Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration

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Summary

• Characterization of spatial and temporal variation of soil respiration coupled with fine root and rhizomorph dynamics is necessary to understand the mechanisms that regulate soil respiration.
• A dense wireless network array of soil CO2 sensors in combination with minirhizotron tubes was used to continuously measure soil respiration over 1 yr in a mixed conifer forest in California, USA, in two adjacent areas with different vegetation types: an area with woody vegetation (Wv) and an area with scattered herbaceous vegetation (Hv).
• Annual soil respiration rates and the lengths of fine roots and rhizomorphs were greater at Wv than at Hv. Soil respiration was positively correlated with fine roots and rhizomorphs at Wv but only with fine roots at Hv. Diel and seasonal soil respiration patterns were decoupled with soil temperature at Wv but not at Hv. When decoupled, higher soil respiration rates were observed at increasing temperatures, demonstrating a hysteresis effect. The diel hysteresis at Wv was explained by including the temperature-dependent component of soil respiration and the variation dependent on photosynthetically active radiation.
• The results show that vegetation type and fine root and rhizomorph dynamics influence soil respiration in addition to changes in light, temperature and moisture.

Key words: CO2 efflux, minirhizotron, mycorrhizas, photosynthesis, rain pulse, temperature-independent respiration, wireless networks.


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Introduction

Soils represent the largest carbon pool in terrestrial ecosystems (Dixon et al., 1994), and understanding the effect of climate variation on soil respiration ($R_s$) is crucial for accurate estimation of the global carbon balance (Schimel, 1995; Raich et al., 2002). $R_s$ is the synthetic result of heterotrophic respiration (by decomposers) and autotrophic respiration (by roots and mycorrhizas). These processes are regulated by several physical (e.g. soil temperature, moisture, and soil porosity) and biological factors (e.g. root density, microbial community, and photosynthesis) that complicate the mechanistic understanding of $R_s$ (Ryan & Law, 2005). Understanding how these factors regulate $R_s$ at different temporal scales is of critical importance in determining the effect of climate variation on terrestrial carbon fluxes.

Roots are the primary belowground structural element of plants and mycorrhizal fungi are obligate symbionts that form a hyphal network that takes up nutrients and water in exchange for newly fixed plant carbon (Allen et al., 2003). Rhizomorphs are large cords of fungal hyphae that transport nutrients and water, and a large proportion appear to be mycorrhizal (Smith & Read, 1997). To date, the relationship between mycorrhizal fungi and $R_s$ has remained unclear because limited studies have been carried out in the field (Langley et al., 2005; Heinemeyer et al., 2006; Heinemeyer...
et al., 2007). Thus, the study of the spatio-temporal dynamics of fine roots and rhizomorphs is a key element in understanding variations in autotrophic respiration and therefore total $R_{e}$ (Hanson et al., 2000; Misson et al., 2006; Vargas & Allen, in press b).

Developments in automated measurements of $R_{e}$ provide an opportunity to study relationships between $R_{e}$ and soil temperature or water content at different temporal scales (Goulden & Crill, 1997; Drewitt et al., 2002). The high frequency of these measurements enables detection of responses to sudden events, such as rain pulses, which are important for the understanding of seasonal patterns (Irvine & Law, 2002; Jassal et al., 2005). Furthermore, diel $R_{e}$ patterns can be studied along with variation in temperature and light (Liu et al., 2006; Carbone & Vargas, 2008). Recent studies have shown that, at the diel scale, $R_{e}$ and soil temperature may be decoupled, showing a hysteresis effect in boreal forests (Liu et al., 2006; Vargas & Allen, in press a), and Mediterranean ecosystems (Tang et al., 2005a; Vargas & Allen, in press b). Several studies have postulated that photosynthesis regulates diel variation in $R_{e}$ rates and may be an explanation of the temperature-independent component of $R_{e}$ (Tang et al., 2005a; Liu et al., 2006). Thus, it is important to test the influence of light, temperature and moisture on $R_{e}$ at multiple spatial and temporal scales.

In this study, we used continuous measurements of soil CO$_2$ concentration in the soil profile in conjunction with minirhizotron measurements to calculate $R_{e}$. The use of minirhizotrons is a nondestructive technique to measure changes in fine roots and rhizomorphs in space and time (Pregitzer et al., 2002; Treseder et al., 2005), and we developed a wireless network array of soil sensors (Allen et al., 2007; Vargas & Allen, in press b). Using this array, we simultaneously quantified $R_{e}$ at multiple points in two adjacent vegetation types of a California mixed conifer forest that included a patch of large trees and an open meadow with scattered herbaceous vegetation. This approach provided the opportunity to test the influence of vegetation type on $R_{e}$ under similarly varying climatic conditions, at different temporal scales, without disturbing the environment. Our objectives were: to determine the environmental factors that regulate fine root and rhizomorph dynamics; to determine the environmental controls on seasonal and diel patterns in $R_{e}$; and to explore the relationship between $R_{e}$ and fine root and rhizomorph dynamics in two adjacent vegetation types.

