Carbon isotope dynamics in *Abies amabilis* stands in the Cascades

N. Buchmann, T.M. Hinckley, and J.R. Ehleringer

Abstract: Carbon isotope ratios ($\delta^{13}C$) of canopy air and carbon isotope discrimination at the ecosystem level were studied in three montane Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) stands, an old-growth and two younger stands. Spatial and temporal variations of canopy CO_2 concentrations ($[CO_2]$) and their $\delta^{13}C$ were strongly related to stand structure. Within the old-growth stand, both daytime canopy $[CO_2]$ and canopy $\delta^{13}C$ stayed close to those of the troposphere, either indicating low overall photosynthetic rates or high turbulent mixing. Pronounced periods of photosynthetic drawdown below baseline $[CO_2]$ accompanied by more enriched canopy $\delta^{13}C$ were observed for the two younger and denser stands. Canopy $[CO_2]$ profiles seemed closely related to changes in soil conditions. Soil respiration rates were positively related to soil temperature, but negatively to soil moisture. $\delta^{13}C$ of soil-respired CO_2 stayed relatively constant at -24.55 ± 0.20‰ during the growing season. Significant relationships existed between canopy $\delta^{13}C$ and $1/[CO_2]$ in all three stands. Using the intercepts of these regressions, we calculated an average $\delta^{13}C$ for ecosystem respiration of -26.4 ± 0.1‰. Ecosystem carbon isotope discrimination (Δ_e), an integrating measure for carbon exchange between the troposphere and the entire ecosystem, stayed relatively constant through time. Δ_e showed no significant stand structure effect (leaf area index, density) and averaged 18.9‰ for the old-growth and 19.2 ± 0.2‰ for the two younger stands.

Résumé : Les ratios isotopiques du carbone ($\delta^{13}C$) de l'air dans la canopée et la discrimination des isotopes du carbone à l'échelle de l'écosystème ont été étudiés dans trois peuplements d'*Abies amabilis* en région montagneuse : un vieux peuplement et deux plus jeunes. Les variations spatiale et temporelle des concentrations de CO_2 de la canopée ($[CO_2]$) et de leurs $\delta^{13}C$ étaient étroitement reliées à la structure du peuplement. Dans le vieux peuplement, le $[CO_2]$ diurne et le $\delta^{13}C$ de la canopée sont demeurés semblables à ceux de la troposphère indiquant soit des taux de photosynthèse généralement faibles, soit un important mixage par turbulence. Des périodes marquées de baisse de la photosynthèse en-dessous du niveau de base de $[CO_2]$, accompagnées par un $\delta^{13}C$ plus enrichi de la canopée ont été observées dans les deux peuplements plus jeunes et plus denses. Les profils de $[CO_2]$ de la canopée semblaient étroitement reliés aux variations dans les conditions du sol. Les taux de respiration du sol étaient positivement corrélés à la température du sol, mais négativement corrélés à l'humidité du sol. Le $\delta^{13}C$ du CO_2 provenant de la respiration du sol est demeuré relativement constant à $-24{,}55 \pm 20$‰ pendant la saison de croissance. Il y avait des corrélations significatives entre le $\delta^{13}C$ de la canopée et $1/[CO_2]$ dans les trois peuplements. Grâce aux points d'intersection de ces régressions, nous avons calculé un $\delta^{13}C$ moyen pour la respiration de l'écosystème de $-26{,}4 \pm 0{,}1$‰. La discrimination de l'isotope du carbone au niveau de l'écosystème (Δ_e), une mesure intégratrice des échanges de carbone entre la troposphère et l'ensemble de l'écosystème, est demeurée relativement constante dans le temps. La structure du peuplement (LAI et densité) n'a pas affecté de façon significative Δ_e qui atteignait 18,9‰ dans le vieux peuplement et $19{,}2 \pm 0{,}2$‰ dans les deux peuplements plus jeunes.

[Traduit par la Rédaction]

Introduction

Understanding global carbon dynamics and the coupling of terrestrial and atmospheric fluxes has become increasingly important, since atmospheric CO_2 concentrations ($[CO_2]$) continue to increase (Komhyr et al. 1985; Conway et al. 1994). Stable carbon isotopes have proved useful as tools for assessing the significance of the terrestrial carbon sink and its contribution to the global carbon fluxes relative to the oceans. When carbon isotope ratios ($\delta^{13}C$) of atmospheric CO_2 are incorporated into global inverse models, the simulations suggest that large carbon sinks occur in the Northern Hemisphere (Ciais et al. 1995; Francey et al. 1995). However, lacking sufficient data from terrestrial ecosystems, important physiologically based input parameters such as the ratio of internal to atmospheric $[CO_2]$ (c_i/c_a) and the carbon isotopic composition of respired CO_2 have been estimated using models for the dominant plant species within different biomes. Further uncertainties arise due to regional and temporal variability of these estimates. Better quantification of ecophysiological parameters and understanding of seasonal variation in these parameters could prove useful in identifying potential mechanisms constraining atmosphere/terrestrial ecosystem dynamics.

The fundamental mechanism underlying carbon isotope studies is the discrimination against the heavier ^{13}C isotope during photosynthesis (Farquhar et al. 1989). While atmospheric CO_2 has a $\delta^{13}C$ of about –8‰, organic material is much more depleted (e.g., –27‰ for a C_3 plant). Since there seems

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to be no significant discrimination during respiration (Lin and Ehleringer 1997), respired CO_2 has a $\delta^{13}C$ close to that of the organic substrate. This information has been successfully used to describe the mixing of tropospheric and respired CO_2 within the canopy of terrestrial ecosystems (Keeling 1958; Sternberg 1989; Lloyd et al. 1996). How does one relate $\delta^{13}C$ to leaf or ecosystem physiology? Farquhar et al. (1989) proposed a relationship between the carbon isotope discrimination of a leaf (Δ_{leaf}) and its c_i/c_a. Further studies revealed close relationships between leaf carbon discrimination and the ratio of CO_2 to water fluxes at the leaf level (water use efficiency; Ehleringer et al. 1993). Lloyd and Farquhar (1994) extended this application and modeled carbon isotope discrimination of entire canopies (Δ_A), using data sets for ecophysiological parameters from the dominant plant species (stomatal responses to leaf-to-air vapor mole fraction differences) and for climate (temperature, precipitation, and relative humidity), which was then scaled for the global distribution of vegetation. They validated their model by calculating the difference between the $\delta^{13}C$ of atmospheric CO_2 within the nocturnal boundary layer and the estimates of $\delta^{13}C$ of respired CO_2. This modeling effort provided encouraging support for such a bottom-up approach, but some initial caution is necessary, since the two terms compared integrate over very different temporal as well as spatial scales: Δ_A estimates integrate over periods of as long as a single growing season and represent values of a few overstory species only; in contrast, the estimates of $\delta^{13}C$ of respired CO_2 represent the carbon respired above ground by all plant species as well as released below ground by roots and microorganisms.

If the goal is to describe the carbon dynamics of the entire ecosystem, then one has to (*i*) consider all species present, including those in the understory, (*ii*) account for microbial and root respiration, and (*iii*) consider isotopic disequilibrium effects (Enting et al. 1993, 1995; Bird et al. 1996; Trumbore et al. 1996). A measure for carbon exchange between terrestrial ecosystems and the troposphere is the ecosystem carbon isotope discrimination, Δ_e (Buchmann et al. 1998), defined as

$$[1] \qquad \Delta_e = \frac{\delta^{13}C_t - \delta^{13}C_r}{1 + \delta^{13}C_r}$$

where $\delta^{13}C_t$ is the carbon isotope ratio of the troposphere and $\delta^{13}C_r$ is the carbon isotope ratio of respired CO_2. Thus, the familiar concept of carbon isotope discrimination at the leaf level is transferred to the ecosystem level.

Δ_e values are based on $\delta^{13}C$ of tropospheric CO_2 and on field measurements of canopy air to estimate $\delta^{13}C$ of respired CO_2. Thus, detailed knowledge about canopy profiles of $[CO_2]$ and $\delta^{13}C$ is needed. Several factors affect the canopy CO_2 concentration and its $\delta^{13}C$: turbulent mixing with the troposphere (Wofsy et al. 1988; Kruijt et al. 1996; Lloyd et al. 1996), carbon exchange responses of over- and under-story plants to abiotic factors, as well as soil carbon exchange as influenced by soil respiration and litter decomposition (Baldocchi and Vogel 1996; Brooks et al. 1997; Buchmann et al. 1996, 1997*a*, 1997*b*; Flanagan et al. 1996). Daily and seasonal variations have been assessed in different biomes, ranging from boreal to temperate to tropical forests (Sternberg 1989; Buchmann et al. 1997*a*, 1997*b*; Flanagan et al. 1996). However, the influence of stand structure on canopy profiles and the isotopic composition of canopy air are less understood (Valentini et al. 1996). Only limited information is available about how Δ_e changes with stand density or leaf area distribution (Buchmann et al. 1997*a*), although feedback mechanisms of stand structure on stand functioning are well known.

