Tree Physiology 26, 833–844

Influences of canopy photosynthesis and summer rain pulses on root dynamics and soil respiration in a young ponderosa pine forest

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Received June 30, 2005; accepted October 7, 2005; published online April 3, 2006

Summary Our first objective was to link the seasonality of fine root dynamics with soil respiration in a ponderosa pine (*Pinus ponderosa* P. & C. Lawson) plantation located in the Sierra Nevada of California. The second objective was to examine how canopy photosynthesis influences fine root initiation, growth and mortality in this ecosystem. We compared CO_2 flux measurements with aboveground and belowground root dynamics. Initiation of fine root growth coincided with tree stem thickening and shoot elongation, preceding new needle growth. In the spring, root, shoot and stem growth occurred simultaneously with the increase in canopy photosynthesis. Compared with the other tree components, initial growth rate of fine roots was the highest and their growing period was the shortest. Both above and belowground components completed 90% of their growth by the end of July and the growing season lasted ~80 days. The period for optimal growth is short at the study site because of low soil temperatures during winter and low soil water content during summer. High photosynthetic rates were observed following unusual late-summer rains, but tree growth did not resume. The autotrophic contribution to soil respiration was 49% over the whole season, with daily contributions ranging between 18 and 87%. Increases in soil and ecosystem respiration were observed during spring growth; however, the largest variation in soil respiration occurred during summer rain events when no growth was observed. Both the magnitude and persistence of the soil respiration pulses were positively correlated with the amount of rain. These pulses accounted for 16.5% of soil respiration between Days 130 and 329.

Keywords: fine root, minirhizotron, photosynthesis, plant-microbes interactions, rhizosphere, soil processes.

Introduction

Forest ecosystems are important in global carbon cycling because 80% of the carbon stored in terrestrial vegetation is in forest biomass (Olson et al. 1985). Forest soil contains around 70% of total soil carbon globally (Post et al. 1982). Soil respiration is estimated to be about 68–80 Pg C $year^{-1}$, the largest component of carbon fluxes from ecosystems to the atmosphere (Raich and Schlesinger 1992). Despite its importance for estimating the global carbon budget, our understanding of soil respiration is still limited because of its high complexity and variability, which are controlled by many biotic and abiotic factors. This is especially true in water-limited ecosystems, which have been under-represented in research networks (Reichstein et al. 2003). Although these ecosystems do not store the greatest amount of carbon globally, they are crucial because they occupy one third of the land surface and are highly vulnerable to climate change (Emanuel et al. 1985, Snyder et al. 2002).

Soil respiration is often modeled as a function of soil temperature without considering the complex responses of root and microbial processes to soil water and substrate availability (Davidson et al. 1998, Högberg et al. 2001, Janssens et al. 2001, Xu and Qi 2001, Reichstein et al. 2003, Xu et al. 2004). The fine root system is a major part of the carbon input belowground and therefore plays an important role in soil carbon cycling (Nadelhoffer and Raich 1992). On average, the contribution of rhizosphere respiration to total soil respiration of forests is ~50%, with values ranging between 10 and 90% (Hanson et al. 2000). Therefore, rhizosphere respiration may be an important belowground process responsible for carbon release. Despite its importance, soil carbon cycling through fine roots is not well understood mainly because of the difficulty in studying this below ground component. Many studies report high rates of soil respiration and high contributions of autotrophic respiration to total soil respiration during the expected period of root growth (Bowden et al. 1993, Epron et al. 1999, Ohashi et al. 2000, Högberg et al. 2001, Widén and Majdi 2001, Rey et al. 2002, Lavigne et al. 2003, 2004, Lee et al. 2003, Bond-Lamberty et al. 2004). However, few of these studies explicitly followed the phenology of root dynamics in

relationship to the rhizosphere contribution to soil respiration. Therefore, the first objective of this paper was to document the link between the seasonality of fine root dynamics (initiation, growth and mortality) and the carbon balance of the ecosystem. We tested the hypothesis that fine root dynamics exert a major control over the seasonal pattern of soil respiration, and that such control is most apparent when roots are actively growing.

Our second objective was to improve our understanding of how canopy photosynthesis influences fine root initiation, growth and mortality. The relationship between carbon availability and fine root dynamics has not been well characterized. Studies in a coniferous boreal forest have shown that it takes 1 to 4 days for the carbon from photosynthesis to become available for roots (Ekblad and Högberg 2001, Högberg et al. 2001). Therefore short-term root dynamics seem to depend partially on allocation of photosynthesis products, but source–sink interactions with other components of the tree are still poorly understood (Farrar and Jones 2000, Pregitzer et al. 2000, Pregitzer 2003). Newly developing leaves are strong carbohydrate sinks and compete with other sinks influencing the pattern of carbon allocation in the tree (Dickson 1990, Farrar and Jones 2000). However, availability of growth limiting resources such as water may alter this pattern (Joslin et al. 2000). Surprisingly, few studies have considered the seasonality of growth for both above-and belowground components together in the field (King et al. 2002, Lyr and Hoffman 1967, Reich et al. 1980). In addition, most root growth studies have been carried out in temperate and boreal forests (Hendrick and Pregitzer 1996, Eissenstat and Yanai 1997, Coleman et al. 2000, Pregitzer et al. 2000, Joslin et al. 2001, Majdi 2001, Pritchard et al. 2001, King et al. 2002, Stevens et al. 2002, Ruess et al. 2003, Tierney et al. 2003, Tingey et al. 2003). Only two studies have been done in severely water-limited sites (Tingey et al. 1995, Lopez et al. 1998, 2001*a*, 2001*b*). Because our site is characterized by low temperatures during the winter and low soil water content during the summer, we predicted that the patterns of root dynamics would differ from those found in other studies. We hypothesized that fine root development would be a high priority and therefore, would be tightly coupled to canopy photosynthesis and available soil water.

To test these hypotheses, we combined CO_2 flux measurements (at ecosystem, soil and leaf levels) with aboveground (shoot, needle, stem) and belowground (fine roots) growth dynamics. We sought to discern temporal patterns of root dynamics, canopy photosynthesis and respiration in reference to environmental conditions at the seasonal timescale. Seasonal drought at the study site was exploited to study the control of water availability on these dynamics.

