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# Dynamics of fine root, fungal rhizomorphs and soil respiration in a mixed temperate forest: integrating sensors and observations

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## Abstract

Fine roots and rhizomorphs have important implications for the global carbon balance, but the processes underlying these carbon sinks are not well understood. This is the first study to couple continuous minirhizotron observations with an array of solid-state $CO_2$ sensors. We calculated soil respiration using a gradient flux method. Using a Kaplan-Maier survival analysis we determined a median longevity of fine roots of 347 days and of 400 days for rhizomorphs. Radiocarbon ($^{14}C$) analysis suggested an age of 7 years for fine roots <1 mm and 17 years for roots of 1 mm in diameter. We found rapid changes in root length (maximum of 38.1 cm $m^{-2}$ $day^{-1}$) and rhizomorph length (maximum of 105.4 cm $m^{-2}$ $day^{-1}$) during sampling of four consecutive days. Changes in rhizomorphs length were more variable than root length and rhizomorphs were negatively correlated with daily changes in soil moisture. The variation in root length may be associated to prior environmental conditions. Fine root length was correlated with daily $CO_2$ production and variation in daily fine root length could contribute up to 4680 g C $ha^{-1}$ $day^{-1}$. We observed a clockwise diurnal hysteresis effect in soil respiration with soil temperature that changed in amplitude and shape along the year. Our results show the importance of shorter intervals of minirhizotron measurements to understand rapid fine roots and rhizomorphs variation. Furthermore, continuous minirhizotron measurements should be couple with continuous measurements of multiple sensor arrays to explain biophysical factors that regulate belowground carbon dynamics.


ABBREVIATIONS: AM , arbuscular mycorrhizae; EM, ectomycorrhizae; PAR, photosynthetically active radiation; VWC, volumetric water content.

# Introduction

The rate that fine roots and rhizomorphs release $CO_2$ to the atmosphere has important implications for global carbon balance, but the mechanisms and processes that regulate carbon dynamics in these pools are not well understood. Fine root production has been estimated to account for up to 33% of global annual net primary production (Gill and Jackson, 2000), but the global contribution of rhizomorphs remains unknown. Rhizomorphs are large cords of fungal hyphae that are involved in transport of nutrients and water (Smith and Read, 1997), and a large fraction of the rhizomorph mass is considered to be mycorrhizal, not saprobic (e.g. Read, 1992). Rhizomorph-forming fungi belong to the Basidomycota, which is a group that includes decomposer and ectomycorrhizal fungi. Rhizomorphs largely consists of newly-fixed carbon directly allocated from the leaves and only passing through the fine roots (Treseder and Allen, 2000; Olsson and Johnson, 2005; Godbold et al., 2006). Therefore, it is crucial to understand the factors controlling fine root and rhizomorphs production at the ecosystem scale for better understanding of $CO_2$ fluxes and nutrient cycles at global scales.

Previous studies have reported a wide range in the rates of fine root production and decay (Hendrick and Pregitzer, 1992; Fitter et al., 1996; Pregitzer et al., 2002; Ruess et al., 2003; Baddeley and Watson, 2005; Majdi and Andersson, 2005). These estimates varied from a few weeks to 1-2 years for first-order ($1^o$) roots, to years to decades for second ($2^o$) and third ($3^o$) -order fine roots. Discrepancies in these results may be explained by several factors. First, the definition of "fine root" may be a problem, as $1^o$ roots appear to have higher nitrogen concentrations and disarticulate readily whereas $2^o$ and $3^o$ roots of similar size order, can also be encased by mycorrhizal fungi, but can live

for much longer periods (Pregitzer et al., 2002). Second, variation in estimates of root longevity may be influenced by the methods used to estimate the structure of the branching order (Pregitzer et al., 2002), the portion of the root used for measurement (Treseder et al., 2004), and the model used to estimate life span (Matamala et al., 2003; Luo et al., 2004; Majdi et al., 2005). Furthermore, there is spatial variation in soils that may influence the estimates of fine root dynamics (Partel and Wilson, 2001, 2002).

In contrast to fine root studies, turnover of rhizomorphs is not well understood despite their importance in plant nutrient and water uptake (Allen et al., 2003). To our knowledge there is only one published study of rhizomorphs turnover using minirhizotrons (Treseder et al., 2005).

There is not a unique approach for studying fine root turnover, and these methods have been reviewed in previous reports (e.g. Majdi et al., 2005). In general, the techniques could be divided into destructive and non-destructive methods. Destructive methods include the collection of soil cores, the use of ingrowth bags (van Noordwijk, 1993), and isotope analysis on fine roots (Gaudinski et al., 2001; Matamala et al., 2003). Non-destructive methods include the use of minirhizotrons (Hendrick and Pregitzer, 1996; Johnson et al., 2001) and ground-penetrating radars (Stover et al., 2007). The frequency of sample collection is an important limitation to the understanding of the mechanisms and processes of roots, rhizomorphs and hyphae dynamics. Destructive methods have the limitation that repeated measurements could not be done on the same sample, while non-destructive methods collect large amount of data that is time consuming to analyze. Therefore, research is usually done by collecting samples with longer time intervals between sampling events. Rapid changes in fine roots and

rhizomorphs may occur between sampling intervals and will be masked by the length of time between observations.

Soil respiration includes heterotrophic respiration (i.e. decomposers) and autotrophic respiration (i.e. respiration from mycorrhizal fungi and living roots). It is regulated by physical (i.e. soil texture, temperature, moisture) and biological factors (i.e. photosynthesis, metabolism), which introduce complexity in the mechanistic understanding of this process (Luo and Zhou, 2006). Roots and microbes contribute to soil respiration in four possible ways: a) maintenance respiration, b) growth respiration, c) grazing by soil invertebrates, and d) upon decomposition, loss of the existing carbon via respiration by other microbes, especially bacteria. Furthermore, it is crucial to understand the mechanisms that regulate soil respiration to better understand the response of terrestrial ecosystems to climate change (Raich et al., 2002).

Traditionally, soil respiration has been measure with soil chambers using point measurements. However, techniques to continuously measure soil respiration have been developed in recent years with automated chambers and the use of solid-state $CO_2$ sensors (King and Harrison, 2002; Hirano et al., 2003; Liang et al., 2003; Savage and Davidson, 2003; Carbone and Vargas, 2008). With improvements in automated techniques it is important to quantify fine roots and rhizomorphs turnover rates in a similar time interval to understand their relationship in multiple temporal and spatial scales (Allen et al., 2007). Recent progress on soil embedded networked systems has provided a prototype for automated image capture and analysis of fine roots and rhizomorphs (Allen et al., 2007).

In this study, we focused on the analysis of minirhizotron images taken during four consecutive days in six sampling campaigns in a mixed conifer forest during the year 2006. This intense analysis of short-term dynamics is the first attempt to understand fast changes in of fine roots and rhizomorphs. It is noteworthy that the minirhizotron technique targets the observation of $1^{o}$ roots, those fine roots where proportions of younger roots decompose faster than older roots and are detected by continuous measurement of minirhizotron images (Allen et al., 2003; Ruess et al., 2003, Fig. 1). As one looks at the broader range of root ages ($2^{o}$ - $4^{o}$), even fine roots may have much longer life spans. In contrast, rhizomorphs are considered to be structures more stable than extraradical hyphae with a lifespan of 11 months (Treseder et al., 2005), but no continuous measurements of short-term turnover has been attempted before.

In addition, we coupled our observations with an array of soil sensors to measure soil temperature, soil moisture and $CO_2$ concentration in the soil profile to estimate soil respiration using the gradient method (Hirano et al., 2003; Jassal et al., 2005; Tang et al., 2005b; Turcu et al., 2005). Therefore, this study integrates for the first time short-term continuous observations of fine roots and rhizomorphs with continuous measurements of soil respiration. We hypothesize that fast changes in fine root and rhizomorphs length may be observed by short-term continuous measurements of minirhizotron images, and these rapid changes may influence soil respiration rates.