The Pacific Northwest of the United States is dominated by dense evergreen coniferous forests that exhibit very high leaf area indices (LAIs) and considerable longevity of both individual trees and foliage (Waring and Franklin 1979; Edmonds 1982). As a result, Pacific Northwest forests not only comprise the largest vegetative and soil carbon pools of the conterminous United States, but they also show the highest net uptake of carbon as well as net carbon release by decay compared with all other regions of the United States (Turner et al. 1995). The Pacific Northwest is characterized by a mild, maritime climate, with high wintertime precipitation, low evaporative demand, and moderate temperatures (Walter 1973). Cloud and fog often occur in summer. The climate and ecophysiological characteristics of the evergreen conifers ensure long periods of carbon gain at low respiratory costs (Waring and Franklin 1979; Teskey et al. 1984; Lassoie et al. 1985; Brooks et al. 1996). Stomata open at low light intensities, maximum stomatal conductance is reached at 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photons (Lassoie et al. 1985), and light saturation occurs at around 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photons (Teskey et al. 1984). Because of low air temperatures, maintenance respiration tends to be low (Sprugel 1990; Brooks et al. 1991). As a result, canopy gradients within Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) stands might be small under varying turbulence regimes, e.g., throughout the growing season, and Δ_e estimates might be rather constant. One might also expect Δ_e values to be higher for Pacific Northwest stands compared with evergreen stands in a much drier environment such as semiarid Utah (Buchmann et al. 1997*a*), where water is a limiting factor and plants develop more water use efficient strategies.

The terrestrial biota is at an isotopic disequilibrium (Enting et al. 1993, 1995) because carbon uptake and carbon release are temporally decoupled. Since the $\delta^{13}C$ of the atmosphere becomes increasingly depleted as a result of fossil fuel combustion (Tans et al. 1990), the $\delta^{13}C$ value of carbon released is not equal to the difference between the tropospheric $\delta^{13}C$ value and the photosynthetic carbon isotope fractionation. Instead, the $\delta^{13}C$ value of carbon released is more positive due to a less depleted tropospheric $\delta^{13}C$ value. Thus, the magnitude of the disequilibrium effect is dependent on the size of the carbon pools involved, their turnover rates, and the fractionation and the isotopic signals of the carbon pools. Since the carbon turnover is relatively slow in Pacific Northwest forests, and carbon pools in both vegetation and soils are large, especially in old-growth stands, one would expect a more enriched (positive) $\delta^{13}C$ of respired CO_2 in an old-growth stand and more depleted signals in younger stands. Thus, we would further expect Δ_e estimates to be lower for an old-growth stand compared with younger stands.

In this study, we chose three montane forest stands of *A. amabilis* that varied in age (40 to >220 years old) and canopy structure (two younger stands: stand density between 2200 and 70 000 trees/ha). We asked two questions: how are vertical profiles of canopy $[CO_2]$ and $\delta^{13}C$ influenced by leaf area distribution in these dense Pacific Northwest stands (LAI >6) and how do canopy profiles and Δ_e estimates vary in stands with different canopy structure, which creates large differences

Table 1. Site characteristics of high-elevation *Abies amabilis* stands in the central Cascade Mountains, Washington.

	Old-growth	Young–high	Young–low
Elevation (m above mean sea level)	1145	1140	1 140
Stand age (years)	>220	47	40
Stand density (ha^{-1})	488	2241	70 000
Maximum height (m)	42	22	8
Leaf area index ($m^2 \cdot m^{-2}$)	6.4	9.4	8.8

Note: Data provided by D. Sprugel and T. Martin (University of Washington). LAI was calculated using projected leaf area.

in turbulence regimes. We were further interested whether the carbon isotopic composition of respired CO_2 and therefore the Δ_e estimates differ among old-growth and young *A. amabilis* stands.

Methods

Sites

The research area was located in the central Cascade Mountains, Washington, U.S.A., within the City of Seattle's Cedar River Watershed, 70 km southeast of Seattle (47°19′N, 121°35′W). Three montane *A. amabilis* stands were chosen ranging in age from 40 to >220 years and in stand density from 488 to 70 000 stems/ha (Table 1). The old-growth stand (located in the Findley Lake Basin) originated after fire (Meier et al. 1985) and was dominated by *A. amabilis* (73 %), with western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) as associated species. Understory vegetation included suppressed *A. amabilis* trees (<1 m tall), *Vaccinium parvifolium* Smith, and *Xerophyllum tenax* (Pursh.) Nutt. Due to higher stand densities and LAI, no understory was present in the two younger stands, the 40-year-old young–low and the 47-year-old young–high, both dominated by *A. amabilis* (approximately 90%, with *T. heterophylla* as associated species). The young–low stand is located outside the Findley Lake Basin, but on its southwestern ridge, and established in 1955 following clear-cutting. The young–high stand is located approximately 10 km southwest of the other two stands and established from released advanced regeneration between 1948 and 1950 after windthrow and salvage cutting. The young–high stand is older, much taller, and supported more leaf area than the young–low stand (Table 1; for more details on LAI determinations, see Martin et al. 1997; Hinckley et al. 1998). Soil nitrogen availability for plant uptake is lower in the young–low stand than in the young–high stand, as reflected by lower foliar nitrogen concentrations (Martin 1997).

The Pacific Northwest is characterized by maritime climate, with high precipitation, low evaporative demand, and moderate temperatures (Walter 1973). Annual mean precipitation at Findley Lake (upper Cedar River Watershed) is 2730 mm, with >80% occurring as snow (Grier et al. 1981). Mean annual temperature averages 5.4°C, with mean air temperatures of –3.2°C in January and 14.4°C in July (Grier et al. 1981). Soils are classified as Typic Cryohumods (Zabowski and Sletten 1991) and show pronounced litter accumulation on the forest floor.

Continuous CO_2 and micrometeorological measurements

Canopy air was sampled from different heights within the canopy (0.3, 2.0, 7.0, 19.0, 30.0, and 40.0 m in the old-growth stand, 0.3, 1.0, 6.7, 11.8, 15.3, and 21.4 m in the young–high stand, and 0.3, 3.7, 6.1, and 8.7 m in the young–low stand). The setup (for more details, see Buchmann et al. 1997*b*) provided continuous air sampling from all heights and two standards (one CO_2-free air source and a calibrated CO_2 source). A run of the entire profile was completed within 10 min. $[CO_2]$ values were measured each second with an infrared CO_2 gas analyzer (LI-6262, LiCor, Lincoln, Nebr.). Every 3 h, both calibration gases were measured. Measurements were taken continuously during 8- to 10-day periods simultaneously in all stands three times during the 1995 growing season: June 8–17, August 13–21, and September 11–20. Air temperatures were measured at 42.0, 21.4, or 8.1 m (old-growth, young–high, and young–low, respectively) and at 1.0 m height (all three stands); soil temperatures were measured at 0.05 m soil depth by using copper–constantan thermocouples. Thermocouples for air temperature were shielded against direct sunlight, but installation allowed free air movement. Photosynthetic active radiation (PAR) was measured at the same heights as air temperatures with a photodiode (GaAsP 1118, Hamamatsu, Bridgewater, N.J.) after calibration against a quantum sensor (LI-190, LiCor, Lincoln, Nebr.).

Exact tropospheric $[CO_2]$ and $\delta^{13}C$ were not known for the area of our study sites. However, within the NOAA Cooperative Flask Sampling Network (Conway et al. 1994), two locations were potentially suitable for comparisons: Cape Meares, Oreg., and Cold Bay, Alaska. Unfortunately, measurements at Cape Meares were stopped in June 1995; thus, the station at Cold Bay (55°12′N, 162°43′W; 11 m above mean sea level) was used for comparison in this study (data provided by T. Conway, NOAA/CMDL, Boulder, Co., and M. Trolier, University of Colorado, Boulder, Co., INSTAAR). On average, tropospheric $[CO_2]$ values during the summer months (May–September) were about 1 ppm higher at Cape Meares than those at Cold Bay. The precision of the NOAA data is <0.5 ppm for $[CO_2]$ and ±0.03‰ for $\delta^{13}C$. Natural temporal variability for data, collected at the same station over a 1-month period, is <0.2‰ (M. Trolier, University of Colorado, INSTAAR, personal communication). Further isotopic shifts may occur as the air mass moves above continental areas before it reaches the study area. However, variability between stations at a similar latitude is between 0.5 and 1 ppm and around 0.25‰ (see Conway et al. 1994 and Ciais et al. 1995, respectively).