Materials and methods

The Blodgett Forest site and ongoing measurements have been extensively described (Goldstein et al. 2000, Misson et al. 2005), therefore, only brief descriptions of the characteristics of the site relevant to this study are presented.

Site description

The study site is part of the AMERIFLUX and FLUXNET networks. It is located at 1315 m above sea level in the Sierra Nevada Mountains of California (35°53′42.9″ N, 120°37′ 57.9″ W), on land owned and managed by Sierra Pacific Industries. In 1990, trees were planted at a density of ~1275 trees ha^{-1}. The plantation is dominated by ponderosa pine (*Pinus ponderosa* P. & C. Lawson) with occasional other tree species. The major understory shrubs are *Arctostaphylos manzanita* Parry (Manzanita) and *Ceonothus cordulatus* Kellogg (Ceanothus).

Common management practices for commercial plantations in the Sierra Nevada were carried out. Shrubs were cut during spring 1999 and the plantation was thinned in May 2000 (Misson et al. 2005, Tang et al. 2005). In spring 2003, tree density was ~510 trees ha^{-1}; stand one-sided projected leaf area index (LAI, allometric method) was 2.49, comprising 72% pines in the overstory and 28% understory shrubs (Manzanita 22% and Ceanothus 6%). In spring 2003, mean tree diameter at breast height (DBH) was 12.0 cm, mean tree height was 4.7 m and basal area was 9.58 m^2 ha^{-1}. The site is characterized by a Mediterranean climate, with warm dry summers and cold wet winters. Since 1998, annual precipitation has averaged 1290 mm, with the majority of precipitation falling between September and May, and almost no rain in summer. Mean daily temperatures range from 14–27 °C during summer to 0–9 °C during winter. The soil is relatively uniform and comprises 60% sand, 29% loam and 11% clay with a pH of 5.5 ± 0.29.

Eddy covariance measurements

Wind velocity and virtual temperature fluctuations were measured at 10 Hz with a three-dimensional sonic anemometer (ATI Electronics, Boulder, CO) mounted on a horizontal beam at 10.5 m above the ground. The CO_2 and H_2O mixing ratios were measured with a closed path infrared gas analyzer (LI-6262, Li-Cor, Lincoln, NE). The raw analog data provided response times of 10 Hz for both gases. Additionally, the canopy vertical profiles of CO_2 and H_2O mixing ratios were measured every 30 min with the Li-Cor LI-6262 by sampling sequentially at five heights for 6 min each.

Since 1997, fluxes of CO_2, H_2O and sensible heat between the forest and the atmosphere have been determined by the eddy covariance method (Baldocchi et al. 1988). Positive fluxes indicate mass and energy transfer from the surface to the atmosphere. The sonic anemometer wind data were rotated to force the mean vertical wind speed to zero and to align the horizontal wind speed onto a single horizontal axis. The time lag for sampling and instrument response was determined by maximizing the covariance between vertical wind velocity (w') and scalar (c') fluctuation. Errors due to sensor separation and damping of high frequency eddies were corrected by spectral analysis techniques as outlined by Rissmann and Tetzlaff (1994). To avoid flux underestimation, storage corrections were applied to the fluxes of CO_2.

Energy balance closure for this ecosystem has been tested by comparing the sum of measured energy fluxes (latent + sensible + soil heat fluxes; LE + H + G in W m^{-2}) to the net radiation measured above the canopy (R_n in W m^{-2}). The linear regression between these terms was: LE + H + G = −2.9 + 0.8 R_n (r^2 = 0.87, P < 0.001). This comparison suggested an imbalance of about 20%. This value is in the medium range of imbalance reported in FLUXNET eddy-covariance studies (Wilson et al. 2002).

Meteorology

Environmental parameters were recorded every 5 s and 30-min means were calculated and stored on a CR10X data logger (see Goldstein et al. (2000) for description of all instruments). The parameters included wind direction and speed, vertical profiles of wind speed at three heights, vertical profiles of air temperature and humidity in aspirated radiation shields at four heights, net radiation, photosynthetically active radiation, soil temperature at 5, 10, 15, 30 and 50 cm depths at three locations, soil water at 10, 30 and 50 cm depths, soil heat flux at 10 cm depth at three locations, rain and atmospheric pressure.

Fine root dynamics

Two plots (20 × 20 m each) were marked out in the footprint area of the canopy flux measurements. In each plot, nine locations at 10-m intervals were marked in a 3 × 3 square grid. At each location, fine root dynamics (root density, growth rate, death rate and diameter classes) were measured by minirhizotron imaging as described by Cheng et al. (1990). In the spring and fall of 2002, minirhizotron tubes (1.5 m in length, 5 cm in inside diameter) were installed at an angle of 45°. Images of a narrow strip (18 mm wide) of the upper soil–tube interface were captured and digitized incrementally with an on-site digitizing system with an indexing handle (Bartz Technologies Minirhizotron, Santa Barbara, CA, combined with a "Video Capture Essentials" video capture card and software from ImperX, Boca Raton, FL). Image changes through time at each tube position have been recorded monthly since April 2003. All digitized images were analyzed with RooTracker 2.0.3 (Duke University National Phytotron, Durham, NC). A root density profile performed in three pits down to 2 m showed that 50% of the fine roots (< 2 mm in diameter) were concentrated in the first 60 cm of the soil and 90% in the first 1.3 m of the soil (1.3 m is ≅ sin(45°) × 1.5 m, where 1.5 m is the length of the minirhizotron tube).

