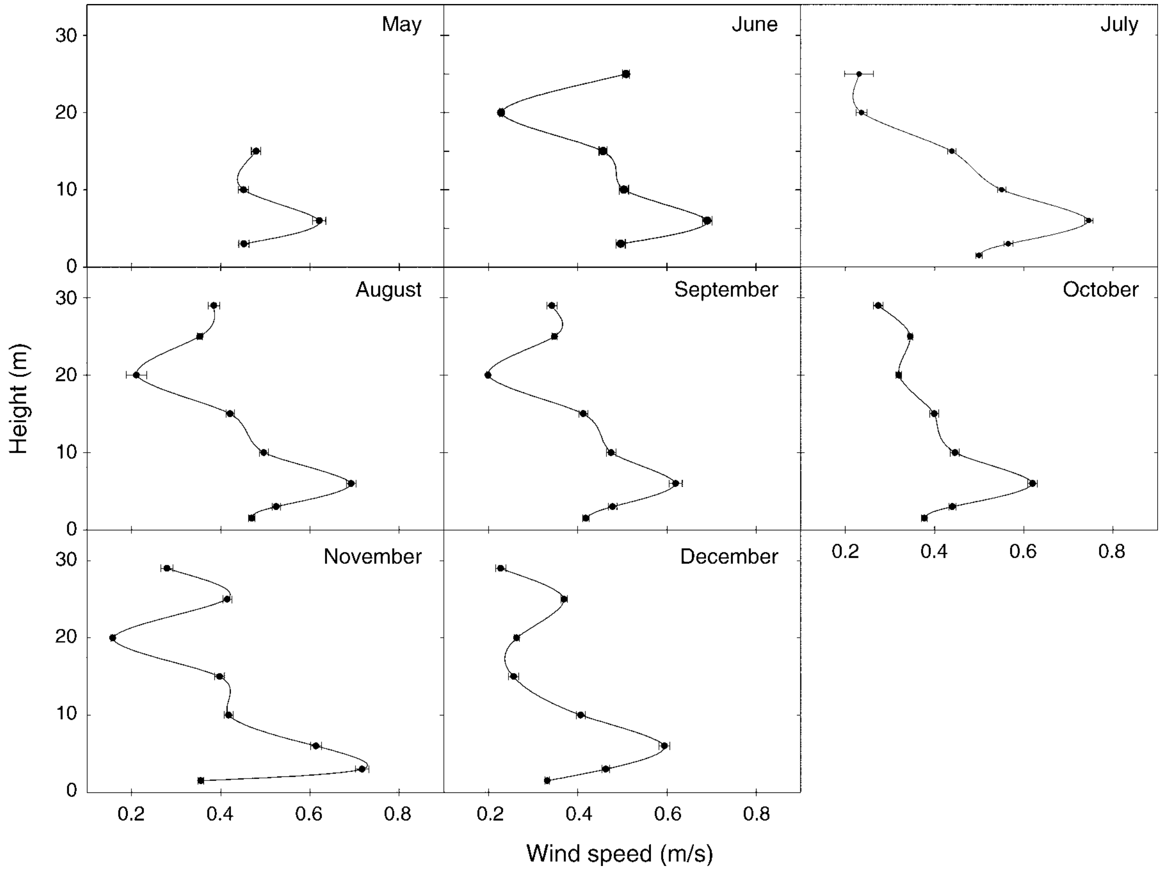

FIG. 2. Mean monthly wind speed profiles during episodes of cold air drainage in the young Douglas-fir watershed from May to December 2003.

temperature was greatest near the canopy top where the greatest quantity of solar radiation is absorbed (Fig. 3b). At all heights, the daily maximum air temperatures occurred at 15:00, after which the air temperatures at all heights steadily declined. The decline was greatest within the canopy air space, and by 20:00 the potential temperature profile became nearly isothermal, indicating that the air was well mixed. The air temperatures remained close to isothermal until the following morning (Fig. 3b).

CO_2 concentration profiles

The CO_2 vertical concentration profiles measured on the towers in young and old-growth watersheds followed a similar pattern to the temperature profiles (Fig. 5). During the day (07:00–20:00), CO_2 concentration varied with height, with the greatest concentrations occurring near the ground. At about 20:00 the air flow in the canopy became well mixed, and the CO_2 concentrations at all heights converged (Fig. 5) at approximately the same time as the potential temperature profile became nearly isothermal (Fig. 4). The CO_2 concentrations steadily increased throughout the night until sunrise. After sunrise, the drainage remained well mixed for 1–2 h, but the CO_2 concentrations began to decline. At approximately 07:00 when the potential temperature profile became stratified, a vertical gradient of CO_2 concentration was re-established. During the course of a night, the range of CO_2 concentration in the well-mixed flow was typically between 30 and 80 ppm in both the young and old-growth forests. The data presented are primarily from the young forest because it contained the taller tower. However, the pattern of CO_2 concentrations was similar at the 10-m tower in the old-growth stand.

Isotopic composition

The range of CO_2 concentration used in the Keeling plots was from 47 to 92 ppm and from 64 to 116 ppm for the young and old-growth forests, respectively (Table 2). There were no discernable differences in the isotopic composition of the air measured at the different heights because the air was well mixed (Fig. 5). Therefore, the samples from the different heights were grouped together to provide an estimate of $\delta^{13}C_{ER}$ for each measurement night.