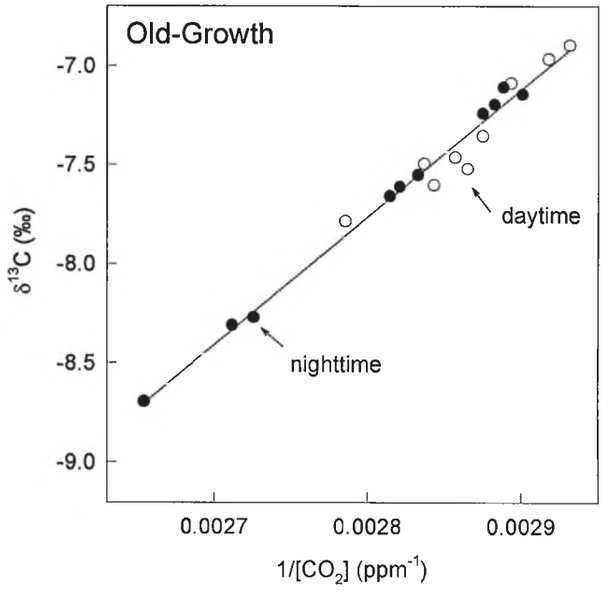
Collection of canopy air for isotope analyses

Canopy air was collected for isotopic analyses from the same heights as used for the continuous CO_2 measurements with a second set of Dekoron tubing (for details, see Buchmann et al. 1997*a*, 1998). Dry air was collected in a preevacuated 1.7-L glass flask (with two high-vacuum stopcocks). After pumping for 20 min, $[CO_2]$ coming out of the flask was measured with a portable photosynthesis system (LI-6200, LiCor, Lincoln, Nebr.), and then, both stopcocks of the flask were closed. Up to four flasks were collected at the same time. Canopy air was collected for isotopic analyses in June, August, and September for both young–high and young–low stands and in August for the old-growth stand. During the 1995 growing season, 48 flasks were collected at night (between 19:30 and 23:00) and 75 flasks during the day (between 08:00 and 17:30).

Soil respiration rates and soil moisture

Soil respiration rates were measured using a soil respiration chamber (LI-6000-09S, LiCor, Lincoln, Nebr.) connected to a portable photosynthesis system (LI-6200). Three PVC tubes (25 cm long, 10 cm inside diameter) to which the chamber could be attached were

Fig. 1. Typical "Keeling plot": relationship between the inverse of canopy [CO_2] and its carbon isotope ratio ($\delta^{13}C$). The August flask data for the old-growth stand are presented. Daytime and nighttime flasks can be described by one regression equation (see Table 2 and text for more details).



inserted into the soil 24 h prior to measurement. To avoid long-term disturbance effects, collars were placed at different locations for each sampling time. The protocol recommended by LiCor (LiCor 6000-09S manual) was changed to five observations of 5 ppm change per measurement (J. Norman, University of Wisconsin, personal communication). CO_2 concentrations within the system were scrubbed with soda lime in an open configuration until the CO_2 level was 50 ppm below ambient. After closing the system, [CO_2] was allowed to increase by 20 ppm before measurements were taken. Four to eight measurements were taken at each site and sampling time (old-growth: August; young–high and young–low: June, August, and September).

Gravimetric water content of litter and soil material (0–0.05 and 0.05–0.10 m depth, respectively) was determined at the sites where soil respiration had been measured. Three replicates were taken per measurement, and sampling containers were sealed in the field with Parafilm. The wet soil samples were weighed, then dried until mass constancy, and reweighed. Soil moisture is expressed as percent dry mass (% dm).

Collection of soil respired CO_2 for isotope analyses

The setup described for soil respiration measurements was modified to collect soil-respired CO_2 for isotopic analyses. A closed system was designed where soil CO_2 efflux was drawn from the soil respiration chamber through the LI-6200 and an ethanol – dry ice water trap into a 1.7-L sampling flask and pushed back into the chamber. The 1.7-L flask was filled with CO_2-free N_2 gas and connected to the top inlet of the soil respiration chamber. The air within the entire system was scrubbed with soda lime for 10–20 min. As soon as [CO_2] dropped below 50 ppm, the soda lime was taken out of the line. The system's [CO_2] was allowed to increase to approximately 350 ppm before the stopcocks of the flask were closed. Three flasks were collected at each site and sampling time (old-growth: August; young–high and young–low: June, August, and September).

Sampling and isotope analyses

Litter and soil samples (0–0.05 and 0.05–0.10 m depth, respectively) were collected at each site and sampling time when soil respiration had been measured (three replicates per site and depth). Litter samples were dried for 48 h at 70°C and then ground with mortar and pestle to a fine powder. Soil materials were acid washed and then sieved (mesh size 1 mm). A 2-mg subsample was combusted and analyzed for $^{13}C/^{12}C$ using an isotope ratio mass spectrometer (delta S, Finnigan MAT, Bremen, Germany).

CO_2 in the flask samples was extracted cryogenically using a four-trap vacuum line (each trap with a triple loop) and transferred into a sampling tube within 12 h after flask collection. Due to possible interferences at mass 44, CO_2 was separated from N_2O by using a gas chromatograph (GC-14A, 3-M Poraplot Q column, Shimadzu Corporation, Kyoto, Japan) prior to isotope analysis. The CO_2 gas was introduced manually into the mass spectrometer and canopy air $\delta^{13}C$ (canopy $\delta^{13}C$) analyzed from the same sample.

The $\delta^{13}C$ was calculated as

$$[2] \quad \delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000‰$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of the sample and the standard (PDB for carbon), respectively (Farquhar et al. 1989). The overall precision of the carbon isotope measurements was ±0.11‰ for organic carbon and 0.03‰ for carbon isotopes in gas samples.

Modeling of canopy $\delta^{13}C$ and estimates of Δ_e

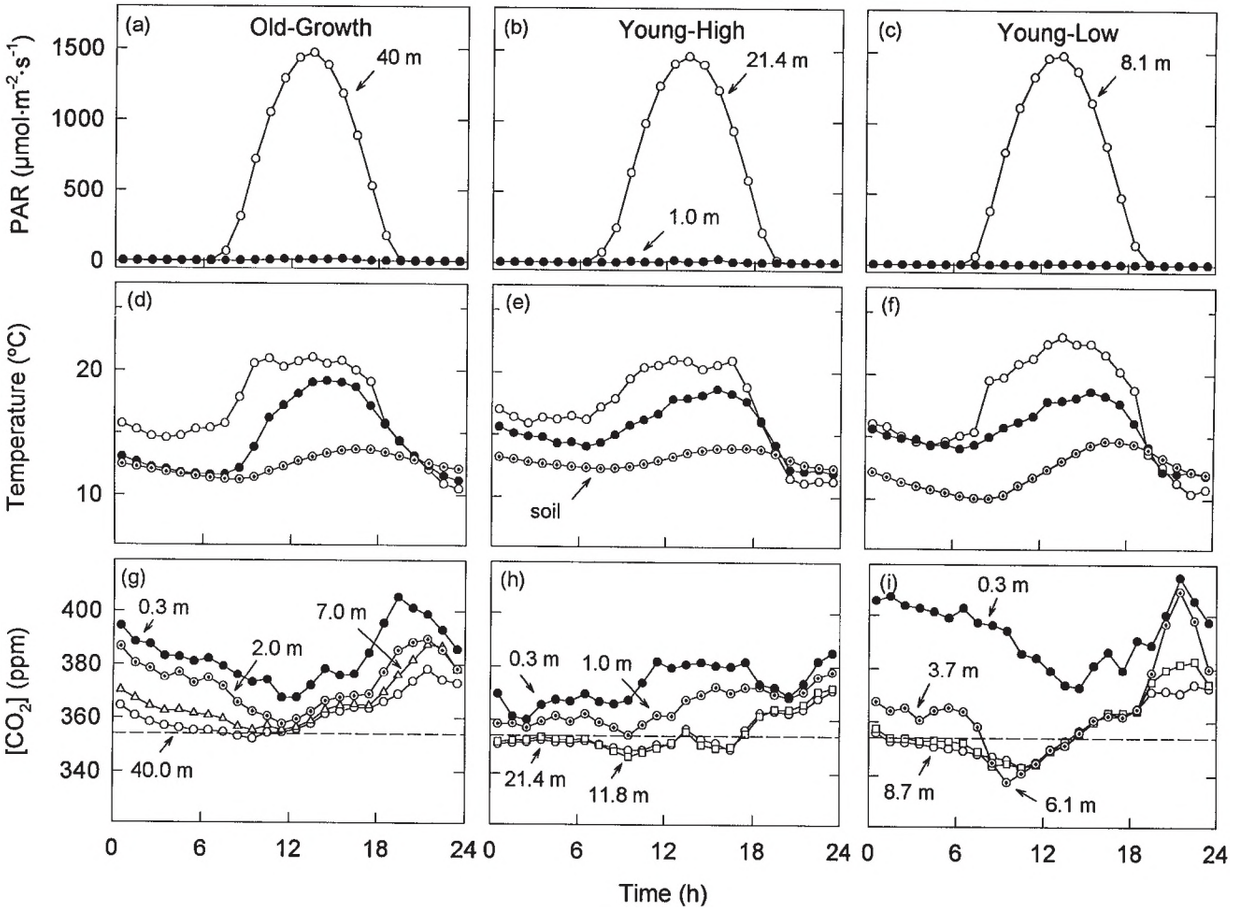
Canopy $\delta^{13}C$ are the result of turbulent mixing of two major CO_2 sources with different $\delta^{13}C$ (tropospheric and respired CO_2) and of a photosynthetic effect due to discrimination during carbon assimilation (Keeling 1958; Sternberg 1989). Thus, canopy $\delta^{13}C$ are linearly related to the inverse of the corresponding canopy [CO_2] (Fig. 1; so-called "Keeling plot").