Soil surface CO_2 flux

Soil respiration was measured monthly from February to November 2003 with a Li-Cor LI-6400-09 soil chamber connected to a LI-6400 portable photosynthesis system at 18 sampling points co-located with the minirhizotron tubes. Soil temperature (at 5 cm depth) was measured simultaneously with soil respiration with the 6000-09TC thermocouple probe. On each date, 2–3 measurements were performed around noon at each sampling point. Soil respiration was also measured at two locations inside a trenched plot (or root exclusion experiment), which allowed us to estimate the influence of rhizosphere respiration on total soil respiration. This trench was dug in August 2001 and measured 0.2 m wide and 1.2 m deep around a 3 × 3 m plot. A tarp was installed in the trench to prevent root regrowth into the plot. Previous studies have shown that the influence of residual decomposing roots on soil respiration should be negligible 2 years after trenching (Hanson et al. 2000). At both the trenched plot and at an untreated location, soil temperature at 5 cm depth and soil water (TDR CS-615, Campbell Scientific, Logan, UT) integrated over the top 30 cm were continuously measured at 5-min time steps.

Soil CO_2 profile

In spring 2003, we installed solid-state CO_2 sensors (GMT-222, Vaisala, Finland) to measure CO_2 concentration profiles in the soil during the vegetation period (Tang et al. 2003). The sensor is a silicon-based, non-dispersive infra-red (NDIR) device that measures CO_2 concentration based on a patented CARBOCAP technique. It assesses CO_2 concentration by detecting the attenuation of single-beam dual-wavelength infra-red (IR) radiation across a fixed distance. We buried three sensors at depths of 2, 8 and 16 cm in the trenched plot (root exclusion) and in an untreated location. The measured gradients of soil CO_2 concentration were used to deduce continuous estimates of CO_2 efflux as described by Tang et al. (2003). The autotrophic or root contribution (RC; %) was calculated according to Hanson et al. (2000) as:

$$\mathrm{RC} = \frac{\left(R_{\mathrm{s,control}} - R_{\mathrm{s,trench}}\right) \times 100}{R_{\mathrm{s,control}}} \quad (1)$$

where $R_{s,control}$ and $R_{s,trench}$ are CO_2 efflux in the untreated and trenched plot, respectively.

We estimated CO_2 efflux from the soil CO_2 profile as described by Tang et al. (2006). Briefly, CO_2 concentration gradient measurements were corrected for variations in temperature and pressure, and used to calculate surface CO_2 efflux. The flux of CO_2 between any two layers of soil was calculated by Fick's first law of diffusion:

$$F = -D_s \frac{\mathrm{d}C}{\mathrm{d}z} \quad (2)$$

where F is CO_2 efflux (μmol m^{-2} s^{-1}), D_s is CO_2 diffusivity in the soil (m^2 s^{-1}), C is the CO_2 mole concentration at a certain depth of soil (μmol m^{-3}) and z is soil depth (m).

Diffusivity was computed with the Moldrup model (Moldrup et al. 1999):

$$\frac{D_s}{D_a} = \phi^2 \left(\frac{\varepsilon}{\phi}\right)^{\beta S} \quad (3)$$

where D_a is CO_2 diffusivity in free air, ε is volumetric air content (air-filled porosity), ϕ is the porosity or sum of the volumetric air content ε and the volumetric water content θ, S is the percentage of mineral soil with size > 2 μm, or S = silt + sand content (S = 0.88 at our site) and β = 2.9 is a constant.

Continuous CO_2 efflux observations from this system were compared with chamber measurements made with a Li-Cor LI-6400 at 18 locations during the growing season. The continuous system provides better temporal resolution, whereas the chamber measurements provide better spatial representation. Notwithstanding these differences, there was good agreement between mean daily soil respiration rates estimated by the two methods. A linear regression between the datasets (x = chamber, y = continuous system) had a non-significant intercept, a significant slope (0.92) at $P < 0.01$ and an $r^2 = 0.97$ (n = 12).

Dendrometric measurements

In 2003, stem growth increment was recorded on 13 trees every 5 days with manual band dendrometers (Series 5, Phytogram, Tucson, AZ). These constant band tension instruments are capable of detecting 0.1 mm changes in circumference. Simultaneously, new needle and new shoot lengths were recorded on the same trees at 1 mm accuracy. Seasonality of leaf area index and biomass (stem, leaf) of the shrubs was estimated every month in 2003 by destructive sampling outside the flux footprint of the tower.

Ecosystem respiration and canopy photosynthesis

Net ecosystem exchange of CO_2 (F_c) was considered to comprise two components, canopy photosynthesis (P) and ecosystem respiration (R_e):

$$F_c = R_e - P \tag{4}$$

A rectangular hyperbola was used to describe canopy photosynthesis:

$$F_c = R_e - \frac{\alpha \mathrm{PAR} P_{max}}{\alpha \mathrm{PAR} + P_{max}} \tag{5}$$

where PAR is measured photosynthetically active radiation, P_{max} is mean maximum canopy photosynthetic flux at saturating irradiance and α is initial canopy quantum yield. The 30-min data of PAR and F_c measured at the top of the tower were use to estimate R_e, P_{max} and α (and thus P) by a nonlinear fitting procedure. This method has been used in several studies to partition F_c into its component processes (e.g., Wofsy et al. 1993, Ruimy et al. 1995). Because it was difficult to fit Equation 5 for each individual day due to the requirement for a certain amount of data, we used a moving 10-day window. The fitting procedure was tested for smaller time windows (down to 5 days) and provided the same seasonal pattern, but with more variability. With smaller time windows, the nonlinear fit sometimes did not converge. The fitting procedure was applied only if the total number of values was higher than 40 and if the number of values at PAR < 800 μmol m^{-2} s^{-1} was higher than 20. Twenty-three percent of the 30-min data were characterized by a friction velocity lower than 0.2 m s^{-1} and were omitted from the analysis. All of the plotted values of R_e and P were values obtained for the last day of the 10-day window. This method allowed us to compare tree growth rate on a given date with mean values of P and R_e calculated over the preceding 10-day period.

Seasonality of canopy photosynthesis closely followed seasonal variations in leaf-level photosynthesis measurements of the three major species in this ecosystem (ponderosa pine, Manzanita, Ceanothus), supporting our method of calculating canopy photosynthesis from F_c data (Misson et al. 2006). In addition, seasonal variations in ecosystem respiration and soil respiration followed the same pattern (r^2 = 0.95) and were similar to the seasonality of monthly soil respiration data measured with the Li-Cor LI-6400 (not shown). This result supports our method of calculating ecosystem respiration from F_c data. This comparison also indicates that soil respiration is a major component of total ecosystem respiration, as shown in a previous study at our site (Xu et al. 2001).

