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

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1   **Summary**

2

3   • Characterization of spatial and temporal variation of soil respiration coupled with fine root and

4   rhizomorph dynamics are necessary to understand the mechanisms that regulate soil respiration.

5   • A dense wireless network array of soil CO_2 sensors was used to continuously measure soil

6   respiration in combination with minirhizotron tubes over one year in two vegetation types:

7   woody vegetation (W_v) and scattered herbaceous vegetation (H_v), in a mixed conifer forest in

8   California, USA.

9   • Annual soil respiration rates and the length of fine root and rhizomorphs were greater at W_v

10   than at H_v. Soil respiration was positively correlated with fine roots and rhizomorphs at W_v but

11   only with fine roots at H_v. Diel and seasonal soil respiration patterns were decoupled with soil

12   temperature at W_v but not at H_v. When decoupled, higher soil respiration rates were observed

13   during increasing temperatures showing a hysteresis effect. The diel hysteresis at W_v was

14   explained by including the temperature-dependent component of soil respiration and the

15   variation dependent on photosynthetically active radiation.

16   • Our results show that vegetation type and fine root and rhizomorph dynamics influence soil

17   respiration in addition to changes in light, temperature and moisture.

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21   **Key words:** CO_2 efflux, minirhizotron, mycorrhizae, photosynthesis, rain pulse, temperature-

22   independent respiration, wireless networks

Introduction

2 Soils represent the largest carbon pool in terrestrial ecosystems (Dixon *et al.*, 1994), and

3 understanding the effect of climate variation on soil respiration (R_s) is crucial for accurate

4 estimation of the global carbon balance (Schimel, 1995; Raich *et al.*, 2002). R_s is the synthetic

5 result of heterotrophic respiration (by decomposers) and autotrophic respiration (by roots and

6 mycorrhizae). These processes are regulated by several physical (e.g. soil temperature, moisture,

7 soil porosity) and biological factors (e.g. root density, microbial community, photosynthesis) that

8 complicate the mechanistic understanding of R_s (Ryan & Law, 2005). Understanding how these

9 factors regulate R_s at different temporal scales is of critical importance in determining the effect

10 of climate variation on terrestrial carbon fluxes.

11 Roots are the primary belowground structural element of plants and mycorrhizal fungal

12 symbionts, associated with fine roots, form a hyphal network that take up nutrients and water in

13 exchange for newly fixed plant carbon (Allen *et al.*, 2003). Rhizomorphs are large cords of

14 fungal hyphae that transport nutrients and water and a large proportion appear to be mycorrhizal

15 (Smith & Read, 1997). To date the contribution of mycorrhizal fungi and their relationship with

16 R_s remains unclear due to the limited studies in the field (Langley *et al.*, 2005; Heinemeyer *et al.*,

17 2006; Heinemeyer *et al.*, 2007). Thus, the study of spatio-temporal dynamics of fine roots and

18 rhizomorphs is a key element to understanding variations in autotrophic respiration and therefore

19 total R_s (Hanson *et al.*, 2000; Misson *et al.*, 2006; Vargas & Allen, in press).

20 Developments on automated measurements of R_s provide an opportunity to study

21 relationships between R_s and soil temperature or water content at different temporal scales

22 (Goulden & Crill, 1997; Drewitt *et al.*, 2002). The high frequency of these measurements can

23 detect responses to sudden events, such as rain pulses, which are important for the understanding

1   of seasonal patterns (Irvine & Law, 2002; Jassal *et al.*, 2005). Furthermore, diel R_s patterns can

2   be studied along with variation in temperature and light (Liu *et al.*, 2006; Carbone & Vargas,

3   2008). Recent studies have shown that at the diel scale, R_s and soil temperature may be

4   decoupled showing a hysteresis effect in boreal forests (Gaumont-Guay *et al.*, 2006), tropical

5   forests, (Vargas & Allen, 2008), and Mediterranean ecosystems (Tang *et al.*, 2005a; Vargas &

6   Allen, in press). Several studies have postulated that photosynthesis regulates diel variation in R_s

7   rates and may be an explanation of the temperature-independent component of R_s (Tang *et al.*,

8   2005a; Liu *et al.*, 2006). Thus, it is important to test the influence of light, temperature and

9   moisture on R_s at multiple spatial and temporal scales.

