Forest thinning and soil respiration in a ponderosa pine plantation in the Sierra Nevada

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Summary Soil respiration is controlled by soil temperature, soil water, fine roots, microbial activity, and soil physical and chemical properties. Forest thinning changes soil temperature, soil water content, and root density and activity, and thus changes soil respiration. We measured soil respiration monthly and soil temperature and volumetric soil water continuously in a young ponderosa pine (Pinus ponderosa Dougl. ex P. Laws. & C. Laws.) plantation in the Sierra Nevada Mountains in California from June 1998 to May 2000 (before a thinning that removed 30% of the biomass), and from May to December 2001 (after thinning). Thinning increased the spatial homogeneity of soil temperature and respiration. We conducted a multivariate analysis with two independent variables of soil temperature and water and a categorical variable representing the thinning event to simulate soil respiration and assess the effect of thinning. Thinning did not change the sensitivity of soil respiration to temperature or to water, but decreased total soil respiration by 13% at a given temperature and water content. This decrease in soil respiration was likely associated with the decrease in root density after thinning. With a model driven by continuous soil temperature and water time series, we estimated that total soil respiration was 948, 949 and 831 g C m⁻² year⁻¹ in the years 1999, 2000 and 2001, respectively. Although thinning reduced soil respiration at a given temperature and water content, because of natural climate variability and the thinning effect on soil temperature and water, actual cumulative soil respiration showed no clear trend following thinning. We conclude that the effect of forest thinning on soil respiration is the combined result of a decrease in root respiration, an increase in soil organic matter, and changes in soil temperature and water due to both thinning and interannual climate variability.

Keywords: carbon cycle, CO₂ efflux, modeling, multivariate analysis.

Introduction

Studies on soil carbon have received much attention because a small change in the soil carbon pool may significantly affect the global carbon cycle and climate system. Soil respiration may accelerate global warming by acting as a positive feedback in the global carbon cycle (Jenkinson et al. 1991, Kirschbaum 1995, Trumbore et al. 1996, Cox et al. 2000). The multiple components of soil respiration, such as root respiration and microbial respiration, and multiple controls, such as soil temperature, soil water, vegetation functional properties, microbial activity, soil organic carbon content, and soil physical and chemical properties, result in high variability in and sensitivity of soil respiration to different factors. Although there has been much consensus on modeling soil respiration in relation to soil temperature, particularly with exponential functions, there is little consensus on the functional form needed to represent effects of water on soil respiration in various ecosystems (Lloyd and Taylor 1994, Fang and Moncrieff 2001, Oi and Xu 2001).

In addition to the temporal and spatial variation in soil respiration caused by natural factors, human disturbance and management affect soil respiration and soil carbon pools. Forest management practices, such as thinning, pruning, harvesting, fertilization and prescribed fire, may influence soil carbon by changing ground surface energy balance, soil water content, nutrient availability and vegetation production. Based on a literature review, Johnson and Curtis (2001) concluded that forest harvesting and fire have no significant effects on soil carbon storage, whereas fertilization and nitrogen-fixing vegetation increase overall soil carbon.

Among published studies of management impacts on soil carbon pools, relatively few have examined the impacts on soil respiration or the dynamics of soil carbon pools. Nakane et al. (1986) found that soil respiration decreased after harvesting because of the cessation of root respiration. Toland and Zak (1994) reported that soil respiration in intact and clear-cut plots did not differ significantly because the increase in microbial respiration in clear-cut plots offset the decrease in root respiration after clear-cutting. Striegl and Wickland (1998) concluded that clear-cutting a mature jack pine woodland reduced soil respiration as a result of disruption of the soil surface and death of tree roots. Ohashi et al. (1999) reported that

soil respiration in a Japanese cedar forest 3–4 years after thinning was higher than in an intact stand, but there was no difference 5 years after the thinning.

Thinning, defined as the partial removal of trees from a plantation, is an important and common silvicultural practice. The purpose of thinning is to reduce competition, improve tree productivity, reduce the wildfire risk and maintain a healthy forest. Thinning decreases stand density and leaf area, increases light and nutrient availability, and changes soil temperature, soil water, belowground root density and the microbial community. Despite the extent of thinning as a forest management practice, there are few studies on the impacts of thinning on plant respiration and carbon allocation (e.g., Lavigne 1988*a*, 1988*b*, 1991), and we are aware of only one published report on the impact of forest thinning on soil respiration (Ohashi et al. 1999).

The purposes of this study were to: (1) investigate and compare the spatial and temporal patterns of soil respiration before and after a pre-commercial thinning; (2) simulate soil respiration using two variables, soil temperature and water, and incorporate the thinning effect into the model; and (3) estimate the annual carbon loss from soil respiration before and after thinning.

Materials and methods

Site description

The study site, a part of the AmeriFlux network, is in a young ponderosa pine (Pinus ponderosa Dougl. ex P. Laws. & C. Laws.) plantation (38°53'42.9" N, 120°37'57.9" W, elevation 1315 m) adjacent to the Blodgett Forest Research Station, a research forest of the University of California, Berkeley. The plantation is dominated by young ponderosa pine planted in 1990 after clear-cutting. Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), white fir (Abies concolor (Gord.) Lindl. ex Hildebr.), incense cedar (Calocedrus decurrens (Torr.) Florin), giant sequoia (Sequoiadendron giganteum (Lindl.) Buchh.) and California black oak (Quercus kelloggii Newb.) occur sparsely in the overstory canopy. The plantation had a mean diameter at breast height (DBH) of 7.6 cm, a mean height (DBH > 3 cm) of 3.4 m and a density (DBH > 3 cm) of 1213 stems ha⁻¹ in 1998. Overstory leaf area index (LAI, all-sided) was about 4.5 at the end of the 1998 growing season. The major shrubs were manzanita (Arctostaphylos spp.) and Ceonothus spp. In 1998, about 58% of the ground area was covered by trees, 24% by shrubs, and the remaining 18% was grass, stumps and bare soil (Goldstein et al. 2000, Xu and Qi 2001a).