## Methods

### Study Site

The study was conducted at the University of California James San Jacinto Mountains Reserve, which is operated by the UC Natural Reserve System. The Reserve has served as the Terrestrial Ecology Observing Systems field site for the Center for Embedded Networked Sensing (CENS, http://cens.ucla.edu) since 2002. The goals of CENS have been to research and develop new environmental and ecological observing systems technologies (Hamilton et al., 2007).

The James Reserve is located at an elevation of 1640 m in the San Jacinto Mountains, California, USA, and surrounded by the San Bernardino National Forest. The James Reserve is a mixed conifer and oak forest with precipitation occurring mostly as rain between the months of November and April with a mean annual precipitation of 507 mm and a mean air temperature of 10.3 °C (measured since 2000). Soils are Entisols with a loamy-sand texture (83% sand, 10% silt, and 7% clay), with a bulk density of 1.2 $g/cm^3$, and underlay by weathered granitic bedrock. Several studies have described the geomorphology of the soils in the area (see Hanawalt and Whittaker, 1976; Graham et al., 1997; Frazier and Graham, 2000).

### Minirhizotron Images

In October 2003, we installed six minirhizotron observation tubes of 5 cm in diameter and 1 m long. The area included individual plants of *Quercus chrysolepis* Liebm. (Canyon live oak), *Q. kelloggii* Newb. (Black Oak), *Calocedrus decurrens* (Torr.) Florin (Incense cedar), *Arctostaphylos pringlei* Parry (Manzanita), and *Pinus lambertiana*

Dougl. (Sugar pine), and understory herbs which constitute a mixture of arbuscular mycorrhizae (AM) and ectomycorrhizae plants (EM). The minirhizotron tubes were installed at an average angle of 42° and inserted as far as possible into the soil. The average vertical depth by the tubes was 40 cm. We allowed roots to recolonize the soil surrounding the tubes for a year before collection of images began. Images from all tubes were collected between 3/2005 and 12/2006 with a total of 104 sampling dates. In addition, we analyzed data from six campaigns of four consecutive days during the year of 2006. These intense image collection campaigns had the objective to capture fast changes in root, rhizomorphs and hyphae along the year (Fig. 1). The campaigns were undertaken from 2/23/2006 to 2/26/2006, 4/29/2006 to 5/2/2006, 6/3/2006 to 6/6/2006, 10/7/2006 to 10/9/2006, 11/11/2006 to 11/14/2006, and 12/9/2006 to 12/12/2006. We will refer to these campaigns throughout the text as C1, C2, C3, C4, C5, and C6, respectively.

The images were collected using a minirhizotron microscope (BTC-10 with I-CAP software, Bartz Technology) with a total area represented in each image of 2.47 $cm^2$. We collected an average of 52 vertical images per tube by inserting the minirhizotron until the bottom of the tube and then moved the lens upward in increments of 1.3 cm. A total of 313 images were taken per day and stored as JPEG files. From all the collected images, we counted the number of roots and rhizomorphs. We randomly selected images to calculate root length (n = 127 images) and rhizomorphs length (n = 170 images) using the line intercept method (Tennant, 1975). We developed linear regression models to predict lengths based on the number of roots and rhizomorphs (Crocker et al., 2003). The models had the form of $y = mx$, where $y$ is the length in cm, $x$

is the number of roots or rhizomorphs, and $m$ is a constant. For roots, $m = 5.013$ ($r^2 = 0.60$, $P < 0.001$), and for rhizomorphs $m = 3.118$ ($r^2 = 0.70$, $P < 0.001$).

## Fine Roots

We collected three soil cores around each minirhizotron tube during February of 2006 to measure fine root (diameter < 2 mm) length and biomass. Fine roots were sorted by hand and rinsed free of organic matter with deionized water. Root length was estimated using the line intercept method (Newman, 1966; Tennant, 1975). Fine roots were oven dried for determination of dry weight, and a linear model to predict root biomass based on root length was developed. The linear model had the form of $y = mx$, where $y$ is the mass in grams, $x$ is the length in centimeters, and $m$ is a constant ($m = 0.003$, $r^2 = 0.91$, $P < 0.001$). This model was used to predict root biomass from root length calculated via minirhizotron image analysis.

We used radiocarbon ($^{14}C$) analysis on fine roots <1 mm and 1 mm in diameter to estimate the mean age of structural carbon in live and dead fine roots according to Gaudinski *et al.* (2001). Briefly, fine roots were washed sequentially in acid (1 N HCl), alkali solution (1 N NaOH), and again acid (1 N HCl) with distilled water rinses after each step. Samples were converted to graphite according to Xu et al. (2007) and measured for radiocarbon using accelerator mass spectrometry at the UC Irvine W. M. Kerck Carbon Cycle AMS facility. To estimate the mean age of carbon in fine roots we assumed that all structural carbon in the root grew in a single year and the average age of the root was determined by comparing the $\Delta^{14}C$ of the structural carbon of the roots to the record of $\Delta^{14}C$ of $CO_2$ in the atmosphere (Gaudinski et al., 2001).

## Soil Respiration

Four minirhizotron tubes were instrumented with solid-state $CO_2$ (Vaisala, CARBOCAP model GMM 220, range 0-10,000 ppm), soil temperature, and soil moisture (Decagon, ECHO) sensors at 2, 8 and 16 cm soil depths during November 2005 (Fig. 2). The $CO_2$ sensors were calibrated every six months after deployment to ensure the quality of the measurements. We calculated soil respiration from the soil using a $CO_2$ gradient flux method based on concentrations of $CO_2$ in the soil profile. The $CO_2$ gradient method has been used in previous studies to understand vertical partitioning of the sources of $CO_2$ in the soil profile (Hirano et al., 2003; Tang et al., 2003; Jassal et al., 2005; Turcu et al., 2005). Measurements of $CO_2$ concentration from the sensors were corrected for temperature and pressure by applying a correction using the ideal gas law according to the manufacturer:

$$CVC = UCR \times \frac{1013 \times (t - 273)}{298 \times p} \quad (1)$$

where CVC is the corrected volume concentration (ppm), UCR is the uncorrected reading, $p$ is ambient pressure (hPa) and $t$ is ambient temperature (°C). These corrected values were used to calculate soil respiration. For modeling soil respiration based on a gradient method we used an approach similar to Tang *et al.* (2005b). Data from $CO_2$ sensors were changed from volume fraction (μmol $mol^{-1}$) to mole concentration (μmol $m^{-3}$). According to Fick's first law of diffusion $CO_2$ diffused from the soil can be expressed as a differential equation:

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

where $F$ is the soil respiration (μmol $m^{-3}$ $s^{-1}$), $D_s$ the gaseous $CO_2$ diffusion coefficient in the soil ($m^2$ $s^{-2}$), $C$ is the mole $CO_2$ concentration (μmol $m^{-3}$) at a $z$ depth, and $z$ is the depth (m). $D_s$ can be estimated as:

$$D_s = D_a \varepsilon \tau \tag{3}$$

where $D_a$ is the $CO_2$ molecular diffusivity of $CO_2$ in the air, $\varepsilon$ is the soil air-filled porosity and $\tau$ is the tortuosity. The product of $\varepsilon\tau$ has been defined as the tortuosity factor $\xi$ (Jury et al., 1991). Then:

$$D_s = D_a \xi \tag{4}$$

The effect of temperature and pressure on $D_a$ is given by:

$$D_a = D_{a_o}\left(\frac{T}{T_o}\right)^{1.75}\left(\frac{P_o}{P}\right) \tag{5}$$

where $D_{a_o}$ is a reference value of $D_a$ (1.47 x $10^{-5}$ $m^2$ $s^{-1}$) at $T_o$ (293.15 K) and $P_o$ (1.013 x $10^5$ Pa) according to Jones (1992). The ratio of diffusivity in the soil ($D_s$) to diffusivity in the air ($D_a$) or tortuosity factor may be calculated using several general models (e.g. Penman, 1940; Marshall, 1959; Millington and Quirk, 1961). We calculated ξ using the Moldrup model (Moldrup et al., 1999) which is based on diffusion through porous media:

$$\frac{D_s}{D_a} = \xi = \phi^2\left(\frac{\varepsilon}{\phi}\right)^{\beta S} \tag{6}$$

where $\beta$ is a constant ($\beta = 2.9$), $S$ = silt + sand content ($S = 93$), and ϕ is the porosity defined as:

$$\phi = 1 - \frac{\rho_b}{\rho_m} = \varepsilon + \theta \tag{7}$$

where $\rho_b$ is the bulk density, $\rho_m$ the particle density with a typical value of 2.65 g $cm^{-3}$, and θ volumetric water content. At our study site, ϕ was a constant value of 0.55.