10   In this study, we coupled continuous measurements of soil CO_2 concentration in the soil

11   profile to calculate R_s in conjunction with minirhizotron measurements. Minirhizotrons are a

12   non-destructive technique to measure changes in fine roots and rhizomorphs in space and time

13   (Pregitzer *et al.*, 2002; Treseder *et al.*, 2005), and we developed a wireless network array of soil

14   sensors (Allen *et al.*, 2007; Vargas & Allen, in press). Using this array, we simultaneously

15   quantified R_s at multiple points in two adjacent vegetation types of a California mixed-conifer

16   forest that included a patch of large trees and an open meadow with scatter herbaceous

17   vegetation. This approach provided the opportunity to test the influence of vegetation type on R_s

18   under similar varying climatic conditions, at different temporal scales, without disturbing the

19   environment. Our objectives were: (i) to determine the environmental factors that regulate fine

20   root and rhizomorph dynamics, (ii) to determine the environmental controls on seasonal and diel

21   patterns in R_s, and (iii) to explore the relationship between R_s and fine root and rhizomorph

22   dynamics in two vegetation types.

23

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, it serves as

the Terrestrial Ecology Observing Systems field site for the Center for Embedded Networked

Sensing, and it 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_v) and an adjacent area with

scattered herbaceous vegetation (H_v). The vascular plants present at W_v were individuals of

Quercus kelloggii Newb. (California black oak), *Calocedrus decurrens* (Torr.) Florin (Incense

cedar), *Arctostaphylos pringlei* Parry (Manzanita), and *Pinus lambertiana* Dougl. (Sugar pine).

All of these species form ectomycorrhizae with the exception of *C. decurrens*, which forms

arbuscular mycorrhizae, and *Q. kelloggii*, which may form both ecto- and arbuscular

mycorrhizae. H_v was dominated by arbuscular mycorrhizal *Eriogonum wrightii* Torr. Ex Benth

(Bastard sage) of less than 10 cm in height and a density of nearly 2 plants m^{-2}. Bastard sage was

also present at the understory of W_v with a similar density as at H_v.

Two 5 m transects were established at both W_v and H_v, as described in Fig. S1. Each

transect was instrumented with three minirhizotron tubes and two sensor nodes as part of a

1   wireless network array (see below). Soil bulk density at W_v was 0.9 g/cm^3 and at H_v 1.2 g/cm^3.

2   Soil texture was 83% sand, 10% silt, and 7% clay at both W_v and H_v. Fine root biomass (0-16

3   cm) was calculated to be 18 g m^{-2} at W_v and 10 g m^{-2} at H_v, and detail fine root and rhizomorph

4   profile distribution is presented in Fig. S2. Fine root nitrogen was 0.58% ($\pm$0.23 s.d.) and 0.53%

5   ($\pm$0.24 s.d.), respectively. Soil carbon (0-16 cm depth) at W_v was 3.1% ($\pm$0.5 s.d.) and at H_v

6   2.4% ($\pm$0.5 s.d.), while soil nitrogen (0-16 cm depth) was 0.08% ($\pm$0.02 s.d.) at W_v and 0.05%

7   ($\pm$0.03 s.d.) at H_v.

8

9   Minirhizotrons

10   During October of 2003 we installed three minirhizotron observation tubes of 5 cm in diameter

11   and 1 m long at each of the 5 m transects (Fig. S1). Collection of images for this research started

12   in January of 2006 to allow fine roots recolonize the soil surrounding the tubes. Images from all

13   the tubes were collected in weekly campaigns between February 2006 and December 2006 with

14   a total of 59 sampling days at intervals that varied from 1 day to 1 month.

15   Minirhizoron images were collected using a minirhizotron microscope (BTC-10 with I-

16   CAP software, Bartz Technology). An average of 52 vertical images were collected per tube, and

17   the number of rhizomorphs and fine roots were counted for all collected images. These images

18   include fine roots and rhizomorphs to an average depth of 60 cm at both vegetation types. We

19   used linear regression models to predict lengths based on the number of roots or rhizomorphs

20   reported by Vargas and Allen (in press) for the study site. We used the information from all 52

21   images and report length of fine roots and rhizomorphs in cm m^{-2}.

