Tree Physiology 21, 309–318

Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California

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Received November 1, 2000

Summary We estimated total ecosystem respiration from a ponderosa pine (*Pinus ponderosa* Dougl. *ex* Laws.) plantation in the Sierra Nevada Mountains near Georgetown, California, from June to October, 1998. We apportioned ecosystem respiration among heterotrophic, root, stem and foliage based on relationships for each component that considered microclimate and vegetation characteristics. We measured each respiration component at selected sampling points, and scaled the measurements up to the ecosystem based on modeled relationships. Over the study period, total mean ecosystem respiration was 5.7 ± 1.3 μmol $m^{-2}s^{-1}$ (based on daily mean), comprising about 67% from soil-surface CO_2 efflux, 10% from stem and branch respiration and 23% from foliage respiration. Shrub leaves contributed about 24% to total foliage respiration, and current-year needles (1998 age class) accounted for 40% of total tree needle respiration. Root respiration accounted for 47% of soil-surface CO_2 efflux. We conclude that ecosystem respiration can be estimated based on daily mean air and soil temperatures through exponential relationships with r^2 values of 0.85 and 0.87, respectively. When based on both air and soil temperatures, about 91% of the variation in total ecosystem respiration could be explained by a linear regression.

Keywords: leaf respiration, microclimate, Q_{10}, soil respiration, soil-surface CO_2 efflux, stem respiration.

Introduction

Forest ecosystems are important in global carbon cycling because 80% of the carbon stored in terrestrial vegetation is forest biomass and forest soil contains more than 70% of the world's soil carbon pool (Post et al. 1982, Olson et al. 1983). Forest ecosystems absorb CO_2 from the atmosphere through photosynthesis and release CO_2 back to the atmosphere through respiration. Because net ecosystem exchange of carbon (NEE) is a small difference between these two large components, NEE is typically an order of magnitude smaller than photosynthesis or respiration (Law et al. 1999*a*, Goulden et al. 1996).

Daytime NEE can be directly measured by the eddy covariance (EC) technique above the canopy. However, nighttime EC measurements may not be reliable at many sites because of the absence of strong turbulence and topography-induced air drainage during the night (Wofsy et al. 1993, Black et al. 1996, Baldocchi et al. 1997, Goldstein et al. 2000). Chamber measurements of respiration of different ecosystem components, such as soil, stem, branch and leaf, provide an independent estimate of ecosystem respiration, which may be used to calibrate or replace the nighttime data measured by EC (Goldstein et al. 2000). Chamber measurements can also be used to examine the contribution of each ecosystem component to total ecosystem respiration.

The ability of a forest ecosystem to sequester atmospheric CO_2 can be enhanced by increasing photosynthetic efficiency or reducing respiration rates or a combination of both. Traditional forest management has focused on maximizing production of timber and non-timber products, and has generally ignored respiration. As concern over CO_2-induced global warming increases globally, forests may in the future be managed not only for timber and non-timber products, but also for CO_2 sequestration. Therefore, ecosystem carbon management may replace traditional forest management as global warming continues to be a focus of research and abatement activities. Ecosystem carbon management demands an understanding of both photosynthesis and respiration because both are important in shaping NEE (Xu 2000), and they may or may not change in concert and magnitude. Although recent research indicates that respiration is the dominant factor determining NEE (Valentini et al. 2000), this remains a controversial issue requiring further examination (Grace and Rayment 2000).

Ecosystem respiration may be partitioned into individual component processes, such as heterotrophic, woody tissue, root, and leaf respiration. Previous studies have extensively focused on one or more of these components (Edwards 1975, Singh and Gupta 1977, Raich and Schlesinger 1992, Ryan et al. 1995, Thierron and Laudelout 1996, Davidson et al. 1998, Epron et al. 1999). Integrative studies of all the major respiration components in one ecosystem have rarely been reported (but see Law et al. 1999*a*), especially in a young ponderosa pine (*Pinus ponderosa* Dougl. *ex* Laws.) ecosystem.

Our long-term goal is to determine how to optimize carbon management of the ponderosa pine ecosystem in northern California. In this study, we used chamber techniques to measure

soil-surface CO_2 efflux (which includes root and heterotrophic respiration), stem respiration and leaf respiration in a young ponderosa pine plantation. We also monitored environmental variables and sampled the vegetation to facilitate scaling up the chamber measurements in both space (to ecosystem scale) and time (to the whole growing season). Our specific objectives were to: (1) quantify the total ecosystem respiration (ER) and the contribution of each component to ER; (2) model heterotrophic, root (including shrub), foliage (including shrub) and stem and branch respiration based on chamber measurements; and (3) examine the effect of temperature on ER.

Materials and methods

Site description

The study site was in a young (approximately 8 years old in 1998) ponderosa pine plantation located (38°53′43″ N, 120°37′58″ W, 1315 m) adjacent to Blodgett Forest Research Station, University of California, Berkeley. The plantation is dominated by ponderosa pine with occasional trees of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gord. & Gelnd.) Lindl.), incense cedar (*Calocedrus decurrens* (Torr.) Florin) and giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz). The major shrubs include manzanita (*Arctostaphylos* spp.) and *Ceonothus* spp.

Based on stems with a diameter at breast height (DBH) greater than 3 cm, the plantation has a mean DBH of 7.6 cm, mean height of 3.4 m, and a density of 1213 stems ha^{-1}. Overstory leaf area index (LAI) was about 4.5 (total needle surface area) in 1998. About 58% of the ground area is covered by trees, 24% by shrubs, and the remaining 18% is grass, stumps and bare soil. The major shrubs had a mean height of about 80 cm and an LAI of 1.6 (total leaf surface area) in 1998.

The site is characterized by a Mediterranean climate with a cold and wet winter and a hot and dry summer. Annual precipitation has averaged 1660 mm since 1961, with the majority of precipitation falling between September and May, and almost no rain in the summer. Mean annual snowfall is 254 cm. The 33-year mean minimum daily temperature in January is 0.6 °C and mean maximum daily temperature in July is 28.3 °C. Trees generally break bud in May and set bud in late July to early August. The year 1998, an El Niño year, was an exception, with new needle elongation starting in June. The following year (1999), a La Niña year, was also an anomalous year, with bud break of the ponderosa pine trees occurring in late April.