Materials and Methods

Study site

This study was conducted at the James San Jacinto Mountains Reserve, which is part of the UC Natural Reserve System. The James Reserve is located in the San Jacinto Mountains, California, USA (33°48′30″N, 116°46′40″W), at an elevation of 1640 m, and is 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). The James Reserve is a test site for the National Ecological Observatory Network, serves as the Terrestrial Ecology Observing Systems field site for the Center for Embedded Networked Sensing, and is instrumented with a large wireless network of environmental sensors (Allen et al., 2007; Hamilton et al., 2007).

In October 2003, we selected an area of woody vegetation ($W_{w}$) and an adjacent area with scattered herbaceous vegetation ($H_{w}$). The vascular plants present at $W_{w}$ were individuals of Quercus kelloggii Newb. (California black oak), Calocedrus decurrens (Torr.) Florin (incense cedar), Arctostaphylos pringlei Parry (manzanita), and Pinus lambertiana Doug. (sugar pine). All of these species form ectomycorrhizas with the exception of C. decurrens, which forms arbuscular mycorrhizas, and Q. kelloggii, which may form both ecto- and arbuscular mycorrhizas. $H_{w}$ was dominated by arbuscular mycorrhizal Eriogonum wrightii Torr. Ex Benth (bastard sage) of < 10 cm in height and at a density of nearly two plants m$^{-2}$. Bastard sage was also present in the understory of $W_{w}$ with a similar density as at $H_{w}$.

Two 5-m transects were established at both $W_{w}$ and $H_{w}$, as described in Supplementary Material Fig. S1. Each transect was instrumented with three minirhizotron tubes and two sensor nodes as part of a wireless network array (see Minirhizotrons and Sensor nodes sections). Soil bulk density was 0.9 g cm$^{-3}$ at $W_{w}$ and 1.2 g cm$^{-3}$ at $H_{w}$. Soil texture was 83% sand, 10% silt, and 7% clay at both $W_{w}$ and $H_{w}$. Fine root biomass (0–16 cm) was calculated to be 18 g m$^{-2}$ at $W_{w}$ and 10 g m$^{-2}$ at $H_{w}$, and a detailed fine root and rhizomorph profile distribution is presented in Supplementary Material Fig. S2. Fine root nitrogen was 0.58% (± 0.23% SD) and 0.53% (± 0.24% SD), respectively. Soil carbon (0–16 cm depth) at $W_{w}$ was 3.1% (± 0.5% SD) and that at $H_{w}$ was 2.4% (± 0.5% SD), while soil nitrogen (0–16 cm depth) was 0.08% (± 0.02% SD) at $W_{w}$ and 0.05% (± 0.03% SD) at $H_{w}$.

Minirhizotrons

During October 2003 we installed three minirhizotron observation tubes 5 cm in diameter and 1 m in length at each of the 5-m transects (Supplementary Material Fig. S1). Collection of images for this research started in January 2006 to allow fine roots to recolonize the soil surrounding the tubes. Images from all the tubes were collected in weekly campaigns between February 2006 and December 2006, with a total of 59 sampling days at intervals that varied from 1 d to 1 month.

Minirhizoron images were collected using a minirhizotron microscope (BTC-10 with I-CAP software; Bartz Technology, Carpinteria, CA, USA). An average of 52 vertical images were collected per tube, and the number of rhizomorphs and fine
roots was counted for all collected images. These images include fine roots and rhizomorphs to an average depth of 60 cm at both vegetation types. We used linear regression models to predict lengths based on the number of roots or rhizomorphs reported by Vargas & Allen (in press b) for the study site. We used the information from all 52 images and report length of fine roots and rhizomorphs in cm m\(^{-2}\).

Sensor nodes

In October 2005 we installed two sensor nodes at each 5-m transect in association with the minirhizotron tubes (Supplementary Material Fig. S1). At W\(_v\), the nodes were within a 2-m radius of plants, and at H\(_v\), within a 1-m radius. At each node we measured photosynthetically active radiation (PAR), air relative humidity, air temperature and barometric pressure at a height of 2 m, and vapor pressure deficit (VPD) was calculated from air temperature and relative humidity. In addition, we installed solid-state CO\(_2\) (GMM 222; Vaisala, Helsinki, Finland), soil temperature, and soil moisture (ECHO EC-20; Decagon, Pullman, WA, USA) sensors at soil depths of 2, 8 and 16 cm (Allen et al., 2007). The soil temperature and moisture sensors were installed horizontally, and the CO\(_2\) sensors were installed vertically, similar to Tang et al. (2005b). All variables were recorded at 5-min intervals and transmitted using a Crossbow Mica2 868/916-Mhz (Crossbow Technology; San Jose, CA, USA) wireless platform to a centralized server at the James Reserve.