22

23

1   Sensor nodes

2   In October of 2005 we installed two sensor nodes at each 5 m transect in association with the

3   minirhizotron tubes (Fig. S1). At W_v the nodes were within a 2 m radius from plants, and at H_v

4   within a 1 m radius. At each node we measured photosynthetically active radiation (PAR), air

5   relative humidity, air temperature and barometric pressure at 2 m height, and vapor pressure

6   deficit (VPD) was calculated from air temperature and relative humidity. In addition, we

7   installed solid-state CO_2 (GMM 222, Vaisala, Helsiniki, Finland), soil temperature, and soil

8   moisture (Decagon, ECHO) sensors at 2, 8 and 16 cm soil depths (Allen *et al.*, 2007). The soil

9   temperature and moisture sensors were installed horizontally, and the CO_2 sensors were installed

10   vertically, similar to Tang et al (2005b). All variables were recorded at 5 minute intervals and

11   transmitted using a Crossbow Mica2 868/916 Mhz wireless platform to a centralized server at the

12   James Reserve.

13

14   Soil CO_2 profile

15   We used a dense array of solid-state CO_2 sensors with a total of 24 sensors among transects (four

16   nodes per area). The CO_2 sensors had a range of 0-10,000 ppm and were calibrated every six

17   months after deployment to ensure the quality of the measurements. To keep the sensors dry, we

18   enclosed them in a watertight container with an opening at the bottom covered with Gortex

19   fabric. R_s was calculated using the flux-gradient method based on concentrations of CO_2 in the

20   soil profile (Tang et al 2005b; Vargas & Allen, in press). Briefly, the CO_2 concentration from the

21   sensors was corrected for temperature and pressure accordingly to the manufacturer (Vaisala,

22   Helsinki, Finland). The corrected CO_2 concentrations were used to calculate R_s using Fick's first

1 law of diffusion, and the diffusivity of soil CO_2 in the soil profile was calculated using the

2 Moldrup model (Moldrup *et al.*, 1999).

3 R_s values from the gradient method were calibrated with R_s values using a soil chamber

4 (Li-8100-102) connected to a soil respiration system (LI-8100, LI-COR Lincoln, NE, USA). We

5 installed 10 cm in diameter PVC soil collars associated with each minirhizotron tube in

6 November 2005. The litter layer was very shallow at both vegetation sites (< 2 cm). Soil

7 respiration was measured two to four times a day (morning and/or afternoon) during the same

8 dates that the minirhizotron images were collected during the year of 2006 (170 measurements in

9 59 days).

10

11 <div align="center">Data analysis</div>

12 Depending on the best statistical fit, we used either a model for R_s using soil temperature as an

13 independent variable:

14 $$R_s = B_o e^{(B_1 * T)} \tag{1}$$

15 or soil temperature and volumetric water content (VWC) as drivers for R_s:

16 $$R_s = B_o e^{(B_1 * T)} e^{(B_2 * \theta) + (B_3 * \theta^2)} \tag{2}$$

17 where R_s is soil respiration in μmol CO_2 m^{-2} s^{-1}, T is soil temperature in °C, θ is the volumetric

18 water content in (m^3 m^{-3}), and B_0, B_1, B_2 and B_3 are model parameters. Similar models have been

19 used previously in Mediterranean ecosystems (Xu *et al.*, 2004; Tang *et al.*, 2005b). To select the

20 best statistical model for R_s, we used the root mean squared error (RMSE), and the Akaike

21 Information Criterion (AIC) as a penalized likelihood criterion (Burnham & Anderson, 2002):

22 $$AIC = -2\ln(L) + 2p \tag{3}$$

1   where L is the likelihood of the fitted model, and p is the total number of parameters in the

2   model. The best statistical model minimizes the value of AIC.

3   To test for diel and seasonal hysteresis effects, we used an F-test as explained by Vargas

4   and Allen (2008). Briefly, we compared the F-values of a single exponential model, using

5   equation (1) and assuming no hysteresis effect, with the sum of the F-values of two independent

6   exponential models (equation 1) by splitting the data into two sets based on maximum and

7   minimum daily temperatures, assuming a hysteresis effect.

8   To model significant daily hysteresis loops we first calculated the temperature-dependent

9   component of R_s based on equation (1). Then the residuals from equation (1) were fit to a linear

10   model based on PAR to explain the diel temperature-independent variation in soil respiration

11   using a similar rational as Liu *et al.* (2006). The final diel R_s model when hysteresis was present

12   took the form:

13
$$R_s = B_o e^{(B_1 * T)} B_2 + (PAR + B_3) \tag{4}$$

14   In addition, repeated measurements using the GLM procedure were used to test for

15   differences between fine root and rhizomorph length between the vegetation types. Pearson

16   correlation coefficients were calculated to test the relationships between the biophysical

17   variables and R_s. All statistical analyses were performed with SPSS v13 (Chicago, IL).