From 2 July to 21 September 2003 (DOY 183–264) the $\delta^{13}C_{ER}$ was estimated to range between −24.5‰ and −27‰ (Table 2). During this same period, the forests received only 6 mm of rainfall (Pypker et al. 2006). As

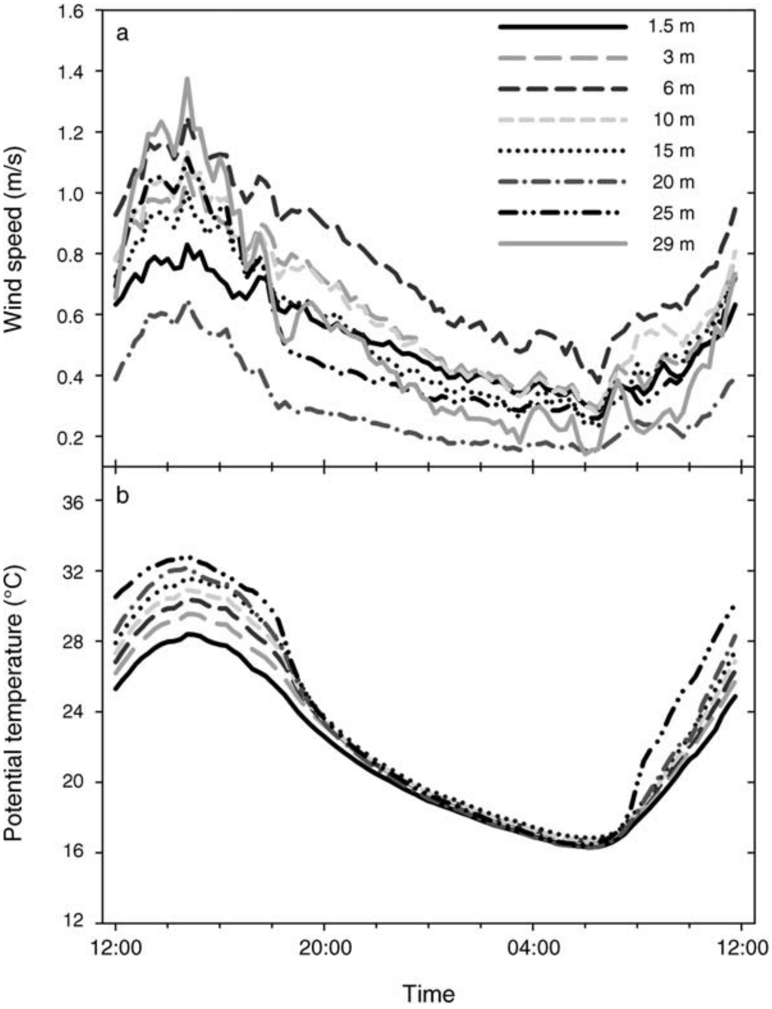

FIG. 3. The mean diurnal (a) wind speeds and (b) potential temperature at multiple heights on the tower at the base of the young Douglas-fir watershed in August 2003.

the seasonal summer dry season progressed and the water potential of the trees decreased (indicating more water stress), the $\delta^{13}C_{ER}$ became more enriched in both watersheds. The first significant rainfall (58 mm) after the summer dry season occurred on 7–9 September 2003 (DOY 250–252) (Pypker et al. 2006). After this rainfall, the $\delta^{13}C_{ER}$ decreased from -25.42 ± 0.65 to -26.43 ± 0.70 (Table 2), but the difference is not significant, as the confidence intervals of each mean overlap.

In contrast with Fessenden and Ehleringer (2002), who reported significant enrichment in $\delta^{13}C_{ER}$ in an old-growth Douglas-fir forest compared with a young forest, we found no consistent difference in $\delta^{13}C_{ER}$ between the young and old-growth watersheds in our study. The $\delta^{13}C_{ER}$ was linearly related to the water potential of the upper canopy trees in the young watershed (linear regression slope P value $= 0.05$, $R^2 = 0.68$, $\alpha = 0.05$), but not in the old-growth watershed (linear regression slope P value $= 0.4$, $R^2 = 0.18$, $\alpha = 0.05$; Fig. 6). Incorporating time lags into the analyses did not substantially improve

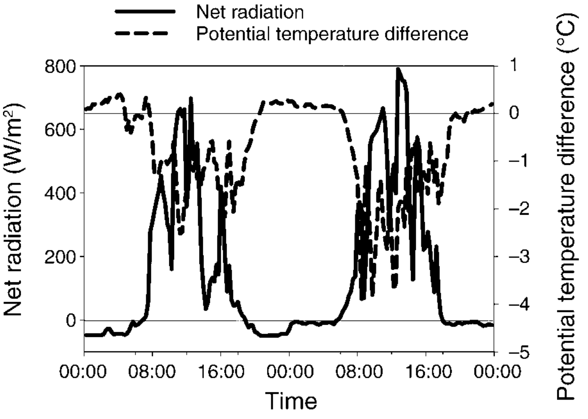

FIG. 4. The net radiation above the canopy (28 m) and the vertical potential temperature difference between the bottom (3 m) and top (28 m) of the tower in the young Douglas-fir watershed on 5 August 2003.