Soil CO\(_2\) profile

We used a dense array of solid-state CO\(_2\) sensors with a total of 24 sensors among transects (four nodes per area). The CO\(_2\) sensors had a range of 0–10 000 ppm and were calibrated every 6 months after deployment to ensure the quality of the measurements. To keep the sensors dry, we enclosed them in a watertight container with an opening at the bottom covered with Gortex fabric. \(R\) was calculated using the flux-gradient method based on concentrations of CO\(_2\) in the soil profile (Tang et al. 2005b; Vargas & Allen, in press b). Briefly, the CO\(_2\) concentration from the sensors was corrected for temperature and pressure according to the manufacturer’s instructions (Vaisala, Helsinki, Finland). The corrected CO\(_2\) concentrations were used to calculate \(R\) using Fick’s first law of diffusion, and the diffusivity of soil CO\(_2\) in the soil profile was calculated using the Moldrup model (Moldrup et al., 1999).

\(R\) values from the gradient method were calibrated with \(R\) values obtained using a soil chamber (Li-8100-102) connected to a soil respiration system (LI-8100; Li-Cor, Lincoln, NE, USA). We installed 10-cm-diameter PVC soil collars associated with each minirhizotron tube in November 2005. The litter layer was very shallow at both vegetation sites (< 2 cm). Soil respiration was measured nearly four times a day (morning and/or afternoon) on the same dates on which the minirhizotron images were collected during the year 2006.

Data analysis

Depending on the best statistical fit, we used either a model for \(R\) using soil temperature as an independent variable:

\[
R = B_0 e^{(B_1 T)}
\]  
Eqn 1

or soil temperature and volumetric water content (VWC) as drivers for \(R\):

\[
R = B_0 e^{(B_1 T)} e^{(B_2 \theta)}
\]  
Eqn 2

\(R\), soil respiration in µmol CO\(_2\) m\(^{-2}\) s\(^{-1}\); \(T\), soil temperature in °C; \(\theta\), volumetric water content in m\(^3\) m\(^{-3}\); \(B_0\), \(B_1\), \(B_2\) and \(B_3\), model parameters.) Similar models have been used previously in Mediterranean ecosystems (Xu et al., 2004; Tang et al., 2005b). To select the best statistical model for \(R\), we used the root mean squared error (RMSE), and the Akaike information criterion (AIC) as a penalized likelihood criterion (Burnham & Anderson, 2002):

\[
AIC = -2\ln(L) + 2p
\]  
Eqn 3

\((L, the likelihood of the fitted model; \(p\), the total number of parameters in the model.) The best statistical model minimizes the value of AIC.

To test diel and seasonal hysteresis effects, we used an F-test as explained by Vargas & Allen (in press a). Briefly, we compared the F-values of a single exponential model, using Eqn 1 and assuming no hysteresis effect, with the sum of the F-values of two independent exponential models (Eqn 1) by splitting the data into two sets based on maximum and minimum daily temperatures, assuming a hysteresis effect.

To model significant daily hysteresis loops we first calculated the temperature-dependent component of \(R\) based on Eqn 1. Then the residuals from Eqn 1 were fit to a linear model based on PAR to explain the diel temperature-independent variation in soil respiration using a similar rational as Liu et al. (2006). The final diel \(R\) model when hysteresis was present took the form:

\[
R = B_0 e^{(B_1 T)} + (B_3 \text{PAR} + B_3)
\]  
Eqn 4

In addition, repeated measurements using the GLM procedure were used to test for differences in fine root and rhizomorph lengths between the vegetation types. Pearson correlation coefficients were calculated to test the relationships between the biophysical variables and \(R\). All statistical analyses were performed with spss v13 (SPSS, Chicago, IL, USA).

Results

Environmental variables

We divided \(R\) into phases from I to VI based on variations in soil temperature and soil VWC during 2006, and we will refer
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to these throughout the text (Fig. 1). Phase I included days of
the year 1 to 50, which corresponded to low soil temperature
and low VWC. Phase III included days 126 to 195, which corresponded to
increasing soil temperature and decreasing VWC. Phase IV
included days 196 to 225 and represents the influence of a
monsoon event. Phase V included days 226 to 330, which corresponded to decreasing temperatures with low VWC.
Phase VI included days 331 to 365, which corresponded to
low temperatures with increasing VWC.

The annual mean soil temperature was 11.9°C at Wv and
10.9°C at Hv. The soil VWC content was higher at Wv, especially
during phases II and III. VPD was lower during phase II
(mean = 0.18 kPa) and higher during phases III and IV (mean
= 0.96 and 0.7 kPa, respectively) in both areas. The monsoon
event reduced the mean soil temperature from nearly 25
to 18°C, increased the mean soil VWC from nearly 0.1 to
0.9 m³ m⁻³ and reduced the mean VPD from nearly 1.4 to
0.28 kPa in both areas.