Results

Seasonal variation of canopy photosynthesis

Weather changes during seasonal transitions were abrupt. After mid-May (Day 130), there was almost no rain and PAR increased sharply, whereas soil water content and relative humidity decreased steadily (Figures 1a–c). The end of October (Day 304) marked the return of regular precipitation, a sharp decrease in PAR and abrupt increases in relative humidity and soil water content as well as a decrease in temperature (Figures 1a–c). Vegetation was most active during the period between Day 130 and Day 304 (5.8 months, 174 days).

Canopy photosynthesis started to increase at the beginning of spring (mid-May, Day 130; Figure 1a). At that time mean daily air temperature started to increase above 8 °C, the daily minimum temperature no longer decreased to sub-freezing values and mean daily PAR was consistently higher than 600 μmol m^{-2} s^{-1} (Figures 1a and 1b). Photosynthetic rates rapidly decreased at the end of June (Day 175) when soil water content and relative humidity dropped below 13% and 45%, respectively (Figures 1a–c). This decrease was correlated with a sharp decrease in canopy stomatal conductance (not shown). From June to the end of July (Day 211), variations in canopy photosynthesis were positively correlated with relative humidity (Figure 1b).

The first summer rain began on July 31 (Day 212 and Day 214, 13.2 mm in total; Figure 1c). This event was correlated with a sharp increase in canopy photosynthesis that lasted 10 days (Figure 1a). We observed several other summer rainstorms during the second part of August (Day 233 to Day 243, 24.6 mm in total), which correlated with increases in photosynthesis until the end of August (Figures 1a and 1c). These two summer rains accounted for only 3% of the annual precipitation in 2003.

Above- and below-ground growth dynamics

Ponderosa pine stems started to elongate at the end of April (Day 120; Figure 2c). Initial growth was slow, although it increased with increasing photosynthesis around Day 130 (Fig-

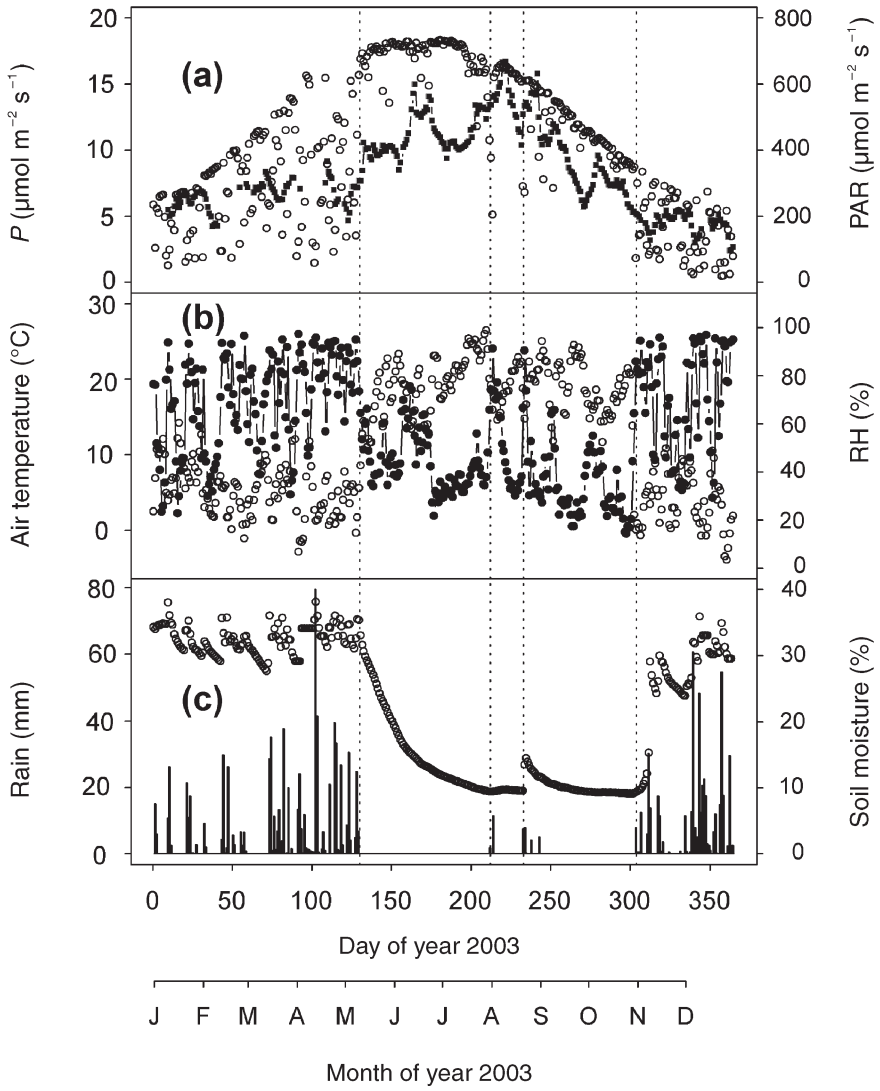

Figure 1. (a) Seasonal variations in canopy photosynthesis (*P*, ■) and mean daily photosynthetically active radiation (PAR, ○). (b) Mean daily air temperature (○) and mean daily relative humidity (RH, ●). (c) Daily rain (vertical bars) and soil water. Vertical dotted lines show the beginning and the end of the growing season and the two summer rain events.

ures 2a and 2c). Ponderosa pine shoots and fine roots started to grow in mid-May (Day 134), two weeks later than the main stems and simultaneously with the increase in canopy photosynthesis (Figures 2a and 2c). The number of living roots existing on any sampling date was closely correlated with observed living root length ($r^2 = 0.94$; $n = 14$). New ponderosa pine needles initiated elongation at the end of May (Day 148) after new shoots had completed 40% of their elongation (Figure 2c). The biomass and leaf area index of the shrubs started to increase by the end of May (data not shown).

