

## Oxygen isotope content of CO<sub>2</sub> in nocturnal ecosystem respiration: 1. Observations in forests along a precipitation transect in Oregon, USA

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[1] The oxygen isotope content of nocturnal ecosystem respiration ( $\delta^{18}\text{O}_R$ ) was examined in forests along a precipitation gradient in Oregon, USA, to determine whether site-to-site variation in  $\delta^{18}\text{O}_R$  was more strongly related to variation in  $\delta^{18}\text{O}$  of precipitation or to evaporative processes that isotopically modify water pools within ecosystems. Measurements were made over 4 years at sites ranging in mean annual precipitation from 227 to 2760 mm. There was a gradient in the isotopic content ( $\delta^{18}\text{O}$ ) of precipitation, with inland sites receiving isotopically depleted precipitation (more negative  $\delta^{18}\text{O}$ ) relative to coastal sites. The  $\delta^{18}\text{O}$  of water in plant xylem generally followed the isotopic pattern of precipitation. Inland forests were drier than coastal forests, leading to a gradient in the vapor pressure deficit of air that caused isotopic enrichment of soil and leaf water. The enriched soil and leaf water pools influenced the isotopic composition of respired CO<sub>2</sub>, leading to variation in observed  $\delta^{18}\text{O}_R$  (Keeling-plot intercepts). Keeling plots with non-significant ( $p > 0.01$ ) regression slopes and those sampled over a time period ( $t$ ) greater than 5 hours yielded unacceptably high uncertainty in  $\delta^{18}\text{O}_R$ . The range of observed  $\delta^{18}\text{O}_R$  was 21.7 to 35.3‰ (VSMOW), with variation within a single site as large as 10.7‰ (range 24.2 to 34.9‰ at different sites). The results suggested a trend of more positive  $\delta^{18}\text{O}_R$  at inland sites relative to those nearer the coast, indicating that fractionation due to evaporative enrichment overshadowed the original isotopic composition of precipitation as a first order control on  $\delta^{18}\text{O}_R$ . **INDEX TERMS:** 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 0365 Atmospheric Composition and Structure: Troposphere—composition and chemistry; 1615 Global Change: Biogeochemical processes (4805); 1818 Hydrology: Evapotranspiration; **KEYWORDS:** carbon cycle, coniferous forest, OTTER, rainfall gradient,  $\delta^{18}\text{O}$

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### 1. Introduction

[2] Since the discovery of a latitudinal pattern in the oxygen isotopic composition ( $\delta^{18}\text{O}$ ) of atmospheric CO<sub>2</sub> [Francey and Tans, 1987], researchers have investigated the utility of oxygen isotopes as potential tracers of biosphere-atmosphere exchange. Oxygen isotopes of CO<sub>2</sub> have been

useful in global scale models to investigate the contributions of carbon uptake by photosynthesis and carbon release by respiration of terrestrial ecosystems [Ciais *et al.*, 1997a, 1997b; Peylin *et al.*, 1999; Cuntz *et al.*, 2003a, 2003b]. These large-scale models are based on an emerging understanding of the mechanisms by which biospheric processes influence  $\delta^{18}\text{O}$  of CO<sub>2</sub> in the atmosphere through net photosynthesis [Farquhar *et al.*, 1993; Flanagan *et al.*, 1994; Yakir *et al.*, 1994; Gillon and Yakir, 2000a, 2000b, 2001], and respiration by roots and heterotrophs in soils [Tans, 1998; Miller *et al.*, 1999; Stern *et al.*, 1999] or foliage [Bowling *et al.*, 2003].

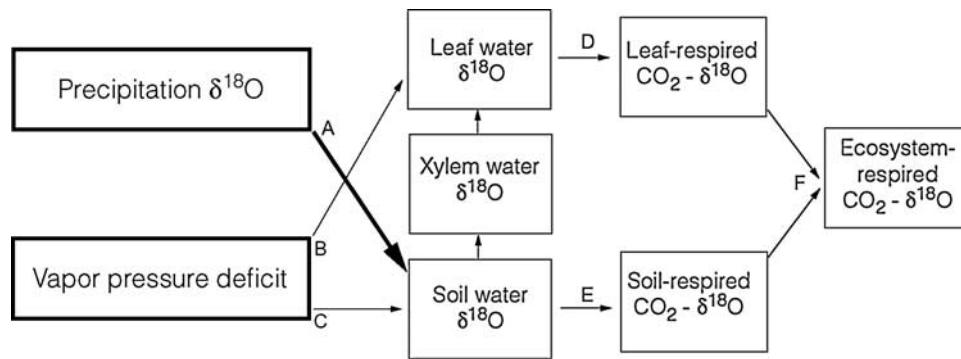
[3] Liquid water in soils and plant leaves imparts distinct stable oxygen isotope signatures to the CO<sub>2</sub> produced by soil and leaf respiration. Leaf water is enriched in oxygen-18 relative to water in stems or in soils due to transpiration [Dongmann *et al.*, 1974; Flanagan *et al.*, 1991; Wang and Yakir, 1995]. During the day, hydration of CO<sub>2</sub> in foliage,

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**Figure 1.** A conceptual diagram of the physical and biological factors influencing  $\delta^{18}\text{O}$  of respired  $\text{CO}_2$ . See text for details.

facilitated by carbonic anhydrase (CA), is followed by retro-diffusion of some  $\text{CO}_2$  molecules back out of the foliage, tending to enrich atmospheric  $\text{CO}_2$  in  $\delta^{18}\text{O}$  (more positive  $\delta^{18}\text{O}$ ) [Flanagan *et al.*, 1997; Buchmann *et al.*, 1997; Harwood *et al.*, 1999]. At night, respiratory  $\text{CO}_2$  within leaves also isotopically equilibrates with leaf water, and upon diffusion out of the leaves should enrich  $\delta^{18}\text{O}$  of  $\text{CO}_2$  within the canopy. Hydration of respiratory  $\text{CO}_2$  produced within soils (by roots or heterotrophs) equilibrates isotopically with soil water [Miller *et al.*, 1999], which is typically quite depleted (more negative  $\delta^{18}\text{O}$ ) relative to leaf water. Hence soil respiration tends to decrease  $\delta^{18}\text{O}$  of atmospheric  $\text{CO}_2$ . These opposing isotopic labels (isotopic enrichment of canopy air by foliar respiration and isotopic depletion by soil respiration) are potentially useful tracers of nocturnal foliar and soil respiratory fluxes, and provide an opportunity to investigate the contribution of each to total nocturnal ecosystem respiration.

[4] A conceptual diagram of the factors that influence  $\delta^{18}\text{O}$  of relevant ecosystem water pools (soil, xylem, and leaf water) and respired  $\text{CO}_2$  is shown in Figure 1. The isotopic content of precipitation initially controls  $\delta^{18}\text{O}$  of soil water (arrow A in Figure 1). Subsequent evaporation of water from the soil surface enriches  $\delta^{18}\text{O}$  of soil water, resulting in an isotopic gradient within the soil. Water is taken up by the roots and is transported through the xylem to the leaves without fractionation [White *et al.*, 1985; Dawson and Ehleringer, 1991], so the isotopic composition of stem water is determined by the isotope ratio of water in the soil in the zone of root uptake. This varies with species (due to differences in rooting depth) and the vertical gradient of moisture in the soil. Vapor pressure deficit (VPD) directly influences the isotopic content of leaf water through the process of evaporative enrichment during transpiration (arrow B in Figure 1) [Rodén and Ehleringer, 1999]. The  $\delta^{18}\text{O}$  of atmospheric water vapor and leaf temperature are other important factors controlling  $\delta^{18}\text{O}$  of leaf water [Flanagan *et al.*, 1991]. VPD also influences the degree of evaporative isotopic enrichment of  $\text{H}_2\text{O}$  in the soil profile (C), particularly near the surface [Allison *et al.*, 1983; Melayah *et al.*, 1996b]. At present, we are aware of no studies that have reported direct measurements of the  $\delta^{18}\text{O}$  content of leaf-respired  $\text{CO}_2$  at night. However, CA-catalyzed isotopic equilibration between  $\text{CO}_2$  inside the

leaf and leaf water influences the isotopic content of  $\text{CO}_2$  respired by the leaves (arrow D in Figure 1). Physical hydration between  $\text{CO}_2$  and water in the soil profile occurs, imparting an isotopic signature to soil-respired  $\text{CO}_2$  that reflects  $\delta^{18}\text{O}$  of soil water (arrow E in Figure 1). The  $\delta^{18}\text{O}$  of respiration by the leaves and by roots and heterotrophs in soil are both influenced by (1) a temperature-dependent equilibrium fractionation factor associated with the hydration reaction between  $\text{H}_2\text{O}$  and  $\text{CO}_2$  [Brenninkmeijer *et al.*, 1983] and (2) a kinetic isotopic fractionation factor associated with diffusion away from the site of respiration [Miller *et al.*, 1999].