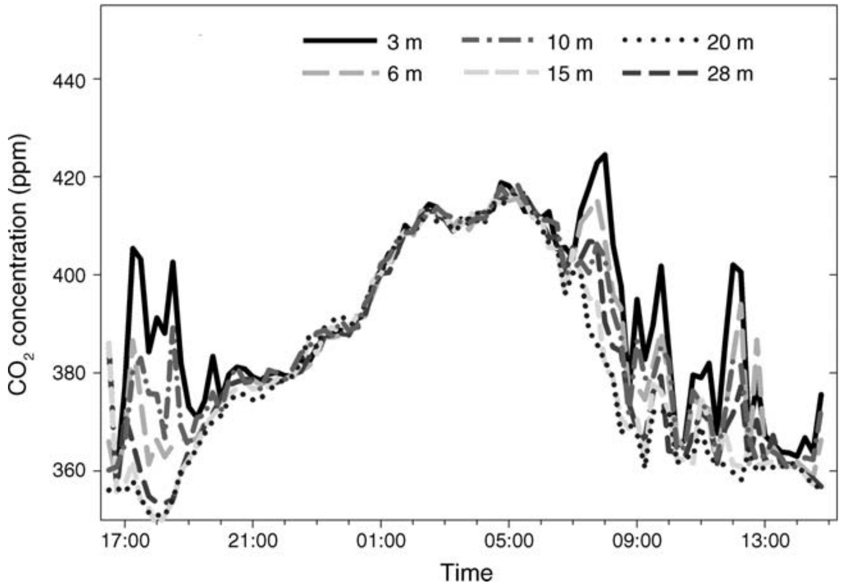

FIG. 5. Nocturnal change in CO_2 concentration measured at multiple heights in the young Douglas-fir watershed on 5–6 August 2003.

the correlations. The $\delta^{13}C_{ER}$ was not linearly related to concurrent vapor pressure deficit or to time-lagged vapor pressure deficit ranging from 1 to 10 days (all P values > 0.05, $\alpha = 0.05$).

Estimates of advected CO_2 flux

Monitoring the air exiting the base of the watershed may also provide an opportunity to quantify nighttime respiration within the watershed using a mass-balance approach. For example, if the valley is treated as an open cuvette, a rough estimate of respiration occurring inside the cuvette (watershed) can be made:

$$R_e = F_0 - F_i + \Delta F_{st} \tag{1}$$

where R_e is the rate of CO_2 input from ecosystem respiration (mol/s), F_0 is the output flux of CO_2 exiting from the valley (mol/s), F_i is the input flux to the valley of atmospheric CO_2 (at background concentration), and ΔF_{st} is the rate of storage of respired CO_2 within the watershed (mol/s). The precision with which R_e can be estimated from Eq. 1 depends on the magnitudes and uncertainties of the other terms on the right-hand side of the equation. If all the CO_2 exiting the valley was in the drainage flow measured below the top of the tower, we could estimate F_0 by treating the cross section of the watershed at the base tower as multiple layers that are perpendicular to the cold air drainage and calculating the product of wind speed and measured CO_2 concentration for each layer. With a similar assumption, the value of F_i could be estimated as the product of wind

TABLE 2. The isotopic composition of ecosystem respiration $\delta^{13}C_{ER}$ for the young and old forests.

Forest	Date	CO_2 range ppm (maximum–minimum)	Max. CO_2 ppm	$\delta^{13}C_{ER}$ (‰)	SE	R^2
Young	2 Jul 2003	92.3	460	−26.42	0.18	0.99
Young	16 Jul 2003	75.6	446	−26.20	0.35	0.99
Young	23 Jul 2003	60.7	431	−26.98	0.35	0.99
Young	30 Jul 2003	69.2	452	−25.99	0.33	0.98
Young	13 Aug 2003	61.8	429	−24.49	0.29	0.99
Young	26 Aug 2003	47.0	411	−25.42	0.65	0.98
Young	7 Sep 2003	55.0	415	−26.43	0.70	0.98
Young	21 Sep 2003	60.4	460	−25.76	0.54	0.98
Old-growth	7 Aug 2003	107	519	−26.12	0.12	0.99
Old-growth	22 Jul 2003	64.6	490	−25.47	0.69	0.97
Old-growth	29 Jul 2003	147	534	−25.54	0.18	0.99
Old-growth	12 Aug 2003	65.6	454	−25.89	0.72	0.97
Old-growth	26 Aug 2003	63.3	428	−25.45	0.55	0.99
Old-growth	21 Sep 2003	116	505	−26.82	0.23	0.99

Notes: The values of $\delta^{13}C_{ER}$ were estimated using geometric mean regression. The R^2 values are for linear regression only.

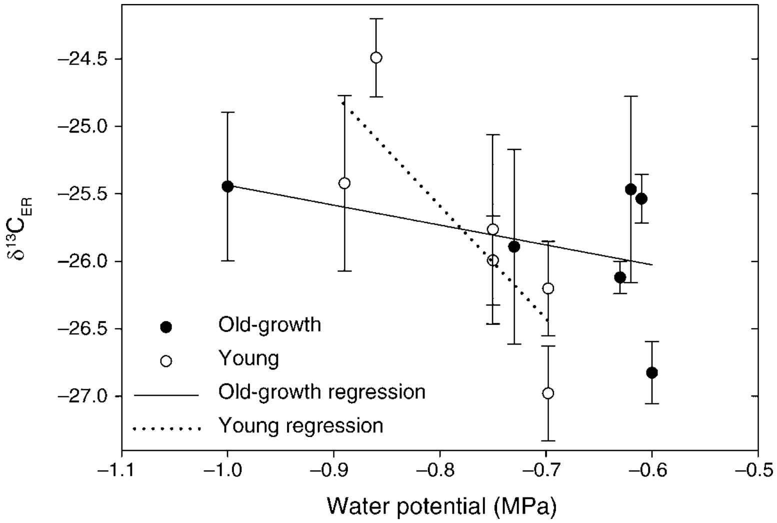

FIG. 6. The relationship between tree pre-dawn water potential and $\delta^{13}C_{ER}$ for a young and old-growth Douglas-fir watershed in 2003. Error bars represent ±SE of the estimate.

speed in each layer and background CO_2 concentration, i.e., if there were no respiration or storage $F_i = F_0$. Thus, watershed-scale respiration R_e would be given by the *net* advected flux ($F_0 - F_i$) plus the storage term ΔF_{st}. In practice, drainage flow and other exchange between air in the watershed and the free atmosphere probably also occur above the top of the tower, so the net advection in the valley cross-section below the tower top $(F_0 - F_i)_t$ is probably an underestimate of the total net advection, as we discuss later.