Compared with the other plant components, initial growth rates of fine roots and shoots were highest and their growing period was shortest (Figure 2c). Almost all new fine roots (84%) appeared between mid-May (Day 136) and mid-July (Day 197). For shoots, 85% of their extension growth was completed by mid-July (Day 190). Main stem elongation initially proceeded more slowly—85% of the expansion was completed by the end of July (Day 209). Needles also completed 85% of their growth by the end of July (Day 209). All four components had completed 90% of their growth by the end of July (Day 210). Increases in biomass and leaf area index of the shrubs was almost complete by the end of July, too (data not shown). In total, the growing period of the summer 2003 at this site lasted 2.7 months (80 days, from ~Day 130 to ~Day 210).

New fine roots appeared mainly between mid-May (Day 136) and mid-July (Day 197; Figure 2c). The daily minimum soil temperature was not continuously higher than 5 °C until mid-May (Day 132; Figure 2b). In July (around Day 200), new roots appeared during a period of low relative humidity (~30%), soil water content (~10%) and photosynthesis, but at a lower rate than in June (Figures 2a and 2c). Only a limited number of new fine roots (16%) appeared in August and during the fall (Figure 2c).

Fine root death rate increased in July (Day 197) when soil water content dropped to 10% and canopy photosynthesis was depressed (Figures 1c, 2a and 2c). Root death rates remained constant until August, even when photosynthesis resumed in

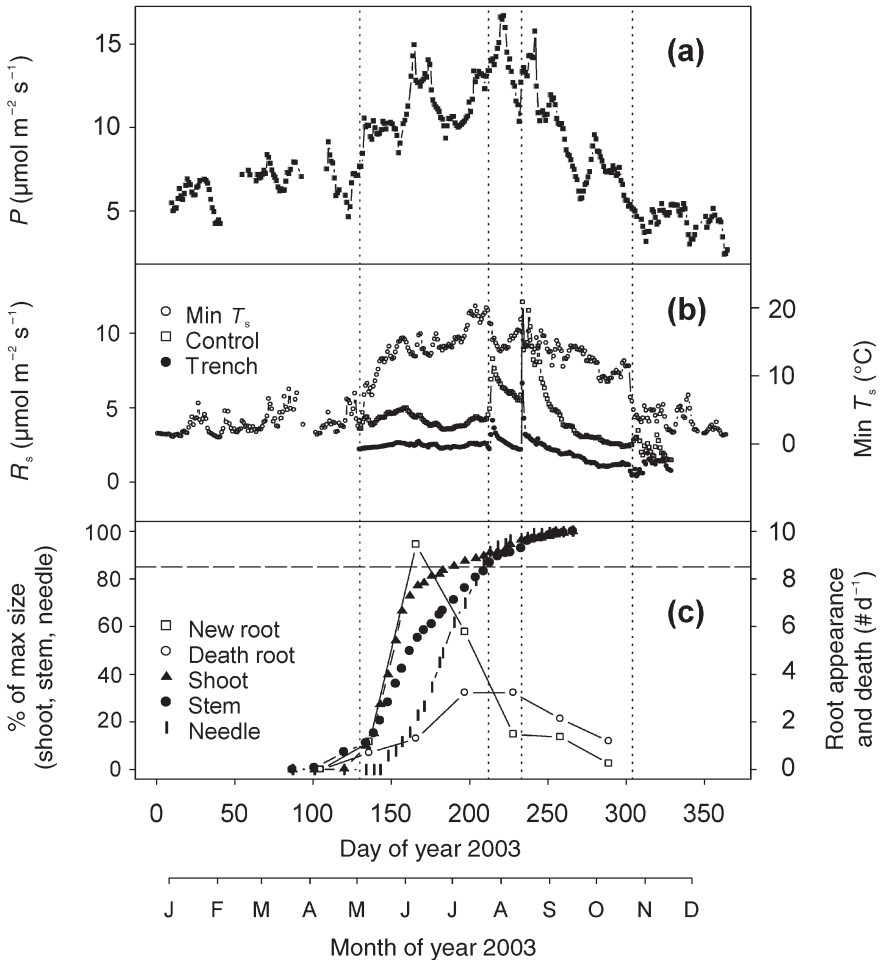

Figure 2. (a) Seasonal variation in canopy photosynthesis (P). (b) Daily minimum soil temperature (T_s, ○), soil respiration in the control (R_s, □) and in the trenched plots (●). (c) Shoot, stem and needle elongation as a percentage of maximum size and root demography (sum of 18 minirhizotron tubes). The broken horizontal line indicates 85% of maximum size. Vertical dotted lines indicate the start and the end of the vegetation season and the two summer rain events.

response to rain events. Mortality rates decreased after August. Survival analysis showed that 38% of the new roots died in the first 2 months and 50% died within 6 months following emergence.

In August, canopy photosynthesis increased and reached its annual maximum during the first summer rain event (Figure 2a). High rates of photosynthesis in August were unaccompanied by an increase in shoot, needle or root growth rate, which, in all cases, was almost nil by the end of July (Figure 2c). Only the stems appeared to elongate slightly during the summer rain events, although these increases were small (< 5%).

Variations in ecosystem and soil respiration

Soil respiration estimated from soil CO_2 concentration profile measurements at the root exclusion site (trench) were lower than at the control site (Figure 2b). The autotrophic contribution was 49% over the whole season, with daily contributions ranging between 18 and 87% (see Equation 1, Figure 3). The contribution increased during the root growth period (Day 136–Day 166), then decreased when roots stopped growing and soil water content declined (Day 166–Day 211; Figure 3). Autotrophic respiration increased again during the summer rain events in August (~Day 212 and ~Day 233).

Differences in soil respiration rates between the control and trenched sites were due not only to the trenching treatment, but also to a difference in environmental conditions because soil temperature was about 3 °C higher at the trenched plot, whereas soil water contents were similar at the trenched and control plots. Based on an exponential temperature function with a Q_{10} of 1.6, we estimated that this temperature difference could lead to an underestimate of RC (Equation 1) by 15% on average.