18

19

20   **Results**

21   Environmental variables

22   We divided R_s in Phases from I to VI based on variations in soil temperature and soil VWC

23   during 2006, and we will refer to them throughout the text (Fig. 1). Phase I included days of the

1   year 1 to 50, which corresponded to low soil temperature and low VWC.   Phase II included days

2   51 to 125, which corresponded to increasing soil temperature and high VWC. Phase III included

3   days 126 to 195, which corresponded to increasing soil temperature and decreasing VWC. Phase

4   IV included days 196 to 225 and represents the influence of a monsoon event. Phase V included

5   days 226 to 330, which corresponded to decreasing temperatures with low VWC. Phase VI

6   included days 331 to 365, which corresponded to low temperatures with increasing VWC.

7   Annual mean soil temperature at W_v was 11.9 °C, and 10.9 °C at H_v. Soil VWC content

8   was relatively higher in W_v, especially during Phases II and III. VPD was lower during Phase II

9   (mean = 0.18 kPa) and higher during Phase III and IV with means of 0.96 and 0.7 kPa,

10   respectively at both areas. The monsoon event reduced the mean soil temperature from nearly 25

11   to 18 °C, increased mean soil VWC from nearly 0.1 to 0.9 m^3 m^{-3} and reduced mean VPD from

12   nearly 1.4 to 0.28 kPa at both areas.

13

14   Fine roots and rhizomorph lengths

15   The minirhizotron measurements showed significant differences in belowground architecture and

16   seasonality of fine roots (F = 171.139, P < 0.001) and rhizomorphs (F = 1714.66, P < 0.001)

17   among vegetation types. Fine root length was significantly higher (P < 0.05) at W_v during Phases

18   I, II, and VI (Fig. 2a). Mean length of fine roots varied from 47.9 to 75.2 cm^1 m^{-2} at W_v and

19   between 29.6 and 56.4 cm^1 m^{-2} at H_v. Greater fine root length was observed during Phase IV at

20   both sites. Fine roots were significantly (P < 0.05) positively correlated with soil temperature at

21   W_v and with soil temperature, VPD and PAR at H_v (Table 1).

22   Rhizomorph length was always significantly (P < 0.05) higher in the W_v with mean

23   values between 123.9 to 205 cm^1 m^{-2}. Length of rhizomorphs associated with H_v ranged from

1   29.4 to 94.2 cm^1 m^{-2} (Fig. 2b). Rhizomorph development responded positively to the monsoon

2   event (Phase IV) at W$_v$ but not at H$_v$. Rhizomorph length was significantly ($P < 0.001$) positively

3   correlated with soil temperature and VPD, and negatively correlated ($P < 0.001$) with VWC at

4   W$_v$ (Table 2). We did not find a significant correlation between rhizomorph length and

5   environmental variables at H$_v$.

6

7   Gradient flux method validation

8   Our calculations of R_s using the gradient method showed a significant positive relationship with

9   R_s using the chamber method during 59 days of measurements. At W$_v$ we found a slope of 0.996

10   with an $r^2 = 0.73$ and $P < 0.001$ (Fig. 3a). At H$_v$ we found a strong relationship with a slope of

11   0.9 and an r$^2 = 0.91$ with $P < 0.001$ (Fig. 3b). At both sites the intercept was not significantly

12   different from zero and the slope was not significantly different from the 1:1 line. The gradient

13   flux method assumes steady state conditions in CO_2 diffusion in the soil. In nearly 5% of our

14   measurements this condition was not met and these measurements were eliminated from the

15   analysis, and the gaps were filled by linear interpolation if they were less than 2 hours.

16

17   Seasonal variation of soil respiration

18   Mean annual R_s at W$_v$ was 2.7 μmol CO_2 m^{-2} s^{-1}, but the mean annual value ranged between 3.3

19   and 1.9 μmol CO_2 m^{-2} s^{-1} with a coefficient of variation (CV) of 15.5 % among nodes (Fig. 4a).