**Fine root and rhizomorph lengths**

The minirhizotron measurements showed significant differences
in belowground architecture and seasonality of fine roots
\((F = 171.139, \ P < 0.001)\) and rhizomorphs \((F = 1714.66,\n\ P < 0.001)\) between vegetation types. Fine root length was
significantly higher \((P < 0.05)\) at Wv during phases I, II, and
VI (Fig. 2a). The mean length of fine roots varied from 47.9
to 75.2 cm² m⁻² at Wv and between 29.6 and 56.4 cm² m⁻²
at Hv. Greater fine root length was observed during phase IV
at both sites. Fine roots were significantly \((P < 0.05)\) positively
correlated with soil temperature at Wv and with soil
temperature, VPD and PAR at Hv (Table 1).

Rhizomorph length was always significantly \((P < 0.05)\) higher
at Wv, with mean values between 123.9 and 205 cm² m⁻².
The length of rhizomorphs associated with Hv ranged from
29.4 to 94.2 cm² m⁻² (Fig. 2b). Rhizomorph development
responded positively to the monsoon event (phase IV) at Wv
but not at Hv. Rhizomorph length was significantly \((P < 0.001)\)
positively correlated with soil temperature and VPD, and
negatively correlated \((P < 0.001)\) with VWC at Wv (Table 2).
We did not find a significant correlation between rhizomorph
length and environmental variables at Hv.

**Gradient flux method validation**

Our calculations of \(R_s\) using the gradient method showed a
significant positive relationship with \(R_s\) using the chamber
method during 59 d of measurements. At Wv, we found a
slope of 0.966 with \(r^2 = 0.73\) and \(P < 0.001\) (Fig. 3a). At Hv,
we found a strong relationship, with a slope of 0.9 and an
\(r^2 = 0.91\) with \(P < 0.001\) (Fig. 3b). At both sites the intercept
was not significantly different from zero and the slope was not
significantly different from the 1 : 1 line. The gradient flux
method assumes steady-state conditions in CO₂ diffusion in
the soil. In nearly 5% of our measurements this condition was
not met and these measurements were eliminated from the
analysis, and the gaps were filled by linear interpolation if they
were less than 2 h.
Table 1 Pearson correlation coefficients between soil respiration ($R_s$), fine root length, rhizomorph length, soil temperature, volumetric water content (VWC), vapor pressure deficit (VPD), and photosynthetically active radiation (PAR) at the woody vegetation ($W_v$) and the herbaceous vegetation ($H_v$) sites

<table>
<thead>
<tr>
<th></th>
<th>Woody vegetation ($W_v$)</th>
<th>Herbaceous vegetation ($H_v$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$R_s$</td>
<td>soil temperature</td>
</tr>
<tr>
<td>Fine root length</td>
<td>1</td>
<td>0.583**</td>
</tr>
<tr>
<td>Rhizomorph length</td>
<td>1</td>
<td>0.143</td>
</tr>
<tr>
<td>Soil temperature</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>VWC</td>
<td>1</td>
<td>0.871***</td>
</tr>
<tr>
<td>VPD</td>
<td>1</td>
<td>0.605***</td>
</tr>
<tr>
<td>PAR</td>
<td>1</td>
<td>0.685***</td>
</tr>
</tbody>
</table>

$n = 59$; *$P < 0.05$; ***$P < 0.001$.

Table 2 Results of regression analyses relating soil respiration to soil water content and soil temperature at the woody vegetation ($W_v$) and the herbaceous vegetation ($H_v$) sites