We calculated values of $(F_0 - F_i)_t$, as described in the Appendix, for data on a typical night of drainage flow in Watershed 1. Fig. 7 shows that $(F_0 - F_i)_t$ ranged from 0.3 to 1.3 mol/s between 20:00 to 05:00 on 5–6 August 2003.

DISCUSSION

Characteristics of nocturnal cold air drainage

During the summer months, nocturnal cold air drainage was frequent in both watersheds (Fig. 1) because summer in western Oregon has little rainfall and mostly clear skies (Taylor and Hannan 1999). These conditions promote cold air drainage, as frequent clear skies increase the occurrence of nocturnal cold air drainage down steep, forested valleys (Whiteman 1990, Whiteman and Doran 1993). Past research has demonstrated that cold air drainages can range from a few meters (e.g., Mahrt and Larsen 1982, Mahrt et al. 2001) to tens or hundreds of meters in depth (e.g., Manins and Sawford 1979, Doran et al. 1990, Whiteman 1990, Smith and Skyllingstad 2005). The nocturnal in-canopy drainage flow at this study site was frequent (Fig. 1), deep (>28 m), and usually well mixed (Fig. 5). The depth of the cold air drainage is consistent with past measurements in forested ecosystems where the cold air drainage extended well above the canopy, with a second maximum near the canopy top (e.g., Komatsu et al. 2003). Given that the dominant wind direction is between 240° and 360° (data not shown), downhill flow generally indicated nocturnal cold air drainage.

The cold air drainage persisted throughout most nights (Fig. 1), but its velocity declined as the night progressed (Fig. 3a). The nocturnal wind speeds may decline during the night because warmer air from above becomes entrained within the drainage, thereby decreasing the buoyancy driving the flow (Barr and Orgill 1989). Alternatively, it might indicate the "damming effect" of a pool of cold air accumulating at the base of the watershed that generates hydrostatic pressure which slows the flow of cold air (e.g., Magono et al. 1982, Yoshino 1984, Maki and Harimaya 1988, Mori and Kobayashi 1996, Iijima and Shinoda 2000, Clements et al. 2003). Regardless of why the wind slows as the night progresses, the data do indicate that cold air drainage in these basins is common during the summer.

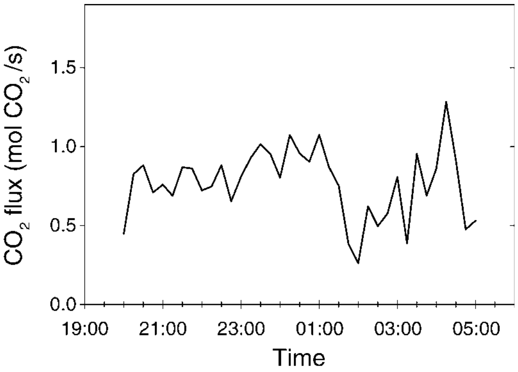

FIG. 7. The estimated flux of CO_2 passing the 28-m tower located at the base of the watershed on 5–6 August 2003. The fluxes were estimated using the method outlined in the Appendix.

Feasibility of quantifying $\delta^{13}C_{ER}$ of the air in the cold air drainage using the "Keeling-plot" approach

Three considerations are involved in evaluating whether air samples from the cold air drainage can be used to determine $\delta^{13}C_{ER}$ using Keeling-plot analyses. First, there must be a sufficient range of CO_2 concentration for accurate estimation of the intercept in the Keeling plot (Pataki et al. 2003). Second, the isotopic composition of the "source" must be stable over the measurement period (Keeling 1958, 1961, Ehleringer et al. 1992). In other words, the flux from the land surface that contributes to respired CO_2 in the samples (i.e., the "footprint") must be stable, and there must not be a significant shift in the components of respiration (i.e., aboveground vs. belowground) or their isotopic characteristics. Third, the observed variations in $\delta^{13}C_{ER}$ should be consistent with environmental variations (Farquhar et al. 1989, Madhavan et al. 1991, Ekblad and Högberg 2001, Bowling et al. 2002).

Is the range of CO_2 concentration adequate for Keeling-plot analyses?—After analyzing Keeling plots from 26 locations in the Americas, Pataki et al. (2003) reported that a minimum value of 75 ppm CO_2 is required to maintain a standard error in $\delta^{13}C_{ER}$ of less than 1‰. Of the 14 sampling nights for the young and old-growth forests in our study, 12 had a range in CO_2 concentration that was greater than 60 ppm (Table 2). While 60 ppm is lower than the desired range suggested by Pataki et al. (2003), the standard errors for estimating the intercept ($\delta^{13}C_{ER}$) were between 0.12‰ and 0.7‰, well below the desired 1‰ (Table 2). However, our precision, along with at least some of data presented in Pataki et al. (2003; e.g., Bowling et al. 2002), was improved because we removed data points that were two standard deviations away from the predicted regression line. As reported in Pataki et al. (2003), the standard error rapidly increases when the range of CO_2 concentration drops below 75 ppm (Table 2). For the two sampling periods when the range in CO_2 concentration was less than 60 ppm, the SE was greater than 0.65‰. Overall, we conclude that the nocturnal variation in CO_2 concentration in the two basins we investigated is more than adequate for accurate determination of the Keeling intercept.