The site is characterized by a Mediterranean climate with a hot dry summer, and a relatively cold wet winter. Most precipitation, which has averaged 1660 mm since 1961 and consists of about 75% rain and 25% snow, falls between September and May with almost no rain in the summer. The site is periodically covered by snow in winter. The mean (over 33 years) minimum daily temperature in January is 0.6 °C and the 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 study site is relatively flat with slopes 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 sandy-loam with 60% sand, 29% silt and 11% clay. Coarse woody debris is scattered on the forest floor from the residuals of the previous harvest (clear-cutting). The soil at 0–30-cm depth had a mean organic matter content of 6.9%, and a total nitrogen content of 0.17% measured in 1998. More detailed site descriptions can be found in Goldstein et al. (2000) and Xu and Qi (2001a).

In spring 1999, most shrubs in this plantation were manually cut at the base of the trunk, but shrubs in the plots where soil respiration was measured were not removed in order to maintain consistent measurements over time. During spring 2000, the whole plantation was thinned including our measurement plots where the thinning was conducted on May 25, 2000. The thinning retained the largest and most valuable trees and evened the distribution of the remaining trees. About 60% of trees and 30% of total biomass and LAI including most shrubs were cut down and mulched mechanically. The locations where we measured soil respiration were carefully protected from soil disturbance during thinning.

Field measurements

We established two $20 \times 20 \text{ m}^2$ sampling plots, 40 m apart within the footprint area of the Blodgett Forest AmeriFlux tower. Soil respiration and soil temperature at 10-cm depth were measured on a 3 × 3 matrix at 10-m intervals resulting in nine sampling points in each plot for a total of 18 measurement locations. We also monitored volumetric soil water at 0-30-cm depth at the center of each plot. Soil respiration was measured with an LI-6400-09 soil chamber connected to an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE) for data collection and storage. A soil collar, with a height of 4.4 cm and a diameter of 11 cm, was permanently inserted in the soil at each sampling point. We used custom-built thermocouple sensors to monitor soil temperature, and a time domain reflectometry system (TDR, CS615 Campbell Scientific, Logan, UT) vertically inserted into the soil to monitor volumetric soil water. Campbell Scientific data loggers (Models CR10X and 23X) were programmed to store temperature and soil water data every 5 min. Air temperature, precipitation and other meteorological parameters were measured every half an hour at the nearby AmeriFlux tower (Goldstein et al. 2000).

Soil respiration measurements started in June 1998. This paper includes data from July 1998 to December 2001. Soil respiration was normally measured once (1–2 days) every month except during winter when snow covered the ground. We typically made 8–10 measurements at each sampling location for each sampling period. We divided all data into two groups: before thinning on May 25, 2000, and after thinning.

Data analysis and modeling

Soil respiration and its temporal and spatial variations were investigated before and after thinning. We developed a model with two independent variables, soil temperature and water, to simulate temporal variation in soil respiration and to investigate changes caused by thinning.

Soil respiration is often simulated by an exponential function, or Q_{10} function, with soil temperature as the driving variable. We found soil water is also a critical variable controlling soil respiration, particularly in the dry Mediterranean summer. A bivariate model more accurately simulates soil respiration in this ecosystem than a univariate model with only temperature as the driver. The water function could be of a different form from the exponential function. Generally, the model is formulated as:

$$F = \beta_0 e^{\beta_1 T} f(\theta) \tag{1}$$

where F (µmol m⁻² s⁻¹) is soil respiration, T (°C) is soil temperature at 10-cm depth, θ (%) is soil volumetric water for the 0–30-cm soil layer, and β_0 and β_1 are model coefficients.

We conducted multivariate analysis to explore the relationship between efflux, temperature and water. Our data indicated that soil water had two opposite effects on soil respiration: when volumetric soil water was low (< 20%), soil respiration increased with increasing soil water; when volumetric soil water was > 20%, soil respiration decreased with increasing soil water. After comparing different functional forms and checking residual plots, we found the following model had a best fit to our data:

$$F = \beta_0 e^{\beta_1 T} e^{\beta_2 \theta + \beta_3 \theta^2} \tag{2}$$

where β_0 , β_1 , β_2 and β_3 are the model coefficients. Equation 2 can be log-transformed to a linear model:

$$ln(F) = ln(\beta_0) + \beta_1 T + \beta_2 \theta + \beta_3 \theta^2$$
 (3)

To explore the effect of thinning on soil respiration, we developed a statistical model to investigate the soil temperature and water effects while considering the influence of thinning. Separate regression analyses before and after thinning could be used to calculate independent sets of parameters for Equation 3, but this approach will not help us analyze the statistical difference of these parameters before and after thinning, nor the effect of thinning on soil respiration. In contrast, a multivariate model with two continuous independent variables and one categorical variable could help us analyze the thinning effect while taking the influence of soil temperature and water into account. We employed a categorical variable "TG," where TG = 0 stands for "before thinning," and TG = 1 stands for "after thinning." Adding this categorical term allowed us to evaluate the effects of temperature and water on soil respiration while considering any changes in these effects caused by thinning. Categorical terms should be accompanied by interaction terms that link the categorical terms with the continuous independent variables and the constant coefficient. Interaction terms allowed us to analyze the differences among dependent variables associated with categorical variables while accounting for the influence of continuous independent variables (see Selvin 1995 for detail). In our case, the interaction terms allowed us to test if the effects of soil temperature and water on soil respiration were the same before and after thinning. Thus, this statistical technique enabled us to evaluate the effect of thinning on soil respiration by normalizing soil temperature and water before and after the thinning.