At a certain depth interval ($z_i$ and $z_{i+1}$) we can calculate the $CO_2$ flux if we know the $CO_2$ concentrations ($C_i$ and $C_{i+1}$). We calculated $CO_2$ fluxes between depths 0.02 - 0.08 m and 0.08 - 0.16 m based on the concentrations measured in the soil profile. For the $CO_2$ flux at the surface ($F_o$) we extrapolated linearly assuming $CO_2$ production constant in the soil profile. For this paper we report soil respiration ($CO_2$ efflux at the soil surface) as a positive upward value and distance below the surface as a negative value.

## Statistics

We used repeated measurements of analysis of variance (ANOVA) to test for changes in root and rhizomorphs length during each campaign. Date of collection was the repeated measures factor for each campaign. We used the Kaplan-Meier survival analysis (Hosmer and Lemeshow, 1999) to test for mean root and rhizomorphs survival. All statistical analyses were performed with SPSS v13 (Chicago, Il).

## Results and Discussion

Minirhizotrons have been used to understand root (Hendrick and Pregitzer, 1996; Johnson et al., 2001) and rhizomorphs (Treseder et al., 2005) dynamics, but few studies have coupled this information with ecosystem fluxes such as water or carbon (Ruess et al., 2003; Allen, 2007; Allen et al., 2007). In addition, most studies have focused on minirhizotron measurements once a month during a year, or once a week during the growing season. This is the first study to integrate continuous measurements of soil sensor arrays with daily measurements of minirhizotron images.

We took minirhizotron images on 106 days during 2005 and 2006 at a range of intervals to better document rapid dynamics. Our data suggest that there was a high seasonal variation in rhizomorphs and root length (Fig. 3a); therefore we attempted to quantify rapid fine root and rhizomorphs growth. For this study we focused on fine roots production and decomposition of rhizomorphs and $1^{o}$ roots branches (Fig. 1). First-order roots are expected to decompose at faster rates because they have higher nitrogen content and, in part, because they may be considered expendable structures if soil temperatures or moisture at the local site is suboptimal. It is unknown how fast these young roots decompose and if this will vary among cohorts of roots. Ruess et al (2003) found that different cohort of roots decompose at different rate in a long-term study. Our results support the hypothesis that rapid turnover times (<4 days) of $1^{o}$ fine roots and rhizomorphs occur based upon continuous observations of minirhizotron images (Fig. 3a). As one looks at $2^{o}$-$4^{o}$ fine roots and mycorrhizal tips, the age should extend out to several years (Pregitzer et al., 2002). In addition, we observed seasonal differences in soil respiration rates associated with our minirhizotron observations (Fig. 3a).

We were also interested in identifying rapid changes in fine roots and rhizomorphs through different temperatures and soil moisture conditions. We expected higher growth rates with warm and moist conditions but slower rates with dry and cold conditions. However, 1° roots and rhizomorphs might readily be sloughed off if temperatures became too hot or soil moisture too low (Fig. 3b). The James Reserve is especially suitable for this research, because temperatures and soil moisture vary widely and rapidly in these forests (Fig. 3b).

## Fine Roots

Minirhizotron images usually are taken relatively infrequent, once a month at the most, but usually at longer time intervals. It is difficult to manually analyze the images, and rapid changes in root production and decomposition are assumed to be relatively slow. We analyzed all root cohorts regardless of birth date between 3/2005 and 12/2006 and estimated a median longevity of roots using a Kaplan-Maier analysis of 347 days (95% confident intervals of 342 and 351 days) or 0.95 years (Fig. 4a). This estimate is similar to the 0.99 years for fine roots in mineral soil (Andersson and Majdi, 2005) or the 0.86 years in the forest floor (Tierney and Fahey, 2001), but higher than the 0.67 years estimates from the upper 30 cm of a hardwood forest (Hendrick and Pregitzer, 1992).

The radiocarbon ($^{14}C$) analysis suggested an age of 7 years (range 5 to 8 years) for structural carbon of fine roots < 1 mm, and 17 years (range 11 to 26 years) for roots of 1 mm in diameter (Fig. 5). These results are similar to the range of 3-18 years of fine roots in deciduous and coniferous forests of the eastern United States (Gaudinski et al., 2001).

Discrepancy between root turnover time calculated from minirhizotron images and radiocarbon dating may be explained by a number of factors. The first depends upon clear demarcation of root branching order. The minirhizotron may emphasize the more rapidly cycling $1^o$ roots, while our radiocarbon data tend to reflect $2^o$ to $4^o$ fine roots that persist much longer in the soil, and branching order is important to estimate fine root radiocarbon age (Gaudinski et al., 2001; Tierney and Fahey, 2002). An alternative hypothesis is that stored carbon from the plant is used occasionally to construct new fine roots as described in a two pool model (Luo et al., 2004). The difference between the 0.95 years from the minirhizotron images and 5-8 years from the $^{14}C$ data would fit this observation as well. Thirdly, the root tips at our site consist of oaks, pines, manzanitas, and ceanothus, and several understory herbs. These represent a mixture of AM and EM plants. Some EM can persist for many years, but the lifespans vary with species of both plant and fungus (Treseder et al., 2004). Finer AM roots tend to have lower C:N ratios that might support rapid turnover, but may have initiated their primary growth and turnover later in the year than our root coring. Thus, the minirhizotron observations could have been biased towards younger ages with a high proportion of the newer AM roots later in the spring and summer, whereas the radiocarbon data towards the longer, more persistent EM roots.

Nevertheless, our data support the hypothesis of variable production and turnover times. Direct observations of changes in root length and biomass of $1^o$ fine roots were based upon continuous observations of minirhizotron images. These observations show that many $1^o$ roots are rapidly produced and turned over. In addition, previous studies have challenged the assumptions of a single live fine-root pool with a unimodal age distribution where root cohorts, branching others, and root diameters may different

turnover times (Gaudinski et al., 2001; Ruess et al., 2003). In complex mixed communities such as our study site, many strategies for root survival may be simultaneously occurring and different methods should be applied to differentiate short- versus long-term dynamics.

We found significant differences ($P < 0.01$) in fine root length of campaigns C1 and C6, but marginal differences ($P = 0.082$) in fine root length during campaign C5 (Fig. 6). These results suggest that during certain times fine roots experience changes in root length that will be missed by less frequent observation periods. During C1 we observed a net loss net loss of 31.2 cm $m^{-2}$ in four consecutive days of observation where the largest loss was in the second day (38.1 cm $m^{-2}$ $day^{-1}$). During C5 we observed a net loss of 0.3 cm $m^{-2}$ with daily variation up to 15.2 cm $m^{-2}$ $day^{-1}$. During C6 we observed a net loss of 0.5 cm $m^{-2}$ with daily variation up to 24.9 cm $m^{-2}$ $day^{-1}$. These results suggest that large fluctuations in gain and loss of daily root length may influence the estimates of turnover times.

We found that mean root length varied among campaigns from 31.6 cm $m^{-2}$ during C1 to nearly 80 cm $m^{-2}$ during C2 and C6 (Table 1). Daily measurements of fine root length were significantly positive correlated with air relative humidity ($r = 0.445$) but not with soil volumetric water content (VWC) and temperature (Table 2). We expected that root turnover would be faster during warm wet conditions therefore we should have seen higher root production during campaigns C2 and C3 (Table 1), but we did not find a significant correlation of fine root counts with soil temperature or soil moisture (Table 2). Therefore, our results suggest that fine root length did not respond to short-term changes in VWC or temperature, but we did see a seasonal pattern that may

influence root length (Fig. 3a). Most likely the root length response may be result of conditions of previous days and the result in growth or mortality should show a lag.