20   Despite the large variation in mean annual R_s, we found a similar seasonal pattern among the

21   nodes at W$_v$, especially in their response to the monsoon event at Phase IV (Fig. 4a, c). During

22   this phase we observed a mean R_s, of 5.6 μmol CO_2 m^{-2} s^{-1}, which represents an increase of

23   nearly 100% from the mean annual rate.

1   Mean annual R_s at H_v was 0.9 µmol CO_2 m^{-2} s^{-1}, and we found that the mean annual value

2   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.

3   4b). The monsoon event (Phase IV) was not evident for nodes 5, 6 and 8, but this event increased

4   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 $R_{s,}$

5   of 1.9 µmol CO_2 m^{-2} s^{-1}, which also represents an increase of nearly 100% from the mean annual

6   rate.

7   The best model to explain seasonal variation in R_s for W_v was a function of soil

8   temperature and soil VWC (Table 2). In addition, we observed a significant (P <0.001)

9   hysteresis effect of R_s with respect to soil temperature with higher rates during increasing

10   temperatures and lower rates during decreasing temperatures (Fig. 5a). During increasing

11   temperatures, R_s at 17 °C on day of the year 136 was 5.7 µmol CO_2 m^{-2} s^{-1}, but during decreasing

12   temperatures, R_s at the same temperature but day of the year 270 was 0.82 µmol CO_2 m^{-2} s^{-1}.

13   This represents a difference of nearly 86% in R_s at similar temperatures. The most parsimonious

14   model to explain R_s at H_v, based on the AIC was soil temperature alone (Fig. 5b). However, the

15   addition of moisture to the model increased the r^2 value and reduced the RMSE (Table 2),

16   suggesting that soil VWC also has an important influence on R_s at H_v.

17   We compared the full data set based on daily averages when all biophysical variables

18   were available (fine roots, rhizomorphs, soil temperature, VWC, VPD, and PAR; $n = 59$ days).

19   At W_v we found that R_s was significantly correlated (P <0.05) with fine roots, soil temperature,

20   VWC, VPD, PAR and rhizomorphs (Table 1). In contrast, R_s at H_v was significantly correlated

21   (P <0.05) with soil temperature, VPD, PAR and fine roots (Table 1).

22

23

2   Diel R_s was processed as the mean for all days during a specific phase for both vegetation types.

3   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

4   decoupled from soil temperature and we observed a significant hysteresis effect ($P < 0.001$)

5   during Phases I, III, V, and VI (Fig. 6). We tested if this effect was an artifact of soil temperature

6   at different depths, but we found the effect to be significant at all measured depths. In addition,

7   soil CO_2 production was higher at the 2-8 cm layer than at the 8-16 layer (data not shown), and

8   root length was also greater at shallow depths (Fig. S2). Thus, we used soil temperature at 8 cm

9   to represent the diel and seasonal patterns. Hysteresis was always clockwise, and maximum R_s

10   rates were between 1300 hr and 1700 hr during all Phases. Although all these loops were

11   significant, Phases III and V showed the largest effects. During Phases with hysteresis, R_s rates

12   were higher during increasing temperatures than during decreasing temperatures (Fig. 6a, c, e, f).

13   The mean difference of R_s between 1100 hr and 2300 hr across Phases was 0.9 μmol CO_2 m^{-2} s^{-1}

14   or 24%. The difference during Phase V between 12 hr and 20 hr was 1.1 μmol CO_2 m^{-2} s^{-1} or

15   69%.

16   The diel hysteresis of R_s with soil temperature at W_v was observed when daily VPD

17   maximums were > 0.6 kPa. At similar VPD values soil temperature was coupled with R_s at H_v

18   (Fig. S3). When diel R_s was decoupled with soil temperature at W_v a model including PAR

19   (equation 4) was able to represent the observed variation with r^2 values between 0.7 and 0.9 (P

20   <0.001) increasing our predictability than if only temperature (equation 1) was used (Table 2). In

21   contrast, at H_v during all Phases R_s was explained by equation (1) with overall r^2 values or nearly

22   0.8 and $P < 0.001$ (Table 2).

23

Discussion

Seasonal variation of soil respiration

We observed larger spatial variation in R_s at W_v than at H_v, 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 up to 30% of the stand-level mean annual R_s at both vegetation types. Our results support the idea that systematic errors, based on spatial heterogeneity, may have large implications for modeling ecosystem R_s (Law *et al.*, 2001).