[5] The potentially contrasting isotopic effects of precipitation and evaporation of water within terrestrial ecosystems on  $\delta^{18}\text{O}$  of ecosystem respiration are the principal focus of this study. The isotopic composition of precipitation at a site is the primary factor that initially controls  $\delta^{18}\text{O}$  of water in the soil, the xylem, and in the leaves. Thus  $\delta^{18}\text{O}$  of nocturnal ecosystem respiration should reflect the isotopic composition of precipitation to some degree. However, soil and leaf water pools will become isotopically enriched through evaporation and transpiration, especially under dry atmospheric conditions or long after a precipitation event or both. The degree to which such evaporative enrichment may influence  $\delta^{18}\text{O}$  of ecosystem respiration has not been established.

[6] The goal of our study was to examine  $\delta^{18}\text{O}$  of nocturnal ecosystem respiration in coniferous forests across a precipitation gradient, where the total annual amount and the isotopic composition of precipitation vary strongly, with a winter-wet summer-dry seasonal pattern of rainfall common to all sites. If  $\delta^{18}\text{O}$  of precipitation varies across the precipitation transect, then the isotopic composition of ecosystem respiration may vary similarly, being most positive at locations where  $\delta^{18}\text{O}$  of precipitation is most positive, and vice versa. Alternatively, if evaporative enrichment of leaf water and especially water in the soil profile occurs,  $\delta^{18}\text{O}_R$  may not even qualitatively reflect the initial isotopic pattern of precipitation. Because the use of Keeling plots with oxygen isotopes of  $\text{CO}_2$  is not well established, a necessary component of our study was to determine if and when the Keeling plot approach (described later) could be used to investigate these isotopic processes.

[7] A companion paper [Bowling *et al.*, 2003] focuses on short-term dynamics in  $\delta^{18}\text{O}_R$  (nightly measurements over

**Table 1.** Experimental Field Sites in the Present Study<sup>a</sup>

Site Code	Dominant Species	Location and Elevation	Distance From Pacific Coast, km	PRISM Modeled 30-Year Mean Precipitation, mm	Years Sampled	Site Reference
<i>Ecosystem Sampling Sites</i>						
A	<i>P. sitchensis</i> , <i>T. heterophylla</i>	45°03'N 123°57'W 240 m	<1	2760	1996, 1997	Gholz [1982], Harcombe et al. [1990], Peterson and Waring [1994] Bowling et al. [2002]
B	<i>P. sitchensis</i> , <i>T. heterophylla</i>	44°07'N 124°07'W 300 m	2	2129	2000, 2001	
C	<i>P. menziesii</i>	44°35'N 123°35'W 290 m	37	1892	2000, 2001	Bowling et al. [2002]
D	<i>P. menziesii</i>	44°36'N 123°16'W 310 m	68	1140	1996, 1997	Bond and Kavanaugh [1999]
E	<i>P. ponderosa</i>	44°30'N 121°37'W 941 m	200	523	1996, 1997 2000, 2001	Anthoni et al. [1999], Law et al. [1999a, 1999b]
F	<i>J. occidentalis</i>	44°18'N 121°20'W 930 m	223	227	1996, 1997 2000, 2001	Gholz [1982], Miller et al. [1992]
<i>Precipitation Sampling Sites</i>						
Alsea	NA	44°23'N 123°37'W 104 m	43	NA	1996, 1997, 2000	Welker [2000]
HJA	NA	44°13'N 122°15'W 436 m	151	NA	1996, 1997, 2000	Welker [2000]

<sup>a</sup>Sites and site codes correspond to work of Bowling et al. [2002] and differ from sites on the original Oregon transect. Site E is an AmeriFlux long-term CO<sub>2</sub> flux study site (Metolius Research Natural Area), and site F is near (but not identical to) the sites used by Gholz [1982] and Miller et al. [1992]. NA, not applicable.

two weeks) at one of the forests described in the present paper, with the goal of using  $\delta^{18}\text{O}$  analyses to quantify the soil and foliar components of total nocturnal ecosystem respiration.

## 2. Methods

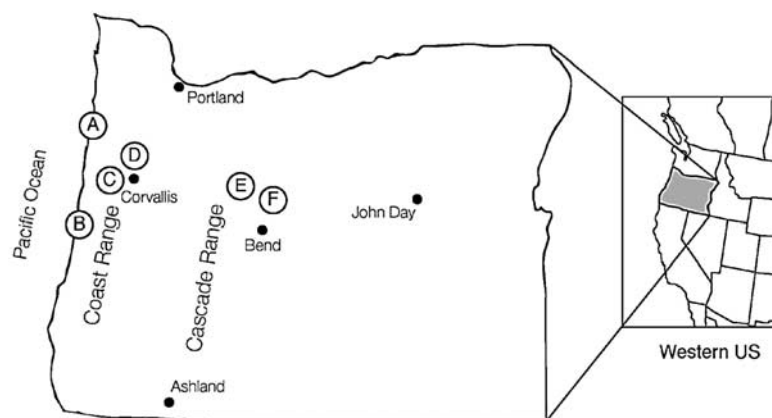
### 2.1. Study Sites

[8] This study was conducted during 1996, 1997, 2000, and 2001, along the Oregon Transect Ecosystem Research project (OTTER [Peterson and Waring, 1994]) in western Oregon, USA. The transect is associated with a substantial precipitation gradient. Total annual precipitation varies by nearly 3000 mm over 250 km, with the wettest sites on the Pacific coast and the driest sites located on the eastern side of the Cascade Mountains. Six study sites in coniferous forests were established along the transect, with mean annual precipitation varying from 227 to 2760 mm (Table 1 and Figure 2). These forests were dominated by *Picea sitchensis* and *Tsuga heterophylla* (mixed Sitka spruce and western

hemlock, sites A and B), *Pseudotsuga menziesii* (Douglas-fir, sites C and D), *Pinus ponderosa* (ponderosa pine, site E), and *Juniperus occidentalis* (western juniper, Site F). A few site details are shown in Table 1; more complete site details are given by Bowling et al. [2002]. Sites and site letter codes are consistent with those of Bowling et al. [2002] and differ from those on the original Oregon transect. Not all sites were sampled in all years (Table 1).

### 2.2. Air Sampling

[9] Air samples were collected at night from a variety of heights within and above the vegetation canopy in each forest, located at 0.2 or 0.8 m height, mid-canopy, and canopy top. Water vapor was chemically removed ( $\text{Mg}(\text{ClO}_4)_2$ ) during sample collection to avoid isotopic effects on  $\delta^{18}\text{O}$  of CO<sub>2</sub> [Gemery et al., 1996]. Samples were stored in glass flasks in the field and returned to the laboratory for analysis of  $\delta^{18}\text{O}$  and CO<sub>2</sub> mole fraction ( $[\text{CO}_2]$ ) following the methods of Bowling et al. [2002]. Samples for a particular sampling period were collected at a

**Figure 2.** Location of study sites in western Oregon.

single site during a single night over time periods varying from 0.7 to 10.2 hours. The number of flasks collected for a flask set averaged 16.1, with a range of 6 to 44 flasks per set. In all, 1258 flask samples were collected during 74 individual sampling periods. Our sampling strategy was designed to maximize the range of  $[\text{CO}_2]$  in the flasks during a single night, which has been shown to minimize the uncertainty in carbon isotope Keeling plot intercepts [Pataki *et al.*, 2003]. Of course, such a strategy often means sampling over an extended time period, which may violate the basic assumption necessary to use the Keeling plot approach for oxygen isotope analysis (described later). This is because the  $\delta^{18}\text{O}$  of leaf water will change as needles adjust from an environment with high VPD during the day to a lower VPD environment at night.