The study site is relatively flat with slopes of less than 3° in our sampling area. The soil is a fine-loamy, mixed, mesic, ultic haploxeralf in the Cohasset series whose parent material was andesitic lahar. It is relatively uniform and dominated by loam and clay-loam soils. Coarse woody debris (a result of previous clear-cut harvesting) is scattered on the forest floor. The soil has a pH of 5.5, and comprises 6.9% organic matter and 0.17% total nitrogen.

Vegetation measurements

We established two 20 × 20-m sampling plots with 40 m between the plots (Figure 1). We measured tree height, DBH and crown width in the plots at the beginning and end of the 1998 growing season. We randomly selected a total of 18 trees in the two plots and measured circumference growth with dendrometers about every 2 weeks. We randomly chose a shoot at different heights on six of these trees to monitor needle phenology by measuring length of new needles (i.e., needles produced in 1998) about every 2 weeks.

In early April 2000, we took advantage of a pre-commercial thinning to select 17 trees representative of the diameter distribution of the plantation for biomass sampling. We measured tree height, DBH and crown width before harvest. We then measured needle, branch and stem biomass by allometric methods. We sampled 100 fascicles of varying ages (1, 2 and 3 years old) on six trees, for a total of 1800 fascicles. We used calipers to measure the diameter of each fascicle, and calculated total leaf surface area assuming cylindrical fascicles. Needle, branch and stem samples were oven-dried at 80 °C for 48 h to obtain dry biomass. Timber specific weight was calculated based on stem and branch dry weights and volumes.

We determined mean diameter and height for each clump of shrubs in each plot to provide shrub coverage by area. To measure shrub growth, we randomly selected six 1 × 1-m subplots for detailed sampling. We measured shrub leaf area and aboveground biomass by harvesting in each of the subplots. Three of the subplots were harvested in June, and the other three were harvested in late August. We measured shrub specific leaf area on a representative sample from each subplot with a leaf area measurement system. We calculated shrub LAI at the site based on specific leaf area.

Microclimate measurements

Soil temperatures at 10- and 20-cm depths were monitored at a total of 18 points in the two 20 × 20-m plots (Figure 1) with custom-built thermocouple sensors connected to data loggers (CR10X and 23X, Campbell Scientific, Inc., Logan, UT) located at the center of each plot. In addition, soil temperature at depths of 0, 5, 15, 30, and 50 cm, air temperature at 1.5 m, and

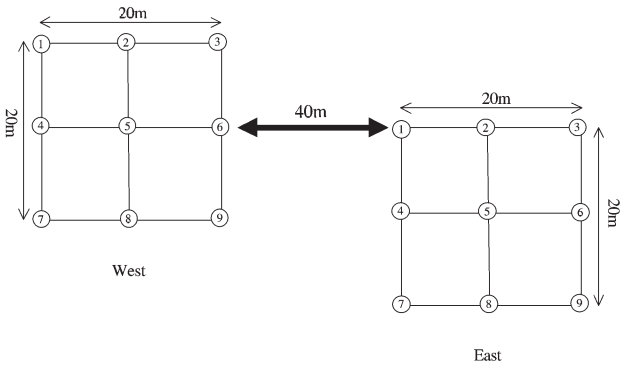

Figure 1. Sample locations for soil respiration and microclimate measurements in the two 20 × 20-m sampling plots.

volumetric soil water (0–30-cm depth average) were monitored at a point in the center of each plot. We used time domain reflectometry (TDR) (CS615 Campbell Scientific, Inc.) to measure volumetric soil water. The data loggers were programmed to sample data every 5 s and store the mean every 5 min, except volumetric soil water data which were sampled and stored every 5 min. Relative humidity and other climate variables were monitored at a meteorological tower on the site.

Soil-surface CO_2 efflux measurement

In each 20 × 20-m plot, soil-surface CO_2 efflux and soil temperature at 5-cm depth were measured on a 3 × 3 matrix spacing 10 m apart (total of 18 sampling locations) (Figure 1). Soil-surface CO_2 efflux was measured with an LI-6400-09 soil chamber (Li-Cor, Inc., Lincoln, NE) connected to a Li-Cor LI-6400 portable photosynthesis system for data collection and storage. Soil temperature was logged with a temperature probe provided with the LI-6400. Healy et al. (1996) provides a complete description of the soil chamber operations. One complete measurement cycle, including chamber setup, attachment, and CO_2 efflux measurement took 1–2 min, depending on the respiration rate.

Soil-surface CO_2 efflux measurement commenced in June 1998 and was performed biweekly through August, followed by monthly measurements through November. In mid-November 1998, we relocated the soil collars to adjacent areas (within 20–30 cm of the original location) and cored the soil at the former location. A soil sample was obtained every 10 cm to a depth of 50 to 70 cm with a 10.4-cm-diameter soil auger. The soil samples were taken to the laboratory to determine root biomass, microbial biomass and physical and chemical properties of the soil.

We separated roots from each soil sample. Roots were classified into three categories: fine (≤ 1 mm), small (1–5 mm), and medium (> 5 mm). We did not find any roots with diameters greater than 5 cm in our samples. Dead and live roots were distinguished by their color and elasticity. Roots were oven-dried at 70 °C for 48 h and weighed (± 0.1 mg). Xu and Qi (2001) provide details on these measurements and their analysis.

Stem respiration measurement

We used the horizontally oriented soil chamber (HOSC) technique to measure stem respiration (Xu et al. 2000). The HOSC technique extends the function of the Li-Cor LI-6400-09 soil chamber to measure stem respiration by means of a soil collar fastened to the stem. The soil chamber (9.9 cm diameter) was connected horizontally to the soil collar (10.1 cm diameter) and held in place with bungee cords during measurements. We chose seven ponderosa pine trees in the western 20 × 20-m plot for stem respiration measurements. The DBH of the selected trees ranged from 8.7 to 15 cm. We measured respiration on both the north and south sides of the stems at a height of about 1.4 m. We also measured respiration at different heights on two trees. We measured stem respiration every 2 to 4 weeks from July to November 1998.