The intercept of this linear regression is an indicator of the isotopic composition of respired CO_2 and was used to estimate ecosystem discrimination against the heavier ^{13}C during photosynthesis of the entire stand (Δ_e). Since results from several dozen forest stands showed that day and night data lie on the same regression line, we used all flask data in this regression approach (Buchmann et al. 1998). Using a Keeling plot to obtain the $\delta^{13}C$ of respired CO_2 has certain advantages over soil respiration chambers or other enclosures. It represents a weighted average of all respiration processes within the ecosystem, not only of a relatively small area. Further, it includes foliage and branch/stem respiration; thus, all respiration fluxes are covered and weighted by their respective flux rates. Provided no fractionation occurs during respiration (Lin and Ehleringer 1997), Δ_e is calculated using eq. 1. Data for $\delta^{13}C_t$ (–8.13‰ in June 1995, –7.47‰ in August 1995, and –7.67‰ in September 1995) were provided by M. Trolier (University of Colorado, INSTAAR); $\delta^{13}C_r$ values were the intercepts of the respective linear regressions (see above). Thus, the error expected with these Δ_e estimates is associated with the error of knowing the $\delta^{13}C$ of tropospheric CO_2 and with the error of determining the $\delta^{13}C$ or respired CO_2. The larger of the two error terms ($\delta^{13}C_r$) is due to the regression analysis. Using this approach for 49 stands in 10 different ecosystems globally, Buchmann et al. (1998) gave a standard error for $\delta^{13}C$ of respired CO_2 of ±0.98‰.

Statistics

The statistical package JMP (version 3, SAS Institute Inc., Cary, N.C.) was used for most of the data analyses. Analyses of variance (ANOVA) were done with site, sampling time, or height as a main factor. We used sampling time as a main factor (and not a repeated measures analysis) because the experimental units (litter, soils, air masses) were not identical for the three sampling times. The Student *t*-test or Tukey–Kramer HSD (honestly significant difference) test (at the 0.05 level) was used to distinguish among the means of two or more groups, respectively. All linear regressions are stated with r^2 adjusted. When both *x* and *y* variables were associated with an error (such as for 1/[CO_2] versus $\delta^{13}C$), slopes and intercepts were calculated by geometric mean regressions (Sokal and Rohlf 1995). Slopes

Fig. 2. Mean daily course of photosynthetic active radiation (PAR), air and soil temperatures, and canopy [CO_2] for three *Abies amabilis* stands at a representative day in September 1995: (*a*, *d*, *g*) old-growth, (*b*, *e*, *h*) young–high, and (*c*, *f*, *i*) young–low. Hourly averages of 10-min records from a 10-day period are presented. If standard error bars are absent, bars are smaller than symbol size. Mean daytime tropospheric [CO_2] for Cold Bay, Alaska, (broken line) was 354.64 ppm (provided by T. Conway, NOAA/CMDL).



and intercepts of regressions were tested against each other by introducing indicator variables ("dummy" variables) into a multiple regression model (Neter et al. 1985).

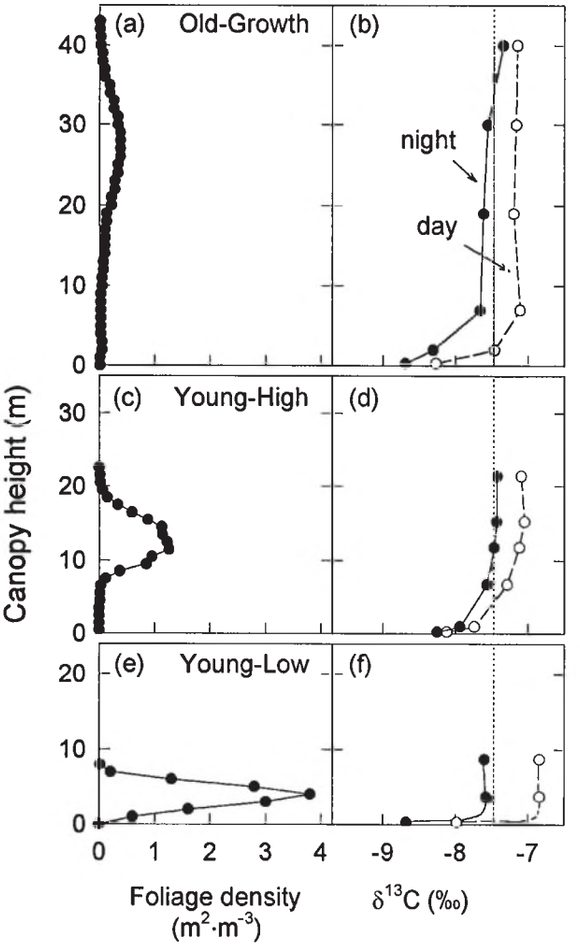
Results

Variations in canopy [CO_2] associated with stand structure

The daily course of canopy [CO_2] on a sunny day in September 1995 differed considerably among the three *A. amabilis* stands (Fig. 2). Although canopy [CO_2] were well stratified in all three canopies (highest [CO_2] near the forest floor and lowest [CO_2] at the top canopy), daily fluctuations, absolute values, as well as overall canopy [CO_2] gradients were different among these three stands. Within the old-growth canopy, [CO_2] rarely dropped below tropospheric background values whereas [CO_2] in both younger and denser stands (see Table 1) showed a pronounced period of photosynthetic drawdown below baseline [CO_2] (up to 8 ppm lower than tropospheric [CO_2] in the young–high stand and up to 17 ppm lower in the young–low stand). Thus, the much higher stem and foliage densities of the young–low stand compared with those of the young–high stand seemed to be reflected in canopy [CO_2]. Canopy [CO_2] gradients in the old-growth stand were maintained throughout the day (daily mean ± SD: 21.7 ± 6.7 ppm), similarly to the gradients in the two younger stands (18.2 ± 7.8 ppm in the young–high stand and 36.9 ± 13.7 ppm in the young–low stand). Wind speeds, recorded above the young–low canopy (T. Martin, College of Forest Resources, University of Washington, Seattle, Wash., personal communication), were low during this day. Maximum speeds (between 1.5 and 1.75 $m \cdot s^{-1}$) were measured between 12:00 and 16:00, while wind direction stayed stable during this time period.

During the night, the buildup of canopy [CO_2] was only minor, before dissipation set in due to turbulent mixing and photosynthetic drawdown in the morning. For example, in the old-growth stand, we found only a 10-ppm difference between 01:00 and 10:00 for [CO_2] at 40.0 m height, about 13 ppm at 7.0 m, and about 20 ppm at 0.30 m height. Concentration differences at 6–7 m in the young–high and young–low stands over this same time period were only about 5 and 14 ppm, respectively. Instead, by early afternoon, [CO_2] throughout the canopies were again increasing (fastest in the young–low stand), although maximum PAR and air temperatures were not

Fig. 3. Height profiles of foliage density and canopy carbon isotope ratio ($\delta^{13}C$) within three montane *Abies amabilis* stands: (*a* and *b*) old-growth, (*c* and *d*) young–high, (*e* and *f*) young–low. Night and afternoon values of original flasks are given. Data on projected foliage leaf area were provided by D. Sprugel (College of Forest Resources, University of Washington). The tropospheric $\delta^{13}C$ (–7.47‰ for Cold Bay, Alaska; vertical broken line) was provided by M. Trolier (University of Colorado, INSTAAR).



reached until 14:00–15:00. However, the increase in afternoon $[CO_2]$ coincided with steadily increasing soil temperatures (while air temperatures stayed constant or decreased; Fig. 2).

Isotopic composition of canopy air

Profiles of canopy $\delta^{13}C$ were affected by foliage leaf area distribution in all three *A. amabilis* canopies (Fig. 3). While the peak leaf area (projected) in the old-growth stand is located near 27 m, maximum foliage leaf area is found at 12 m in the young–high stand and at about 4 m in the young–low stand. Understory vegetation is only present in the old-growth stand; however, some branches in the young–low stand extend almost to the forest floor. Higher foliage density in the young–low stand resulted in more enriched daytime canopy $\delta^{13}C$, with $\delta^{13}C$ above the background value of the troposphere (by 0.4–0.7‰), reflecting carbon isotope discrimination during photosynthesis. Highest canopy $\delta^{13}C$ values were found throughout the young–low canopy. Near to the forest floor, most depleted $\delta^{13}C$ were found. Similar to the $[CO_2]$ gradients, daytime gradients of canopy $\delta^{13}C$ were highest in the stand with highest stem and foliage densities (young–low) and the least in the least dense stand (old-growth). Nighttime $\delta^{13}C$ in the main canopy were quite similar among all stands and were near to the tropospheric background values.