## Fungi

This is the first study on rapid changes rhizomorph lengths. We analyzed all cohorts of rhizomorphs regardless of birth date between 3/2005 and 12/2006 and estimated a median longevity using a Kaplan-Maier analysis of 400 days (95% confident intervals of 396 and 403 days) or 1.1 years (Fig. 4b). Rhizomorphs have been observed to live up to 11 months in a pinyon-juniper woodland, New Mexico showing that their construction by fungi may be a mechanism for long-term nutrient immobilization (Treseder et al., 2005).

We found significant differences ($P< 0.05$) in rhizomorph length in campaigns C1, C2, C4, C5 and C6 (Fig. 6). Our results support the hypothesis that turnover times can be observed by changes in rhizomorph length based upon continuous observations of minirhizotron images. Similarly to the patterns in fine root length, rhizomorphs experience changes that could be missed by longer observation periods. During C2 we observed a net loss gain of 29.4 cm $m^{-2}$ in four consecutive days of observation where the largest gain was in the second day (30.8 cm $m^{-2}$ $day^{-1}$). During C4 we observed a net loss of 72.6 cm $m^{-2}$, where the largest loss was seen in the third day with 105.4 cm $m^{-2}$ $day^{-1}$. Campaigns C5 and C6 also shown losses in rhizomorph lengths with net losses of 45.6 and 2.8 cm $m^{-2}$, respectively. Maximum variation in rhizomorphs lengths for these campaigns was 26.3 cm $m^{-2}$ $day^{-1}$ for C5 and 39.08 cm $m^{-2}$ $day^{-1}$ for C6.

Our results show that rhizomorph length was more variable than root length during the sampled campaigns and the standard deviations were larger, suggesting large spatial and temporal variability. The survival analysis shows larger median longevity of rhizomorphs, but our data suggests that these structures fluctuate in length during their lifespan. During the sampled campaigns the length of the rhizomorphs was negatively correlated with VWC. Rhizomorphs grew rapidly (2-week period) with low soil VWC (below 1% in July, Fig. 3) and are crucial for water transport in arid soils (Allen, 2007). During these dry conditions water may be redistributed via hydraulic lift by the nearby oaks and the rhizomorphs to the soil, mycorrhizal fungi, and even into adjacent plants (Querejeta et al., 2003; Egerton-Warburton et al., 2007; Querejeta et al., 2007). Therefore, we further hypothesize that plants may invest in carbon for rhizomorphs in exchange of water during harsh conditions.

Rhizomorphs are more stable structures than extra radical hyphae. Previous laboratory observations have shown that an AM hyphal network grows out for a week, then dies back, with a lifespan of the 6-8$^{o}$ branch only surviving for a day or two, and the 1$^{o}$ branch living for up to 2-3 weeks (Friese and Allen, 1991; Allen et al., 2003). More recent studies using radiocarbon have found that most AM hyphae survive on average 5 to 6 days showing that a large rapid mycorrhizal pathways of carbon to the soil (Staddon et al., 2003). Observing individual hyphae with minirhizotrons is difficult because the image quality and resolution of the most minirhizotrons is inadequate for this level of observation. Nevertheless, during the summer of 2005, we undertook some high-resolution images of individual root tips. The finer hyphae (3-4$^{o}$ AM branches) tended to live for no more than a week. The coarse AM runner hyphae persisted for between 16 and

20 days. Some individual hyphae were observed to persist for over a month. More work is needed to study individual hyphae, but our initial observations suggest that most have short life spans, but some can persist for surprisingly long periods.

## Soil Respiration

Our results show a high amount of variation in soil respiration rates tied to fluctuations in soil VWC and soil temperature among the campaigns. We observed rapid changes in root and rhizomorphs length among the different campaigns that may suggests an autotrophic contribution to soil respiration rates. Soil respiration was highly correlated with soil and air temperature, and with photosynthetically active radiation (PAR; Table 2). Temperature is a major driver for soil respiration in temperate forests. Soil VWC was also correlated with soil respiration and may be a key driver for seasonal soil respiration as seen in other sites with precipitation during the winter months (Davidson et al., 1998). However, at short time-scale measurements, increasing volumetric water can actually reduce respiration by decreasing the diffusion coefficient (Warrick, 2003).

It is important to corroborate the modeled flux with measured values using soil respiration systems. We compare the daily average of modeled and measured soil respiration during the campaigns, and found that the gradient flux method shows slightly higher values compared with the Li-Cor 8100 ($r^2 = 0.939$ $P < 0.001$, Fig. 7). More studies are needed to compare the gradient flux method with the chamber method in other ecosystems and it may be necessary to determine site-specific diffusivity models to better estimate soil respiration rates (Jassal et al., 2005).

Root length was significantly positive correlated with $CO_2$ concentration at 2, 8 and 16 cm, but not with soil respiration (Table 2). The production of soil $CO_2$ is a function of root and microbial biomass, but soil respiration also depends on the diffusivity of $CO_2$ in the soil, which is a function soil temperature and soil water content, and the driving atmospheric pressure gradient (Moldrup et al., 2003). Importantly, the concentration of $CO_2$ in the soil was correlated with soil respiration (Table 2). Therefore, fine root biomass may affect soil respiration rates. Assuming a 50% of carbon in fine roots biomass, we calculate a net loss of 4680 g C $ha^{-1}$ $day^{-1}$ via rapid fine root turnover during campaign C1. It is unclear what proportion of the carbon stored in fine roots would be rapidly incorporated to the soil organic matter or respired contributing to total soil respiration.

We observed a clockwise hysteresis effect that changed in amplitude and shape during campaigns C3, C5 and C6 (Fig. 8). A hysteresis loop was not observed in the other campaigns, therefore hysteresis appears to organize and disorganize along the year. It is clear that changes in soil temperature and soil moisture affect soil $CO_2$ diffusivity in the soil profile (Moldrup et al., 2003), and changes in photosynthesis rates may affect the contribution of roots to soil respiration (Tang et al., 2005a). Hysteresis effects have been observed in boreal forests (Gaumont-Guay et al., 2006), oak grass savanna (Tang et al., 2005a), and tropical forests (Vargas, 2007), but there is not a clear mechanistic explanation on the controls of this response. It is unclear how fine roots and rhizomorphs may influence hysteresis in soil respiration, but this effect may be regulated by a combination of physical and biological processes. We observed that campaigns C3 and C5 were associated with higher values of rhizomorphs length, but it was not the case for

C6 (Table 1). Root length did not show a relationship with diurnal soil respiration patterns. Therefore, it is not only necessary to monitor production and death of fine roots and rhizomorphs structures, but also their metabolic activity to determine their contribution to daily patterns of soil respiration.

## Conclusion

Complexity of root and rhizomorph dynamics can be understood most effectively through the synthesis and integration of information across relevant temporal and spatial scales. More studies using continuous measurements are needed to quantify rapid changes in root length and to understand the physical and biological drivers of these changes. Our study suggests that continuous measurements of fine roots and rhizomorphs are crucial because short-term dynamics may be missed using longer sampling periods. This was evident by the intense sampling campaigns that detected nearly 40 cm $m^{-2}$ $day^{-1}$ of change in root length but over 100 cm $m^{-2}$ $day^{-1}$ of change in rhizomorph length. Changes in roots and rhizomorphs lengths and their metabolic activity may influence soil respiration rates at seasonal and diurnal scales, and biophysical processes may explain the observed hysteresis effects on soil respiration with respect to temperature. However, further studies are needed to integrate the influence of fine roots and rhizomorphs on soil respiration at different temporal scales. Embedded Networked Sensing technology is a promising field to develop sensors to remotely continuously monitor the dynamics of environmental variables (Hamilton et al., 2007). Furthermore, the combination of multiple sensors to study rhizosphere dynamics may help to understand root and

rhizomorphs dynamics and their contribution to the global carbon cycle (Allen et al., 2007).