[10] Air samples were analyzed for isotopic content ( $\delta^{18}\text{O}$ ) of  $\text{CO}_2$  by continuous-flow isotope ratio spectrometry (CF-IRMS; details given by Bowling *et al.* [2002]). Precision for  $\delta^{18}\text{O}$  was determined daily by comparison to known standards and was typically 0.15 to 0.2‰. We report all  $\delta^{18}\text{O}$  values, for  $\text{CO}_2$  or  $\text{H}_2\text{O}$ , relative to the Vienna Standard Mean Ocean Water (VSMOW) scale [Coplen, 1996].  $[\text{CO}_2]$  in each flask sample was analyzed either during collection in the field (during 1996, 1997, 2000) or in the lab (2000, 2001) using infrared gas analysis as described by Bowling *et al.* [2001, 2002]. The precision of  $[\text{CO}_2]$  determination for the field measurements was  $1.0 \mu\text{mol mol}^{-1}$ , and for the lab measurements,  $0.3 \mu\text{mol mol}^{-1}$ .  $\text{CO}_2$  mole fraction is reported relative to World Meteorological Organization  $\text{CO}_2$  standards.

### 2.3. Keeling Plots

[11] The oxygen isotope ratio of whole-ecosystem respired  $\text{CO}_2$  ( $\delta^{18}\text{O}_R$ ) was determined as the intercept of a geometric mean regression of  $\delta^{18}\text{O}$  versus  $1/[\text{CO}_2]$  [Keeling, 1958]. Flasks from all heights that were sampled during a particular night were combined into a single Keeling plot. We report the uncertainty in  $\delta^{18}\text{O}_R$  as the standard error of the intercept. Outliers were removed on individual Keeling plots as described for carbon isotope Keeling plots by Bowling *et al.* [2002]. Seventy flask samples were determined to be outliers using this method (5.6% of the total). We examined the significance of the regression between  $\delta^{18}\text{O}$  and  $1/[\text{CO}_2]$  using the Student's t-distribution [Sokal and Rohlf, 1995].

### 2.4. Xylem, Spring, and Soil Water

[12] During 2000 and 2001 at sites B, C, E, and F, stem and soil samples were collected (typically at dawn) on the nights of air sampling. Stems were collected from live branches within reach of the ground at most sites or sampled with a shotgun (at site E where branches were inaccessible from the ground). Bark was removed. Stems were 5–10 mm in diameter and 5–7 cm long. Soil samples were collected from the top 10 cm of mineral soil at each site. A vertical face was excavated from the soil with a hand trowel, a 10-cm-tall column was isolated and removed, mixed within a dry plastic bag, and then subsampled. At site E, water samples were also collected from a spring flowing into the Metolius River roughly 2 km from the study site.

[13] Stem, soil, and spring water samples were stored in screw-cap glass vials covered with wax film and kept refrigerated or frozen until analysis. Water was extracted from stem and soil samples in the laboratory by cryogenic distillation under vacuum. The  $\delta^{18}\text{O}$  of water was determined by CF-IRMS [Fessenden *et al.*, 2002].

### 2.5. Meteorological Data

[14] Meteorological variables were measured at site E during all four sampling years as described by Anthoni *et al.* [1999]. During 2001, meteorological measurements were also made at sites B, C, and F. Measurements included air temperature and relative humidity at canopy top (HMP45A, Vaisala, Inc., Woburn, Massachusetts), soil temperature at 10 cm depth (Cu-Co thermocouples), soil moisture (CS615, Campbell Scientific, Inc., Logan, Utah), and precipitation (TR-525M-R2, Texas Electronics, Dallas, Texas). Sensors were sampled every 5 s, and data were stored as hourly averages. Although Bowling *et al.* [2002] compiled data from nearby climate stations in their carbon isotope analysis of the same sites, only meteorological data that were obtained on-site were used in the present study.

### 2.6. The $\delta^{18}\text{O}$ of Precipitation

[15] Collection of precipitation for isotopic analysis requires sophisticated collectors or frequent site visits to prevent isotopic fractionation due to evaporation. Since our primary study sites were remote, collection of robust isotope samples at each site was not logistically feasible. We present data collected at other sites in Oregon (Table 1) as part of the National Atmospheric Deposition Program [Welker, 2000]. Weekly precipitation samples were collected in 1996, 1997, and 2000 at the Alsea Guard Ranger Station and the H. J. Andrews Experimental Forest. These samples were stored at  $4^\circ\text{C}$  until  $\delta^{18}\text{O}$  determination using a water- $\text{CO}_2$  equilibration technique and CF-IRMS.

### 2.7. Modeling $\delta^{18}\text{O}$ of Leaf Water and Leaf- and Soil-Respired $\text{CO}_2$

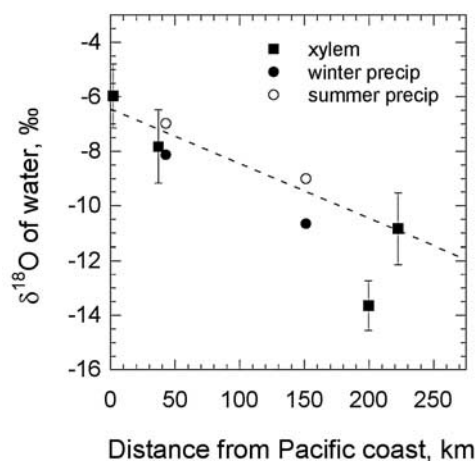
[16] A combination of measurements and modeling were used to determine theoretical upper and lower limits for the isotopic composition of  $\text{CO}_2$  respired from ecosystem components. The goal was not to calculate exactly what measured isotopic values should be, but instead to determine the range of  $\delta^{18}\text{O}_R$  across the Oregon transect that may result from site differences in precipitation, temperature, and humidity. For this purpose, mean climatic data measured during summer 2001 were used, with only nocturnal values used where appropriate.

[17] The Craig-Gordon model of evaporative enrichment [Craig and Gordon, 1965; Flanagan *et al.*, 1991] was used to model the isotopic composition of water in leaf tissue. This model predicts  $\delta^{18}\text{O}$  of leaf water based on four factors: (1)  $\delta^{18}\text{O}$  of xylem water, (2)  $\delta^{18}\text{O}$  of atmospheric water vapor, (3) relative humidity, and (4) leaf temperature. Mean summertime values for relative humidity and air temperature were used (days 150–250). We assumed that leaf temperature was identical to air temperature [Jarvis and McNaughton, 1986; Martin *et al.*, 1999], and we neglected leaf boundary layer conductance as described by Flanagan

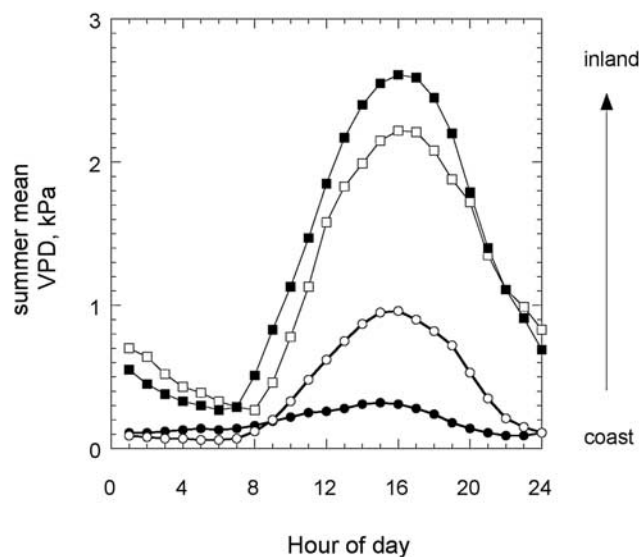
*et al.* [1997]. We used the mean of all observations for  $\delta^{18}\text{O}$  of xylem water, and estimated  $\delta^{18}\text{O}$  of atmospheric water vapor by assuming isotopic equilibrium with xylem water at the mean summer temperature. The validity of this assumption is not well-established, but collection of water vapor for isotopic analysis at remote field sites is labor intensive, and can take several hours under low humidity conditions. The equations of *Majoube* [1971] were used to compute the temperature dependent fractionation factor for water liquid-vapor equilibrium.

[18] Modeled values for  $\delta^{18}\text{O}$  of leaf water were used to compute  $\delta^{18}\text{O}$  of leaf-respired  $\text{CO}_2$  by applying a temperature-dependent fractionation factor for  $\text{CO}_2\text{-H}_2\text{O}$  equilibrium [*Brenninkmeijer et al.*, 1983] and assuming an additional diffusive fractionation of 8.8‰ as  $\text{CO}_2$  diffuses from the leaf. We do not know if this 8.8‰ fractionation is fully expressed for  $\delta^{18}\text{O}$  of leaf respired  $\text{CO}_2$  nor do we know how established variations in carbonic anhydrase activity among plants [*Gillon and Yakir*, 2001] might alter  $\delta^{18}\text{O}$  of leaf-respired  $\text{CO}_2$ . However, conifers in general have high equilibrium between  $\text{CO}_2$  and water in plant leaves [*Gillon and Yakir*, 2001].