Seasonal patterns of R_s were explained by a function that combined soil temperature and VWC at W_v. A similar function has been used to explain seasonal R_s 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 H_v included only soil temperature, our results suggest that soil VWC is an important driver for R_s, 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 R_s to variation in environmental factors. Thus, our results suggest that the processes that regulate R_s at W_v may be more complex than at H_v.

We found a seasonal hysteresis effect on R_s at W_v with higher rates during increasing temperatures early in the growing season. The high rates were associated with higher soil VWC, increasing soil temperatures and higher lengths of fine roots and rhizomorphs. Lower rates of R_s were associated with decreasing temperatures, the late summer drought conditions and a decrease in rhizomorphs. A similar pattern of seasonal hysteresis on R_s with respect to soil temperature, VWC and root production have been observed in a boreal aspen stand (Gaumont-Guay *et al.*, 2006). In contrast, an opposite pattern in seasonal hysteresis was observed in other

1   temperate forests where R_s was lower in early summer (Moren & Lindroth, 2000; Drewitt *et al.*,

2   2002). These sites exhibited an increase in R_s that was attributed to high soil microbial activity in

3   response to the warming of deeper soil layers during late summer. We did not find a seasonal

4   hysteresis effect on R_s at H_v, therefore, we further hypothesize that (a) this effect may be a result

5   of a differential contribution of heterotrophic and autotrophic components to R_s and their

6   response to changes in soil temperature and soil VWC, or (b) there could be a difference in the

7   relative contributions of growth respiration and maintenance respiration in the autotrophic

8   component of R_s that may vary seasonally and may contribute to the hysteresis effect at W_v.

9   Further studies coupling automated measurements of R_s, fine roots and rhizomorphs with

10   isotopic techniques may help to separate the contribution of the components of R_s. Carbone *et al.*

11   (2008) have reported the advantages of combining autochambers and isotope measurements to

12   partition soil respiration in arid ecosystems.

13   Our research provides evidence that the study of fine root and rhizomorph dynamics may

14   help to interpret seasonal variation and pulses of R_s. Our data suggest that rhizomorph length was

15   correlated with R_s at the seasonal scale. Furthermore, rhizomorphs appeared to be crucial to

16   maintaining activity during drier events and the ability to access water from the smaller

17   micropores in the soil (Allen, 2007). It has been observed that rhizomorph length can change up

18   to 100 cm m^2 in less than four days showing the large plasticity of these structures, and could

19   influence R_s rates (Vargas & Allen, in press).

20   Fine root dynamics followed a similar seasonal pattern at both sites but this was not the

21   case for rhizomorphs. Rhizomorphs showed greater variation at W_v suggesting higher activity

22   than at H_v. At the end of Phase III, soil VWC decreased to nearly 10% with soil temperatures of

23   nearly 25 °C, decreasing R_s in both vegetation types. During the monsoon event (Phase VI), we

1   observed an increase in R_s associated with an increase in root and rhizomorph length at W_v, but

2   only of fine roots at H_v. This pulse in R_s represented an increase of 100% over the annual mean

3   rate, and is comparable with previous studies (Tang *et al.*, 2005b; Misson *et al.*, 2006). Similar

4   responses in R_s following rain events have been attributed to an increase in CO_2 production in the

5   soil due to enhanced decomposition of available carbon compounds and microbial population

6   growth (Xu *et al.*, 2004; Jassal *et al.*, 2005). We found that during this Phase R_s is coupled with

7   soil temperature, but our results suggest that a fraction of the enhancement of CO_2 production

8   may be associated with an increment in fine root and rhizomorph metabolic activity as seen in a

9   previous study (Heinemeyer *et al.*, 2007). Therefore, subsequent studies should aim to partition

10 heterotrophic and autotrophic sources (accounting for root and rhizomorph components) of R_s

11 during rain pulses in this ecosystem.