A major departure from the seasonal variation in soil respiration (R_s) was observed during the summer rain events in August in both the trenched and the control plots (Figure 2b); however, the magnitude of the response to rain and the timing of decay differed between the plots. Following Xu et al. (2004), we calculated the dynamic time constant (τ) to quantify the decay rate of R_s after the rain event by fitting the data to the function:

$$R_s = b_0 + b_1 e^{-t/\tau} \quad (6)$$

where t is number of days after the rain event. Coefficients b_0 and b_1 represent the background and the enhancement of R_s. Coefficient τ represents the time required for R_s to decline to $1/e$ (~37%) of its peak value. These parameters were fitted

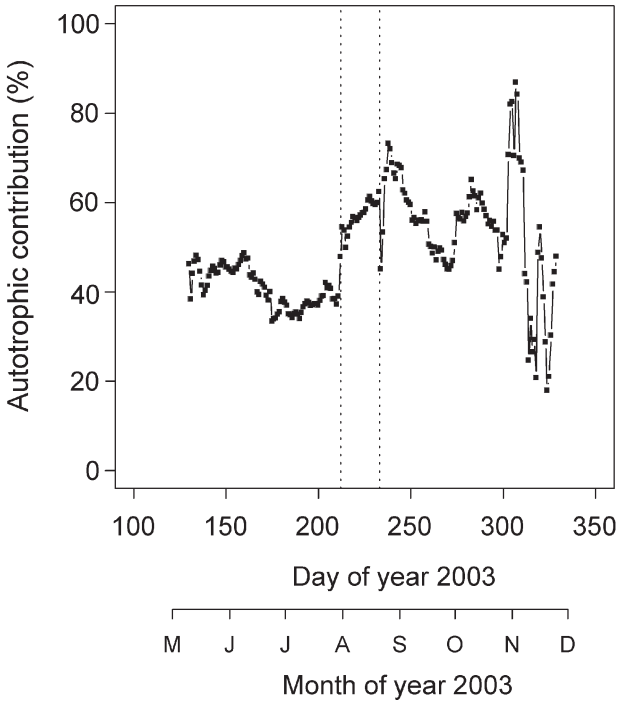

Figure 3. Autotrophic contribution to soil respiration during 2003 (Equation 1). The vertical dotted lines indicate the two summer rain events.

with a nonlinear fitting procedure (S-PLUS 6.0). Table 1 shows that the time constant τ and coefficient b_1, representing the enhancement, were higher for the control site than for the trenched site. Both parameters were also higher during the second rain event, which was characterized by higher precipitation (24.6 versus 13.2 mm; Table 1).

To determine the increase in soil respiration due to the two rain events, we calculated the sum of any extra respiration, between Day 212 and Day 304, that was higher than the initial rate before the first rain event. The respiration pulses greatly enhanced total soil respiration for the season: together the two pulses increased respiration by 16.5% at the control site and ~1% at the trenched site (Table 1). At both sites, the respiration pulse was higher for the second rain event, which was characterized by higher precipitation.

A Q_{10} function based on soil temperature at 10 cm depth was fitted to ecosystem respiration (R_e), excluding data that were affected by the summer rains (Days 211 to 280). We found a Q_{10} of 1.4 and a base respiration rate of 1.8 μmol m^{-2} s^{-1}. These parameters were used to adjust ecosystem respiration to a 25 °C soil temperature reference value based on the Q_{10} exponential temperature function. Ecosystem respiration adjusted for temperature ($R_{e,25}$) was plotted as a function of soil water content (Figure 4). Figure 4 shows that during winter, $R_{e,25}$ was relatively constant and ranged between 3 and 5 μmol m^{-2} s^{-1}. During the period of active growth (Day 13–Day 210), $R_{e,25}$ increased slightly up to an average of 5.5 μmol $m^{-2}s^{-1}$ for soil water contents > 13%. When soil water content decreased below 13% during the growth period, $R_{e,25}$ fell to 2.5 μmol m^{-2} s^{-1}. Large pulses of $R_{e,25}$ occurred following two summer rain events (~Day 212 and ~Day 233). Although the rain events resulted in high CO_2 efflux, they did not appreciably rewet the soil down to a depth of 10 cm where the TDR probe was located. Soil respiration was also adjusted for temperature variation ($R_{s,25}$) by the same method as described for ecosystem respiration; seasonal variation in $R_{s,25}$ showed the same pattern as $R_{e,25}$ when plotted as a function of soil water content.

Discussion

Photosynthetic controls on root growth

Depending on climatic regime, functional group and adaptive strategy, trees can exhibit fixed root growth (single flush), free growth (multiple flushes) or a mixed growth pattern (Vogt et al. 1996, Joslin et al. 2001). Temperate and boreal forests are characterized by relatively long production periods, where new root initiation and growth occur throughout the growing season (Hendrick and Pregitzer 1992, Ruess et al. 2003). Several flushes of roots have been observed in these forests, but more root growth usually occurs in spring (Hendrick and Pregitzer 1992, Joslin et al. 2001, King et al. 2002, Ruess et al. 2003). Whether root growth peaks before or after maximum shoot and leaf expansion seems to depend on soil temperature and soil water. In cool and moist climates, root growth in spring seems to be delayed until cumulative soil heat reaches a threshold (Pregitzer et al. 2000, Ruess et al. 2003). Subsequently, more root growth occurs after aboveground growth

Table1. Parameters of the exponential decay model (Equation 6) in the control and trenched location for the two rain events in summer 2003. Standard errors are in parenthesis. Abbreviations: b_0 = base respiration (μmol m^{-2} s^{-1}); b_1 = enhancement (–); τ = time constant (days); r^2 = coefficient of determination; and Increase (%) = increase in respiration due to rain event.

		b_0	b_1	τ	r^2	Increase (%)
First rain event	Control	5.5 (0.1)	3.1 (0.1)	6 (0.7)	0.97	5.8
(Days 215–232)	Trenched	2.2 (0.1)	2.2 (0.1)	5 (0.5)	0.99	0.1
Second rain event	Control	2.2 (0.1)	9.3 (0.2)	17 (1.1)	0.96	10.7
(Days 234–301)	Trenched	1.2 (0.1)	3.2 (0.2)	15 (2.1)	0.98	0.8