<table>
<thead>
<tr>
<th>Period</th>
<th>Model</th>
<th>Vegetation type</th>
<th>$B_0$</th>
<th>$B_1$</th>
<th>$B_2$</th>
<th>$B_3$</th>
<th>$r^2$</th>
<th>$P$ value</th>
<th>RMSE</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>I</td>
<td>$W_v$</td>
<td>1.396</td>
<td>0.049</td>
<td>–</td>
<td>–</td>
<td>0.354</td>
<td>&lt;0.0001</td>
<td>1.21</td>
<td>1444</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>$H_v$</td>
<td>0.516</td>
<td>0.053</td>
<td>–</td>
<td>–</td>
<td>0.750</td>
<td>&lt;0.0001</td>
<td>0.11</td>
<td>956</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>$W_v$</td>
<td>0.193</td>
<td>0.089</td>
<td>22.149</td>
<td>–61.202</td>
<td>0.919</td>
<td>&lt;0.0001</td>
<td>0.42</td>
<td>611</td>
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<tr>
<td></td>
<td>II</td>
<td>$H_v$</td>
<td>0.168</td>
<td>0.059</td>
<td>22.095</td>
<td>–97.273</td>
<td>0.899</td>
<td>&lt;0.0001</td>
<td>0.09</td>
<td>1205</td>
</tr>
<tr>
<td>Diel</td>
<td>I</td>
<td>$W_v$</td>
<td>0.002</td>
<td>0.614</td>
<td>1.791</td>
<td>0.001</td>
<td>0.734</td>
<td>&lt;0.0001</td>
<td>0.009</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>$H_v$</td>
<td>0.518</td>
<td>0.059</td>
<td>–</td>
<td>–</td>
<td>0.787</td>
<td>&lt;0.0001</td>
<td>0.005</td>
<td>–</td>
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<tr>
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<td>II</td>
<td>$W_v$</td>
<td>2.008</td>
<td>0.042</td>
<td>–</td>
<td>–</td>
<td>0.812</td>
<td>&lt;0.0001</td>
<td>0.003</td>
<td>–</td>
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<tr>
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<td>II</td>
<td>$H_v$</td>
<td>0.547</td>
<td>0.033</td>
<td>–</td>
<td>–</td>
<td>0.835</td>
<td>&lt;0.0001</td>
<td>0.001</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>$W_v$</td>
<td>1.943</td>
<td>0.034</td>
<td>0.855</td>
<td>0.001</td>
<td>0.941</td>
<td>&lt;0.0001</td>
<td>0.019</td>
<td>–</td>
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<tr>
<td></td>
<td>III</td>
<td>$H_v$</td>
<td>1.075</td>
<td>0.013</td>
<td>–</td>
<td>–</td>
<td>0.876</td>
<td>&lt;0.0001</td>
<td>0.003</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>IV</td>
<td>$W_v$</td>
<td>3.794</td>
<td>0.019</td>
<td>–</td>
<td>–</td>
<td>0.859</td>
<td>&lt;0.0001</td>
<td>0.017</td>
<td>–</td>
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<tr>
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<td>IV</td>
<td>$H_v$</td>
<td>1.509</td>
<td>0.013</td>
<td>–</td>
<td>–</td>
<td>0.673</td>
<td>&lt;0.0001</td>
<td>0.004</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>V</td>
<td>$W_v$</td>
<td>0.028</td>
<td>0.164</td>
<td>1.152</td>
<td>0.001</td>
<td>0.912</td>
<td>&lt;0.0001</td>
<td>0.025</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>V</td>
<td>$H_v$</td>
<td>0.662</td>
<td>0.25</td>
<td>–</td>
<td>–</td>
<td>0.894</td>
<td>&lt;0.0001</td>
<td>0.005</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>VI</td>
<td>$W_v$</td>
<td>0.002</td>
<td>0.745</td>
<td>1.505</td>
<td>0.001</td>
<td>0.846</td>
<td>&lt;0.0001</td>
<td>0.008</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>VI</td>
<td>$H_v$</td>
<td>0.493</td>
<td>0.031</td>
<td>–</td>
<td>–</td>
<td>0.799</td>
<td>&lt;0.0001</td>
<td>0.005</td>
<td>–</td>
</tr>
</tbody>
</table>

Model I has the form $R_s = B_0e^{(B_1T)}$, model II the form $R_s = B_0e^{(B_1T)}/\theta^{(B_2)}$, and model III the form $R_s = B_0e^{(B_1T)}B_3 + (\text{VPD} + B_3)$.

The best-fit model parameters ($B_0$, $B_1$, $B_2$, and $B_3$) are reported for each model together with the squared coefficient of regression ($r^2$), the root mean squared error (RMSE) and the Akaike information criterion (AIC; for the seasonal estimates). $T$ is temperature ($^\circ$C) at a depth of 8 cm, $\theta$ is volumetric water content (m$^{-3}$ m$^{-3}$), PAR is photosynthetically active radiation (mol m$^{-2}$ s$^{-1}$), and $R_s$ is soil respiration (µmol CO$_2$ m$^{-2}$ s$^{-1}$).

Model parameters were estimated using the Levenberg–Marquardt method.
Seasonal variation of soil respiration

Mean annual $R_s$ at Wv was 2.7 µmol CO$_2$ m$^{-2}$ s$^{-1}$, but the mean annual value ranged between 3.3 and 1.9 µmol CO$_2$ m$^{-2}$ s$^{-1}$ with a coefficient of variation (CV) of 15.5% among nodes (Fig. 4a). Despite the large variation in mean annual $R_s$, we found a similar seasonal pattern among the nodes at Wv, especially in their response to the monsoon event at phase IV (Fig. 4a,c). During this phase we observed a mean $R_s$ of 5.6 µmol CO$_2$ m$^{-2}$ s$^{-1}$, which represents an increase of nearly 100% from the mean annual rate.

The mean annual $R_s$ at Hv was 0.9 µmol CO$_2$ m$^{-2}$ s$^{-1}$, and we found that the mean annual value at this site ranged between 0.6 and 1.2 µmol CO$_2$ m$^{-2}$ s$^{-1}$ with a CV of 5% among nodes (Fig. 4b). The monsoon event (phase IV) was not evident for nodes 5, 6 and 8, but this event increased $R_s$ at node 7 to nearly 5 µmol CO$_2$ m$^{-2}$ s$^{-1}$ (Fig. 3b,d). During this phase we observed a mean $R_s$ of 1.9 µmol CO$_2$ m$^{-2}$ s$^{-1}$, which also represents an increase of nearly 100% from the mean annual rate.