After adding a categorical term and the interaction terms, our original model (Equation 3) had three continuous independent variables T, θ and θ^2 , one binary variable TG (thinning), and three interaction terms $T_{\rm TG}$ ($T \times$ thinning), $\theta_{\rm TG}$ ($\theta \times$ thinning), and $\theta_{\rm TG}^2$ ($\theta^2 \times$ thinning):

$$\ln(F) = \beta_0 + \beta_1 T + \beta_2 \theta + \beta_3 \theta^3 + \beta_4 TG + \beta_5 T_{TG} + \beta_6 \theta_{TG} + \beta_7 \theta_{TG}^2$$
(4)

We used a backward elimination approach, i.e., we first employed all possible variables in our model and then eliminated any variables that failed to pass the statistical *t*-tests and *F*-tests. By adding the categorical variable we could pool the data from before and after thinning to conduct multivariate analysis. We used the statistical package Stata (Stata Corporation, College Station, TX) to conduct multivariate linear regression analysis. The regression results and associated *t*-test and *F*-test results allowed us to finalize our model and estimate coefficients of each variable.

Results

Seasonal variation in soil respiration

Figure 1 shows the seasonal variation in periodically measured soil respiration (a), and soil temperature and volumetric soil water (b) over 3.5 years, from July 1998 to December 2001. Each value represents the mean of measurements over the day-time (0700–1900 h) over 18 locations.

Soil respiration was strongly correlated with both soil temperature and volumetric soil water. Soil temperature and water content were negatively correlated. In the Mediterranean climate in California, soil temperature peaked in July and August when soil water was at a minimum for the year. Volumetric soil water reached peak values in the January–March period when soil temperature was at its lowest. Soil respiration increased in spring and peaked in May–June, in phase with the increasing soil temperature when soil water content was moderate. Soil respiration then decreased after June, dominantly controlled by decreasing soil water in the summer and autumn despite the still increasing soil temperature. In the early winter, although the autumnal rain substantially enhanced soil water content, soil respiration was still low because of the low soil temperature.

Spatial variation in soil respiration

Spatial variation in soil respiration was determined based on measurements at 18 sampling locations before and after thinning. We averaged soil respiration from each sample location over the year before thinning and the year after thinning, compared the spatial mean value and standard deviation over 18 locations before and after thinning, and statistically tested the

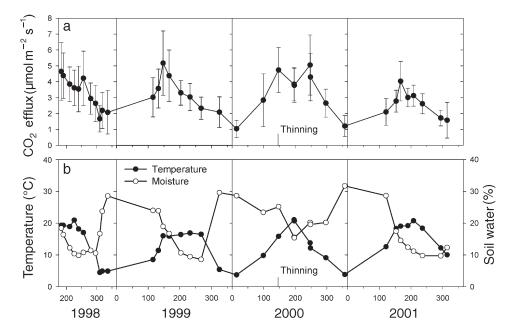


Figure 1. Seasonal variation in soil respiration (a) and soil temperature and soil water (b) before and after thinning conducted on DOY146 (May 25) in 2000. Error bars in (a) indicate standard deviations for 18 samples.

difference in mean values. Before thinning, mean soil respiration was 3.26 µmol m⁻² s⁻¹ over the spatial samples. After thinning, mean soil respiration increased to 3.78 µmol m⁻² s⁻¹, but the increase was not statistically significant (P=0.18 for the t-test). However, variation in soil respiration decreased from 31.9% of the mean with a standard deviation (SD) of 1.04 µmol m⁻² s⁻¹ before thinning to 23.4% with an SD of 0.89 µmol m⁻² s⁻¹ after thinning. The spatial variation in soil temperature over the 18 locations decreased slightly from 11.9% before thinning to 10.1% after thinning. The decreases in spatial variation in soil respiration and temperature suggest that thinning increased the spatial homogeneity of soil respiration and temperature.

Effects of thinning

To study effects of thinning on soil respiration, the spatially averaged measurements of soil respiration, soil temperature and soil water before and after thinning were pooled with a categorical variable, TG, to separate the two stages. We conducted a multivariate linear regression analysis to optimize the parameters in Equation 4. We found that coefficients β_5 , β_6 and β_7 did not pass the t-test at a 95% confidence level with P = 0.309, 0.065 and 0.365, respectively. We further conducted three pairs of two-variable F-tests (T_{TG} and θ_{TG} ; T_{TG} and θ^2_{TG} ; and θ_{TG} and θ^2_{TG}) and confirmed that the coefficients β_5 , β_6 and β_7 were not significantly different from zero and thus the null hypothesis ($\beta_5 = \beta_6 = \beta_7 = 0$) was accepted. Therefore, we dropped the variables corresponding to coefficients β_5 , β_6 and β_7 from Equation 4, giving a refined and simplified model with only four variables including a binary one, namely T, θ , θ^2 and TG (Equation 5). Equation 5 allowed us to test the sensitivity of soil respiration to soil temperature and volumetric soil water and to assess the change in soil respiration after thinning.