Is the isotopic composition of respired CO_2 consistent over the measurement period?—In this study, we were not able to evaluate whether the "footprint," or the aboveground/belowground components, of respiration varied over the course of nocturnal measurement periods. However, if there were a significant change in the isotopic composition of the source over the time that samples were taken, it should be apparent as a "kink" or curve in the Keeling plot line (because the ordinate is plotted as $1/CO_2$ concentration, and CO_2 concentration tended to increase over time for each set of samples; Fig. 5). We found no evidence of kinks or curves in any of the data we collected, so we conclude there is no evidence for variation in the isotopic composition of the source during measurements. However, these questions require closer investigation in the future.

Relationship of $\delta^{13}C_{ER}$ to environmental variables.—The technology involved in collecting samples for determination of $\delta^{13}C_{ER}$ is rapidly evolving. Although the laboratory precision of $\delta^{13}C$ determination in our samples was excellent, our methods for collecting air samples and determining CO_2 concentration in this study were somewhat primitive and labor intensive. We have subsequently developed a more precise, automated system for collecting air samples and have improved methods for measuring CO_2 concentration in the laboratory. Nevertheless, the methods used in this study reveal that considerable variation in $\delta^{13}C_{ER}$ is likely due to short-term variations in canopy physiology, demonstrating that the approach is well worth pursuing further.

The $\delta^{13}C_{ER}$ values measured in this study follow an expected pattern, for a region with a seasonal summer dry season (Bowling et al. 2002), ranging between −24.5 and −27‰ (Table 2). Past research reported $\delta^{13}C_{ER}$ for Douglas-fir forests in the Pacific Northwest to range between −24‰ and −33‰ (Bowling et al. 2002, Fessenden and Ehleringer 2002, Ponton et al. 2006). In this study, the seasonal trend for $\delta^{13}C_{ER}$ was to gradually increase as the summer dry season progressed (Table 2). Only after a significant rainfall in September did the $\delta^{13}C_{ER}$ appear to decrease (Table 2). Bowling et al. (2002) monitored $\delta^{13}C_{ER}$ at six forested sites in Oregon that stretched along a precipitation gradient. Two of these sites were young Douglas-fir forests (~13 and 30 years old) and, as at the study site here, Bowling et al. (2002) reported that from June to September the $\delta^{13}C_{ER}$ for the 13 and 30 year old Douglas-fir forests increased from approximately −29.5‰ to −25.5‰ and from −27‰ to −25.5‰, respectively. Furthermore, Ponton et al. (2006), when monitoring seasonal changes in $\delta^{13}C_{ER}$ during the seasonal summer dry season at a ~50 yr-old Douglas-fir forest on Vancouver Island, British Columbia, Canada, found that between May and September the $\delta^{13}C_{ER}$ increased from approximately −27.5‰ to −24.8‰. To prevent xylem cavitation and embolism, Douglas-fir trees use their stomata to regulate water potential in the tree (Phillips et al. 2002, Domec et al. 2004). By closing their stomata, the isotopic signature of the recently fixed photosynthate is thus expected to increase (Farquhar et al. 1989, Madhavan et al. 1991). Hence, past researchers have shown $\delta^{13}C_{ER}$ to be sensitive to changes in vapor pressure deficit or soil moisture (Ekblad and Högberg 2001, Bowling et al. 2002). However, despite following seasonal changes in water availability, the variation in the $\delta^{13}C_{ER}$ was not closely correlated with any one of the environmental variables we investigated.

In contrast with studies of Ekbald and Högberg (2001) and Bowling et al. (2002), the variation of $\delta^{13}C_{ER}$ was not significantly related to vapor pressure deficit using any time lag when compared using linear regression ($R^2 =$

0.01 with no time lag). There was a significant correlation between $\delta^{13}C_{ER}$ and pre-dawn water potential of dominant trees in the young forest, but not the old-growth forest (Fig. 6). It is not surprising that $\delta^{13}C_{ER}$ cannot be explained by such simple environmental parameters because the isotope signal integrates a large number of variables. As McDowell et al. (2002) noted, environmental variations that affect canopy physiology (e.g., temperature, humidity, soil moisture) are also likely to affect the relative contribution of different respiratory sources (e.g., foliage, litter, roots, bulk soil), thereby affecting $\delta^{13}C_{ER}$ in more complex ways.

The larger sampling area increases the heterogeneity of the components contributing to the $\delta^{13}C_{ER}$ measured at the tower. One of the benefits of monitoring the isotopic signal contained within the cold air drainage is that it provides an integrated signal of the $\delta^{13}C_{ER}$ for all or part of a watershed. However, the larger sampling area incorporates respiration from riparian and upslope positions. Given that the microclimates at these locations are likely very different, it is possible that the lack of correlation between vapor pressure deficit and $\delta^{13}C_{ER}$ may result, in part, because of this heterogeneity.