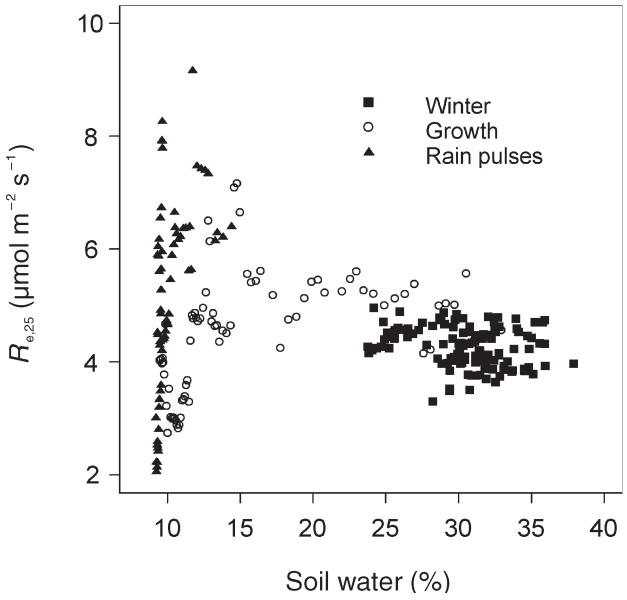

Figure 4. Ecosystem respiration adjusted for temperature variation ($R_{e,25}$; see text) as a function of soil water at 10 cm. Winter, growth and rain pulse periods are shown.

has slowed down because carbon allocation to roots is likely postponed until carbon demand for the construction of spring foliage is reduced (Lyr and Hoffman 1967, Kuhns et al. 1985, Fahey and Hughes 1994, Joslin et al. 2001). In drier climates, soil temperature is usually higher and imposes less limitation on root expansion in early spring. In these conditions, root growth can precede shoot growth by several weeks, thus providing the canopy with water for leaf expansion (Hendrick and Pregitzer 1996, King et al. 2002).

In a typical Mediterranean climate, Lopez et al. (1998) showed that root production occurs all year long, but the cycle is reversed in comparison with temperate and boreal ecosystems: production is higher in winter when soil water availability is highest and soil temperature is not limiting, whereas it is lower in summer because of limitations imposed by low soil water content (cf. Lopez et al. 2001*a*). Because our ecosystem is located in a mountainous Mediterranean climate in the Sierra Nevada of California, both soil temperature and soil water limit root growth, but at different times of the year. During winter, soil is rarely below freezing, but daily minimum temperatures are typically between 0 and 5 °C, which, it has been suggested, are too low for root growth (Pregitzer et al. 2000). During summer, soil water content quickly drops below 15%. The period for optimal root growth is, thus, very short, being limited to spring and early summer (Figure 2c).

During spring and early summer, both root and shoot elongation rates are high (Figure 2c), whereas stem diameter growth proceeds more slowly. Higher rates and a shorter season for shoot extension growth than for shoot diameter growth has also been observed in ponderosa pine in northern California (Tingey et al. 1996). Because needles form along new shoots, their development is highly dependent on shoot elongation. Therefore, although the elongation rate of needles was high, foliage development lagged behind root, shoot and stem growth. Similarly, high rates of needle elongation have also been observed for ponderosa pine by Grulke et al. (1998).

During the first part of the vegetation period, shoot and root development were coincident with canopy photosynthesis (Figures 2a and 2c). Part of this growth was probably fueled by utilization of nonstructural carbohydrates. Root mortality increased and peaked shortly after root initiation and elongation, at the time that drought stress started to increase and depress photosynthesis. Fine root initiation, growth and mortality all seem to be coupled to canopy photosynthesis at our site, at least during the first part of the vegetation period. In 2003, minirhizotron images were taken on a monthly basis and this coarse temporal resolution did not allow us to track fine temporal changes. In 2004 and 2005, minirhizotron images were taken on a biweekly basis throughout the year.

Only one flush of growth for roots, shoots and needles was observed at our site. Growth did not resume during the second part of the vegetation period, even though summer rain events caused an increase in photosynthesis. Stem diameter growth rates showed a small increase (< 5%) in response to the rain events, but it is difficult to determine if this increase was due to cell division and differentiation or to a swelling of the tissue due to rehydration of the living (phloem, xylem) or nonliving (bark) tissues, or both (Kuroda and Kiyono 1997). Root mortality remained high in August during the second part of the vegetation period, even when soil water content and photosynthesis increased after the rain events. In August, daily maximum soil temperature at 10 cm was < 25 °C and so is unlikely to be responsible for the observed high rates of root mortality (Pregitzer et al. 2000). We conclude, therefore, that root growth and mortality, as well as shoot, stem and needle growth were partially decoupled from photosynthesis and soil water content during the second part of the vegetation period.

The pattern of tree growth at our site seems to be highly fixed and not at all plastic, following the concept of "phenological programming" as proposed by Hendrick and Pregitzer (1996) and further developed by Joslin et al. (2001). The species that we studied have evolved in an environment where drought stress is the norm and appear to be "programmed" to produce one burst of growth when air and soil temperature, soil water content and air relative humidity are favorable and the supply of carbohydrate is adequate. However, this theory does not explain the data presented by Tingey et al. (1996), which showed that young ponderosa pine in northern California experiencing soil temperatures similar to ours, but without soil water limitation (> 30%) exhibited several flushes of shoot and stem growth during the growing season. We found that fine roots exhibited a single peak of growth in June, whereas Tingey et al. (1996) observed root production almost all year long, suggesting that "phenological programming" can be overridden by physiological adaptation if soil water is not limiting.