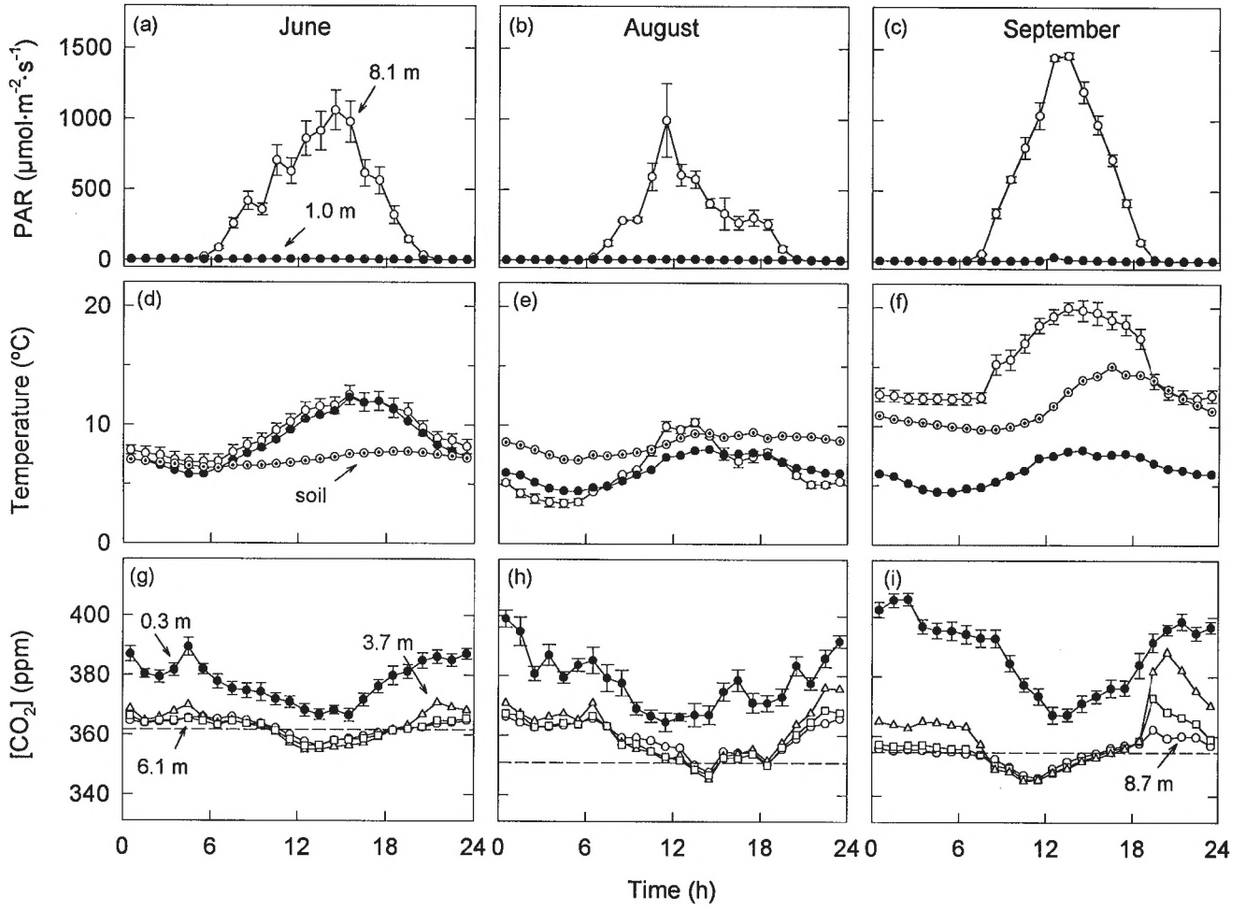
Seasonal variations of canopy $[CO_2]$

Comparing canopy $[CO_2]$ or $\delta^{13}C$ within a stand during the course of a growing season, one has to account for changes in the physiological and metabolic activities of plants and microorganisms as well as for changes in the turbulence regime. The seasonal comparison of canopy $[CO_2]$ within the young–low stand revealed that average daytime $[CO_2]$ decreased steadily throughout the growing season (by 10–15 ppm), although the tropospheric $[CO_2]$ started to increase again in September (Fig. 4, broken lines). While turbulent mixing of canopy and tropospheric air is responsible for the uniform $[CO_2]$ profiles (very small gradients), CO_2 depletion of canopy air can only be due to photosynthetic activity. $[CO_2]$ just above the forest floor (0.3 m height) increased steadily from June to September, as did nighttime $[CO_2]$ (by up to 20 ppm). Such changes near to the forest floor could be due to (*i*) entrainment of air with higher $[CO_2]$ from the convective boundary layer or (*ii*) higher respiratory fluxes from the forest floor (autotrophic or heterotrophic respiration). As seen earlier, the greatest daily fluctuations in canopy $[CO_2]$ and the largest canopy gradients were observed at higher temperatures, especially higher soil temperatures. Since stronger turbulent mixing (e.g., in September) should have resulted in smaller, not larger, canopy gradients and soil respiration generally dominates the ecosystem respiratory flux (e.g., Goulden et al. 1996), we conclude that soil respiration was the major reason for the observed $[CO_2]$ gradients that did not collapse during the day. The young–high stand exhibited similar temporal and spatial patterns, but with smaller absolute fluctuations of $[CO_2]$ (data not shown).

Soil respiration

Soil respiration, an indicator of root and soil microbial activities, fluctuated seasonally due to changes in soil temperature and soil moisture, factors apparently affected by stand structure (Fig. 5). However, differences among stands were small. Multiple regression analysis revealed that soil temperature and soil moisture at 0.10 m soil depth were the most important parameters in explaining the variance in soil respiration rates ($r^2 = 0.34$; coefficients of partial determination were 0.20 and 0.18, respectively). Soil CO_2 efflux increased with increasing soil temperature and decreasing soil moisture at 0.10 m depth. Thus, soil water status influenced CO_2 exchange negatively in these Pacific Northwest forest soils. Adding moisture of the litter layer and soil moisture at 0.05 m depth into the multiple regression model increased the r^2 to 0.45 (coefficients of partial determination were 0.13 and 0.05, respectively). During the 1995 growing season, this negative effect of soil moisture on soil respiration resulted in the highest soil respiration rates being noted in the young–low stand, the stand maintaining the lowest levels of soil moisture throughout the soil profile. This observation might be associated with differences in soil physical properties (e.g., water

Fig. 4. Mean daily course of photosynthetic active radiation (PAR), air and soil temperatures, and canopy [CO_2] for a young, nitrogen-poor *Abies amabilis* stand (young–low) throughout the 1995 growing season: (*a*, *d*, *g*) June, (*b*, *e*, *h*) August, and (*c*, *f*, *i*) September. The 10-min records of the entire sampling period are averaged and presented as hourly means over a day. If standard error bars are absent, bars are smaller than symbol size. Mean daytime tropospheric [CO_2] for Cold Bay, Alaska (broken line) was 361.64 ppm in June, 350.82 ppm in August, and 354.64 ppm in September (provided by T. Conway, NOAA/CMDL).



holding capacity) or with greater rain interception (less throughfall) in this very dense stand compared with the old-growth and young–high stands (see Table 1). The same mechanism might be responsible for the high soil moisture values in the old-growth stand during August 1995, where lower foliage densities might be related to low rain interception and therefore high throughfall inputs.

$\delta^{13}C$ of respired CO_2 and ecosystem discrimination

For all three *A. amabilis* stands, tight relationships existed between canopy $\delta^{13}C$ and $1/[CO_2]$ (Table 2). Stands differing in overstory LAI by almost 3 $m^2 \cdot m^{-2}$ (old-growth versus young–low) showed very similar intercepts, with a maximum difference of 0.9‰ (well within the error range of this coefficient; see Methods). Moreover, relationships did not change significantly with sampling time during the 1995 growing season, indicating that the $\delta^{13}C$ of ecosystem respiration ($\delta^{13}C_{ER}$) and the photosynthetic effect on canopy [CO_2] stayed relatively stable during the study period. Actual measurements of the $\delta^{13}C$ of soil-respired CO_2 ($\delta^{13}C_{SR}$) confirmed that the $\delta^{13}C$ of biogenic sources did not change significantly during the 1995 growing season (Fig. 6; ANOVA with time as main factor: $P = 0.12$ for young–high, $P = 0.66$ for young–low). The average $\delta^{13}C_{SR}$ value for all three *A. amabilis* stands was –24.55 ± 0.20‰ (Table 3), slightly more enriched than the overall intercept (–26.17 ± 0.74‰; Table 2). The average $\delta^{13}C$ of soil organic carbon ($\delta^{13}C_{SOC}$) did not show a clear trend among the three *A. amabilis* stands. $\delta^{13}C_{SOC}$ values became more enriched with increasing soil depth (2‰ for old-growth and young–high and 3‰ for young–low), indicating age effects or fractionation during litter decomposition and soil organic matter formation in these Pacific Northwest forest soils.