Advected CO_2 flux estimates

Estimates of the net advected flux of carbon dioxide $(F_0 - F_i)_t$ through the valley cross-section below the top of the tower range from 0.3 mol/s to 1.3 mol/s (Fig. 7). Past work in similar forests of this region suggests that the respiratory flux per unit ground area is approximately 7 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ (Harmon et al. 2004, Campbell and Law 2005). Given that the floor area of the valley is about 96 ha, this corresponds to a watershed-scale respiratory flux R_e of approximately 7 mol/s. Therefore, this method estimates that the advected flux passing the 28-m tower accounts only for approximately 5–18% of the total ecosystem respiration within the 96-ha watershed. If our advection calculations and assumptions are accurate, the remaining respired CO_2 must have either been advected in drainage flow above the tower or have exited the flow by becoming entrained in the overlying air or have been stored in the sub-canopy airspace up valley from the tower. An alternative explanation is that the source area of the CO_2 measured in the drainage flow (the footprint of the tower) may not have included the entire watershed, so that the CO_2 in the cold air drainage that advected past the tower was only a small fraction of the watershed respiration.

Quantifying advective fluxes using a single vertical profile measured at the base of the watershed is uncertain, as windspeeds and CO_2 concentrations are assumed to be horizontally homogeneous (King 1989). In the present case, the drainage flow was well mixed, so homogeneity of CO_2 concentration is a reasonable assumption (Fig. 5). However, wind speeds were not likely to be horizontally homogeneous. For example, wind speeds measured above the canopy are unlikely to represent wind speeds on the adjacent vegetated slope at the same elevation because of frictional drag exerted by the foliage (e.g., Fons 1940, Allen 1968, Landsberg 1971, Shaw 1977, Turnipseed et al. 2003). King (1989) concluded that calculations based on a single vertical profile overestimated the advected volume flux of air out of a watershed in Colorado by a factor of two.

Although CO_2 storage in canopy airspace is unlikely to be a significant term in the mass balance over long sampling times, it is probably not negligible on the time scale of Fig. 7. The largest cause of the difference between $(F_0 - F_i)_t$ and R_e is probably the footprint of the tower being smaller than the area of the watershed. To more accurately estimate fluxes the depth of the cold air drainage and the footprint of the tower must be determined. We plan future studies with a taller tower, an inert tracer gas, and improved spatial sampling of temperature gradients in the watershed to determine whether CO_2 mass balance studies can be refined to provide better estimates of ecosystem respiration in steep terrain.

CONCLUSION

Nocturnal air drainage within the canopies of two steep, forested watersheds was strong and deep. The flow became well mixed at roughly the same time as net radiation above the canopy became negative and a temperature inversion formed at the canopy top. The well-mixed regime persisted through the night and into the early morning. These deep, well-mixed drainage systems offer opportunities to monitor and quantify ecosystem function on the basin or sub-basin scale in complex, mountainous terrain. Nocturnal drainage carries a large quantity of ecosystem-respired CO_2. The carbon isotope composition of CO_2 in the drainage system holds promise as an indicator of variation in basin-scale physiological processes. We found that the range of CO_2 concentration over a single evening was sufficient to estimate $\delta^{13}C_{ER}$ from Keeling plot analyses and that variation in $\delta^{13}C_{ER}$ over a summer dry season and early fall rains generally followed expected trends. Estimates of the advected CO_2 flux in the cold air drainage were much smaller than the likely respiration from the entire watershed. Eventually, it may be possible to quantify variations in ecosystem respiration rates from mass balance measurements in these flows. However, to quantify the mass flux of carbon and to use $\delta^{13}C_R$ to monitor intra- and interannual variations in ecosystem metabolism on the basin scale requires further work, particularly better knowledge of vertical and lateral advective transfer within the ecosystem and a deeper understanding of the interactions between environmental drivers and the short-term dynamics of carbon cycling.

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LITERATURE CITED

Allen, L. H., Jr. 1968. Turbulence and wind speed spectra within a Japanese larch plantation. Journal of Applied Meteorology 7:73–78.

Aubinet, M., B. Heinesch, and M. Yernaux. 2003. Horizontal and vertical CO_2 advection in a sloping forest. Boundary-Layer Meteorology 108:397–417.

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 Environment 20:1108–1122.

Barbour, M. M., J. E. Hunt, R. J. Dungan, M. H. Turnbull, G. W. F. Brailsford, G. D. Farquhar, and D. Whitehead. 2005. Variation in the degree of coupling between ^{13}C of phloem sap and ecosystem respiration in two mature *Nothofagus* forests. New Phytologist 166:497–512.

Barr, S., and M. M. Orgill. 1989. Influence of external meteorology on nocturnal valley drainage winds. Journal of Applied Meteorology 28:497–517.

Black, T. A., et al. 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. Global Change Biology 2:219–229.

Bowling, D. R., N. G. McDowell, B. J. Bond, B. E. Law, and J. A. Ehleringer. 2002. ^{13}C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. Oecologia 131:113–124.

Buchmann, N., and J. A. Ehleringer. 1998. CO_2 concentration profiles, and carbon and oxygen isotopes in C_3 and C_4 crop canopies. Agricultural and Forest Meteorology 89:45–58.

Buchmann, N., J.-M. Guehl, T. S. Barigah, and J. R. Ehleringer. 1997. Interseasonal comparison of CO_2 concentrations, isotopic composition, and carbon dynamics in an Amazonian rainforest (French Guiana). 110:120–131.

Campbell, J. L., and B. E. Law. 2005. Forest soil respiration across three climatically distinct chronosequences in Oregon. Biogeochemistry 73:109–125.

Canadell, J. G., et al. 2000. Carbon metabolism of the terrestrial biosphere: a multitechnique approach for improved understanding. Ecosystems 3:115–130.