To measure the temperature of sapwood, we hand-drilled a hole about 5 cm below the collar, and about 3 cm deep into the stem, corresponding to an approximate depth of 1 cm past the cambium into the sapwood. This opening allowed insertion of the soil temperature probe to measure the sapwood temperature during respiration measurements. This method was later improved by using thermocouples connected to a data logger to reduce sampling error and provide continuous temperature data.

Leaf respiration measurement

Nighttime leaf respiration was measured monthly from May through August 1998 with a Li-Cor LI-6400 portable photosynthesis system (Goldstein et al. 2000, Panek and Goldstein 2000). Fascicles on branches at different heights and orientations were chosen within the crowns of six trees. Needles of various ages were selected for respiration measurements, and needle temperature was simultaneously monitored.

Biomass data analysis

Based on our analysis of 17 representative trees harvested during the April 2000 pre-commercial thinning, we developed an equation to estimate stem and branch biomass (M_{sb}) as a function of DBH (Figure 2):

$$M_{sb} = \exp[4.78 + 2.11 \ln(\mathrm{DBH})] \quad (r^2 = 0.99, n = 17, P < 0.0001). \tag{1}$$

The relationship between stem and branch biomass and DBH appeared to be nonlinear. Xu (2000) provides additional details on this curve fitting process and results. We used the best-fit equation to estimate stem and branch biomass for each tree in each sampling plot at the beginning and end of the growing season. Sapwood volume was derived by dividing branch and stem biomass by specific weight (0.42 g cm^{-3}), which assumes no heartwood in the young trees.

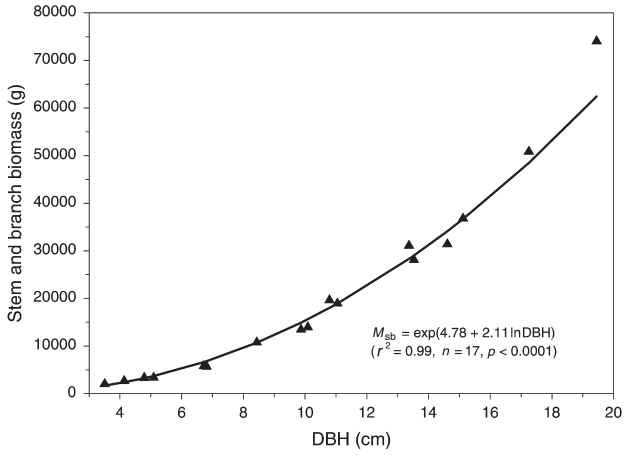

Figure 2. Relationship between stem + branch biomass and tree diameter at breast height (DBH).

Seasonal dynamics of woody biomass growth were estimated by distributing the entire season's measured growth according to a nonlinear process (Xu 2000). Based on our dendrometer readings, we fitted a Rayleigh distribution curve to estimate seasonal diameter growth (Figure 3) (Abramowitz and Stegun 1972). Based on seasonal diameter growth, we estimated seasonal biomass dynamics with Equation 1.

We used Equation 1 and the seasonal woody tissue growth distribution curve presented in Figure 3, to predict the dynamics of stem and branch biomass per unit ground area during the 1998 growing season (Figure 4). As illustrated, most biomass growth occurred in July and August (approximately Days 185 through 235).

Leaf area data analysis

Based on our analysis of trees harvested during the pre-commercial thinning in April 2000, leaf area by age class was calculated by multiplying specific leaf area (0.90 $m^2\ g^{-1}$ for new needles, 0.81 $m^2\ g^{-1}$ for old needles) with needle biomass (by age class). We then used these results to develop an equation to estimate leaf area per tree (LA) by age class as a function of DBH (Figure 5):

$$\text{LA (new needles)} = 0.402\,\text{DBH}^{1.67} \quad (r^2 = 0.97,\ n = 17,\ P < 0.0001), \tag{2}$$

$$\text{LA (old needles)} = 0.305\,\text{DBH}^{1.83} \quad (r^2 = 0.93,\ n = 17,\ P < 0.0001). \tag{3}$$

New needles were defined as those grown in 1999, and old needles were those grown in 1998 and earlier. Figure 5 indicates a nonlinear relationship between ponderosa pine LA and DBH, and including tree height in the equation did not significantly improve the fitting. We computed tree LAI in each 20 × 20-m plot by summing the estimated leaf area of each tree in the plot and dividing by the total area of the plot. Shrub LAI was derived from shrub specific leaf area and total leaf biomass. Total leaf biomass was obtained by scaling the data from the 1 × 1-m subplots up to the 20 × 20-m plots.

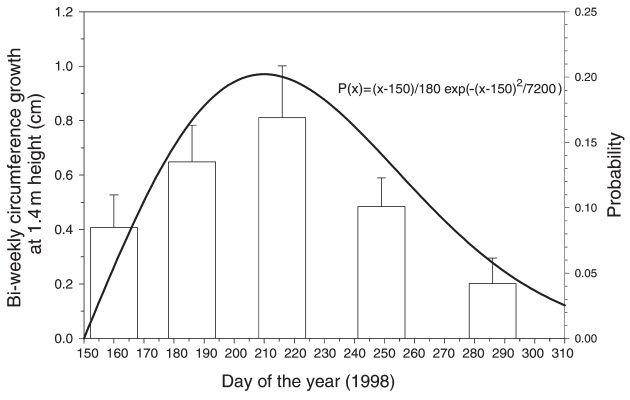

Figure 3. Seasonal tree diameter growth and its curve fitting based on a Rayleigh distribution.