$$ln(F) = \beta_0 + \beta_1 T + \beta_2 \theta + \beta_3 \theta^2 + \beta_4 TG$$
 (5)

After checking the variance and normality of the residual plot, we conducted the regression analysis for Equation 5, which gave us the best-fitted coefficients with $\beta_0=-1.148,$ $\beta_1=0.0439,$ $\beta_2=0.200,$ $\beta_3=-0.00506,$ and $\beta_4=-0.137.$ In other words, after replacing TG with 0 or 1, the model has the form:

$$F = 0.317 e^{0.0439T} e^{(0.2\theta - 0.00506\theta^2)}, \text{ before thinning}$$

$$F = 0.277 e^{0.0439T} e^{(0.2\theta - 0.00506\theta^2)}, \text{ after thinning}$$

$$(R^2 = 0.69, n = 169, P < 0.001)$$

Dropping the coefficients β_5 , β_6 and β_7 indicated that thinning had no interaction with soil temperature and volumetric soil water; i.e., thinning did not cause a statistically significant change in the correlation of soil respiration with soil temperature and soil water content. The best fit of coefficient β_4 indicated that thinning changed the magnitude of soil respiration by decreasing the constant coefficient β_0 by about 13%.

A plot of the three-dimensional (3D) shape of the model output before thinning is shown in Figure 2. Soil respiration after thinning had a 3D-surface 13% lower than before thinning (data not shown). Figure 2 indicates that, at any soil water content, soil respiration increases exponentially with soil temperature. At a given soil temperature, soil respiration is maximal when volumetric soil water is about 20%.

The constant coefficient β_0 , or basal respiration, represents biotic factors related to soil microbes, soil organic carbon content, root biomass and root respiration. Soil microbial biomass and soil organic carbon content contribute to microbial decomposition; root biomass and root respiration contribute to total root respiration. Coefficient β_0 is a site-specific constant that may change after a significant disturbance, such as thin-

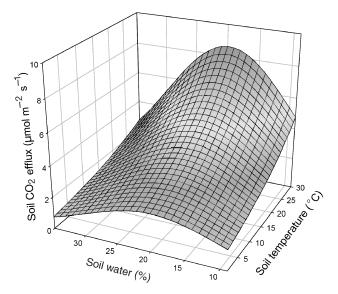


Figure 2. The 3D shape of the soil respiration model before thinning with driving variables of soil temperature and soil water.

ning, with corresponding changes in root biomass, root activity, soil microbial biomass and soil organic carbon content.

The above parameterization was based on data spatially averaged from 18 locations. Similarly, we also explored the correlations between soil respiration and soil temperature and volumetric soil water at each spatial location. We found no statistical difference in the correlations among the 18 locations except for the difference in β_0 , reinforcing our interpretation that β_0 represents the combination of biotic effects of the site and may vary with the thinning event.

Equation 6 allowed us to examine the correlation of soil respiration with soil temperature normalized by soil water. To plot soil respiration versus soil temperature, we normalized soil respiration measurements by the water term and the constant term (influenced by thinning) in Equation 6. Figure 3 shows soil respiration versus temperature (a) and normalized soil respiration versus temperature (b). We found that, after correcting for the effect of soil water, the correlation between soil respiration and temperature significantly increased (R^2 increased from 0.40 to 0.52). Figure 3a suggests that the variance of soil respiration increased with soil temperature when temperature is less than 18 °C. After normalizing for soil water (Figure 3b), the deviation in soil respiration from a fitted exponential curve substantially decreased in the intermediate temperature region.

Equation 6 also allowed us to assess the sensitivity of soil respiration to changes in soil temperature and soil water. Holding volumetric soil water constant, we calculated from Equation 6 that $Q_{10} = 1.55$. This means that, if soil water does not change while temperature is increased by 10 °C, soil respiration will increase by 55% of the original value. This situation may explain the diurnal or day-to-day variation in efflux at our site, but cannot explain the seasonal variation because the seasonal changes in soil temperature are always accompanied by changes in soil water and other variables. The effect of in-

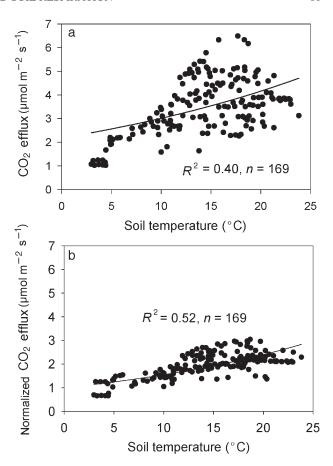


Figure 3. Soil respiration as a function of soil temperature (a), and soil respiration, normalized by soil water, as a function of soil temperature (b).

creased soil temperature on soil respiration may be either offset or enhanced by the corresponding changes in soil water and other factors that influence soil respiration.

Equation 6 indicates that soil water had two opposite effects on soil respiration. The quadratic term in the exponent indicates that soil respiration was maximal when volumetric soil water was 20%. Given a constant soil temperature, when volumetric soil water is increased to less than 20%, soil respiration increases; however, when volumetric soil water is increased to greater than 20%, soil respiration decreases with further increases in soil water. The model suggests that a volumetric soil water value of about 20% is optimal for soil respiration.