Clements, C. B., C. D. Whiteman, and J. D. Horel. 2003. Cold air-pool structure and evolution in a mountain basin: Peter Sinks, Utah. Journal of Applied Meteorology 42:752–768.

Domec, J.-C., J. M. Warren, F. C. Meinzer, J. R. Brooks, and R. Coulombe. 2004. Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigated by hydraulic redistribution. Oecologia 141:7–16.

Doran, J. C., T. W. Horst, and C. D. Whiteman. 1990. The development and structure of nocturnal slope winds in a simple valley. Boundary-Layer Meteorology 52:41–68.

Ehleringer, J. R., A. E. Hall, and G. D. Farquhar. 1992. Stable isotopes and plant carbon-waster relations. Academic Press, San Diego, California, USA.

Ekblad, A., and P. Högberg. 2001. Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. Oecologia 127:305–308.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40: 503–537.

Farquhar, G. D., S. von Caemmerer, and J. A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. Planta 149:78–90.

Fessenden, J. E., and J. R. Ehleringer. 2002. Age-related variations in $\delta^{13}C$ of ecosystem respiration across a coniferous forest chronosequence in the Pacific Northwest. Tree Physiology 22:159–167.

Flanagan, L. B., J. R. Brooks, G. T. Varney, S. C. Berry, and J. A. Ehleringer. 1996. Carbon isotope discrimination during photosynthesis and the isotope ratio of respired CO_2 in boreal forest ecosystems. Global Biogeochemical Cycles 10: 629–640.

Flanagan, L. B., and J. A. Ehleringer. 1998. Ecosystem–atmosphere CO_2 exchange: interpreting signals of change using stable isotope ratios. Trends in Ecology and Evolution 13:10–14.

Fleagle, R. G. 1950. A theory of air drainage. Journal of Meteorology 7:227–232.

Fons, W. L. 1940. Influence of forest cover on wind velocity. Journal of Forestry 38:481–486.

Franklin, J. F., et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399–423.

Gray, A. N., and T. A. Spies. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. Journal of Ecology 84:635–645.

Harmon, M. E., K. Bible, M. G. Ryan, D. C. Shaw, H. Chen, J. Klopatek, and X. Li. 2004. Production, respiration, and overall carbon balance in an old-growth *Pseudotsuga-Tsuga* forest ecosystem. Ecosystems 7:498–512.

Hawkes, H. B. 1947. Mountain and valley winds with special reference to the diurnal mountain winds of the Great Salt Lake Region. Ohio State University, Columbus, Ohio, USA.

Iijima, Y., and M. Shinoda. 2000. Seasonal changes in the cold air pool formation in a subalpine hollow, central Japan. International Journal of Climatology 20:1471–1483.

Keeling, C. D. 1958. The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas. Geochimica et Cosmochimica Acta 13:322–334.

Keeling, C. D. 1961. The concentration and isotopic abundances of carbon dioxide in rural and marine air. Geochimica et Cosmochimica Acta 24:277–298.

King, C. W. 1989. Representativeness of single vertical wind profiles for determining volume flux in valleys. Journal of Applied Meteorology 28:463–466.

Klaassen, W., F. Bosveld, and E. deWater. 1998. Water storage and evaporation as constituents of rainfall interception. Journal of Hydrology 212–213:36–50.

Komatsu, H., N. Yoshida, H. Takizawa, I. Kosaka, C. Tantasirin, and M. Suzuki. 2003. Seasonal trend in the occurrence of nocturnal drainage flow on a forested slope under a tropical monsoon climate. Boundary-Layer Meteorology 106:573–592.

Landsberg, J. J., and G. B. James. 1971. Wind profiles in plant canopies: studies on an analytical model. Journal of Applied Ecology 8:729–741.

Lavigne, M. B., et al. 1997. Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. Journal of Geophysical Research 105:28977–28985.

Madhavan, S., I. Treichel, and M. H. O'Leary. 1991. Effects of relative humidity on carbon isotope fractionation in plants. Botanica Atca 104:292–294.

Magono, C., C. Nakamura, and Y. Yoshida. 1982. Nocturnal cooling of the Moshiri Basin, Hokkaido in midwinter. Journal of the Meteorological Society of Japan 60:1106–1116.

Mahrt, L. 1986. Nocturnal topoclimatology. WCP-117, World Meteorological Organization, Geneva, Switzerland.

Mahrt, L., and S. Larsen. 1982. Small scale drainage front. Tellus 34:579–587.

Mahrt, L., D. Vickers, R. Nakamura, M. R. Soler, J. Sun, S. Burns, and D. H. Lenschow. 2001. Shallow drainage flow. Boundary-Layer Meteorology 101:243–260.

Maki, M., and T. Harimaya. 1988. The effect of advection and accumulation of downslope cold air on nocturnal cooling in basins. Journal of the Meteorological Society of Japan 66: 581–597.

Manins, P. C., and B. L. Sawford. 1979. Katabatic winds: a field study. Quarterly Journal of the Meteorological Society 105:1011–1025.

McDowell, N. G., N. Phillips, C. Lunch, B. J. Bond, and M. G. Ryan. 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. Tree Physiology 22:763–774.

Monteith, J. L., and M. H. Unsworth. 1990. Principles of environmental physics. Second edition. Edward Arnold, New York, New York, USA.

Moore, G. W., B. J. Bond, J. A. Jones, N. Phillips, and F. C. Meinzer. 2004. Structural and compositional controls on transpiration in a 40- and 450-yr-old riparian forest in western Oregon, USA. Tree Physiology 24:481–491.