The best model to explain seasonal variation in $R_s$ for Wv was a function of soil temperature and soil VWC (Table 2). In addition, we observed a significant ($P < 0.001$) hysteresis effect of $R_s$ with respect to soil temperature, with higher rates when temperatures were increasing and lower rates when temperatures were decreasing (Fig. 5a). When temperatures were increasing, $R_s$ at 17°C on day of the year 136 was 5.7 µmol CO$_2$ m$^{-2}$ s$^{-1}$, but when temperatures were decreasing, $R_s$ at the same temperature but on day of the year 270 was 0.82 µmol CO$_2$ m$^{-2}$ s$^{-1}$. This represents a difference of nearly 86% in $R_s$ at similar temperatures. The most parsimonious model to explain $R_s$ at Hv, based on the AIC, was soil temperature alone (Fig. 5b). However, the addition of moisture to the model...
increased the $r^2$ value and reduced the RMSE (Table 2), suggesting that soil VWC also has an important influence on $R_s$ at H_v.

We compared the full data set based on daily averages when all biophysical variables were available (fine root length, rhizomorph length, soil temperature, VWC, VPD, and PAR; $n = 59$ d). At W_v, we found that $R_s$ was significantly correlated ($P < 0.05$) with fine root length, soil temperature, VWC, VPD, PAR and rhizomorph length (Table 1). By contrast, $R_s$ at H_v was significantly correlated ($P < 0.05$) with soil temperature, VPD, PAR and fine root length (Table 1).

Diel variation of soil respiration

Diel $R_s$ was processed as the mean for all days during a specific phase for both vegetation types. During all phases, diel $R_s$ showed higher rates at W_v than at H_v. At W_v, we observed that $R_s$ was decoupled from soil temperature and we observed a significant hysteresis effect ($P < 0.001$) during phases I, III, V, and VI (Fig. 6). We tested whether this effect was an artefact of soil temperature at different depths, but we found the effect to be significant at all measured depths. In addition, soil CO$_2$ production was higher in the 2–8-cm layer than in the 8–16-cm layer (data not shown), and root length was also greater at shallower depths (Supplementary Material Fig. S2). Thus, we used soil temperature at 8 cm to represent the diel and seasonal patterns. Hysteresis was always clockwise, and maximum $R_s$ rates were between 13:00 and 17:00 h during all phases. Although all these loops were significant, phases III and V showed the largest effects. During phases with hysteresis, $R_s$ rates were higher when temperatures were increasing than when temperatures were decreasing (Fig. 6a,c,e,f). The mean difference in $R_s$ between 11:00 and 23:00 h across phases was 0.9 µmol CO$_2$ m$^{-2}$ s$^{-1}$ or 24%. The difference during phase V between 12:00 and 20:00 h was 1.1 µmol CO$_2$ m$^{-2}$ s$^{-1}$ or 69%.

The diel hysteresis of $R_s$ with soil temperature at W_v was observed when daily VPD maximums were > 0.6 kPa. At
similar VPD values soil temperature was coupled with Rs at Hv (Supplementary Material Fig. S3). When diel Rs was decoupled with soil temperature at Wv, a model including PAR (Eqn 4) was able to represent the observed variation, with $r^2$ values between 0.7 and 0.9 ($P < 0.001$), increasing the predictability compared with the use of temperature alone (Eqn 1; Table 2). By contrast, at Hv during all phases Rs was explained by Eqn 1, with an overall $r^2$ value of nearly 0.8 and $P < 0.001$ (Table 2).

Discussion

Seasonal variation of soil respiration

We observed larger spatial variation in Rs at Wv than at Hv, suggesting higher variation at small scales in the presence of woody vegetation and with greater root and rhizomorph length. Furthermore, we found that individual nodes can vary by up to 30% of the stand-level mean annual Rs in both vegetation types. Our results support the idea that systematic errors, based on spatial heterogeneity, may have large implications for modeling ecosystem Rs (Law et al., 2001).

Seasonal patterns of Rs were explained by a function that combined soil temperature and VWC at Wv. A similar function has been used to explain seasonal Rs in Mediterranean ecosystems where water is limiting during the dry season (Xu et al., 2004; Tang et al., 2005b). Although the most parsimonious model for Hv included only soil temperature, our results suggest that soil VWC is an important driver for Rs at Hv, as is expected for a site with hot, dry summers and cold, moist winters. However, differences in model structures reflect differences in the response of the autotrophic and heterotrophic components of Rs to variation in environmental factors. Thus, our results suggest that the processes that regulate Rs at Wv may be more complex than at Hv.