Estimation of interannual soil respiration

We used Equation 6 to estimate annual cumulative soil respiration based on continuous soil temperature and water data. Figure 4a shows estimated continuous daytime (0700–1900 h) mean soil respiration from July 1 (DOY182), 1998, to December 31 (DOY365), 2001, compared with periodic measurement values. Mean daytime soil temperature and soil water are shown in Figure 4b. Because we have only daytime measurements of soil respiration, we used daytime mean values of temperature and water to drive the model for comparing measured data with model results. The model matches most of the mea-

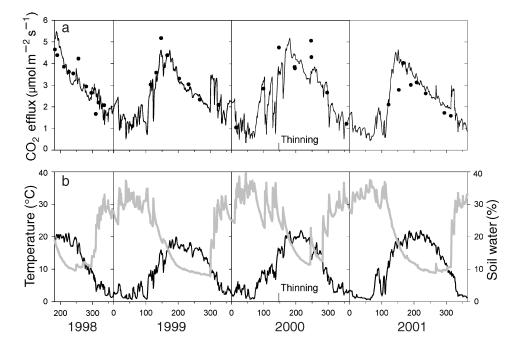


Figure 4. (a) Estimated daytime (0700 – 1900 h) soil respiration values (solid line) with periodic measurement values (filled circles), and (b) soil temperature (solid line) and soil water (gray line) from July 1 (DOY182), 1998, to December 31 (DOY365), 2001.

surement data. However, within 3 months after thinning in 2000, the measured data did not match well with the model, suggesting a complicated response of soil respiration immediately after the thinning.

Annual cumulative soil respiration was calculated with the model driven by year-round half-hour-interval data of soil temperature and volumetric soil water. Total soil respiration was estimated to be 578 g C m⁻² for July to December 1998. In years 1999, 2000 and 2001, total soil respiration was 948, 949 and 831 g C m⁻² year⁻¹, respectively. Between DOY148, 1999, and DOY147, 2000 (365 days before thinning), cumulative soil respiration was 915 g C m⁻² year⁻¹, and between DOY148, 2000, and DOY146, 2001 (365 days after thinning), cumulative soil respiration was 918 g C m⁻² year⁻¹.

Although our model indicates that thinning decreases soil respiration at a given temperature and water content, because of the change in microclimate following thinning and the natural variability in climate, the change in soil respiration following thinning was not significant. We plotted three years of monthly and annual magnitudes of total precipitation, mean air temperature, mean soil temperature, mean soil water content and cumulative soil respiration in Figure 5. Figure 5a indicates that the interannual variability in precipitation was significant. Year 2001 was relatively dry with precipitation about 300 mm lower compared with Years 2000 and 1999. The seasonal pattern of precipitation also changed year by year. Unlike the preceding two years, there was almost no rainfall between May and October in 2001. However, precipitation in November and December 2001 was higher than in November and December 2000 and 1999. Mean air temperature (Figure 5b) in 2000 was lower than in 2001 and 1999. In response to the combination of natural variability and thinning, soil temperature and soil water varied annually but in different patterns from air temperature and precipitation. Mean annual soil temperature (Figure 5c) measured at 10-cm depth gradually

increased from 9.4 °C in 1999, to 10.0 °C in 2000 and 10.5 °C in 2001, even though the lowest air temperature among the three years occurred in 2000. Mean volumetric soil water (Figure 5d) increased from 21.1% in 1999 to 25.1% in 2000 despite similar precipitation in 1999 and 2000. The seasonal pattern of soil water suggests that water in summer 2000 remained high compared with summer 1999 because of reduced evapotranspiration following thinning. Mainly because of low precipitation, mean soil water declined to 21.7% in 2001, but was still slightly higher than in 1999 because of a combination of decreased water input (precipitation) and output (evapotranspiration following thinning).

As a result of these patterns of changes in soil temperature and soil water, cumulative soil respiration (Figure 5e) was approximately constant in 1999 and 2000, and then decreased in 2001. Seasonally, soil respiration was relatively high in summer 2000 after thinning compared with the other two years, despite reduced root density, corresponding with the high soil water content as a result of the reduced evapotranspiration following thinning. Soil respiration in winter and spring of 2000 was relatively low compared with 1999, probably reflecting reduced root density when soil water was not limited. The decreased soil respiration in 2001 was correlated with decreased precipitation but may also be related to thinning. In summary, interannual variation in soil respiration could be explained by multiple factors, including natural climate variability and thinning effects (changed soil temperature, water and biotic factors) but not by the variation in any single factor.

Discussion

Thinning

The effects of forest thinning on soil respiration are complex. They are determined by many interactive factors including changes in soil temperature, soil water, microbial respiration rate, root respiration rate and decomposition of dead roots and leaf and branch litter. These factors are influenced both by thinning, as a result of changes in canopy structure and energy balance, and by natural variability in climate such as precipitation and temperature. Thinning decreases canopy density, root density, leaf area index, total photosynthesis and evapotranspiration. It may also change the components of the energy balance, such as the ratio of sensible heat to latent heat (Bowen ratio), and soil heat flux. Because thinning decreases crown closure and increases bare areas subject to direct solar radiation, diurnal variation in soil temperature may increase. These changes will lead to corresponding changes in soil respiration.

Because of the lack of control plots, we assessed the effects of thinning on the same plot before and after thinning. Therefore, changes in soil respiration caused by natural climate variability have to be considered.