[19] Measured  $\delta^{18}\text{O}$  of soil water was used in the same fashion (using measured soil temperature and also applying a diffusive fractionation factor of 8.8‰) to compute  $\delta^{18}\text{O}$  of soil-respired  $\text{CO}_2$ . The exact value of the appropriate diffusive fractionation factor in the soil is not well-known, and is likely to differ with soil physical and biological



**Figure 3.** The  $\delta^{18}\text{O}$  of precipitation (weighted by precipitation amount) and xylem water across the Oregon transect. Precipitation samples were collected in 1996, 1997, and 2000 at Alsea Guard Ranger Station and H. J. Andrews Experimental Forest, and are separated into summer (days 150–250, solid circles) and winter (all other days, open circles) periods. Xylem water (squares) was collected during 2000 and 2001 at sites B, C, E, and F, and data are presented as means and standard deviations ( $n = 9$  to 13). The dashed line is a regression through the xylem values for all sites except site E, which has access to a groundwater source that is recharged from high elevation moisture.



**Figure 4.** Diel pattern of mean vapor pressure deficit (VPD) of air during summer 2001 (days 150–250) measured at sites B (solid circles), C (open circles), E (open squares), and F (solid squares).

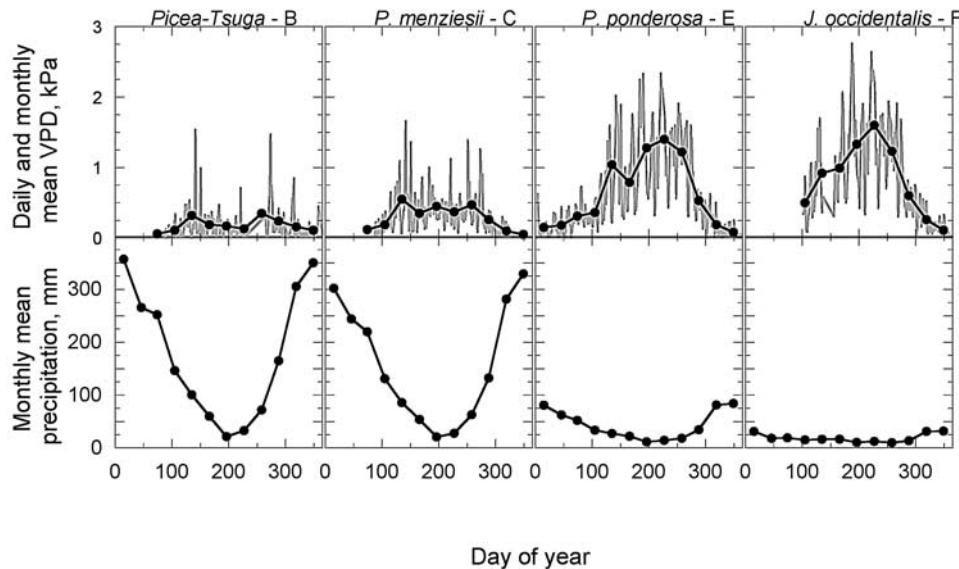
properties across our sites [*Miller et al.*, 1999]. We chose to treat all sites identically, sampling soil water at identical depths and applying the same fractionation factors to all sites.

### 3. Results and Discussion

#### 3.1. Precipitation and Humidity Patterns

[20] The isotopic composition of precipitation across the Oregon transect is shown in Figure 3. These data conform to the well-established pattern called the continental effect, where  $\delta^{18}\text{O}$  of precipitation generally becomes depleted in  $^{18}\text{O}$  (more negative  $\delta^{18}\text{O}$ ) as storms move inland and isotopically heavier precipitation falls first [*Rozanski et al.*, 1993]. “Distance from coast” is often used as an index of the continental pattern of  $\delta^{18}\text{O}$  of precipitation [e.g., *Rozanski et al.*, 1993], and we present our data in a similar fashion where relevant. In general, precipitation was more enriched in  $^{18}\text{O}$  at the coast and became depleted farther inland, with an average isotopic gradient of  $-2\text{‰}$  per 100 km. The strength of the isotopic gradient in Oregon is larger than has been observed on transects across Eurasia and South America ( $-0.2$  to  $-0.3\text{‰}$  per 100 km). This is likely due to the additional influence of elevational changes as storms cross the Coast and Cascade mountain ranges in western Oregon [*Welker*, 2000]. The  $\delta^{18}\text{O}$  values of precipitation were more depleted in the winter than in the summer at all sites (Figure 3), which is commonly observed due to seasonal changes in ocean and air temperatures [*Gat*, 1996].

[21] The mean summertime (days 150–250) diel pattern of vapor pressure deficit of air is shown in Figure 4. There was a strong gradient in VPD across the transect that persisted through the summer, with inland sites showing considerably higher diel amplitudes and peak values. The daily (24 hours) and monthly mean VPD patterns at these



**Figure 5.** (top) Seasonal pattern of mean vapor pressure deficit of air during 2001, where shaded lines are 24-hour means and solid circles are monthly means and (bottom) the long-term mean monthly precipitation at each site (monthly averages). Precipitation data were generated for each site using the PRISM model [Daly *et al.*, 1994, 1997] as described by Bowling *et al.* [2002]. Sites are arranged in order of increasing distance from the coast (left to right, with the coastal sites on the left) in this and Figures 6 and 11.

sites are shown in Figure 5, arranged left to right from the coast for consistency with the precipitation patterns in Figure 3. The passage of cool storm fronts (low VPD) and periods of hot dry weather (high VPD) across western Oregon was apparent, with consistent troughs and peaks observed at all sites (Figure 5, top panels). Daily mean VPD was high inland and approached 3 kPa at site F (*J. occidentalis*), with hourly observations peaking near 5 kPa (not shown). The long-term monthly mean precipitation at each site (Figure 5, bottom panels) shows the distinct wet winter and dry summer pattern characteristic of western Oregon [Waring and Franklin, 1979; Taylor and Hannan, 1999]. Periods of minimal summer rain coincide with maximum VPD (high evaporation potential), leading to the possibility of substantial evaporative isotopic enrichment of soil and leaf water pools in the summer. Thus the isotopic composition of precipitation was depleted (more negative  $\delta^{18}\text{O}$ ) at the inland forests, contrasting with greater potential for evaporative enrichment at inland sites (leading to more positive  $\delta^{18}\text{O}$ ). The degree to which these contrasting isotopic effects are transferred to respired  $\text{CO}_2$  was the primary subject of our study.

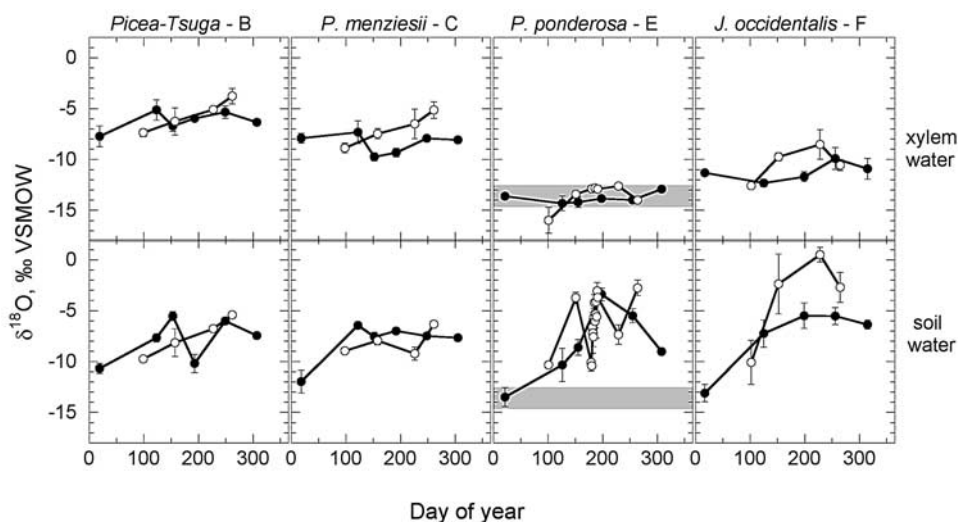
### 3.2. The $\delta^{18}\text{O}$ of Xylem and Soil Water

[22] In general, the isotopic composition of xylem water followed the pattern of  $\delta^{18}\text{O}$  of precipitation (Figure 3), with more enriched xylem water at coastal sites. Temporal patterns in  $\delta^{18}\text{O}$  of xylem and soil water are shown in Figure 6. All sites showed some degree of seasonal variation. The  $\delta^{18}\text{O}$  of xylem water varied within a season at a single site by 1.4 (site E, *P. ponderosa*, 2000) to 4.1‰ (site F, *J. occidentalis*, 2001). There was a general

pattern of more enriched xylem water during 2001 (relative to 2000) at the inland sites (sites E and F, Figure 6), but clear year-to-year trends were not apparent at the coastal sites.