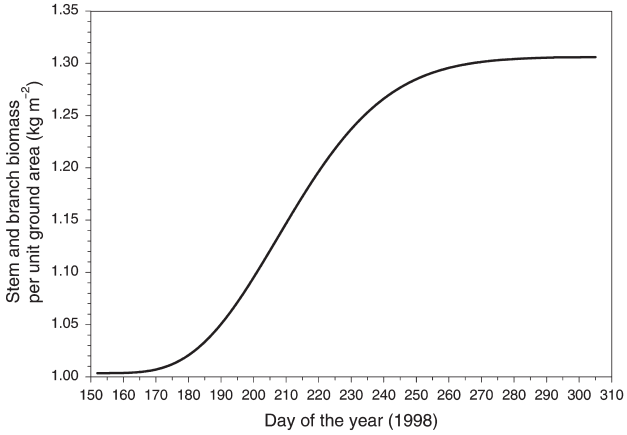

Figure 4. Cumulative stem + branch biomass per unit ground area over the period of measurement (1998).

Figure 6 shows leaf growth dynamics during the 1998 growing season for trees and shrubs. We distributed the increase in tree and shrub LAI during the growing season based on our measurement of new needle growth and linear interpolation between individual measurements. Xu (2000) has presented the details of the seasonal dynamics of LAI. The range of LAI for shrubs and trees was 0.7–1.6 and 2.8–4.6, respectively. Shrub LAI tended to increase faster in the early part of the growing season, whereas tree LAI tended to increase more quickly near the middle of the growing season.

Respiration data analysis

Equation 4 was used to estimate needle respiration by age class:

$$R_{\text{leaf}} = \text{LAI}\ a\ \exp\{b(T_{\text{leaf}} - T_{\text{ref}})\}, \tag{4}$$

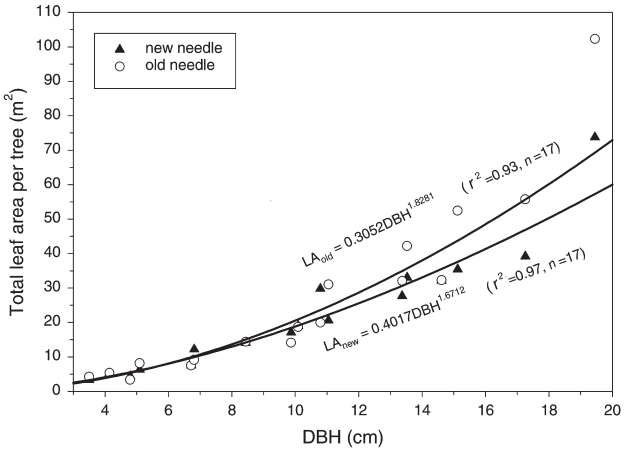

Figure 5. Relationship between total tree leaf area and tree diameter at breast height (DBH) for new (grown in 1999) and old (grown in 1998 and earlier) needles. The results are based on an analysis of trees harvested in April 2000.

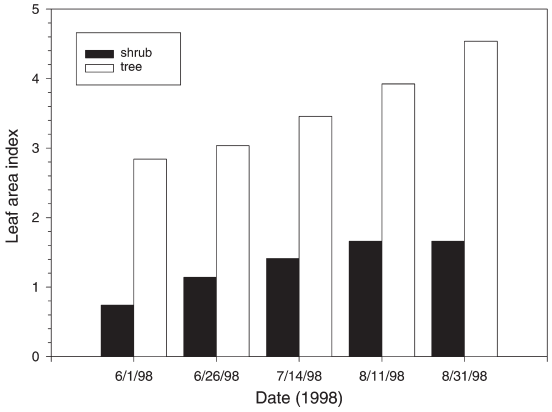

Figure 6. Tree and shrub leaf area index development during the measurement period (1998).

where R_{leaf} is ecosystem scale leaf respiration (μmol $m^{-2}s^{-1}$), LAI is leaf area index, T_{ref} is reference temperature (10 °C), and T_{leaf} is leaf temperature (°C). Parameters a and b were empirically fit to the dark respiration measurements for both old ($a = 0.17$, $b = 0.047$, $r^2 = 0.85$) and new ($a = 0.17$, $b = 0.090$, $r^2 = 0.80$) needles (Goldstein et al. 2000). We represented leaf growth dynamics by applying a time-dependent LAI, and used air temperature as a proxy for needle temperature.

Leaf respiration of shrubs was calculated with Equation 4 and the parameter values derived for old ponderosa pine needles. Similar to our ponderosa pine needle respiration calculation, we assumed air temperature adequately approximated shrub leaf temperature and we applied a time-dependent LAI to represent leaf growth dynamics.

We used least square techniques to model the relationship between stem respiration and sapwood temperature by a nonlinear curve:

$$R = \beta_0 e^{\beta_1 T}, \tag{5}$$

where R is measured stem respiration (μmol $m^{-1}s^{-2}$), T is sapwood temperature (°C), and β_0 and β_1 are fitting parameters. This exponential relationship is commonly used to represent respiration rate as a function of temperature (Ryan et al. 1995, Carey et al. 1996, Edwards and Hanson 1996, Lavigne and Ryan 1997). We used a separate equation (i.e., unique fitting parameter values) for each month to capture changes in phenology. The Q_{10} values were calculated as:

$$Q_{10} = e^{10\beta_1}. \tag{6}$$

Because we lacked continuous measurements of sapwood temperature in 1998, we used soil temperature at 5-cm depth to estimate sapwood temperature because it has a similar thermal inertia. Sapwood and soil temperatures were highly correlated (data not shown):

$$T_{sapwood} = 3.06 + 0.92 T_{soil} \quad (r^2 = 0.93,\ n = 77,\ P < 0.0001). \tag{7}$$

We used the estimated sapwood temperature to calculate woody respiration for the whole study period.