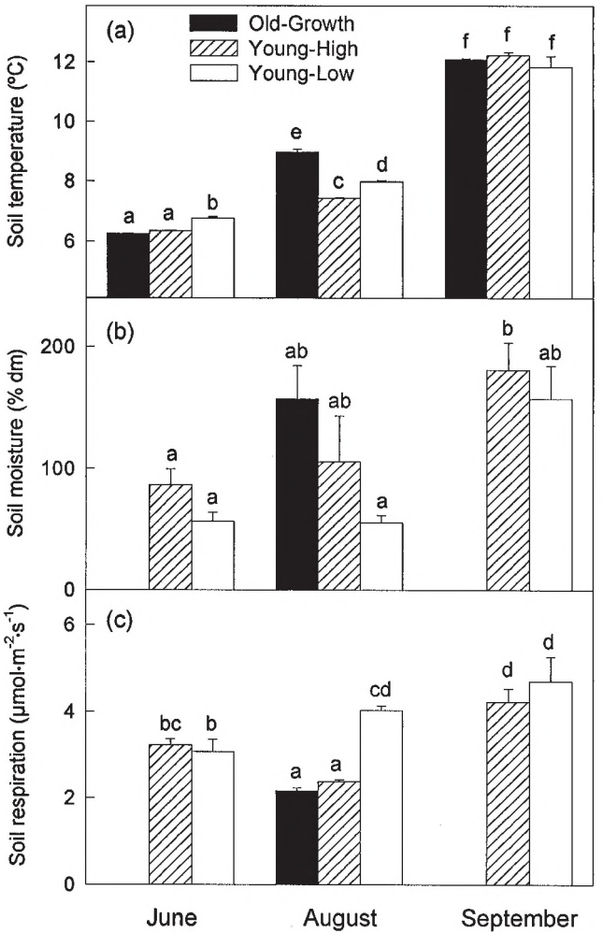
Since tropospheric $\delta^{13}C$ values at Cold Bay also changed by 0.7‰ within the study period and due to the errors associated with the Δ_e estimates, the small seasonal trend in ecosystem discrimination for *A. amabilis* stands was not significant (Fig. 6). Furthermore, average Δ_e estimates for the stand with highest stand and foliage densities (young–low: 19.2 ± 0.3‰) were almost identical to those for the stand with the highest LAI (young–high: 19.1 ± 0.4‰), indicating similar foliar c_i/c_a and low intrinsic water use efficiency of all stands. Comparing August data only, both young stands showed very similar

Table 2. Linear regressions between canopy carbon isotope ratio ($\delta^{13}C$) and the inverse of canopy [CO_2] for three *Abies amabilis* stands with different age and leaf area index (LAI) throughout the 1995 growing season.

	LAI	Site	Regression	r^2	n	F
June 8–20	8.8	Young–low	$y = 6779(\pm483)x - 26.67(\pm1.31)$	0.93	15	184
	9.2	Young–high	$y = 6689(\pm366)x - 26.35(\pm1.02)$	0.94	22	314
Aug. 10–21	6.4	Old-growth	$y = 6484(\pm223)x - 25.92(\pm0.63)$	0.98	19	830
	8.8	Young–low	$y = 6881(\pm861)x - 26.74(\pm2.38)$	0.85	12	64
	9.2	Young–high	$y = 6712(\pm398)x - 26.78(\pm1.14)$	0.93	20	267
Sept. 11–20	8.8	Young–low	$y = 6404(\pm441)x - 26.13(\pm1.24)$	0.94	13	199
	9.2	Young–high	$y = 6399(\pm156)x - 26.00(\pm0.43)$	0.99	22	1674
Overall		All	$y = 6546(\pm256)x - 26.17(\pm0.72)$	0.82	123	535

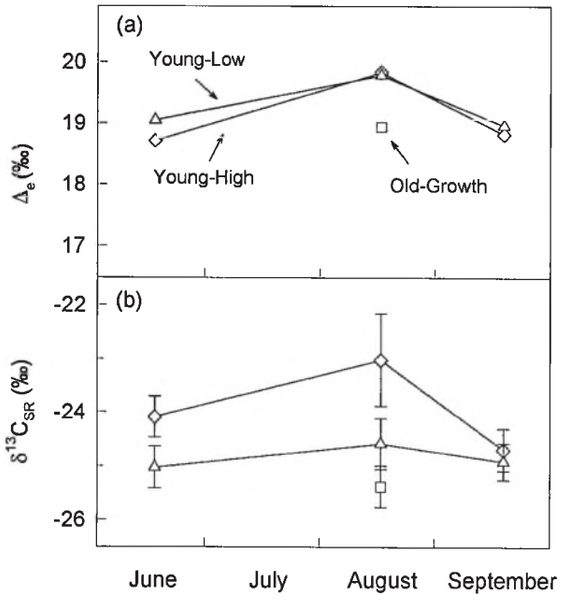
Note: Equations are given with 1 SE in parentheses; $P < 0.0001$ for all equations. No significant differences were found among the regression equations (F-test at the 0.05 level).

Fig. 5. (*a*) Soil temperature and (*b*) soil moisture at 0.10 m depth as well as (*c*) soil respiration rates for three *Abies amabilis* stands throughout the 1995 growing season. Means (±SE) are presented ($n = 4–8$). Different letters within a panel represent significantly different means (Tukey–Kramer test at the 0.05 level).



Δ_e estimates (young–low: 19.79‰; young–high: 19.84‰) whereas the old-growth stand, as expected, exhibited a lower Δ_e value (18.9‰).

Fig. 6. Seasonal course of estimates of (*a*) ecosystem discrimination (Δ_e) and (*b*) carbon isotope ratios of soil-respired CO_2 ($\delta^{13}C_{SR}$) for three *Abies amabilis* stands during the 1995 growing season.



Discussion

Spatial and temporal variations of canopy [CO_2] and its $\delta^{13}C$ were strongly related to stand structure of *A. amabilis* stands in the Pacific Northwest. Canopy gradients of [CO_2] and $\delta^{13}C$ seemed to be more closely related to changes in soil temperatures than to changes in light. $\delta^{13}C_{SR}$ stayed relatively constant during the 1995 growing season as did $\delta^{13}C_{ER}$. Δ_e estimates for the two younger *A. amabilis* stands showed no significant differences resulting from differences in stand structure. However, the Δ_e estimate for the old-growth stand was almost 1‰ lower than for the two younger stands.

The amount and distribution of foliage as well as stand density had profound effects on canopy [CO_2] and $\delta^{13}C$. In the old-growth stand, the stand with the lowest LAI and the most uniform vertical leaf area distribution (Fig. 3), canopy gradients of [CO_2] and $\delta^{13}C$ were small. Daytime [CO_2] and $\delta^{13}C$ close

Table 3. Carbon isotope ratios of ecosystem respiration ($\delta^{13}C_{ER}$, intercepts from Table 2, August), soil-respired CO_2 ($\delta^{13}C_{SR}$), and soil organic carbon ($\delta^{13}C_{SOC}$) at three soil depths.

	Old-growth (LAI = 6.4)	Young–high (LAI = 9.2)	Young–low (LAI = 8.8)	*P*
$\delta^{13}C_{ER}$ (‰)	–25.9±0.6	–26.8±1.1	–26.7±2.4	0.44
$\delta^{13}C_{SR}$ (‰)	–25.4±0.3*a*	–23.9±0.4*b*	–24.9±0.2*a*	0.0151
$\delta^{13}C_{SOC}$ (‰)				
Litter	–28.1±0.4*b*	–27.8±0.2*b*	–28.8±0.1*a*	0.0015
0.05 m	–26.7±0.1	–25.6±0.3	–26.8±0.4	0.0560
0.10 m	–26.4±0.1	–25.7±0.2	–26.0±0.2	0.0624

Note: LAI, leaf area index. Different letters following the means represent significantly different $\delta^{13}C$ among the stands (Tukey–Kramer test at the 0.05 level). The *P*-values are given for one-way ANOVA. For $\delta^{13}C_{SR}$, sampling time and interaction term (sampling time × site) were not significant ($P = 0.0853$ and 0.2988, respectively); $n = 3$ (old-growth) and $n = 9$ (young–high and young–low). For $\delta^{13}C_{SOC}$, sampling time and interaction terms (sampling time × site) were not significant (lowest $P = 0.194$ and 0.195, respectively); $n = 6$ (old-growth) and $n = 9$ (young–high and young–low) for each horizon.

to tropospheric baseline values implied that either the photosynthetic activity of the old-growth canopy was lower or that the daytime turbulent mixing was relatively higher than for the two younger stands. Since the old-growth stand had the lowest LAI and foliage densities throughout the canopy (Table 1), turbulent mixing may be the dominant factor responsible for the observed patterns. However, ecophysiological processes coincide with micrometeorological fluxes in forest stands. Several studies have shown that decreasing productivity with stand age (Gholz 1982) is not due to increased maintenance respiration of a tree, but to reduced foliage growth and net photosynthesis (Grier et al. 1981; Yoder et al. 1994). Mature old-growth forests, an important feature in the Pacific Northwest, appear to have foliar overstory production similar in magnitude to litterfall (Long 1982). Thus, one could speculate that these ecosystems are functioning ecophysiologically near a carbon equilibrium, where fluxes of respired CO_2 equal photosynthetic fluxes, as modeled by Cohen et al. (1996). Then, one would expect diurnal variations in canopy $[CO_2]$ mainly due to turbulent mixing, and no pronounced photosynthetic drawdown of $[CO_2]$ or ^{13}C enrichment of canopy air, similar to the patterns observed (Figs. 2 and 3). Unfortunately, eddy covariance measurements above old-growth forests are rare (Hollinger et al. 1994), although they could provide the means to describe the carbon exchange and verify our observations. Nevertheless, net ecosystem carbon exchange, defined as the difference between net primary productivity and heterotrophic respiration, is generally reduced by 30 to 50% for forests older than 100 years compared to maximum values (Buchmann and Schulze, in preparation[2]).