[23] The  $\delta^{18}\text{O}$  of xylem water at site E was considerably more depleted ( $-13.7\text{‰}$ ) than expected based on its distance from the coast ( $-10.4\text{‰}$ , dashed line in Figure 3). *Pinus ponderosa* at this site has access to deep soil moisture [Anthoni *et al.*, 1999; Irvine *et al.*, 2002] which may be recharged by snowmelt from upper elevation watersheds [Dutton *et al.*, 2002]. The presence of deep soil moisture is a strong control on respiratory activity in the soil at site E [Irvine and Law, 2002]. Xylem water at site E was isotopically indistinguishable from water in a nearby spring (Figure 6) and the Metolius River (data not shown). James *et al.* [2000] have argued that the Metolius River is recharged from a high elevation mountain basin (roughly 2100 m inferred recharge elevation compared to the site E elevation of 941 m). Thus the altitudinal influence on  $\delta^{18}\text{O}$  of precipitation in the recharge basin is a likely cause of the unusually depleted  $\delta^{18}\text{O}$  of xylem water at site E relative to other sites across the Oregon transect.

[24] Soil and xylem water at the inland sites were more enriched in 2001 (Figure 6), despite the fact that these sites received almost twice as much summer rainfall in 2001 compared to 2000 [Irvine and Law, 2002]. This apparent contradiction is resolved for site E if water in the rooting zone is primarily recharged by winter precipitation. The larger enrichment in xylem water at site F during 2001 may reflect some uptake of summer rain by *Juniperus occidentalis* trees, although *J. osteosperma* makes limited use of summer rains in Utah [Flanagan *et al.*, 1992;



**Figure 6.** Seasonal pattern of  $\delta^{18}\text{O}$  measured in (top) xylem water and (bottom) soil water (0–10 cm depth) during 2000 (solid circles) and 2001 (open circles). The shaded bar on plots for site E shows the range of  $\delta^{18}\text{O}$  measured in spring water collected near the site (–12.5 to –14.7‰).

Donovan and Ehleringer, 1994]. Alternatively, hydraulic redistribution of summer rains by the shrubs *Artemisia tridentata* [Caldwell et al., 1998] or *Purshia tridentata* at site F may influence the  $\delta^{18}\text{O}$  of *J. occidentalis* xylem water, or water at substantial rooting depth (many tens of centimeters) could be enriched in  $^{18}\text{O}$  by soil evaporation [Hsieh et al., 1998].

[25] The isotopic composition of soil water in the top 10 cm showed more variability than stem water (Figure 6), and did not generally follow the isotopic pattern of precipitation across the transect. Variation in  $\delta^{18}\text{O}$  as large as 10.7‰ was observed within a season at site F (*J. occidentalis*), with highly enriched values during summer drought. During 13 rain-free days in summer 2001,  $\delta^{18}\text{O}$  of soil water at site E (*P. ponderosa*) varied from –10.4 to –3.1‰ in response to hot dry weather (Figure 6) [see also Bowling et al., 2003; McDowell et al., 2003].

[26] The dynamic nature of the isotopic composition of xylem and particularly soil water should result in considerable variability in  $\delta^{18}\text{O}$  of ecosystem respiration across the Oregon transect. Further, even if  $\delta^{18}\text{O}$  of xylem water remained constant,  $\delta^{18}\text{O}$  of leaf water and leaf respiration should respond to changes in atmospheric moisture through the process of evaporative enrichment of leaf water.

### 3.3. Evaluation of Keeling Plots for Use With $\delta^{18}\text{O}$ of Ecosystem Respiration

[27] In a now-classic paper, Keeling [1958] presented a two-ended graphical isotopic mixing model to interpret the isotopic signature of  $\text{CO}_2$  produced by ecosystem respiration. The model has been used extensively to interpret the carbon isotopic content of nocturnal ecosystem respiration and considerable insight about ecosystem carbon cycling is emerging from its use [Lancaster, 1990; Flanagan et al., 1996; Bowling et al., 2002; Ometto et al., 2002; Pataki et al., 2003]. Although Keeling’s original paper did not

advocate the use of the model for  $\delta^{18}\text{O}$  of nocturnal ecosystem respiration ( $\delta^{18}\text{O}_R$ ), several recent studies have applied it in this context [Yakir and Wang, 1996; Buchmann et al., 1997; Buchmann and Ehleringer, 1998; Flanagan et al., 1997, 1999; Harwood et al., 1999; Bowling et al., 1999; Mortazavi and Chanton, 2002; J. P. Ometto et al., Oxygen isotope ratios of waters and respired  $\text{CO}_2$  in Amazonian forest and pasture ecosystem, submitted to Ecological Applications, 2003]. However, this approach should be used with caution for reasons that are discussed below.

[28] The Keeling approach assumes that a forest with some initial background  $\text{CO}_2$  mole fraction  $C_b$  and isotopic composition  $\delta_b$  experiences an increase in  $[\text{CO}_2]$  due to nocturnal respiration by all ecosystem components. Conservation of mass requires that any measured mole fraction  $C_m$  will be composed of a contribution from the initial background  $\text{CO}_2$  present ( $C_b$ ) and the  $\text{CO}_2$  added by respiration ( $C_R$ ),

$$C_m = C_b + C_R. \quad (1)$$

Each of these quantities has an associated isotope ratio so that

$$\delta_m C_m = \delta_b C_b + \delta_R C_R, \quad (2)$$

and combining these equations yields

$$\delta_m = C_b(\delta_b - \delta_R)/C_m + \delta_R. \quad (3)$$

Equation (3) is the basis for a Keeling plot, in which the measured quantities  $\delta_m$  and  $1/C_m$  are regressed to obtain the y-intercept  $\delta_R$ , which is the isotopic composition of the  $\text{CO}_2$  that was added by respiration. A potential problem of the Keeling method is that the intercept is obtained by extrapolation some distance away from the region of the plot which is well-constrained by measurements. An

alternative mathematical form based on the same physical principles has recently been proposed [Miller and Tans, 2003] which may alleviate this concern.

[29] The Keeling plot approach is based on a two-component mixing model, and its application assumes a priori that either (1) all isotopic variation in the ecosystem air samples comes from a respiratory source with a single isotopic composition,  $\delta_R$ , or (2) that the relative contributions of component fluxes that might differ in isotopic composition (such as foliar and soil respiration) do not change over the time in which the Keeling plot is constructed. The first assumption is unlikely in an ecosystem context [e.g., Miller and Tans, 2003], but the second is usually satisfied for carbon isotopes of ecosystem respiration. The situation is more complex for oxygen isotopes. Expanding equations (1) and (2) to allow for contributions from the soil and foliar respiratory fluxes,

$$C_m = C_b + C_{\text{foliage}} + C_{\text{soil}} \quad (4)$$

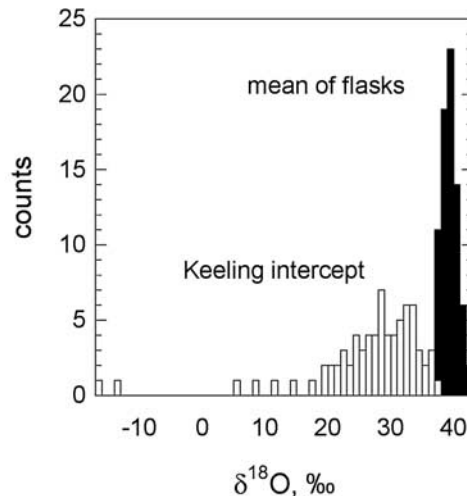
$$\delta_m C_m = \delta_b C_b + \delta_{\text{foliage}} C_{\text{foliage}} + \delta_{\text{soil}} C_{\text{soil}}, \quad (5)$$

where  $\delta_{\text{foliage}}$  and  $\delta_{\text{soil}}$  represent the oxygen isotope ratios of the foliar and soil fluxes. (Note that these equations could alternatively be expressed based on fluxes rather than mole fractions.) To satisfy the assumptions of the Keeling plot approach for this system, the right-hand sides of equations (2) and (5) must be equal, which occurs only when

$$\delta_R = (\delta_{\text{foliage}} C_{\text{foliage}} + \delta_{\text{soil}} C_{\text{soil}}) / C_R = \text{constant}. \quad (6)$$