To estimate stem respiration of the entire 20 × 20-m plot, we converted stem respiration from a surface area to a sapwood volume based respiration as follows:

$$E_v = \frac{S}{V} E_s = \frac{\pi D\, h \times 10^{-2}}{S_{sapwood}\, h \times 10^{-4}} = \frac{100\,\pi D}{\pi D^2/4} E_s, \quad E_v = \frac{400 E_s}{D}, \tag{8}$$

where E_v is CO_2 efflux per unit of sapwood volume (μmol m^{-3} s^{-1}), E_s is CO_2 efflux per unit stem surface area (μmol m^{-2} s^{-1}), D is stem diameter (cm), S and V are stem surface area (m^2) and sapwood volume (m^3), respectively, of the stem cylinder cross section defined by the top and bottom of the soil respiration chamber, h is height of the stem cylinder (also the diameter of the soil respiration chamber) (m), and $S_{sapwood}$ is sapwood cross-sectional area (cm^2). Based on our estimate of sapwood volume from biomass measurements, we converted E_V to total stem respiration for each 20 × 20-m plot.

Soil-surface CO_2 efflux was modeled using soil temperature (10-cm depth) and soil volumetric water (0–30 cm average) by the following equation:

$$F = \beta_0 W^{\beta_1} e^{\beta_2 T}, \tag{9}$$

where F is soil-surface CO_2 efflux rate (μmol m^{-2} s^{-1}), W is soil volumetic water (%), T is soil temperature (°C at 10 cm), and β_0, β_1, and β_2 are constants fitted by the least square technique. Most modeling approaches assume $\beta_1 = 1$, but we found a better fit by introducing β_1 as a parameter. We used a separate equation (i.e., unique fitting constant values) for each month to capture changes in phenology. Xu and Qi (2001) have a detailed description of this model.

We separated root respiration from soil-surface CO_2 efflux by using a regression between soil-surface CO_2 efflux and root density (Kucera and Kirkham 1971, Behera et al. 1990). Based on our categorization of roots, we compared soil-surface CO_2 efflux and various groupings of root size, and found that soil-surface CO_2 efflux and fine root biomass were significantly correlated through a simple linear regression:

$$R = 2.36 + 0.001 M_r \quad (r^2 = 0.52,\ n = 18,\ P < 0.001), \tag{10}$$

where R is soil-surface CO_2 efflux (μmol m^{-2} s^{-1}), M_r is fine and small root biomass (g; < 5 mm) in the 0–50 cm soil layer. By using the y-intercept value to estimate mean heterotrophic respiration, we calculated that root respiration accounts for 46.7% of total soil-surface CO_2 efflux during the growing season. This ratio was used to apportion our soil-surface CO_2

efflux measurement between root respiration and heterotrophic respiration. We note that this equation does not consider seasonal changes in root biomass, and there may be a bias in the root respiration apportionment because of the root biomass present in November.

To compare the contribution of each respiration component to ER, we converted all respiration fluxes to units of μmol s^{-1} per square meter of ground surface. We note that the converted respiration fluxes were calculated based on our field measurements and the modeled relationships. Other tree species occasionally encountered in our plots were treated as ponderosa pine trees for the purpose of estimating ER; however, their influence on the results is marginal because there was a total of only five white fir and three Douglas-fir trees in the two plots.

Results

Microclimate

Figure 7 presents daily mean air and soil (5 cm) temperatures measured during the 1998 growing season. Generally, these temperatures varied concurrently, although soil temperature lagged air temperature because of the soil's higher heat capacity. Figure 7 shows daily mean relative humidity and volumetric soil water versus day of the year for 1998. Relative humidity varied dramatically during the season, whereas volumetric soil water declined steadily during the hot, dry Mediterranean summer.

Soil-surface CO_2 efflux

We used Equation 9 to model daily mean soil-surface CO_2 efflux based on the daily mean soil temperature and volumetric soil water data (Figures 7 and 8). Figure 8 shows the variations in daily mean soil-surface CO_2 efflux, heterotrophic respiration, and root respiration over the 1998 growing season. Soil-surface CO_2 efflux was allocated to heterotrophic and root respiration based on the analysis of Equation 10. There may be a bias in the root respiration estimate because it was based on a single sampling of root biomass in November. Volumetric soil water peaked around Day 160 and then declined during the remainder of the season, whereas soil-surface CO_2 efflux peaked around Day 190 because of the joint effects of soil temperature and water content on heterotrophic and root respiration. Although daily mean soil temperature peaked near Days 215 and 225, volumetric soil water had declined sufficiently to constrain soil-surface CO_2 efflux to about 80% of its maximum on Day 160.

Stem respiration

Figure 9 shows stem respiration as a function of sapwood temperature for four of our seven subject trees during 1998. Sapwood temperature explained 82–96% of the variation in stem respiration. Although the trees were of similar age and DBH and grew under similar conditions, they exhibited different respiration characteristics on a unit area basis. The Q_{10} values (indicative of temperature sensitivity) also varied from 2.4 to 2.9 among the trees.

Based on the correlation between sapwood and soil temperature (Equation 8) and the estimated sapwood volume for both 20 × 20-m plots, we calculated stem and branch respiration per unit ground area for the growing season (Figure 10). Stem and branch respiration varied in unison with soil temperature (see Figure 7) based on the linear regression between these param-

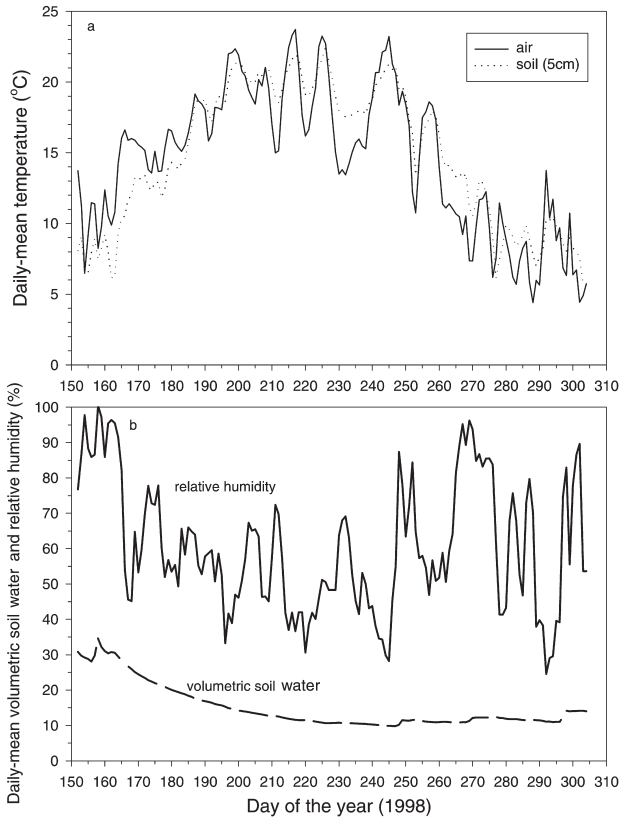

Figure 7. Seasonal trends in (a) daily mean air (at 1.5 m aboveground) and soil (at 5-cm depth) temperature and (b) daily mean relative humidity (%) and volumetric soil water (%; 0–30 cm mean depth).