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## Tables

TABLE 1. Summary statistics of measured variables according to sampling campaigns. The campaigns were: C1 (2/23/2006 to 2/26/2006), C2 (4/29/2006 to 5/2/2006), C3 (6/3/2006 to 6/6/2006), C4 (10/7/2006 to 10/9/2006), C5 (11/11/2006 to 11/14/2006), and C6 (12/9/2006 to 12/12/2006). Standard deviations are in parenthesis.

| | Sampling campaigns | | | | | |
|---|---|---|---|---|---|---|
| | C 1 | C 2 | C 3 | C 4 | C 5 | C 6 |
| Fine Roots ($cm\ m^{-2}$) | 31.6 | 81.5 | 57.6 | 43.2 | 53.7 | 80.7 |
| | (18.5) | (7.6) | (6.5) | (6.0) | (8.6) | (13.2) |
| Rhizomorphs ($cm\ m^{-2}$) | 111.7 | 123.8 | 147.3 | 128.5 | 163.2 | 122.5 |
| | (7.5) | (14.5) | (15.2) | (53.9) | (21.5) | (19.3) |
| Hyphae (% hyphae / tube) | 11.5 | 10.3 | 17.7 | 9.5 | 15.1 | 19.4 |
| | (2.7) | (3.2) | (2.8) | (7.6) | (1.1) | (4.9) |
| Soil Temperature (°C) | 4.3 | 12.9 | 18.7 | 12.4 | 10.3 | 5.2 |
| | (0.6) | (0.4) | (0.3) | (0.5) | (0.4) | (0.4) |
| Volumetric water content ($m^{-3}\ m^{-3}$) | 0.17 | 0.185 | 0.105 | 0.03 | 0.04 | 0.12 |
| | (0.001) | (0.003) | (0.002) | (0.001) | (0.001) | (0.013) |
| $CO_2$ flux ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) | 1.8 | 4.4 | 5.4 | 1.1 | 0.7 | 2.0 |
| | (0.2) | (0.2) | (0.1) | (0) | (0.1) | (0.1) |
| $CO_2$ at 2 cm (ppm) | 780.7 | 1507.6 | 1511.1 | 658.3 | 621 | 934.4 |
| | (5.9) | (13) | (10.1) | (7.5) | (5.9) | (74.4) |
| $CO_2$ at 8 cm (ppm) | 1232 | 2565 | 2505 | 832 | 794 | 1346 |
| | (34) | (34) | (32) | (9) | (3) | (106) |
| $CO_2$ at 16 cm (ppm) | 1569 | 3174 | 3312 | 1046 | 1095 | 1869 |
| | (29) | (68) | (29) | (17) | (15) | (173) |
| PAR ($\mu E\ m^{-2}\ s^{-1}$) | 246.5 | 376.3 | 332.5 | 226.4 | 167 | 105.6 |
| | (14.4) | (2.3) | (36.6) | (15) | (5.2) | (25.8) |
| Relative Humidity (%) | 58.3 | 63.5 | 39 | 59.2 | 54.7 | 86.3 |
| | (3.1) | (3.8) | (5.7) | (5.8) | (7) | (7.7) |
| Air temperature (°C) | 3.5 | 11.8 | 18.2 | 8.5 | 7.3 | 3 |
| | (0.8) | (0.5) | (0.7) | (1.2) | (0.6) | (0.8) |

TABLE 2. Pearson correlation coefficients of fine roots length, rhizomorphs length, and daily average of soil respiration ($CO_2$ flux in μmol $CO_2$ $m^{-2}$ $s^{-1}$ ). Soil $CO_2$ concentration is expressed in parts per million (ppm). PAR is photosynthetically active radiation. *P* values are in parenthesis.

| | Soil Temperature (°C) | VWC ($m^{-3}$ $m^{-3}$) | $CO_2$ flux | $CO_2$ at 2 cm (ppm) | $CO_2$ at 8 cm (ppm) | $CO_2$ at 16 cm (ppm) | PAR (μE) | Relative Humidity (%) | Air Temperature (°C) |
|---|---|---|---|---|---|---|---|---|---|
| Fine Root length | 0.086 | 0.252 | 0.321 | **0.489** | **0.438** | **0.457** | 0.01 | **0.445** | 0.079 |
| *P* value | (0.695) | (0.245) | (0.136) | **(0.018)** | **(0.036)** | **(0.028)** | (0.965) | **(0.033)** | (0.721) |
| Rhizomorphs length | 0.357 | **-0.471** | -0.022 | -0.057 | -0.073 | -0.046 | -0.098 | -0.38 | 0.285 |
| *P* value | (0.094) | **(0.023)** | (0.922) | (0.798) | 0.739 | (0.833) | (0.656) | (0.074) | (0.187) |
| $CO_2$ flux | **0.678** | **0.498** | 1 | **0.970** | **0.975** | **0.978** | **0.793** | -0.333 | **0.791** |
| *P* value | **(> 0.001)** | **(0.016)** | - | **(> 0.001)** | **(> 0.001)** | **(> 0.001)** | **(> 0.001)** | 0.12 | **(> 0.001)** |

# Figures

FIG. 1. Expected relationship between fine root decomposition time and root age at death of two cohorts of fine roots where younger roots decompose faster than older roots (Allen et al., 2003; Ruess et al., 2003). This study focused on the shaded area where young roots are expected to decompose at faster rates.

FIG. 2. Soil sensor array at the San Jacinto Mountains James Reserve in southern California. Minirhizotron tubes where equipped with soil moisture, temperature and $CO_2$ sensors at three depths (2, 8 and 16 cm). Soil respiration using the gradient flux method (see methods for details) was validated using the chamber method with a Licor 8100 soil respiration system.

FIG. 3. Length of fine roots ( ○ ) and rhizomorphs ( ● ), and soil respiration during the year of 2006 (A) at the James Reserve, CA. Relationship of soil temperature and soil moisture during the year of 2006 (B). DOY means day of the year.

FIG. 4. Fine root survival curve (A), and rhizomorphs survival curve (B) for days between 3/17/2005 and 12/31/2006. The x axis is numbers of days after 3/17/2005 and the y axis is the cumulative survival percentage.

FIG. 5. Radiocarbon data of structural carbon in fine roots <1 m in diameter and fine roots of 1mm in diameter. Error bars are ±1 standard deviation.

FIG. 6. Mean daily root length ( ○ ) and rhizomorphs length ( ● ) per campaign. *P* values indicate significant differences using repeated measurements ANOVA. The null hypothesis was that length should not change in four consecutive days (sampling campaigns). The campaigns were: C1 (2/23/2006 to 2/26/2006, A), C2 (4/29/2006 to 5/2/2006, B), C3 (6/3/2006 to 6/6/2006, C), C4 (10/7/2006 to 10/9/2006, D), C5 (11/11/2006 to 11/14/2006, E), and C6 (12/9/2006 to 12/12/2006, F). DOY means "day of the year" during 2006. Error bars are ±1 standard deviation.

FIG. 7. Soil respiration using the gradient flux method vs. soil respiration using the chamber method during the sampling campaigns (see methods for details). Soil respiration is expressed as $CO_2$ flux in μmol $CO_2$ $m^{-2}$ $s^{-1}$. Error bars are ±1 standard deviation.

FIG. 8. Relationship between soil respiration (expressed as $CO_2$ flux in μmol $CO_2$ $m^{-2}$ $s^{-1}$) and soil temperature (°C) at the James Reserve during the sampled campaigns. Black circles indicate increasing temperature and open circles indicate decreasing temperatures in a diurnal cycle. The campaigns were: C1 (2/23/2006 to 2/26/2006, A), C2 (4/29/2006 to 5/2/2006, B), C3 (6/3/2006 to 6/6/2006, C), C4 (10/7/2006 to 10/9/2006, D), C5 (11/11/2006 to 11/14/2006, E), and C6 (12/9/2006 to 12/12/2006, F).