If the relative contributions of the foliar and soil respiratory fluxes (i.e.,  $C_{\text{foliage}}/C_R$  and  $C_{\text{soil}}/C_R$ ) to total ecosystem respiration do not change, then  $\delta_R$  may remain constant even if  $\delta_{\text{foliage}}$  and  $\delta_{\text{soil}}$  differ by a large amount. Even within a single night,  $\delta_{\text{soil}}$  and particularly  $\delta_{\text{foliage}}$  vary over time, since soil and leaf temperatures and  $\delta^{18}\text{O}$  of leaf water vary over the course of a night [Bowling *et al.*, 2003]. Any analysis (such as ours) which combines flasks collected at different heights, potentially influenced by different biota with different temporal dynamics, should proceed cautiously. We did not generally collect enough flasks at each height to robustly examine height variation in isotopic content or height effects on Keeling plot intercept. However, if the flask sampling for a Keeling plot can be accomplished quickly relative to the change in isotopic signatures of the fluxes, then the variation in both  $\delta_{\text{soil}}$  and  $\delta_{\text{foliage}}$  will be minimized. Bowling *et al.* [2003] examined the nightly temporal variation in these quantities at site E during flask sampling, and showed that isotopic variation of each could be constrained to a few ‰, much smaller than the isotopic difference in the two fluxes. Hence there are periods when the assumption of constant isotopic signatures for  $\delta^{18}\text{O}$  of respired  $\text{CO}_2$  from ecosystem components is valid, and the use of Keeling plots will yield useful biological information. Bowling *et al.* [2003] present a detailed analysis of the variation in nightly  $\delta_{\text{foliage}}$  and  $\delta_{\text{soil}}$  over a 2-week period.

[30] The Keeling analysis predicts a linear relationship between  $\delta^{18}\text{O}$  of atmospheric  $\text{CO}_2$  and  $1/C_m$ , which pro-

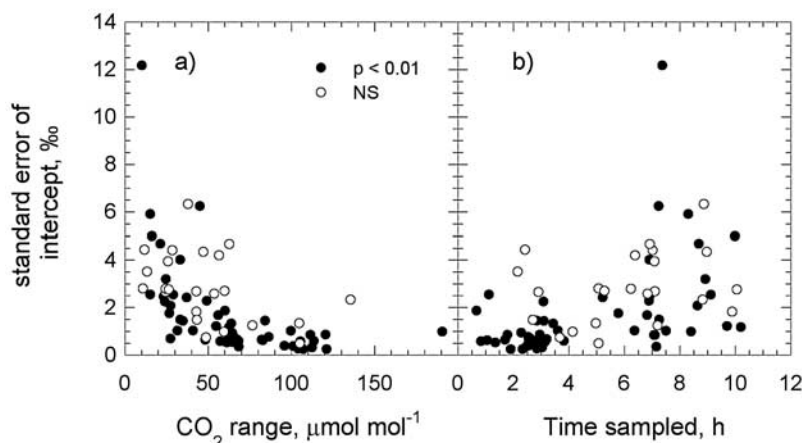


**Figure 7.** Frequency histograms of  $\delta^{18}\text{O}$  of ecosystem respiration derived from Keeling plots ( $\delta^{18}\text{O}_R$ , open bars), and the mean  $\delta^{18}\text{O}$  values of atmospheric  $\text{CO}_2$  (solid bars) of all the flasks in a particular flask set. Bins are 1‰ wide.

vides an opportunity for an empirical test of the robustness of the Keeling plot in a particular instance. If a linear relationship is not apparent, then equation (3) does not adequately describe the system. Flanagan *et al.* [1997] used the statistical significance of the Keeling regression to determine when  $\delta^{18}\text{O}_R$  values obtained from Keeling plots could be viewed as legitimate. If a significant regression was not obtained, the mean  $\delta^{18}\text{O}$  of the flasks (rather than the Keeling plot intercept) was used as a substitute measure of  $\delta^{18}\text{O}_R$ . Frequency distributions of  $\delta^{18}\text{O}_R$  and mean  $\delta^{18}\text{O}$  from the present study are shown in Figure 7. In all cases, the mean  $\delta^{18}\text{O}$  was more enriched than the respective Keeling plot intercept, by as much as 17.0‰. The average difference (mean  $\delta^{18}\text{O}$  in a flask set minus the Keeling plot intercept of that flask set) was  $12.8 \pm 9.0$ ‰ (mean  $\pm$  SD,  $n = 74$ ). This is not surprising since mixing of ecosystem-respired  $\text{CO}_2$  (which typically has a  $\delta^{18}\text{O}$  content  $\delta_R$  of 20–35‰ as we will show later) with background air (typically  $\delta_b \approx 40$ ‰) generally provides a positive slope on a Keeling plot [Bowling *et al.*, 2003]. The intercept of such a relationship ( $\delta^{18}\text{O}_R$ ) is almost certain to be more negative than the average of the measured flasks since the intercept is distant from the measurements.

[31] Pataki *et al.* [2003] showed that, for carbon isotope Keeling plots, the uncertainty in the isotopic composition of respired  $\text{CO}_2$  (which is the standard error of the intercept) is inversely related to the range of  $[\text{CO}_2]$  obtained in the flask samples used to construct the plot. The same is true for Keeling plots used to examine the oxygen isotope content of atmospheric  $\text{CO}_2$  (Figure 8a). In general, to determine  $\delta^{18}\text{O}_R$  with an uncertainty less than 2‰, a  $\text{CO}_2$  range of  $75 \mu\text{mol mol}^{-1}$  is required, even for Keeling plots with highly significant regressions (Figure 8a). However, the time required to collect air samples in order to construct a Keeling plot is very important. Since  $\delta_{\text{soil}}$  and  $\delta_{\text{foliage}}$  vary with time during a single night [Bowling *et al.*, 2003], longer sampling periods are associated with more variability





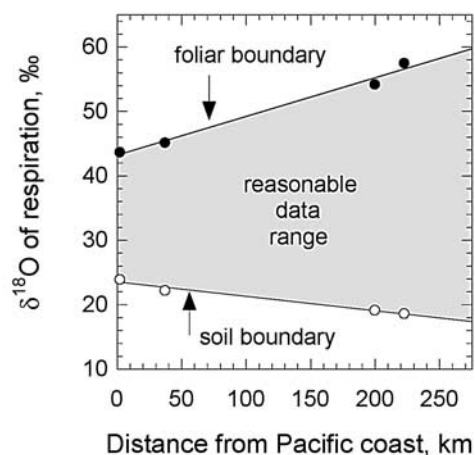
**Figure 8.** Standard error of the Keeling intercept versus (a) the  $\text{CO}_2$  range in flask sets and (b) the sampling time over which flasks were collected for each Keeling plot. Data are shown separately for those Keeling plots which were associated with significant ( $p < 0.01$ , Student's t-test, solid circles) and non-significant (NS, open circles) regressions.

in the isotopic composition of the foliar and soil respiratory fluxes. This variability is in essence a violation of the assumptions on which a Keeling plot is based (discussed above). Minimizing the sampling time is a potentially useful way to minimize the degree to which Keeling-plot assumptions are violated. However, shorter sampling times are generally associated with smaller ranges in  $[\text{CO}_2]$  which lead to greater uncertainty in  $\delta^{18}\text{O}_R$  (Figure 8b), an important tradeoff.