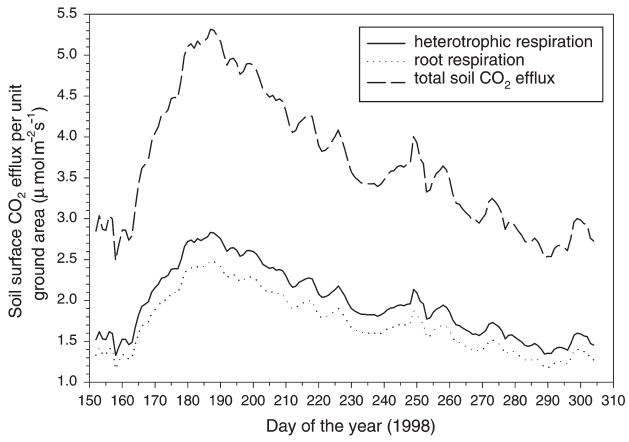

Figure 8. Seasonal trends in soil and root respiration per unit ground area.

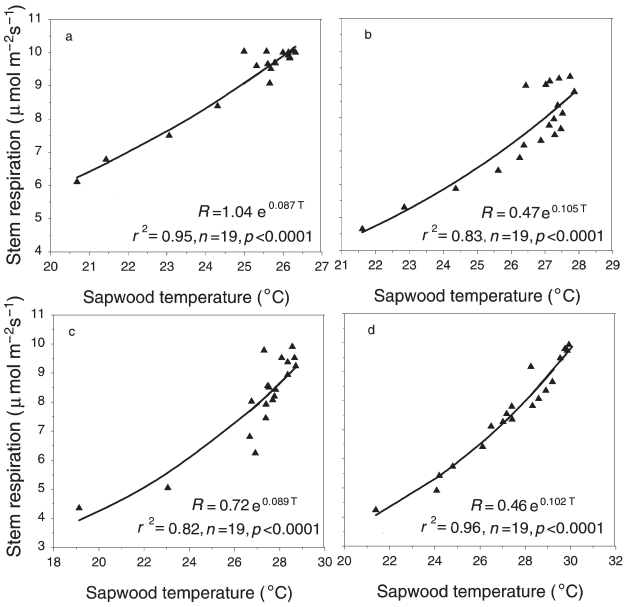

Figure 9. Exponential curve fitting between stem respiration and sapwood temperature for four representative ponderosa pine trees.

eters. Stem and branch respiration had a strong seasonal variation, ranging from a minimum of about 0.2 μmol m^{-2} s^{-1} to a maximum of 0.85 μmol m^{-2} s^{-1} in August. Short-term variation (1–2 week time scale) was also detected (Figure 10).

Leaf respiration

Figure 11 illustrates respiration of both new (1998 age class) and old (1995–97 age class) needles during the growing season. Although needle respiration is driven by air temperature, variations in needle respiration did not track variations in air temperature closely because needle LAI increased during the growing season. However, the major peaks and troughs in Figure 11 corresponded to similar air temperature fluctuations. Total needle respiration increased rapidly from 0.5 μmol m^{-2} s^{-1} in June to about 2.0 μmol m^{-2} s^{-1} in early August, followed by a sharp decrease to about 1.0 μmol m^{-2} s^{-1} in late August. Needle respiration reached an annual peak of 2.4 μmol m^{-2} s^{-1} in early September, followed by a rapid decrease to about 0.6 μmol m^{-2} s^{-1} in late fall.

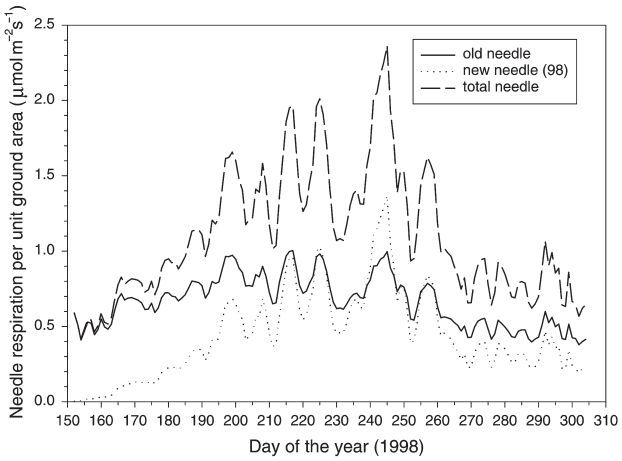

Figure 11. Seasonal trend in tree needle respiration per unit ground area.

Although LAI of new needles was only about half that of old needles in midsummer, the magnitude of new needle respiration was equivalent to old needle respiration (see parameter values for Equation 4). In addition, respiration of new needles was more sensitive to temperature fluctuations. Respiration of old needles was fairly constant throughout the season, varying from about 0.4 to 0.9 μmol m^{-2} s^{-1}.

Shrub respiration followed a similar seasonal pattern to that of needle respiration (Figure 12). Shrub respiration increased rapidly from 0.1 μmol m^{-2} s^{-1} in June to an annual peak of about 0.6 μmol m^{-2} s^{-1} in early August, followed by a sharp decrease to about 0.35 μmol m^{-2} s^{-1} in late August. Shrub respiration recovered to about 0.55 μmol m^{-2} s^{-1} in early Septem-

Figure 10. Seasonal trend in stem + branch respiration per unit ground area.