Despite the complexity of thinning effects, the simulation model (Equation 5) helped simplify the assessment. Use of temperature alone to simulate soil respiration is not applicable at our site because variability in soil respiration in the summer is largely driven by soil water content. We treated soil temperature and soil water as driving variables for soil respiration, and incorporated other factors into the basal respiration and a categorical factor varying with thinning. Because maximum soil respiration occurs in the middle of the volumetric soil wa-

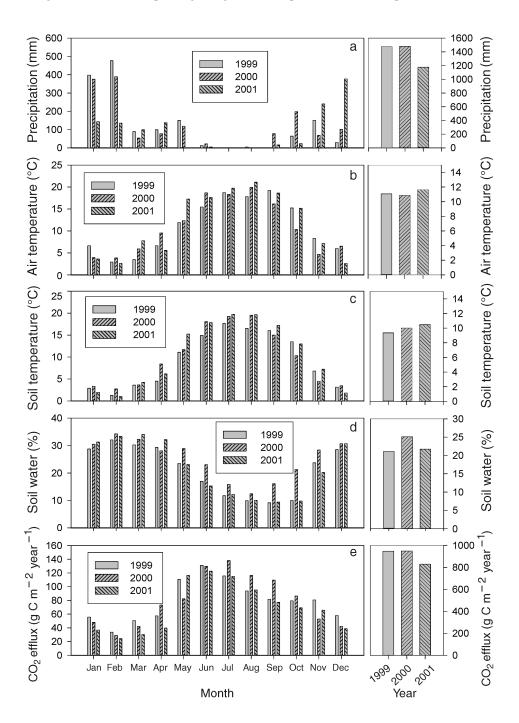


Figure 5. Three years of monthby-month variation in total precipitation (a), mean air temperature (b), mean soil temperature (c), mean soil volumetric water (d) and total soil respiration (e).

ter range, we treated the water variable as a quadratic form in the exponent term. The reason for decreased soil respiration at the high volumetric soil water range (20–40%) is probably associated with decreases in air porosity in soils and oxygen availability to microbes. The model allowed us to normalize temperature and water while comparing the magnitude of soil respiration before and after thinning. The model indicates that soil respiration will decrease in the first 1–2 years after thinning if soil temperature and soil water content do not change.

Multivariate regression after pooling data from before and after thinning facilitated examination of the effect of thinning on soil respiration while removing the influence of temperature and water. By adding appropriate categorical variables and pooling data, this multivariate analysis technique can be applied to evaluating other forest management practices, such as the effects of clear-cutting or fertilizing treatments on soil respiration. For example, the categorical variable TG (thinning) in Equation 5 can be removed or replaced by other forest management treatments or continuous variables. By removing TG, Equation 5 changes to a soil respiration model with two variables (Equation 3) that can simulate soil respiration over periods of time with no major disturbance. The two variables, temperature and water, represent only the major climatic controls on soil respiration. Other factors, such as fine root biomass, microbial biomass, organic carbon availability, nitrogen availability, and soil chemical and physical composition, also influence carbon efflux. If these factors vary significantly, either spatially, temporally or because of major disturbances, we need to add more variables, either binary or continuous, to simulate soil respiration in different stages or locations.

Temperature sensitivity of soil respiration

Temperature sensitivity of soil respiration (Q_{10}) has been widely discussed in modeling soil respiration (e.g., Lloyd and Taylor 1994, Gulledge and Schimel 2000, Xu and Qi 2001b). Based on Equation 6, we can theoretically analyze Q_{10} . By definition, Q_{10} is a constant when an exponential function is used to model CO_2 flux (F):

$$Q_{10} = \frac{F(T+10)}{F(T)} = \frac{\beta_0 e^{\beta_1 (T+10)}}{\beta_0 e^{\beta_1 T}} = e^{10\beta_1}$$
 (7)

However, Q_{10} can be a function of temperature if other functional forms, such as linear, quadratic or Arrhenius functions, are used to model flux because the temperature term cannot be cancelled when we compute Q_{10} . It has been widely recognized (Lloyd and Taylor 1994, Kirschbaum 1995, Thierron and Laudelout 1996) that the Q_{10} value is temperature dependent. By adding another variable, soil water, to simulate soil respiration, as we did in this study, Q_{10} becomes more complex. The 3D surface in Figure 2 indicates that many flux-temperature curves may occur with varying Q_{10} if soil water is allowed to change; however, when holding volumetric soil water constant, Q_{10} becomes a constant if an exponential function is used to express the effect of temperature. If soil water varies when temperature is increased by 10 °C, Q_{10} can be a function of water because the water term cannot be removed. This has

been empirically observed by Xu and Qi (2001b) in a previous study at this site. In addition, Q_{10} may vary with different ecosystem types. If we add another variable to represent site effect or treatment effects, Q_{10} may vary with this additional variable, which is consistent with many reports that Q_{10} varies widely with ecosystem types (e.g., Raich and Schlesinger 1992, Kirschbaum 1995, Davidson et al. 1998). Therefore, when considering multiple variables controlling soil respiration, the value of Q_{10} varies and depends on how the variables other than temperature are treated: Q_{10} may be a constant if temperature is increased while other variables are held constant; or Q_{10} may vary if other variables vary with temperature.

At our site before and after thinning, we found Q_{10} was a constant if computed within a day or several days when volumetric soil water did not change substantially. However, Q_{10} may vary seasonally when water changes. We found that Q_{10} did not vary in response to thinning. This result disagrees with a previous study showing that root respiration had a significantly greater Q_{10} than soil heterotrophic respiration (Boone et al. 1998). If this result is true at our site, one would expect a decrease in Q_{10} after thinning, because thinning reduces root biomass and the proportion of root respiration over total respiration. Further studies are needed to examine the temperature sensitivity of subcomponents of soil respiration in a Mediterranean climate.