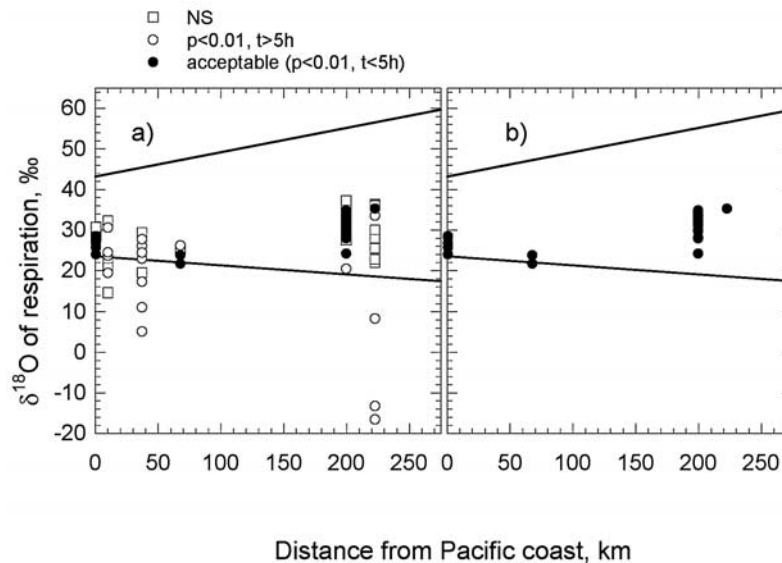
### 3.4. The $\delta^{18}\text{O}$ of Ecosystem Respiration

[32] We can take advantage of our understanding of the factors that influence  $\delta^{18}\text{O}$  in respiratory fluxes to help determine whether or not a Keeling plot can provide a useful estimate of  $\delta^{18}\text{O}_R$ . Several studies have focused on the mechanistic details of leaf water enrichment through transpiration [Flanagan *et al.*, 1991; Wang and Yakir, 1995; Wang *et al.*, 1998; Roden and Ehleringer, 1999; Helliker and Ehleringer, 2000], photosynthetic discrimination against  $\text{C}^{18}\text{O}^{16}\text{O}$  [Farquhar *et al.*, 1993; Flanagan *et al.*, 1994; Yakir *et al.*, 1994; Gillon and Yakir, 2000a, 2000b, 2001], soil water enrichment through evaporation [Barnes and Allison, 1983; Mathieu and Bariac, 1996; Melayah *et al.*, 1996a], and the processes by which soil-respired  $\text{CO}_2$  is isotopically altered by interactions with soil water [Amundson *et al.*, 1998; Tans, 1998; Miller *et al.*, 1999; Stern *et al.*, 2001]. While many of these processes are now well understood and can be fairly accurately modeled, such models required detailed accompanying measurements which were impossible to obtain at all of our sites for all sampling periods.

[33] Here we use our available measurements to loosely constrain measured  $\delta^{18}\text{O}_R$  values. On the basis of the observations of  $\delta^{18}\text{O}$  of xylem and soil water in Figure 6, and measured VPD (Figure 4), air, and soil temperature (not shown), we modeled the isotopic composition of the foliar and soil-respired fluxes at four sites across the Oregon transect (Figure 9). These modeled signatures are not likely



**Figure 9.** Theoretical bounds for  $\delta^{18}\text{O}$  of  $\text{CO}_2$  produced by respiration across the Oregon transect. The upper line represents the maximum reasonable values for  $\delta^{18}\text{O}$  of foliar respiration, and the lower line represents the minimum reasonable values for  $\delta^{18}\text{O}$  of soil respiration. The range is narrower at the wetter end of the transect (near the coast) because atmospheric humidity and temperature are restricted to narrower ranges. Sites at the drier end of the transect experience larger variation in precipitation  $\delta^{18}\text{O}$ , temperature, and humidity. Data points are not measured; they are based on modeling and observations (air and soil temperatures, humidity, and  $\delta^{18}\text{O}$  of xylem and soil water) at four sites as described in the text. Boundary lines are simply regressions through the modeled data points, and should be interpreted as rough estimates of the theoretical bounds for  $\delta^{18}\text{O}$  of ecosystem respiration. Legitimate Keeling plot intercepts ( $\delta^{18}\text{O}_R$ ) should fall within these bounds. Regression lines are  $y = 0.0601x + 43.217$ ,  $r^2 = 0.985$  (foliar boundary) and  $y = -0.0224x + 23.556$ ,  $r^2 = 0.976$  (soil boundary).



**Figure 10.** The  $\delta^{18}\text{O}$  of ecosystem respiration (Keeling plot intercepts) versus distance from the coast across the Oregon transect. The theoretical boundaries of Figure 9 are shown for comparison (lines). (a) All data ( $n = 74$ ), separated into acceptable data (solid circles), data with nonsignificant (NS, open squares) regressions, and data with significant regressions that did not meet the 5-hour sampling minimum (open circles). (b) “Acceptable” data based on two criteria, (1) a significant linear relationship ( $p < 0.01$ ) and (2) sampling completed in less than 5 hours. Acceptable data were obtained at only four of the six sites (A, D, E, and F). Site B is shown offset to the right from site A for clarity.

to be exactly correct for any given site at any given time. However, they provide a broad and conservative set of constraints with which to evaluate the Keeling plot data, and as we will show, some Keeling plot data do not conform to these broad expectations. A detailed comparison between modeled isotopic signatures and measurements at site E (*P. ponderosa*) during an intensive study period is provided in the companion paper [Bowling *et al.*, 2003].

[34] Generally, the modeled  $\delta^{18}\text{O}$  of foliar respiration was more enriched at inland sites (points on upper line in Figure 9) due to the strong influence of summertime evaporative enrichment of leaf water. In contrast, the modeled soil-respired  $\delta^{18}\text{O}$  signature decreased slightly at inland sites (points on lower line, Figure 9). The minimum (most negative) observed values for  $\delta^{18}\text{O}$  in soil water (Figure 6) were used to construct the soil line in Figure 9, and those were sampled in winter (Figure 6). Had summertime means or maxima been used instead, the modeled soil line would move upward by 5–12‰, and would be a bit more positive at inland sites relative to the coast. These boundaries represent the maximally isotopically enriched (upper line) and maximally depleted (lower line)  $\delta^{18}\text{O}$  of nocturnal respiratory fluxes based on all measurements of  $\delta^{18}\text{O}$  of xylem and soil water made in the present study. To conform to our mechanistic understanding of oxygen isotope effects associated with leaf and soil respiration and associated physical processes, any measured  $\delta^{18}\text{O}$  of ecosystem respiration must fall in the region between these lines.

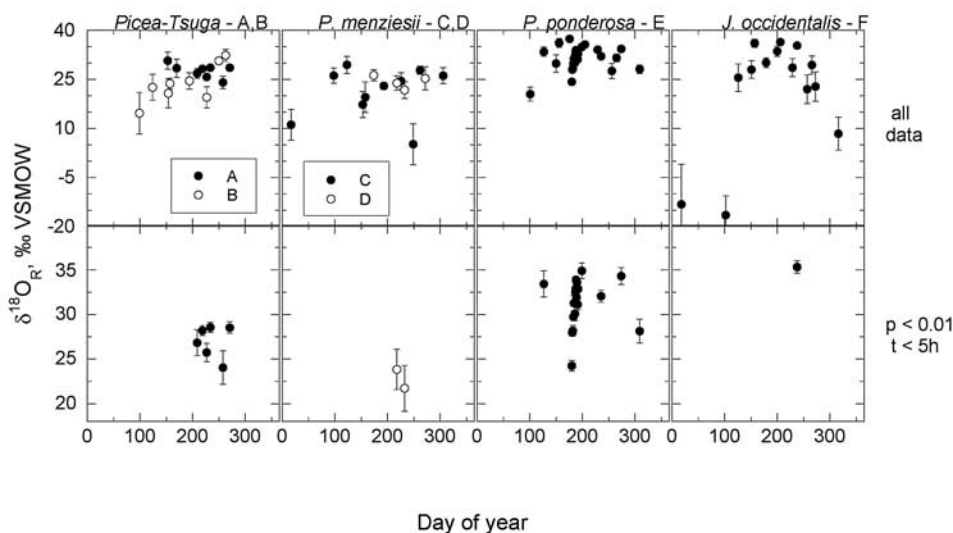
[35] Keeling plot intercepts from our six sites across the Oregon transect are shown in Figure 10. In 12 out of 74 cases, Keeling plot intercepts did not fit within the expected range. Keeling plots that were associated with

both significant ( $p < 0.01$ ) and nonsignificant (NS) regressions were found within the theoretical bounds. Replacement of NS points with the flask mean, as advocated by Flanagan *et al.* [1997], would move the squares in Figure 10a in the more positive direction by 12.8‰ on average (Figure 7), a fairly large shift compared to the observed variation (Figure 10). It is unclear that the use of either the mean or the intercept in the case of a NS regression will provide biologically useful information. We feel that mean replacement may artificially bias the estimates of  $\delta^{18}\text{O}_R$  and recommend instead that those data sets with NS regressions be rejected (or at least used with caution).