We found a seasonal hysteresis effect on Rs at Wv, with higher rates when temperatures were increasing early in the growing season. The high rates were associated with higher soil VWC, increasing soil temperatures and greater lengths of fine roots and rhizomorphs. Lower rates of Rs were associated with decreasing temperatures, the late summer drought conditions and a decrease in rhizomorph lengths. A similar pattern of seasonal hysteresis effect on Rs with respect to soil temperature, VWC and root production has been observed in a boreal aspen (Populus tremuloides) stand (Gaumont-Guay et al., 2006). By contrast, an opposite pattern of seasonal hysteresis was observed in other temperate forests where Rs was lower in early summer (Moen & Lindroth, 2000; Drewitt et al., 2002). These sites exhibited an increase in Rs that was attributed to high soil microbial activity in response to the warming of deeper soil layers during late summer. We did not find a seasonal hysteresis effect on Rs at Hv; therefore, we further hypothesize that either (1) this effect may be a result of a differential contribution of heterotrophic and autotrophic components to Rs and their response to changes in soil temperature and soil VWC, or (2) there could be a difference in the relative contributions of growth respiration and maintenance respiration in the autotrophic component of Rs that may vary seasonally and may contribute to the hysteresis effect at Wv. Further studies combining automated measurements of Rs, fine root length and rhizomorph length with isotopic techniques may help to separate the contributions of the components of Rs. Carbone et al. (in press) have reported the advantages of combining autochambers and isotope measurements to partition soil respiration in arid ecosystems.

Our research provides evidence that the study of fine root and rhizomorph dynamics may help in interpreting seasonal variation and pulses of Rs. Our data suggest that rhizomorph length was correlated with Rs at the seasonal scale. Furthermore, rhizomorphs appeared to be crucial to maintaining activity during drier events and to the ability to access water from the

![Fig. 5](image-url) Relationship between daily mean soil respiration and daily soil temperature at a depth of 8 cm for (a) woody vegetation and (b) herbaceous vegetation. Open circles, increasing temperatures; closed circles, decreasing temperatures during the year of 2006. Solid line, best fit of an exponential equation (see Table 1).
smaller micropores in the soil (Allen, 2007). It has been observed that rhizomorph length can change by up to 100 cm m⁻² in < 4 d, demonstrating the high plasticity of these structures, and could influence Rₚ rates (Vargas & Allen, in press b).

Fine root dynamics followed a similar seasonal pattern at both sites but this was not the case for rhizomorphs. Rhizomorphs showed greater variation at Wv, suggesting higher activity than at Hv. At the end of phase III, soil VWC decreased to nearly 10%, with soil temperatures of nearly 25°C, resulting in decreases in R in both vegetation types. During the monsoon event (phase VI), we observed an increase in R, following rain events that have been attributed to an increase in CO₂ production in the soil as a result of enhanced decomposition of available carbon compounds and microbial population growth (Xu et al., 2004; Jassal et al., 2005). We found that during this phase R was coupled with soil temperature, but our results suggest that a fraction of the enhancement of CO₂ production may be associated with an increase in fine root and rhizomorph metabolic activity, as seen in a previous study (Heinemeyer et al., 2007). Therefore, subsequent studies should aim to partition heterotrophic and autotrophic sources (accounting for root and rhizomorph components) of R during rain pulses in this ecosystem.

Fig. 6 Diel patterns of soil respiration and soil temperature at a depth of 8 cm for woody vegetation (closed circles) and herbaceous vegetation (triangles). Open circles, increasing temperatures during the day under woody vegetation. The arrows indicate the direction of the hysteresis effect, and time in parentheses indicates maximum soil respiration rates. Letters indicate different phases during 2006: (a) phase I, (b) phase II, (c) phase III, (d) phase IV, (e) phase V, and (f) phase VI (see Fig. 1 for details).
Diethyl variation of soil respiration

Our results show that diel patterns of $R_s$ were different depending on the vegetation type, suggesting the influence of different plant physiological factors influencing $R_s$. We found that diel $R_s$ at $H_v$ was coupled with soil temperature, while diel $R_s$ at $W_v$ was always higher when temperatures were increasing than when temperatures were decreasing, producing a clockwise hysteresis loop. We postulate that this pattern may be regulated by photosynthesis of woody plants, as the temperature-independent component of the diel variation was explained by variation in PAR, as seen in a previous study (Liu et al., 2006).

These results add to the increasing evidence that photosynthesis may play a role in regulating diel $R_s$ (Högberg et al., 2001; Bowling et al., 2002; Irvine et al., 2005; Tang et al., 2005a; Liu et al., 2006), and we observed lags between $R_s$ and PAR of up to 5 h that are comparable with the photosynthesis lags from hours to days that have been reported (Bowling et al., 2002; McDowell et al., 2004; Tang et al., 2005a; Carbone & Trumbore, 2007). The diel hysteresis effect was observed at $W_v$ when VPD values were higher than 0.6 kPa. These plants are deep-rooted and may have access to deeper water at the site. Many studies have shown that higher VPD promotes partial stomatal closure which decreases photosynthesis, especially in ecosystems with low soil moisture (Baldocchi, 1997; Arneth et al., 1998; Hunt et al., 2002). We postulate that, under stress conditions of low soil moisture and higher VPD values, woody vegetation may experience lags between photosynthesis and $R_s$. A similar pattern has been observed during the dry season in another Mediterranean ecosystem (Tang et al., 2005a). Furthermore, under these conditions we observed an increase in rhizomorph lengths, suggesting a carbon investment from the plants to the fungi that may also influence autotrophic $R_s$ rates.