FIG. 1. Expected relationship between fine root decomposition and time

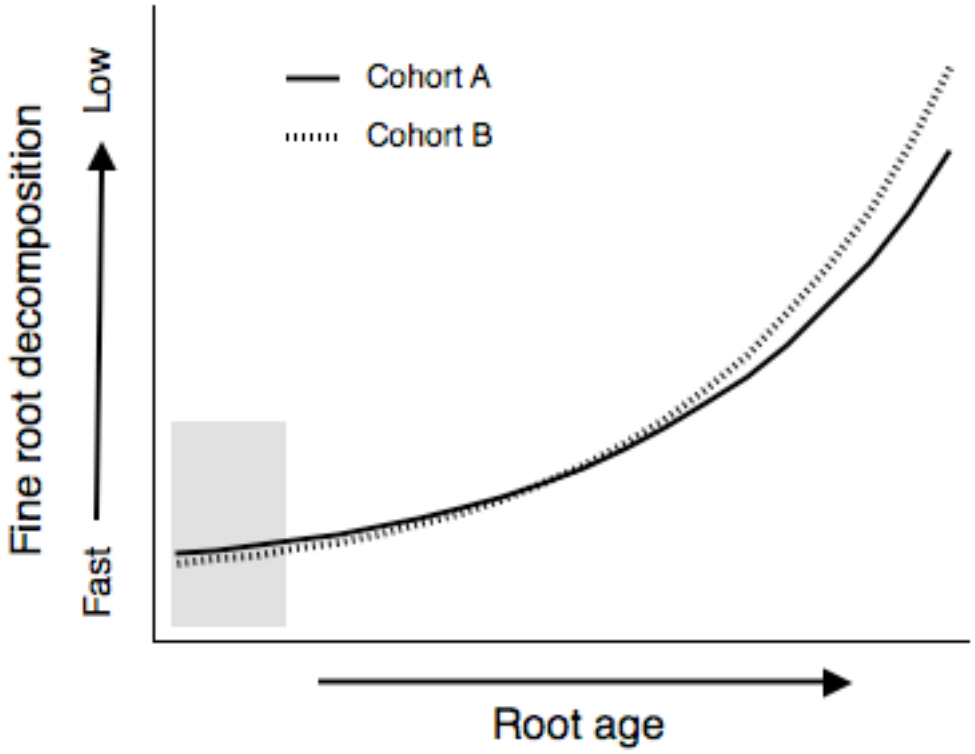


FIG. 2. Soil sensor array.

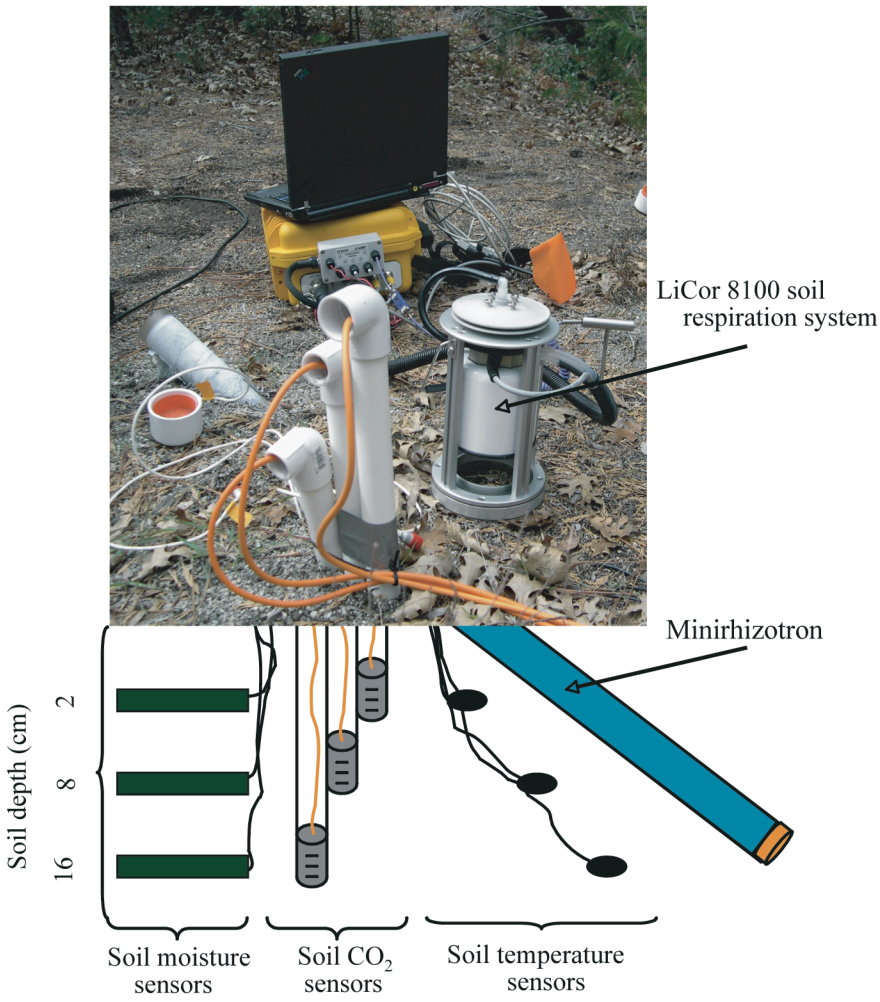


FIG. 3. Roots, rhizomorphs, soil $CO_2$, temperature and soil moisture at the James Reserve