In contrast, $[CO_2]$ depletions up to 17 ppm below the tropospheric background and pronounced ^{13}C enrichments of canopy air were observed in the youngest *A. amabilis* stand with the highest stand and foliage densities (young–low). Patterns were even more pronounced than those in the young–high stand despite similar LAIs (8.8 versus 9.2). Thus, LAI alone might not be the appropriate factor to explain the observed canopy profiles; leaf area densities might be the more appropriate index. $[CO_2]$ and $\delta^{13}C$ of tropospheric air will also change when air masses move over continental areas. However, the observed daytime CO_2 depletions and ^{13}C enrichments were much larger than any daytime tropospheric fluctuation (see Methods). Furthermore, for canopies with relatively low overstory LAI (<4.5, *Acer* spp. and trembling aspen (*Populus tremuloides* Michx.)) in semiarid environments, even doubling the overstory LAI did not affect upper canopy CO_2 concentrations or $\delta^{13}C$, when turbulent mixing was high (Buchmann et al. 1996, 1997*a*). However, canopy gradients of $[CO_2]$, $\delta^{13}C$, and $\delta^{18}O$ were greater in a dense riparian *Acer* spp. stand (LAI = 4.5) than in an open stand (LAI = 2.1). Yet, these differences were mainly due to the presence of a vigorous understory vegetation in the open stand, resulting in a large photosynthetic drawdown of $[CO_2]$ below and ^{13}C enrichment above tropospheric baseline values. Stand density and foliage distribution affected canopy $[CO_2]$ and $\delta^{13}C$ more than just overstory LAI. Unfortunately, these factors are more difficult to obtain, e.g., by remote sensing, than LAI. Thus, scaling from representative forest stands to larger scales such as a region remains a challenging step in ecosystem modeling.

Since stand structure has profound effects on stand microclimate, we found an interesting interaction between soil moisture and soil temperature on soil respiration rates. A multiple regression analysis revealed that soil moisture in 0.10 m depth had a negative effect on soil CO_2 efflux, while soil temperature affected soil respiration positively. This pattern in a wet temperate climate is very similar to conditions in tropical rainforests where soil CO_2 efflux decreased by about 40% after strong rain events, resulting in a rapid decrease of $[CO_2]$ just above the forest floor by about 50 ppm (Buchmann et al. 1997*b*). Thus, high soil moisture contents (>150 % dm) might have limited soil CO_2 efflux considerably in the old-growth stand, probably related to larger throughfall amounts (less rain interception) than received by the two denser stands (young–high and young–low; Fig. 5). This inhibition by environmental factors even compensated the higher fine root production and the distribution of roots in more shallow horizons in the old-growth stand compared with that in the young–low stand (Grier et al. 1981; Meier et al. 1985). Although slow decomposition rates in the Pacific Northwest are reflected by the large buildup of organic matter (Long 1982), it remains unclear to what extent soil respiration by roots compared with decomposition by microorganisms contributed to the total soil CO_2 exchange.

In agreement with previous observations in boreal (Flanagan et al. 1996) and tropical forests (Buchmann et al. 1997*b*), $\delta^{13}C_{SR}$ remained stable throughout the season (Fig. 6), implying that the carbon sources for soil respiration stay relatively constant over a single growing season. A similar pattern was observed for $\delta^{13}C_{ER}$ (Table 2). Interestingly, both parameters differed from each other by approximately 2‰. One can speculate on whether this difference might have been associated with an isotopic disequilibrium between the soil and the above-ground components. The term "isotopic disequilibrium" (Enting et al. 1993) has been used to describe the difference between the carbon isotope ratios of soil respiration and above-ground (plant) respiration. This difference is thought to be associated with older soil carbon that was fixed

[2] Buchmann, N., and Schulze, E.D. Net CO_2 and H_2O fluxes of terrestrial ecosystems.

under conditions when the tropospheric $\delta^{13}C$ was different than it is today. Ecosystem respiration is the sum of autotrophic respiration (including root, stem, and foliage respiration) and heterotrophic respiration, with the latter being the dominant fraction (up to 85%; Fan et al. 1990; Wofsy et al. 1993). Since there is no fractionation during mitochondrial respiration (Lin and Ehleringer 1997), above-ground respired CO_2 should have a similar carbon isotope ratio to newly fixed carbon; in our case, approximately –28.9‰ for 0- and 1-year-old foliage (Buchmann et al., in preparation[3]). However, $\delta^{13}C_{SR}$ will depend on the $\delta^{13}C$ and the different fractions of older soil organic matter that are being respired and on root respiration which would be similar to that of the above-ground components. Because turnover rates in the soil are slow and the atmospheric signal was more positive several decades ago (Tans et al. 1990), the $\delta^{13}C$ value of soil respiration should be more positive than that of current above-ground respiration (assuming constant carbon isotope discrimination over time). This theoretical consideration is consistent with the more positive $\delta^{13}C$ we measured for soil respiration and soil organic matter in deeper horizons (–25 to –26‰ compared with –29‰ for foliage), although the soil respiration signal still includes some root respiration.

Since ecosystem respiration is integrating over both autotrophic and heterotrophic respiration, its $\delta^{13}C$ (overall mean about –26‰) reflects the stand history, including decades when the tropospheric $\delta^{13}C$ signal was less depleted than today. Furthermore, these disequilibrium effects should become more pronounced the older the respired organic matter. Thus, we might expect a more positive $\delta^{13}C_{ER}$ and a smaller Δ_e estimate for the old-growth compared with the two younger stands (Table 3; Fig. 6). However, hydraulic limitation of gas exchange characteristics of older trees might confound this interpretation, since older and taller trees often show lower stomatal conductance rates which are then reflected in more positive foliar $\delta^{13}C$ (Ryan and Yoder 1997). The $\delta^{13}C$ values of sunlit foliage (current and 1 year old) marginally support this latter possibility, however; the differences of foliar $\delta^{13}C$ values among stands were minor ($P = 0.07$; Buchmann et al., in preparation[3]).

Changes in Δ_e during the growing season were small, but consistent for both younger stands: August Δ_e values tended to be slightly higher than those in June or September (Fig. 5). This small seasonal course for *A. amabilis* stands agreed well with results reported for boreal evergreen forests, where Δ_e remain constant throughout the growing season (Flanagan et al. 1996). However, the balance between photosynthesis and stomatal conductance (intrinsic water use efficiency) of forest canopies might also influence carbon isotope discrimination at the ecosystem level, which may explain some of the observed variations in Δ_e estimates among coniferous forests. Δ_e of boreal black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.) stands averaged 19‰ (Flanagan et al. 1996). Estimates for the two younger *A. amabilis* stands in the Pacific Northwest were on average 19.2‰ (this study). Δ_e for temperate evergreen forests were about 18.3‰ for lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands during a very wet and cool year (Buchmann et al. 1997*b*) as well as for *Pinus* spp. stands in California and Montana (calculated from Lancaster 1990 flask data by using tropospheric data from Francey et al. 1995). On regional or global scales, a decreased Δ_e might therefore reflect an increased assimilation to conductance ratio among biomes, under conditions when precipitation decreases and (or) the evaporative demand increases. Understanding the ecophysiology of entire ecosystems will help to interpret these variations in $\delta^{13}C_{ER}$ and Δ_e among stands. Although estimates of Δ_e from a wide variety of ecosystems are important for interpreting global CO_2 flask data, these data sets are still uncommon (Buchmann et al. 1998). In the future, $\delta^{13}C_{ER}$ and Δ_e data will be needed to validate the modeled $[^{13}C]CO_2$ exchange between ecosystems and the atmosphere and to improve our estimates of the extent to which terrestrial ecosystems serve as sinks or sources in the global carbon budget.

[3] Buchmann, N., Hinckley, T.M., and Ehleringer, J.R. Intra-canopy variation in the carbon isotope composition of *Abies amabilis* needles.

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References

Baldocchi, D.D., and Vogel, C.A. 1996. Energy and CO_2 flux densities above and below a temperate broad-leaved forest and a boreal pine forest. Tree Physiol. **16**: 5–16.

Bird, M.I., Chivas, A.R., and Head, J. 1996. A latitudinal gradient in carbon turnover times in forest soils. Nature (Lond.), **381**: 143–146.

Brooks, J.R., Hinckley, T.H., Ford, E.D., and Sprugel, D.G. 1991. Foliage dark respiration in *Abies amabilis* (Dougl.) Forbes: variation within the canopy. Tree Physiol. **9**: 325–338.

Brooks, J.R., Sprugel, D.G., and Hinckley, T.M. 1996. The effects of light acclimation during and after foliage expansion on photosynthesis of *Abies amabilis* foliage within the canopy. Oecologia, **107**: 21–32..

Brooks, J.R., Flanagan, L.B., Varney, G.T., and Ehleringer, J.R. 1997. Vertical gradients in photosynthetic gas exchange characteristics and refixation or respired CO_2 within boreal forest canopies. Tree Physiol. **17**: 1–12.

Buchmann, N., Kao, W.Y., and Ehleringer, J.R. 1996. Carbon dioxide concentrations within forest canopies — variation with time, stand structure, and vegetation type. Global Change Biol. **2**: 421–432.

Buchmann, N., Kao, W.Y., and Ehleringer, J.R. 1997*a*. Influence of stand structure on carbon-13 of vegetation, soils, and canopy air

within deciduous and evergreen forests in Utah (USA). Oecologia, **110**: 109–119.