Mori, M., and T. Kobayashi. 1996. Dynamic interaction between observed nocturnal drainage winds and a cold air lake. Journal of the Meteorological Society of Japan 74: 247–258.

Parsons, E. A., P. W. Mote, A. Hamlet, N. Mantua, A. Snover, W. Keeton, E. Miles, D. Canning, and K. Gray Ideker. 2001. Potential consequences of climate variability and change for the Pacific Northwest. Pages 247–280 *in* N. A. S. Team, editor. Climate change impacts of the United States: the potential consequences of climate variability and change: foundation report. Cambridge University Press, New York, New York, USA.

Pataki, D. E., J. A. Ehleringer, L. B. Flanagan, D. Yakir, D. R. Bowling, C. Still, N. Buchmann, J. O. Kaplan, and J. A. Berry. 2003. The application and interpretation of Keeling plots in terrestrial carbon cycle research. Global Biogeochemical Cycles 17:1022.

Paw U, K. T., et al. 2004. Carbon dioxide exchange between an old-growth forest and the atmosphere. Ecosystems 7:513–524.

Phillips, N., B. J. Bond, N. G. McDowell, and M. G. Ryan. 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. Tree Physiology 22:205–211.

Ponton, S., L. B. Flanagan, K. Alstad, B. G. Johnson, K. Morgenstern, N. Kljun, T. A. Black, and A. G. Barr. 2006. Comparison of ecosystem water-use efficiency among Douglas-fir forest, aspen forest and grassland using eddy covariance and carbon isotope techniques. Global Change Biology 12:294–310.

Pypker, T. G., B. J. Bond, T. E. Link, D. Marks, and M. H. Unsworth. 2005. The importance of canopy structure in controlling the interception loss of rainfall: examples from a young and an old-growth Douglas-fir forest. Agricultural and Forest Meteorology 130:113–129.

Pypker, T. G., M. H. Unsworth, and B. J. Bond. 2006. The role of epiphytes in rainfall interception by forests in the Pacific Northwest. II. Field measurements at the branch and canopy scale. Canadian Journal of Forest Research 36:819–832.

Schimel, D. S., T. G. F. Kittel, S. W. Running, R. K. Monson, A. A. Turnipseed, and D. E. Anderson. 2002. Carbon sequestration studies in Western US mountains. EOS 83: 445–448.

Shaw, R. H. 1977. Secondary wind speed maxima inside plant canopies. Journal of Applied Meteorology 16:514–521.

Smith, C. M., and E. D. Skyllingstad. 2005. Numerical simulation of katabatic flow with changing slope angle. Monthly Weather Review 135:3065–3080.

Sokol, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. Third edition. Freeman, New York, New York, USA.

Soler, M. R., C. Infante, P. Buenestado, and L. Mahrt. 2002. Observations of nocturnal drainage flow in a shallow gully. Boundary-Layer Meteorology 105:253–273.

Staebler, R. M., and D. R. Fitzjarrald. 2004. Observing subcanopy CO_2 advection. Agricultural and Forest Meteorology 122:139–156.

Stull, R. B. 1988. An introduction to boundary layer meteorology. Kluwer Academic Publishers, Boston, Massachusetts, USA.

Swanson, F. J., and M. E. James. 1975. Geology and geomorphology of the H. J. Andrews Experimental Forest, Western Cascades, Oregon. Pacific Northwest Forest and Range Experiment Station, Forest Service, USDA Research Paper PNW-188:1–14.

Taylor, G. H., and C. Hannan. 1999. The climate of Oregon: from rainforest to desert. Oregon State University Press, Corvallis, Oregon, USA.

Tu, K. P., P. D. Brooks, and T. E. Dawson. 2001. Using septum-capped vials with continuous-flow isotope ratio mass spectrometeric analysis of atmospheric CO_2 for Keeling plot applications. Rapid Communications in Mass Spectrometry 15:952–956.

Turnipseed, A. A., D. E. Anderson, P. D. Blanken, W. M. Baugh, and R. K. Monson. 2003. Airflows and turbulent flux measurements in mountainous terrain. Part 1. Canopy and local effects. Agricultural and Forest Meteorology 119:1–21.

Wallace, J. M., and P. V. Hobbs. 1977. Atmospheric science: an introductory survey. Academic Press, New York, New York, USA.

Whiteman, C. D. 1986. Temperature inversion buildup in Colorado's Eagle Valley. Meteorology and Atmospheric Physics 35:220–226.

Whiteman, C. D. 1989. Morning transition tracer experiments in a deep narrow valley. Journal of Applied Meteorology 28: 626–635.

Whiteman, C. D. 1990. Observations of thermally developed wind systems in mountainous terrain. Pages 5–42 *in* W. Blumen, editor. Atmospheric processes over complex terrain. American Meteorological Society, Boston, Massachusetts, USA.

Whiteman, C. D., and J. C. Doran. 1993. The relationship between overlying synoptic-scale flows and winds within a valley. Journal of Applied Meteorology 32:1669–1682.

Yoshino, M. M. 1984. Thermal belt and cold air drainage on the mountain slope and cold air lake in the basin at quiet, clear night. GeoJournal 8.3:235–250.

Zobitz, J. M., J. P. Keener, H. Schnyder, and D. R. Bowling. 2006. Sensitivity analysis and quantification of uncertainty for isotopic mixing relationships in carbon cycle research. Agricultural and Forest Meteorology 136:56–75.

APPENDIX

Estimation of the net flux $(F_0 - F_i)_t$ of CO_2 in the valley cross-section below the tower top (*Ecological Archives* A017-029-A1).