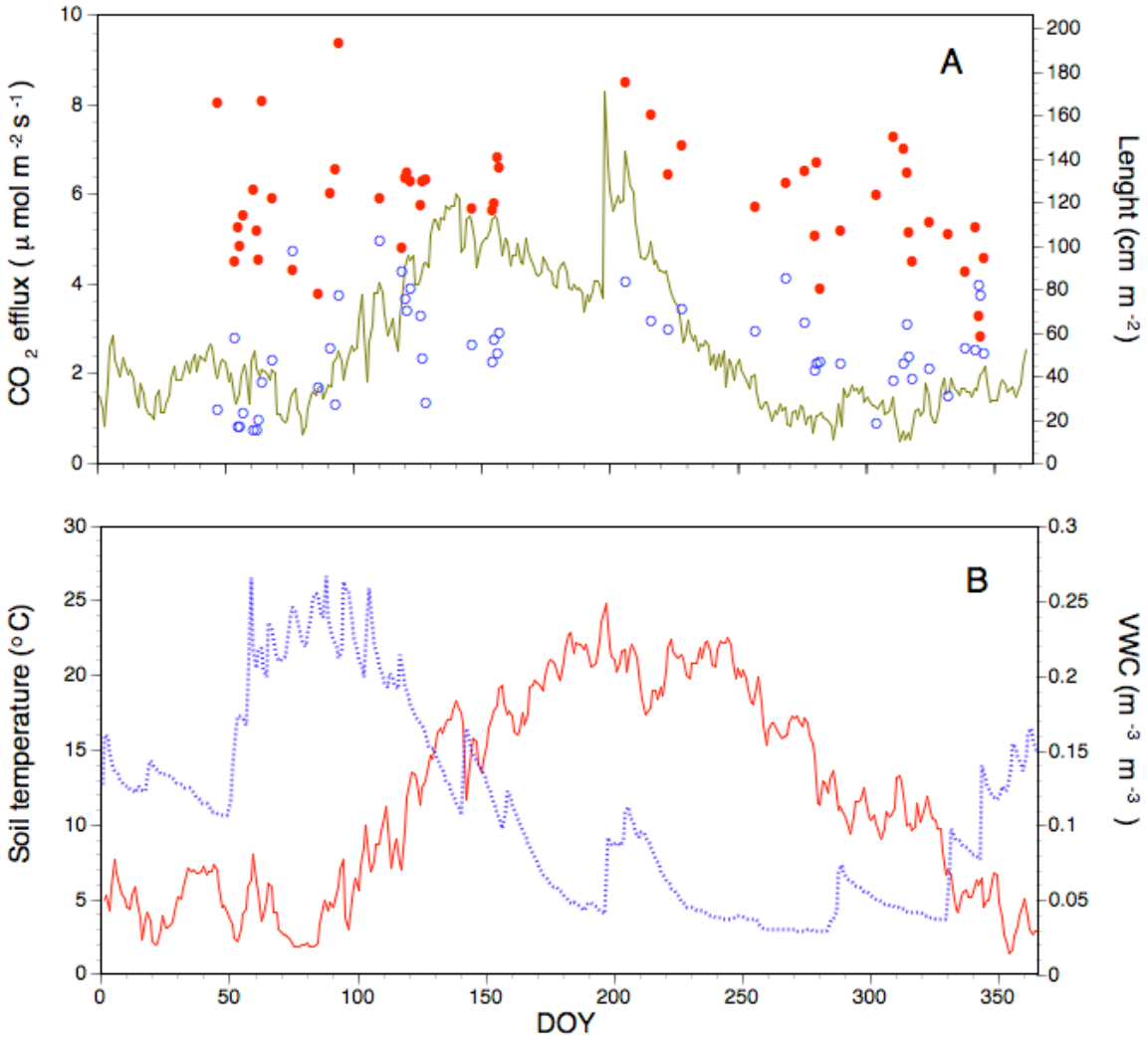


FIG. 4. Survival curves for fine roots and rhizomorphs

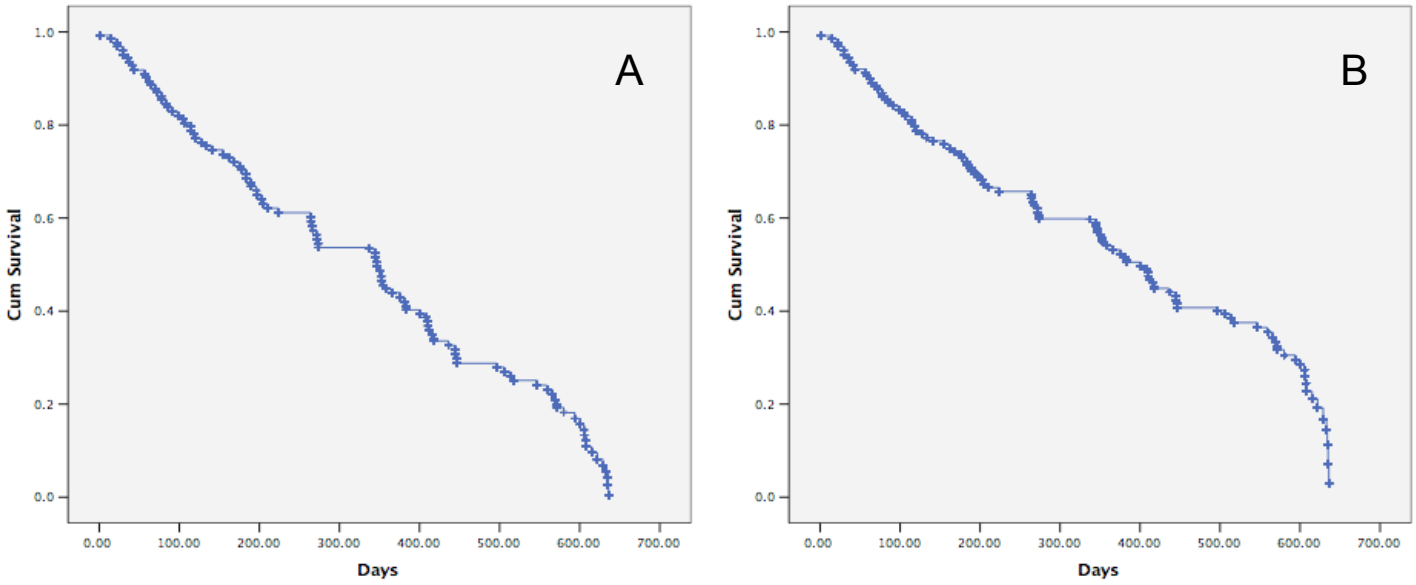


FIG. 5. Radiocarbon data for fine roots

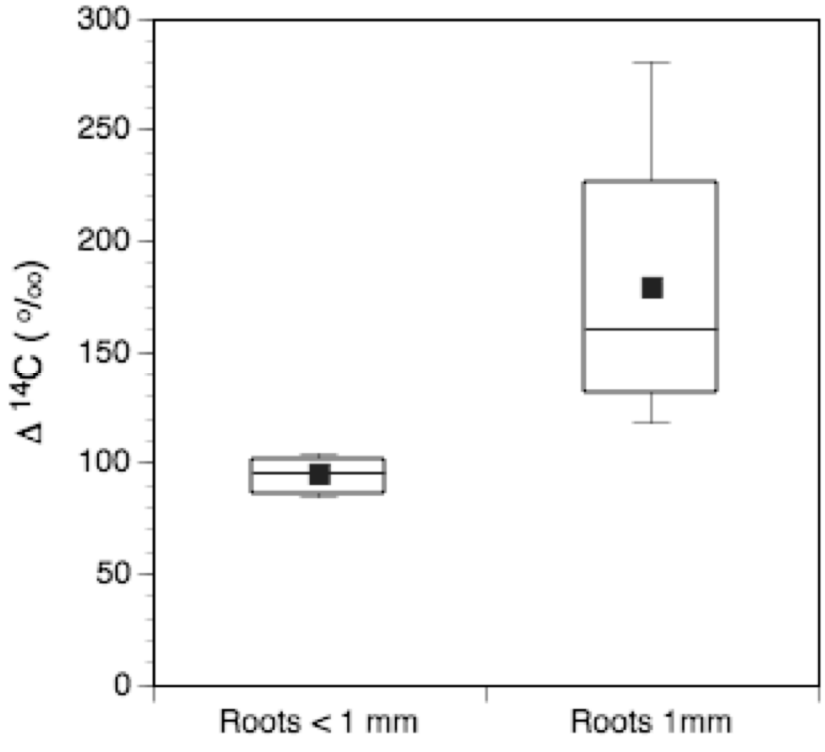


FIG. 6. Mean daily root length and rhizomorphs length.