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

Buchmann, N., Brooks, J.R., Flanagan, L.B., and Ehleringer, J.R. 1998. Carbon isotope discrimination of terrestrial ecosystems. *In* Stable Isotopes and the integration of biological, ecological and geochemical processes. *Edited by* H. Griffiths, D. Robinson, and P. Van Gardingen. BIOS Scientific Publishers Ltd., Oxford, U.K. pp. 203–221.

Ciais, P., Tans, P.P., Trolier, M., White, J.W.C., and Francey, R.J. 1995. A large northern hemisphere terrestrial CO_2 sink indicated by the $^{13}C/^{12}C$ ratio of atmospheric CO_2. Science (Washington, D.C.), **269**: 1098–1102.

Cohen, W.B., Harmon, M.E., Wallin, D.O., and Fiorella, M. 1996. Two decades of carbon flux from forests of the Pacific Northwest. BioScience, **46**: 836–844.

Conway, T.J., Tans, P.P., Waterman, L.S., Thoning, K.W., Kitzis, D.R., Masarie, K.A., and Zhang, N. 1994. Evidence for interannual variability of the carbon cycle from the National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnosis Laboratory Global Air Sampling Network. J. Geophys. Res. **99**: 22 831 – 22 855.

Edmonds, R.L. 1982. Analysis of coniferous forest ecosystems in the western United States. US/IBP Synthesis Series 14. Hutchinson Ross Publishing Co., Stroudsburg, Pa.

Ehleringer, J.R., Hall, A.E., and Farquhar, G.D. 1993. Stable isotopes and plant carbon–water relations. Academic Press, San Diego, Calif.

Enting, I.G., Trudinger, C.M., Francey, R.J., and Granek, H. 1993. Synthesis inversion of atmospheric CO_2 using the GISS tracer transport model. Tech. Pap. No. 29, Division of Atmospheric Research, CSIRO, Canberra, Australia.

Enting, I.G., Trudinger, C.M., and Francey, R.J. 1995. A synthesis inversion of the concentration and $\delta^{13}C$ of atmospheric CO_2. Tellus Ser. B Chem. Phys. Meteorol. **47**: 35–52.

Fan, S.M., Wofsy, S.C., Bakwin, P.S., and Jacob, D.J. 1990. Atmospheric–biosphere exchange of CO_2 and O_3 in the Central Amazon Forest. J. Geophys. Res. **95:** 16 851 – 16 864.

Farquhar, G.D., Ehleringer, J.R., and Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. **40**: 503–537.

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

Francey, R.J., Tans, P.P., Allison, C.E., Enting, I.G., White, J.W.C, and Trolier, M. 1995. Changes in oceanic and terrestrial carbon uptake since 1982. Nature (Lond.), **373**: 326–330.

Gholz, H.L. 1982. Environmental limits on above-ground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology, **63**: 469–481.

Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C., and Wofsy, S.C. 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Global Change Biol. **2**: 169–182.

Grier, C.C., Vogt, K.A., Keyes, M.R., and Edmonds, R.L. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can. J. For. Res. **11**: 155–167.

Hinckley, T.M., Sprugel, D.G., Brooks, J.R., Brown, K.J., Martin, T.A., Roberts, D.A., Schaap, W., and Wang, D. 1998. Scaling and integration in trees. *In* Ecological scale: theory and applications. *Edited by* D.L. Peterson and V.T. Parker. Columbia University Press, New York. In press.

Hollinger, D.Y., Kelliher, F.M., Byers, J.N., Hunt, J.E., McSeveny, T.M., and Weir, P.L. 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. Ecology, **75**: 134–150.

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

Komhyr, W.D., Gammon, R.H., Harris, T.B., Waterman, L.S., Conway, T.J., Taylor, W.R., and Thoning, K.W. 1985. Global atmospheric CO_2 distribution and variations from 1968–1982 NOAA/GMCC CO_2 flask sample data. J. Geophys. Res. **90**: 5567–5596.

Kruijt, B., Lloyd, J., Grace, J., McIntyre, J., Farqhuar, G.D., Miranda, A.C., and McCracken, P. 1996. Source and sinks of CO_2 in Rondonian tropical rainforest, inferred from concentrations and turbulence along a vertical gradient. *In* Amazonian deforestation and climate. *Edited by* J.H.C. Gash, C.A. Nobre, J. Roberts, and R.L. Victoria. John Wiley & Sons, New York. pp. 331–351.

Lancaster, J. 1990. Carbon-13 fractionation in carbon dioxide emitting diurnally from soils and vegetation at ten sites on the North American continent. Dissertation, University of California, San Diego, Calif.

Lassoie, J.P., Hinckley, T.M., and Grier, C.C. 1985. Coniferous forests of the Pacific Northwest. *In* Physiological ecology of North American plant communities. *Edited by* B.F. Chabot and H.A. Mooney. Chapman and Hall, New York. pp. 127–161.

Lin, G., and Ehleringer, J.R. 1997. Carbon isotopic fractionation does not occur during dark respiration in C_3 and C_4 plants. Plant Physiol. **114**: 391–394.

Lloyd, J., and Farquhar, G.D. 1994. ^{13}C discrimination during CO_2 assimilation by the terrestrial biosphere. Oecologia, **99**: 201–215.

Lloyd, J., Kruijt, B., Hollinger, D.Y., Grace, J., Francey, R.J., Wong, S.C., Kelliher, F.M., Miranda, A.C., Gash, K.H.C., Vygodskaya, N.N., Wright, I.R., Miranda, H.S., Farquhar, G.D., and Schulze, E.D. 1996. Vegetation effects on the isotopic composition of atmospheric CO_2 at local and regional scales: theoretical aspects and a comparison between rain forest in Amazonia and a boreal forest in Siberia. Aust. J. Plant Physiol. **23**: 371–399.

Long, J.N. 1982. Productivity of western coniferous forests. *In* Analysis of coniferous forest ecosystems in the western United States. *Edited by* R.L. Edmonds. US/IBP Synthesis Series 14. Hutchinson Ross Publishing Co., Stroudsburg, Pa. pp. 89–125.

Martin, T.A. 1997. Transpiration and boundary layer resistance from the shoot to the canopy scale in *Abies amabilis* forests. Ph.D. dissertaion, University of Washington, Seattle, Wash.

Martin, T.A., Brown, K.J., Cermak, J., Ceulemans, R., Kucera, J., Meinzer, F.C., Rombold, J.S., Srugel, D.G., and Hinckley, T.M. 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. Can. J. For. Res. **27**: 797–808.

Meier, C.E., Grier, C.C., and Cole, D.W. 1985. Below- and aboveground N and P use by *Abies amabilis* stands. Ecology, **66**: 1928–1942.

Neter, J., Wasserman, W., and Kutner, M.H. 1985. Applied linear statistical models. Irwin, Homewood, Ill.

Ryan, M.G., and Yoder, B.J. 1997. Hydraulic limits to tree height and tree growth. BioScience, **47**: 235–242.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. W.H. Freeman and Company, New York.

Sprugel, D.G. 1990. Components of woody-tissue respiration in young *Abies amabilis* (Dougl.) Forbes trees. Trees (Berl.), **4**: 88–98.

Sternberg, L.S.L. 1989. A model to estimate carbon dioxide recycling in forests using $^{13}C/^{12}C$ ratios and concentrations of ambient carbon dioxide. Agric. For. Meteorol. **48**: 163–173.

Tans, P.P., Fung, I.Y., and Takahasi, T. 1990. Observational constraints on the atmospheric CO_2 budget. Science (Washington, D.C.), **247**: 1431–1438.

Teskey, R.O., Grier, C.C., and Hinckley, T.M. 1984. Change in photosynthesis and water relations with age and season in *Abies amabilis*. Can. J. For. Res. **14**: 77–84.

Trumbore, S.E., Chadwick, O.A., and Amundson, R. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science (Washington, D.C.), **272**: 393–396.

Turner, D.P., Koerper, G.J., Harmon, M.E., and Lee, J.J. 1995. A carbon budget for forests of the conterminous United States. Ecol. Appl. **5**: 421–436.

Valentini, R., DeAngelis, P., Matteucci, G., Monaco, R., Dore, S., and Scarascia Mugnozza, G.E. 1996. Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. Global Change Biol. **2**: 199–207.

Walter, H. 1973. Vegetation of the Earth. Springer-Verlag, Heidelberg, Germany.

Waring, R.H., and Franklin, J.F. 1979. Evergreen coniferous forests of the Pacific Northwest. Science (Washington, D.C.), **204**: 1380–1386.

Wofsy, S.C., Harriss, R.C., and Kaplan, W.A. 1988. Carbon dioxide in the atmosphere over the Amazon Basin. J. Geophys. Res. **93**: 1377–1387.

Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.M., Bakwin, P.S., Daube, B.C., Bassow, S.L., and Bazzaz, F.A. 1993. Net exchange of CO_2 in a mid-latitude forest. Science (Washington, D.C.), **260:** 1314–1317.

Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., and Kaufmann, M.R. 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. **40**: 513–527.

Zabowski, D., and Sletten, R.S. 1991. Carbon dioxide degassing effects on the pH of Spodosol soil solution. Soil Sci. Soc. Am. J. **55**: 1456–1461.