[36] Not surprisingly, the majority of points that fell outside the expected range were sampled over time periods greater than 5 hours (Figure 10a), and those points which were farthest outside the boundaries were in this category. These data clearly illustrate that sampling times must be minimized when attempting to determine  $\delta^{18}\text{O}_R$  via Keeling plots. Our samples were primarily collected for analysis of carbon isotope ratios in ecosystem respiration [Bowling *et al.*, 2002] where the sampling time does not appear to be an important constraint [Pataki *et al.*, 2003].

[37] Data in the present study were deemed “acceptable” if they were associated with (1) significant regressions (a cutoff of  $p < 0.01$  was used to define significance), and (2) sampling periods less than 5 hours. Acceptable data are plotted in Figure 10b, and generally fall within the theoretical boundaries.

[38] Our study describes the largest data set presently available with which to evaluate the validity of Keeling plots in determining the oxygen isotope ratio of nocturnal ecosystem respired  $\text{CO}_2$ . While our two acceptability crite-



**Figure 11.** The  $\delta^{18}\text{O}$  of ecosystem respiration plotted versus day of year at six sites. Sites A and B, and C and D, are combined in the left-most panels. Each datum represents flasks collected during a single night, during 1996, 1997, 2000, or 2001 ( $n = 74$  flask sets total). The top panels show all data ( $n = 74$ ); the bottom panels show only acceptable data as described in Figure 10 and the text. The scales of the  $y$  axes differ in the top and bottom panels.

ria are arbitrary, there are several reasons to adopt them (or similar ones) as a general guide to determine data quality. First, it makes no sense to try to interpret an intercept from a nonsignificant regression relationship. Second, the regression cutoff of  $p < 0.01$  was selected based on a comparison with coefficients of determination ( $r^2$ ) for the  $\delta^{18}\text{O}$  versus  $1/[\text{CO}_2]$  regressions (data not shown), which showed moderate improvement in  $r^2$  over cutoffs of  $p < 0.05$  or  $0.1$ . We elected to use the more stringent statistical test of  $p < 0.01$ . On average,  $r^2$  for the acceptable data was  $0.86 \pm 0.17$  (mean  $\pm$  SD,  $n = 28$ ) and  $0.44 \pm 0.30$  for the unacceptable data ( $n = 46$ ). Third,  $\delta_{\text{soil}}$  and  $\delta_{\text{foliage}}$  will change over time within a single night [Bowling *et al.*, 2003], so sampling periods of several hours or more involve non-static isotopic conditions in respiratory fluxes and lead to a violation of the single-source (or mixed source) assumption of the Keeling plot. Fourth, we also calculated  $\delta^{18}\text{O}_R$  based on an alternative regression model proposed for carbon isotope Keeling plots by Miller and Tans [2003]. This model determines  $\delta^{18}\text{O}_R$  from equations (1) and (2) as the slope of a regression of  $\delta^{18}\text{O}^* [\text{CO}_2]$  versus  $[\text{CO}_2]$ . Very large isotopic differences (5–40‰) were obtained between the slope-based and the (Keeling) intercept-based methods when used for flask sets with NS regressions and/or longer sampling times. Finally, use of these criteria eliminates nearly all the outliers from the modeled reasonable data range shown in Figures 9 and 10, without necessitating direct measurements of ecosystem soil, xylem, and leaf water isotope ratios (which were required to establish the boundaries in Figure 10).

[39] Keeling-plot estimates of  $\delta^{18}\text{O}$  in ecosystem respiration across the Oregon transect are shown in Figure 11. The top panels include all data regardless of their acceptability, and the bottom panels show only the data deemed acceptable. Considerable variation was observed at all sites when

all Keeling plots were examined, and individual estimates of  $\delta^{18}\text{O}_R$  were often found to be theoretically unrealistic (top panels in Figure 11, Figure 10a). Application of our data quality criteria reduced the number of Keeling plots from 74 to 28, and only four of our six sites retained usable estimates of  $\delta^{18}\text{O}_R$  (A, D, E, and F). On average, the isotopic composition of ecosystem respiration at the sites that were closer to the Pacific coast (sites A and D) was  $25.9 \pm 2.5\text{‰}$  (mean  $\pm$  SD,  $n = 8$ ), and  $\delta^{18}\text{O}_R$  of the inland sites (E and F) was  $31.5 \pm 2.8\text{‰}$  ( $n = 20$ ). The pattern of more positive  $\delta^{18}\text{O}_R$  at inland forests is opposite the general isotopic pattern of precipitation and xylem water ( $-2\text{‰}$  per 100 km) across the sites ( $\delta^{18}\text{O}$  of these water pools was more positive at the coast, Figure 3). The influence of dry atmospheric conditions at inland sites (Figure 4) during the period of summer drought led to substantial evaporative enrichment of soil water (Figure 6), which was conferred to  $\delta^{18}\text{O}_R$ . This resulted in a spatial gradient in the isotopic content of ecosystem respiration (during the summer) of roughly  $3\text{‰}$  per 100 km (coastal versus inland sites) which opposed the isotopic gradient of precipitation ( $-2\text{‰}$  per 100 km) in sign. As noted, the isotopic gradient in precipitation along the Oregon transect is among the highest observed [Welker, 2000].

[40] Leaf area index (LAI) and aboveground biomass decrease substantially with precipitation across the transect [Grier and Running, 1977; Gholz, 1982], so one might expect the proportion of soil-respired  $\text{CO}_2$  relative to total respiration fluxes to be greater in low-LAI inland forests. This could cause greater influence of enriched  $\delta^{18}\text{O}$  of soil water at the drier sites due to the higher relative  $\text{CO}_2$  fluxes from the soil. However, more leaf area leads to greater litterfall and more substrate for decomposition. Studies in deciduous and coniferous forests of LAI in the range 2.1 to

4.5  $\text{m}^2 \text{m}^{-2}$  have reported a fairly narrow proportion of soil-respired  $\text{CO}_2$  relative to total respiration (67–77%) [Goulden *et al.*, 1996; Law *et al.*, 1999a, 1999b, 2001; Xu *et al.*, 2001]. Across a wide range of forest types, total annual respiration is tightly linked to total annual litterfall [Davidson *et al.*, 2002], and total respiration from the coastal sites is likely to be much higher than the inland sites. Hence the isotopic influence of respiration by Oregon forests on atmospheric  $\text{CO}_2$  should be greatest in the coastal forests.

[41] These data illustrate the complex ways in which ecosystem respiration can directly influence the isotopic composition of atmospheric  $\text{CO}_2$ . As a community, we now have a fairly solid understanding of the mechanisms with which ecosystem water pools interact with  $\text{CO}_2$  to influence  $\delta^{18}\text{O}$  of respiration fluxes. This understanding lends itself to modeling at a variety of scales. Our results suggest that for modeling at any scale to successfully predict  $\delta^{18}\text{O}$  of respiration, the temporal dynamics of the isotopic composition of relevant water pools (precipitation, and xylem, leaf, and especially soil water) must be adequately characterized in the models.

#### 4. Conclusions

[42] We have examined the isotopic composition of ecosystem respiration and a variety of related ecosystem components across a strong precipitation gradient in Oregon, USA. We observed a spatial gradient in  $\delta^{18}\text{O}$  of precipitation, and  $\delta^{18}\text{O}$  of xylem water followed the general precipitation pattern. At site E where the dominant trees had access to groundwater recharged by snowmelt from higher elevations, the xylem water was more depleted than expected based on distance from the coast. Spatial and temporal variability was observed in  $\delta^{18}\text{O}$  of xylem water, and especially of soil water, across the transect. The soil water isotopic patterns were consistent with isotopic enrichment associated with evaporation, which was strongest at the drier inland sites. A general set of guidelines was adopted which allowed us to assess the quality of Keeling-plot data used to determine  $\delta^{18}\text{O}$  of ecosystem respiration. Data sets with nonsignificant Keeling regressions, or those that were collected over time periods longer than 5 hours, were found to conflict with expectations based on theory and were rejected. Data which met these quality criteria suggest that  $\delta^{18}\text{O}$  of ecosystem respiration was more enriched at inland sites than at sites nearer the coast. This pattern contrasts directly with the isotopic pattern of precipitation across the transect which was most enriched at the coast.

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are those of the authors and do not necessarily reflect the views of USDA, NSF, or DOE.

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