Root control of soil respiration

On average, the annual contribution of rhizosphere respiration to total soil respiration reported for forests is ~50%, but values

range between 10 and 90% (Hanson et al. 2000). This wide span is associated with functional differences in ecosystems as well as with variability in the methods and the extent of the season used to estimate this contribution. Based on a trenching experiment, we determined a mean seasonal rhizosphere contribution of 49% from the beginning of May to the end of November, with daily contributions ranging between 18 and 87%. The trenching method for separating rhizosphere respiration from heterotrophic respiration has many confounding factors (Hanson et al. 2000) and was not replicated in our study; hence, our value of 49% is only an approximation. In addition, we showed that the autotrophic contribution (RC) might be underestimated by 15% as a result of temperature differences between the trenched and the control sites. Large seasonality in RC was likely a result of variation in biomass, specific activity and sensitivity to the soil environment of the roots and the heterotrophs. In many studies, high rates of soil respiration and of root contributions have been linked to the expected period of root growth (Bowden et al. 1993, Epron et al. 1999, Ohashi et al. 2000, Widén and Majdi 2001, Högberg et al. 2001, Rey et al. 2002, Lavigne et al. 2003, 2004, Lee et al. 2003, Bond-Lamberty et al. 2004); however, none of these studies explicitly followed the phenology of root growth relative to the rhizosphere contribution to soil respiration.

Our experimental design allowed us to demonstrate that increasing rates of soil respiration and rhizosphere contributions in the spring were coincident with a period of fast root growth (Figures 2b–c and 3). Increased respiration during this period provides the energy and the carbon skeletons necessary for the synthesis of new root biomass (Atkin et al. 2000); however, the increase in respiration was relatively small. During the period of root growth, standardized ecosystem respiration ($R_{e,25}$) increased by only ~1 μmol $m^{-2} s^{-1}$ and the rhizosphere contribution to soil respiration increased by 10% compared with values during the previous winter (Figures 3 and 4). A similar small increase in the contribution of rhizosphere respiration has been found at our site based on soil chamber data (Tang et al., unpublished data). Other studies have reported higher increases (30 to 50%) in the contribution of autotrophic respiration to total soil respiration during the growing season (Lee et al. 1999, Ohashi et al. 1999, Epron et al. 2001, Högberg et al. 2001).

The spring increase in soil respiration was small and transient. The major seasonal variation in soil respiration occurred during unusual rain events in August, in the trenched and the control plots, with a significant departure from the otherwise fairly smooth seasonal variation in soil respiration (Figure 2b). Other studies in forests located in arid, semi-arid or temperate climates have shown rapid increases in soil respiration with summer rainfall (Irvine and Law 2002, Flanagan et al. 2002, Reichstein et al. 2002, Rey et al. 2002, Emmerich 2003, Xu and Baldocchi 2004, Lee et al. 2004, Xu et al. 2004). Such increases can be attributed partly to the stimulation of root activity and heterotrophic respiration, whereas the effect of CO_2 displacement by the rain is thought to be minimal (Lee et al. 2004). In our study, we can exclude any longer term (> 4–5 days) influence of root growth respiration because root growth did not occur following the rain events. Analysis of the range of conditions reported in the studies cited above indicate that respiration pulses after a rain event are larger and occur for longer at the drier sites, but many other factors must play a role including the quality and quantity of the substrate, the type of heterotrophic population and the previous environmental conditions (Xu et al. 2004). At our site, the enhancement and time constant of the respiration pulses were positively correlated with the amount of precipitation, in accordance with results reported by Xu et al. (2004).

Several recent studies have provided seasonal information on the effects of rain events on carbon exchange between field plots and the atmosphere. In a temperate mixed forest, the respiration pulse accounted for 5–10% of the annual net ecosystem production following a single intensive summer storm (Lee et al. 2004). Xu et al. (2004) found that one rain event during the dry season was equivalent to 10% of annual gross primary productivity in arid grassland. In our case, two soil respiration rain pulses during the summer 2003 accounted for an additional 16.5% of soil respiration seasonally. In the root exclusion plot, summer rain events enhanced respiration by less than 1%, which may indicate that roots stimulated respiration during the rain events by ~15.5%. There was heavy mortality in these roots, as suggested by survival analysis, and they likely provided fresh labile carbon as a substrate for decomposers. In addition, root activity might have increased just after the rain because water uptake increased. These results provide information on how the presence of roots controls soil respiration directly by using carbon for their maintenance and growth, but also indirectly by having a positive effect on decomposition processes. When associated with rain during the dry season, carbon release from the soil can be substantial. As reported by Xu and Baldocchi (2004), we found that the timing of rain events can play a bigger role in influencing carbon fluxes of some ecosystem than total annual precipitation.

In conclusion, our hypotheses that fine root development at our site is a high priority and is tightly coupled to canopy photosynthesis and available soil water was partially supported and mainly holds for the first part of the vegetation period when increases in photosynthesis and root growth coincided. We found that the period for optimal root growth is short at our site because of low soil temperatures during the winter and low soil water content during summer. High rates of photosynthesis were observed following summer rains during the second part of the vegetation period when temperature was optimal, but root growth did not resume and mortality rates did not decrease. It is likely that fine root dynamics is controlled by both environmental variables (mainly soil temperature and soil water content) and endogenous factors (mainly carbohydrate supplies and phenological signals).

Our second hypothesis that fine roots exert a major control over the seasonal patterns of soil respiration, and that such control is most apparent when roots are actively growing, was also partially confirmed because increases in soil and ecosystem respiration corrected for temperature variations were observed during the period of active root growth. This provides evidence for a direct link between canopy photosynthesis, and

ecosystem and soil respiration. However, increases in respiration during root growth were relatively small. The largest variation in soil respiration at our site occurred during unusual rain events in the summer, which had no effect on root growth. Such increases in soil respiration can mostly be attributed to the stimulation of heterotrophic respiration; however, the activity of these heterotrophs was highly dependent on the earlier soil inputs of fresh labile carbon by the roots. This provides evidence for an indirect link between canopy photosynthesis, root growth and soil respiration.

Acknowledgments

This work was made possible by grants from the Kearney Foundation of Soil Science, the University of California Agricultural Experiment Station and the Office of Science, Biological and Environmental Research Program (BER), U.S. Department of Energy, through the Western Regional Center of the National Institute for Global Environmental Change (NIGEC) under Cooperative Agreement No. DE-FCO2-03ER63613. Financial support does not constitute an endorsement of the views expressed in this article. We gratefully acknowledge Sierra pacific Industries for allowing us to carry this research in their property and the Blodgett Forest crew for their invaluable support. We are grateful to Daniel Epron and four anonymous reviewers for their contribution to the improvement of this manuscript.

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