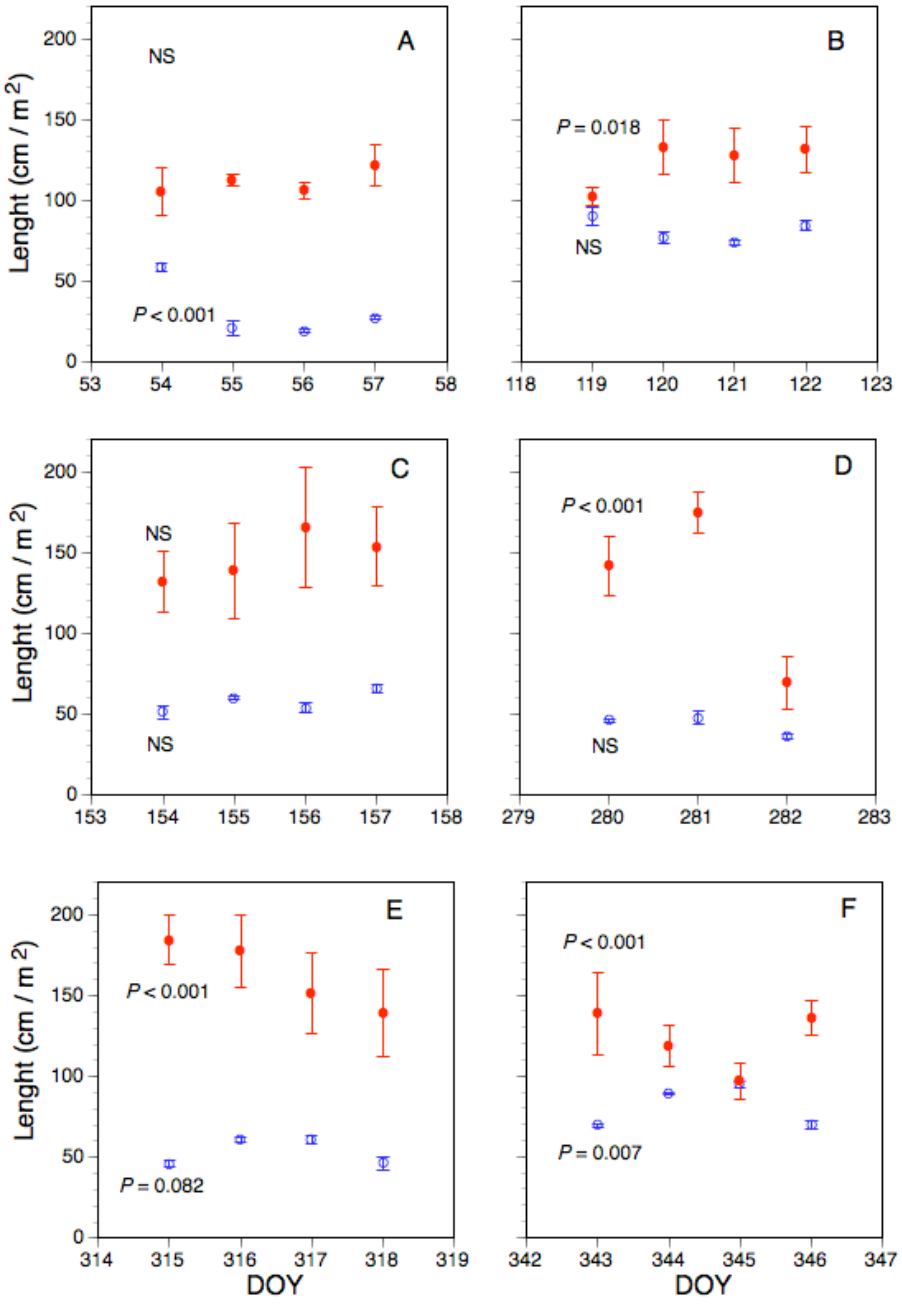


Fig. 7. Method comparison for soil respiration

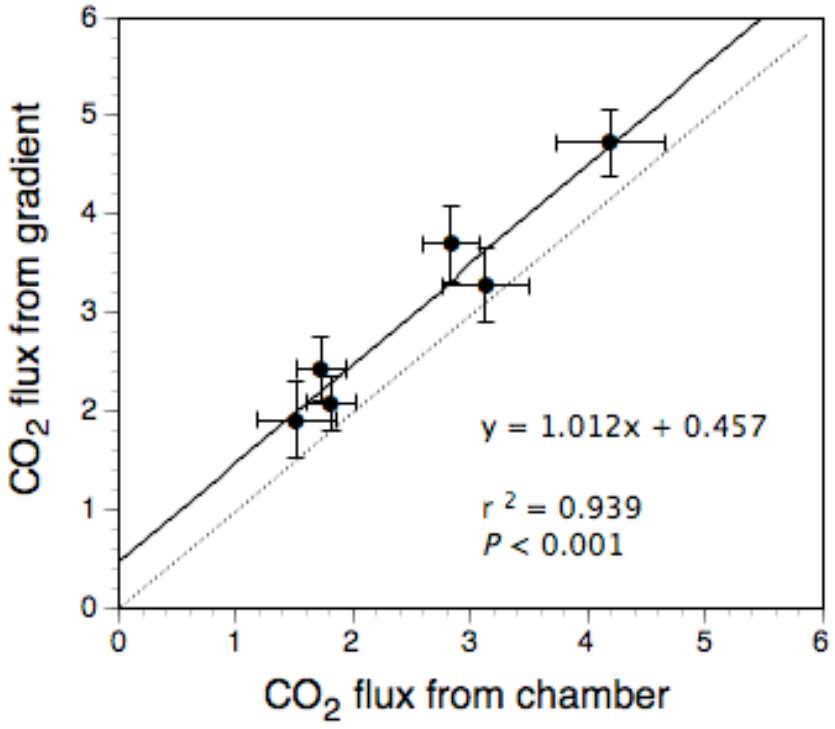
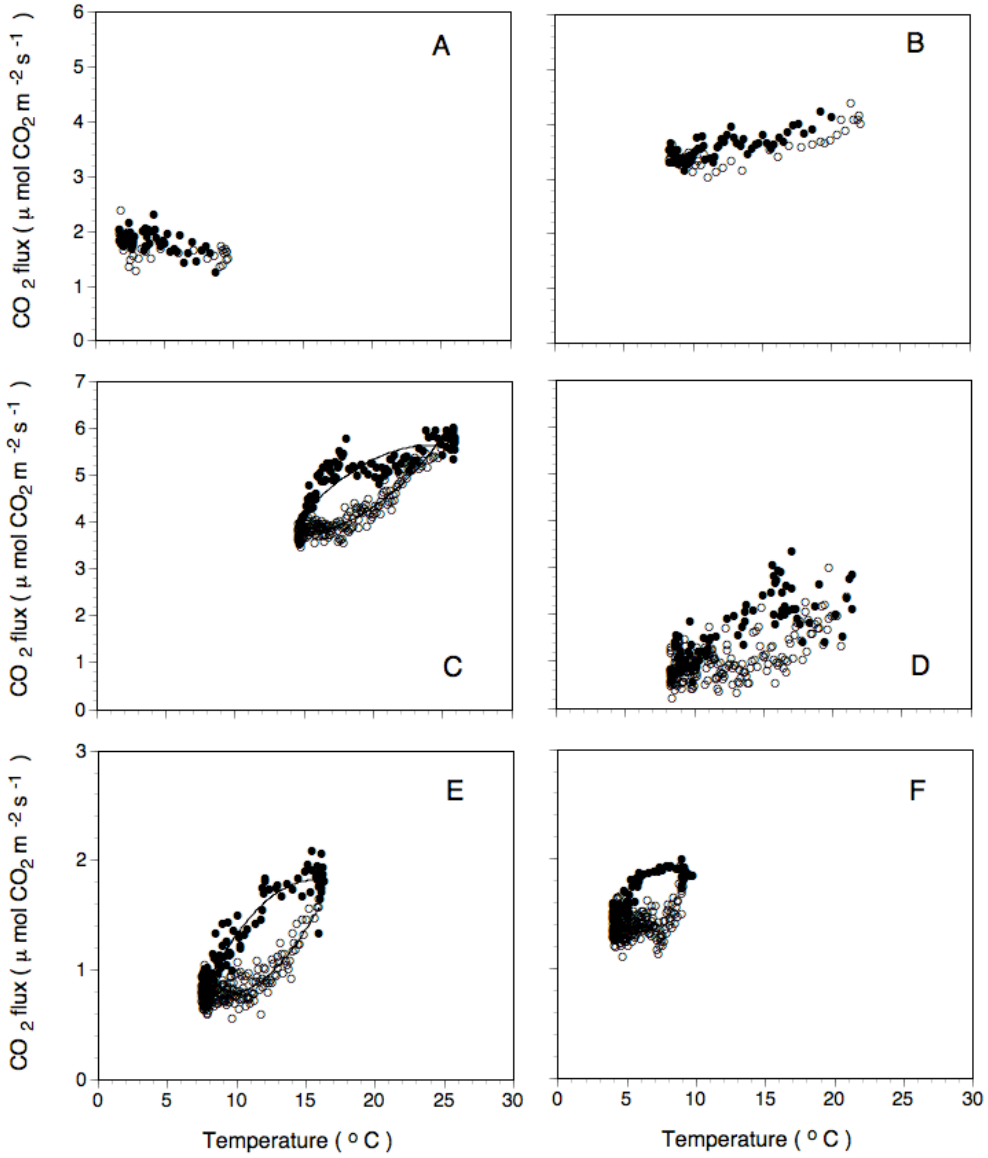


FIG. 8. Relationship between soil respiration and soil temperature



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