We cannot exclude the possibility that diel $R_s$ may be regulated by a combination of physical and biological processes. It is known that changes in soil temperature and soil moisture affect soil CO$_2$ diffusivity in the soil profile (Simunek & Suarez, 1993). Other studies suggest that time lags associated with photosynthesis and soil respiration are independent of photosynthesis and are commensurate with timescales of CO$_2$ diffusion from the roots to the soil surface (Stoy et al., 2007), or caused by wind-induced pressure pumping (Flechard et al., 2007). $W_v$ and $H_v$ have similar soil texture and soil bulk density and at both sites we observed higher CO$_2$ production from the 2–8-cm soil depth; therefore, we do not attribute diel lags to diffusion differences. The implications of not accounting for daily or seasonal hysteresis at $H_v$ may result in overestimation or underestimation of $R_s$ depending on the shape and direction of the loop. In the case of a large daily asymmetric loop, as in phase V, daily mean $R_s$ when temperatures were increasing was 2.3 µmol CO$_2$ m$^{-2}$ s$^{-1}$, while the daily mean calculated for decreasing temperatures was 1.6 µmol CO$_2$ m$^{-2}$ s$^{-1}$. These calculations represent a difference of +28 and −11%, respectively, from the daily mean value of 1.8 µmol CO$_2$ m$^{-2}$ s$^{-1}$, accounting for hysteresis. If this exercise is performed for all days during phase V, then the results for cumulative carbon loss vary from a high of 247.9 g C m$^{-2}$ to a low of 172.8 g C m$^{-2}$, and a measured value of 195.5 g C m$^{-2}$ accounting for hysteresis. At the seasonal scale, $R_s$ at $H_v$ had a mean value of 3.1 µmol CO$_2$ m$^{-2}$ s$^{-1}$ when temperatures were increasing and a mean value of 2.3 µmol CO$_2$ m$^{-2}$ s$^{-1}$ when temperatures were decreasing, representing a difference of nearly ±15%, respectively, from the annual mean value of 2.7 µmol CO$_2$ m$^{-2}$ s$^{-1}$. These results suggest that ecosystem soil respiration may be under- or overestimated if systematic measurements are made at maximum or minimum soil respiration rates when a hysteresis effect is present both at diurnal and at seasonal scales. More research is needed to identify how common this effect is in other ecosystems, the biophysical factors that regulate it, and the implications for daily, annual and interannual $R_s$ modeling.

Conclusions

A novel aspect of this study was the integration of multiple points of continuous measurements of soil CO$_2$ profiles with detailed observations of fine roots and rhizomorphs using minirhizotrons. Our results show that higher soil respiration ($R_s$) rates were associated with woody vegetation ($W_v$) at both seasonal and diel scales. Further, vegetation at $W_v$ tended to have greater numbers of fine roots and greater rhizomorph lengths than the sparse herbaceous vegetation at $H_v$. Environmental variables may influence the changes in the lengths of fine roots and rhizomorphs in different ways in the different vegetation types studied. Of note, $R_s$ was positively correlated with fine roots and rhizomorphs at $W_v$ but only with fine roots at $H_v$. We found a hysteresis loop for seasonal $R_s$ at $W_v$, where a difference of up to 86% in $R_s$ was observed between increasing and decreasing temperatures. We observed a pulse of $R_s$ during a monsoon event equivalent to a 100% increase compared with the mean annual value of $R_s$ in both vegetation types. This pulse was associated with an increase in fine roots and rhizomorphs at $W_v$, but only of fine roots at $H_v$. $R_s$ was decoupled from soil temperature at the diel scale and we found a significant hysteresis effect at $W_v$ but not at $H_v$. The temperature-independent component of $R_s$ was explained by variation in PAR and in combination with the temperature-dependent component we were able to model the diel hysteresis loops at $W_v$. In addition, the diel hysteresis was only present at higher VPD values and during periods of rhizomorph growth, suggesting further biological controls on $R_s$. We suggest that failure to account for possible hysteresis in $R_s$ at diel and seasonal scales may result in the over- or underestimation of $R_s$ depending on the shape and direction of the loop. Further research is needed to fully understand the biophysical controls on the diel and seasonal patterns of $R_s$ and how plant types and dynamics of fine roots and rhizomorphs influence these patterns.
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Supplementary Material

The following supplementary material is available for this article online:

Fig. S1 Experimental design at the James San Jacinto Mountains Reserve, a mixed temperate forest in Southern California, USA.

Fig. S2 Profile of fine roots and rhizomorphs at the woody vegetation and the scatter herbaceous vegetation sites.

Fig. S3 Diel patterns of vapor pressure deficit (VPD), photosynthetically active radiation (PAR), and soil respiration at the James Reserve.

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