Seasonal and spatial variation in soil respiration

Our measurement data indicate that soil respiration was controlled by both temperature and water. Soil respiration peaked in May–June when both soil temperature and soil water content were moderate. During this period, soil microbes had optimal environmental conditions and trees were starting the growing season. Thus, both root respiration and microbial decomposition had a high value, corresponding to a peak value of total soil respiration.

Our model satisfactorily simulated the temporal variation in soil respiration and thinning effects. However, the model could not explain the spatial variation. Instead, we used spatially measured data to analyze the thinning effect on spatial variation. Based on measurements of 18 spatial samples of soil respiration over 3.5 years, we found that the spatial variation in soil respiration decreased after thinning. Selective cutting of small trees and clustered trees to achieve more regular spatial intervals made the site more homogeneous in terms of canopy, and probably also root, distribution. As a result, the spatial variation in soil temperature decreased slightly from 11.9 to 10.1%, because the 30% reduction in LAI reduced the shaded areas. Decreased variations in root distribution and soil temperature may explain the decreased spatial variation in soil respiration.

Root respiration and microbial decomposition

Root or rhizosphere respiration is an important component of soil respiration. It may account for 10-90% of total soil respiration over various vegetation types and seasons of the year, with a mean value of 45.8% for forest vegetation (Hanson et al. 2000). Xu et al. (2001) reported that root respiration accounted

for 47% of total soil respiration at our site. Soil respiration is expected to decrease in the short term after thinning because of the decrease in live root biomass. Our model indicates that soil respiration decreased by 13% after thinning at a given soil temperature and soil water content. If root respiration accounts for 47% of total respiration, and if root respiration decreased by 30% after thinning because of a 30% decrease in root biomass, soil respiration should have decreased by 14%, which is consistent with our model result.

Although total root respiration may decrease after thinning, root respiration rate from the remaining trees may increase as a result of increases in photosynthetic rate and growth of new roots and the decrease in competition. Thinning typically increases photosynthetic rates at the leaf level, especially in the lower crowns (Ginn et al. 1991, Peterson et al. 1997, Tang et al. 1999). Root respiration or soil respiration may depend more on photosynthesis and vegetation productivity than on temperature (Hogberg et al. 2001, Janssens et al. 2001, Kuzyakov and Cheng 2001), and thus may increase following thinning. At our site, increased root respiration per tree may have partially offset the loss of total root respiration because of the reduction in root biomass after thinning.

Dead roots from thinned trees may also contribute more carbon efflux from soil after thinning. Based on a study with trenched plots that cut the connection between roots and trees, Bowden et al. (1993) observed that root decomposition ceased to influence soil respiration from trenched plots 9 months after trenching, whereas Epron et al. (1999) estimated that root decomposition will influence soil respiration for 2 years after trenching. At our site, it is likely that decomposition of dead roots from thinned trees influenced total soil respiration throughout the repeated measurement period after thinning.

Thinning and mulching of aboveground biomass increased woody debris at the soil surface, increased organic carbon in the surface layer, and may have influenced soil respiration, which includes the decomposition of surface debris. However, the increase in decomposition of the woody and leaf debris after thinning may be small. Before thinning, our site was covered by woody debris from clear-cutting before replanting in 1990. It was also covered by leaf debris from live trees, but the decomposition rate of surface debris was low. In the Mediterranean summer when temperature is high, the surface soil is dry, prohibiting the decomposition of surface debris. In the other seasons, temperature limits the rapid decomposition of surface debris. A litter-bag study at this site (data not shown) indicated that woody and leaf debris accounted for only 1 and 4% of total soil respiration, respectively. Hence, we speculate that the increased surface debris due to thinning contributed only a small part (less than 2%) to the soil CO₂ efflux.

In summary, the biotic factors influencing soil respiration after thinning include reduced root respiration per ground area, increased root respiration rate from remaining trees, and increased organic carbon content and correspondingly increased decomposition from soil microbes and surface debris. Within the short period (1–2 years) after thinning in this young plantation, and holding abiotic factors unchanged, reduced root respiration per ground area likely accounted for the decrease in total soil respiration.

Conclusions

Soil temperature alone could not completely explain the temporal variation in soil respiration. Combining soil temperature and soil water content explained most of the temporal variations in soil respiration at our site. The spatial variation in soil respiration was not only due to variations in soil temperature and soil water, but also to variations in root biomass, soil organic matter and other soil properties. Thinning 60% of the trees corresponding to 30% of the biomass significantly changed the microclimate in the forest and decreased the spatial variation in soil respiration.

Based on multivariate regression analysis with two continuous variables and one categorical variable, we conclude that thinning did not significantly change the relationship between soil respiration and soil temperature and soil water content. Forest thinning significantly decreased soil respiration at a given temperature and water content. The decrease was most likely a result of the decrease in root density after thinning. Although the model indicates that thinning theoretically decreases soil respiration, because of the variation in soil temperature and soil water driven by both thinning effects and natural climate variability, actual cumulative soil respiration did not change markedly in response to the thinning event. The effect of forest thinning on soil respiration is the combined result of a decrease in root respiration, an increase in soil organic matter, and changes in soil temperature and soil water content. As a result, total soil respiration remained similar in 1999 (948 g C m⁻² year⁻¹) and 2000 (949 g C m⁻² year⁻¹), because of slight increases in soil temperature and soil water from 1999 to 2000 and a decrease in root biomass. In 2001, soil respiration decreased to 831 g C m⁻² year⁻¹, consistent with the decrease in soil water caused by a long dry period in the summer of 2001.

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References

Boone, R.D., K.J. Nadelhoffer, J.D. Canary and J.P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396:570–572.