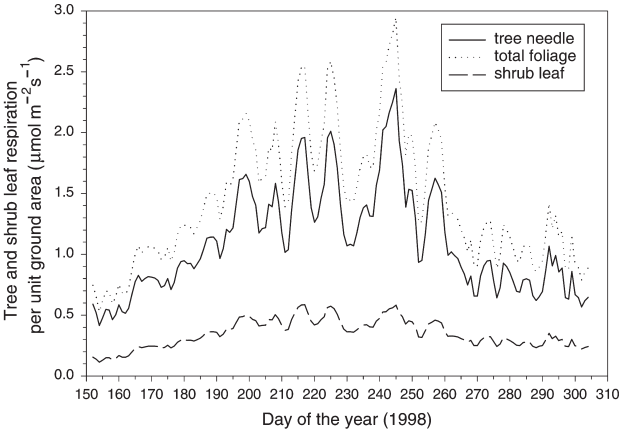

Figure 12. Comparison of the seasonal trends in total foliage respiration, tree needle respiration and shrub leaf respiration per unit ground area.

ber, followed by a steady decrease to about 0.25 μmol m^{-2} s^{-1} in late fall. Total foliage respiration was dominated by needle respiration in magnitude and pattern (Figure 12). Total foliage respiration varied from about 0.5 to 2.9 μmol m^{-2} s^{-1}. The contribution of shrub respiration to total foliage respiration was less than 23%.

Ecosystem respiration (ER)

Total ecosystem respiration per unit ground area varied from 3.4 to 7.8 μmol m^{-2} s^{-1} (Figure 13). The seasonal pattern of ER was asymmetric. It increased rapidly from the seasonal minimum (in early June) to the seasonal maximum (in mid-July), followed by a gradual decrease punctuated by short-term (~1 week) spikes and troughs through early September. From early September to early October, ER dramatically decreased from about 7.5 to 3.5 μmol m^{-2} s^{-1}.

Figure 14 shows the relative contribution of heterotrophic, woody tissue (root and stem + branch), and foliage respiration to ER. We included roots as part of woody tissue, but note that this grouping contrasts with previous studies that considered only aboveground woody tissue (stem and branches). On average, woody tissue, heterotrophic, and foliage respiration accounted for 40, 35, and 25% of ER, respectively (Table 1). Although the ratio of woody tissue respiration to ER varied from 34 to 45%, it was the dominant component throughout the season. The contribution of heterotrophic respiration to ER gradually declined from 40% in early June to 26% in late August, followed by an increase to 35% in early October. The ratio of foliage respiration to ER increased from 15% in early June to about 40% in early September, followed by a sharp decrease by mid-September, before fluctuating around 25% through to the end of the season. The ratio of foliage respiration to ER exhibited significantly greater short-term variability than the ratios of the other components.

Based on our modeling work, root respiration and heterotrophic respiration contributed roughly equally to soil-surface CO_2 efflux, which comprises 65% of ER. Root respiration dominated woody tissue respiration, contributing 76% to the total. Stem and branch respiration comprised about 10% of ER (Table 1).

Figure 13. Seasonal trend in total ecosystem respiration per unit ground area.

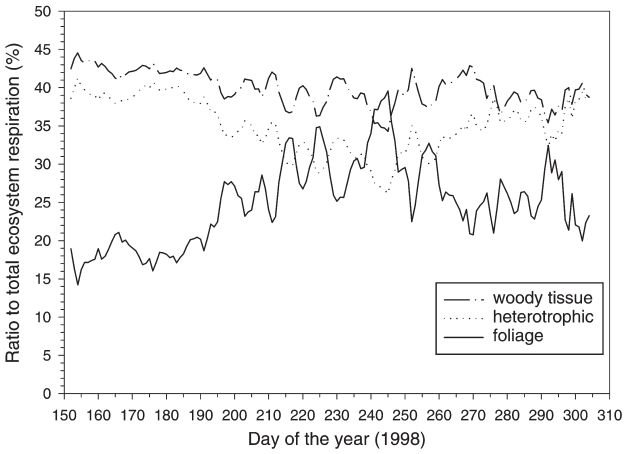

Figure 14. Seasonal patterns of the contribution of woody tissue (root + stem + branch), heterotrophic, and total foliage respiration to total ecosystem respiration.

Ecosystem respiration and temperature

Air and soil temperature were strongly correlated with ER, explaining 85 and 87% of the variation in ER, respectively. The r^2 values based on linear and exponential fitting were close. The exponential fits were:

$$ER = 2.93\, e^{0.0436 T_a} \quad (r^2 = 0.85,\ n = 153,\ P < 0.0001), \tag{11}$$

$$ER = 2.86\, e^{0.0448 T_s} \quad (r^2 = 0.87,\ n = 153,\ P < 0.0001), \tag{12}$$

where ER is daily mean ecosystem respiration (μmol m^{-2} s^{-1}), T_a and T_s are daily mean air (°C at 1.5 m) and soil temperature (°C at 5 cm in depth), respectively. The Q_{10} value was about 1.6 for both air and soil temperature.

When based on both air and soil temperatures, about 91% of the variation in ER could be explained by a linear regression:

$$ER = 1.97 + 0.12 T_a + 0.13 T_s \quad (r^2 = 0.91,\ n = 153,\ P < 0.0001), \tag{13}$$

where T_a is air temperature and T_s is soil temperature.

Discussion

A seasonal mean ER rate of 5.7 ± 1.3 μmol m^{-2} s^{-1} was calculated from the daily mean respiration rates for each component. This value is generally higher than other published values for ponderosa pine ecosystem respiration. Anthoni et al. (1999) reported an ER rate of 3.4 and 4.2 μmol m^{-2} s^{-1} for the 1996 and 1997 growing seasons, respectively, for a stand that is a mixture of old-growth (250-year-old) and young

Table1. Ecosystem respiration (ER) components and their contribution. Mean, minimum and maximum are derived from the daily mean respiration rate.