Bowden, R.D., K.J. Nadelhoffer, R.D. Boone, J.M. Melillo and J.B. Garrison. 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can. J. For. Res. 23:1402–1407.

Cox, P.M., R.A. Betts, C.D. Jones, S.A. Spall and I.J. Totterdell. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:750–750.

Davidson, E.A., E. Belk and R.D. Boone. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biol. 4:217–227.

- Epron, D., L. Farque, E. Lucot and P.M. Badot. 1999. Soil CO₂ efflux in a beech forest: the contribution of root respiration. Ann. For. Sci. 56:289–295.
- Fang, C. and J.B. Moncrieff. 2001. The dependence of soil CO₂ efflux on temperature. Soil Biol. Biochem. 33:155–165.
- Ginn, S.E., J.R. Seiler, B.H. Cazell and R.E. Kreh. 1991. Physiological and growth responses of 8-year-old loblolly pine stands to thinning. For. Sci. 37:1030–1040.
- Goldstein, A.H., N.E. Hultman, J.M. Fracheboud, M.R. Bauer, J.A. Panek, M. Xu, Y. Qi, A.B. Guenther and W. Baugh. 2000. Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA). Agric. For. Meteorol. 101:113–129.
- Gulledge, J. and J.P. Schimel. 2000. Controls on soil carbon dioxide and methane fluxes in a variety of taiga forest stands in interior Alaska. Ecosystems 3:269–282.
- Hanson, P.J., N.T. Edwards, C.T. Garten and J.A. Andrews. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48: 115–146.
- Hogberg, P., A. Nordgren, N. Buchmann, A.F.S. Taylor, A. Ekblad, M.N. Hogberg, G. Nyberg, M. Ottosson-Lofvenius and D.J. Read. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–792.
- Janssens, I.A., H. Lankreijer, G. Matteucci et al. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biol. 7:269–278.
- Jenkinson, D.S., D.E. Adams and A. Wild. 1991. Model estimates of carbon dioxide emissions from soil in response to global warming. Nature 351:304–306.
- Johnson, D.W. and P.S. Curtis. 2001. Effects of forest management on soil C and N storage: meta analysis. For. Ecol. Manage. 140: 227–238.
- Kirschbaum, M.U.F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biol. Biochem. 27:753–760.
- Kuzyakov, Y. and W. Cheng. 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. Soil Biol. Biochem. 33:1915–1925.
- Lavigne, M.B. 1988a. Growth and net assimilation rates in thinned and unthinned stands of balsam fir. Can. J. For. Res. 18: 1205–1210.
- Lavigne, M.B. 1988b. Stem growth and respiration of young balsam fir trees in thinned and unthinned stands. Can. J. For. Res. 18: 483–489.

- Lavigne, M.B. 1991. Effects of thinning on the allocation of growth and respiration in young stands of balsam fir. Can. J. For. Res. 21:186–192.
- Lloyd, J. and J.A. Taylor. 1994. On the temperature dependence of soil respiration. Funct. Ecol. 8:315–323.
- Nakane, K., H. Tsubota and M. Yamamoto. 1986. Cycling of soil carbon in a Japanese red pine forest 2. Changes occuring in the first year after a clear-felling. Ecol. Res. 1:47–58.
- Ohashi, M., K. Gyokusen and A. Saito. 1999. Measurement of carbon dioxide evolution from a Japanese cedar (*Cryptomeria japonica* D. Don) forest floor using an open-flow chamber method. For. Ecol. Manage. 123:105–114.
- Peterson, J.A., J.R. Seiler, J. Nowak, S.E. Ginn and R.E. Kreh. 1997. Growth and physiological responses of young loblolly pine stands to thinning. For. Sci. 43:529–534.
- Qi, Y. and M. Xu. 2001. Separating the effects of moisture and temperature on soil CO₂ efflux in a coniferous forest in the Sierra Nevada mountains. Plant Soil 237:15–23.
- Raich, J.W. and W.H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus Ser. B Chem. Phys. Meterol. 44:81–99.
- Selvin, S. 1995. Practical biostatistical methods. Wadsworth Publishing, Belmont, CA, pp 152–166.
- Striegl, R.G. and K.P. Wickland. 1998. Effects of a clear-cut harvest on soil respiration in a jack pine–lichen woodland. Can. J. For. Res. 28:534–539.
- Tang, Z.M., J.L. Chambers, S. Guddanti and J.P. Barnett. 1999. Thinning, fertilization, and crown position interact to control physiological responses of loblolly pine. Tree Physiol. 19:87–94.
- Thierron, V. and H. Laudelout. 1996. Contribution of root respiration to total CO_2 efflux from the soil of a deciduous forest. Can. J. For. Res. 26:1142–1148.
- Toland, D.E. and D.R. Zak. 1994. Seasonal patterns of soil respiration in intact and clear-cut northern hardwood forests. Can. J. For. Res. 24:1711–1716.
- Trumbore, S.E., O.A. Chadwick and R. Amundson. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science 272:393–396.
- Xu, M. and Y. Qi. 2001a. Soil-surface CO₂ efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. Global Change Biol. 7:667–677.
- Xu, M. and Y. Qi. 2001b. Spatial and seasonal variations of Q₁₀ determined by soil respiration measurements at a Sierra Nevadan forest. Global Biogeochem. Cycles 15:687–696.
- Xu, M., T.A. DeBiase, Y. Qi, A. Goldstein and Z.G. Liu. 2001. Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California. Tree Physiol. 21:309–318.