Components	Components	Mean ($\mu mol\ m^{-2}s^{-1}$)	Minimum ($\mu mol\ m^{-2}s^{-1}$)	Maximum ($\mu mol\ m^{-2}s^{-1}$)	Conribution to ER (%)
Leaf	All	1.45	2.94	0.53	25.4
	Shrub	0.35	0.59	0.11	6.1
	New needle	0.44	1.40	0.00	7.7
	Old needle	0.66	1.00	0.38	11.6
Soil	Heterotrophic	2.00	2.80	1.30	34.6
Woody Tissue	All	2.27	3.10	1.41	39.8
	Root	1.72	2.50	1.20	30.2
	Stem and Branch	0.54	0.86	0.21	9.5

(45-year-old) ponderosa pine trees in central Oregon. Law et al. (1999*b*) reported a nocturnal ER rate of 3.6 $\mu mol\ m^{-2}\ s^{-1}$ for the 1997 growing season, with an annual mean of 2.4 $\mu mol\ m^{-2}\ s^{-1}$ (Law et al. 1999*a*) at the same site. We believe the high organic matter input from previous harvesting around 1990 and the higher annual precipitation (1660 versus 600 mm) at our site partially explains the difference in ER between the two sites (Xu and Qi 2001). Soil-surface CO_2 efflux (heterotrophic + root respiration) is a major component of ER at both sites, and is sensitive to soil water, temperature, and soil organic matter content (Davidson et al. 1998, Fang et al. 1998, Epron et al. 1999, Xu and Qi 2001). The mean soil-surface CO_2 efflux for July and August was 2.5 $\mu mol\ m^{-2}\ s^{-1}$ at the Oregon site versus 4.3 $\mu mol\ m^{-2}\ s^{-1}$ at our site.

The contribution of leaf respiration, stem + branch respiration, and soil-surface CO_2 efflux to ER was 17.6, 6.0, and 76.4%, respectively, in a ponderosa pine forest in Oregon (Law et al. 1999*a*). The corresponding values at our site were 25.4, 9.5, and 64.8%, respectively. The lower percentage of leaf respiration to ER at the Oregon site is primarily a result of the low LAI at that site (1.5 hemi-leaf surface area). In addition, shrub respiration was negligible at the Oregon site, whereas it accounted for about 6% of ER at our site. The higher percentage of stem + branch respiration at our site than at the Oregon site (9.5 versus 6%) may be caused by the higher growth rate of our young trees. Raich and Schlesinger (1992) estimated that soil-surface CO_2 efflux was 48 to 71% of ER, and our result (64%) is within the upper part of this range.

Our estimates of soil-surface CO_2 efflux are generally higher than those for the Oregon site (0.5–3.7 $\mu mol\ m^{-2}\ s^{-1}$; Law et al. 1999*a*) and for a beech forest in France (0.4–4.0 $\mu mol\ m^{-2}\ s^{-1}$; Epron at al. 1999). Again, the high soil organic matter from previous harvesting and high growth rate of the young trees may have contributed to this difference. However, our estimates of soil-surface CO_2 efflux are lower than those of Thierron and Laudelout (1996), who reported that daily mean CO_2 efflux varied from 3.2 to 10.7 $\mu mol\ m^{-2}\ s^{-1}$ in June in a deciduous forest in France. The different tree species and different climate regimes may explain this difference.

We found that root respiration accounted for 47% of total soil-surface CO_2 efflux, which is within the reported range of 30–90% (Bowden et al. 1993, Thieron and Laudelout 1996, Epron et al. 1999). By comparing root respiration in different forest types, Nakane et al. (1996) concluded that the proportion of root respiration to soil-surface CO_2 efflux may approach 50% irrespective of forest type, when the cycle of soil carbon is near a dynamic equilibrium in a forest ecosystem. Our regression method for estimating the ratio of root respiration to total soil-surface CO_2 efflux may not accurately quantify the seasonal pattern of root respiration because we applied one ratio to the whole growing season. We also sampled root biomass in November when root biomass may be near its seasonal peak, which would tend to overestimate the root respiration component. In addition, the assumption that the spatial variation of soil-surface CO_2 efflux is caused by the spatial variation of root biomass may be inaccurate because of the heterogeneity of the soil and forest floor (Behera et al. 1990). Sample size may also introduce biases to the results (Nakane et al. 1996). However, some researchers have successfully used the regression method to separate root respiration from soil-surface CO_2 efflux (Kucera and Kirkham 1971, Behera et al. 1990). Furthermore, application of this regression method will not influence the overall estimates of soil-surface CO_2 efflux and ecosystem respiration.

Scaling up based on stem respiration rate measurements and sapwood volume may underestimate total stem respiration rates because younger woody tissues will have higher respiration rates. On the other hand, scaling up based on stem and branch surface area will overestimate stem respiration. We measured stem respiration at different heights on two trees, and these unpublished data corroborate this assertion. Future studies are required to develop a more accurate scaling up scheme.

A detailed knowledge of the seasonal behavior of total ecosystem respiration and its apportionment between the different components is critical to understanding ecosystem carbon balance. It is important to examine ecosystem respiration at annual and longer temporal scales, because interannual and decadal variation of climate and vegetation may influence the contribution of each component to the total ecosystem respiration. Further studies at different temporal and spatial scales are needed. This study is among the efforts aimed at understand-

ing ecosystem respiration at a specific scale.

Acknowledgments

We thank Wenzhi Zhao, Chang Che, Jianwu Tang, Qinghua Guo, Meredith Bauer, Megan McKay, Jeanne Panek, Gunnar Schade, Michael Dillon, Margaret Torn, Kevin Tu, Robert Heald, David Rambeau and Sheryl Rambeau for their assistance in field data collection. We thank Dennis Baldocchi for his constructive comments. We also thank Dr. John Battles for allowing us to use his leaf area imaging system. The University of California at Berkeley funded this study. Terry DeBiase was supported by the W.S. Rosecrans and William Siggins Fellowships.

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