12

13   Diel variation of soil respiration

14 Our results show that diel patterns of R_s were different depending on the vegetation type

15 suggesting the influence of different plant physiological factors influencing R_s. We found that

16 diel R_s at H_v was coupled with soil temperature, while diel R_s was always higher during

17 increasing temperatures than during decreasing temperatures describing a clockwise hysteresis

18 loop at W_v. We postulate that this pattern may be regulated by photosynthesis of woody plants,

19 since the temperature-independent component of the diel variation was explained by variation in

20 PAR as seen in a previous study (Liu *et al.*, 2006). These results support the increasing evidence

21 that photosynthesis may play a role in regulating diel R_s (Högberg *et al.*, 2001; Bowling *et al.*,

22 2002; Irvine *et al.*, 2005; Tang *et al.*, 2005a; Liu *et al.*, 2006), and we observed lags between R_s

23 and PAR of up to 5 hours that are comparable with photosynthesis lags reported from hours to

1   days (Bowling *et al.*, 2002; McDowell *et al.*, 2004; Tang *et al.*, 2005a; Carbone & Trumbore,

2   2007). The diel hysteresis effect was observed at W_v when VPD values were higher than 0.6 kPa.

3   These plants are deep rooted and may have access to deeper water at the site. Many studies have

4   shown that higher VPD promotes partial stomata closure that decreases photosynthesis,

5   especially in ecosystems with low soil moisture (Baldocchi, 1997; Arneth *et al.*, 1998; Hunt *et*

6   *al.*, 2002). We postulate that, under stress conditions of low soil moisture and higher VPD

7   values, woody vegetation may experience lags between photosynthesis and R_s. A similar pattern

8   has been observed during the dry season in another Mediterranean ecosystem (Tang *et al.*,

9   2005a). Furthermore, during these conditions we observed an increase in rhizomorph lengths,

10   suggesting a carbon investment from the plants to the fungi that may also influence autotrophic

11   R_s rates.

12   We cannot exclude the possibility that diel R_s may be regulated by a combination of

13   physical and biological processes. It is known that changes in soil temperature and soil moisture

14   affect soil CO_2 diffusivity in the soil profile (Simunek & Suarez, 1993). Other studies suggest

15   that time lags associated with photosynthesis and soil respiration are commensurate with CO_2

16   diffusion timescales from the roots to the soil surface and independent from photosynthesis (Stoy

17   *et al.*, 2007), or by wind-induced pressure pumping (Flechard *et al.*, 2007). W_v and H_v have

18   similar soil texture and soil bulk density and at both sites we observed higher CO_2 production

19   from the 2-8 cm soil depth, therefore we do not attribute diel lags based on diffusion differences.

20   The implications of not accounting for daily or seasonal hysteresis at H_v may result in

21   overestimation or underestimation of R_s depending on the shape and direction of the loop. In the

22   case of a large daily asymmetric loop, as in phase V, daily mean R_s during increasing

23   temperatures was 2.3 μmol CO_2 m^{-2} s^{-1}, while the daily mean calculated for decreasing

1   temperatures was 1.6 µmol CO_2 m^{-2} s^{-1}. These calculations represent a difference of +28 and -

2   11%, respectively, from the daily mean value of 1.8 µmol CO_2 m^{-2} s^{-1} accounting for hysteresis.

3   If this exercise is done for all days during phase V, then the results for cumulative carbon loss

4   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

5   m^{-2} accounting for hysteresis. At the seasonal scale, R_s at H$_v$ during increasing temperatures had

6   a mean value of 3.1 µmol CO_2 m^{-2} s^{-1} and during decreasing temperatures of 2.3 µmol CO_2 m^{-2} s^{-}

7   ^{1}, representing a difference of nearly ±15%, respectively, from the annual mean value of 2.7

8   µmol CO_2 m^{-2} s^{-1}. These results suggest that ecosystem soil respiration may be under or

9   overestimated if systematic measurements are done at maximum or minimum soil respiration

10   rates when hysteresis effect is present both at diurnal and seasonal scales. More research is

11   needed to identify how common this effect is in other ecosystems, the biophysical factors that

12   regulate it, and the implications for daily, annual and interannual R_s modeling.

13

14   **Conclusion**

15   A novel aspect of this study was the integration of multiple points of continuous measurements

16   of soil CO_2 profiles with intense observations of fine roots and rhizomorphs using

17   minirhizotrons. Our results show that higher soil respiration (R_s) rates were associated with

18   woody vegetation (W$_v$) at both seasonal and diel scales. Further, W$_v$ tended to have greater

19   numbers of fine roots and higher lengths of rhizomorphs than the sparse herbaceous vegetation

20   (H$_v$). Environmental variables may influence the changes in length of fine roots and rhizomorph

21   among the studied vegetation types in different ways. Of note, R_s was positively correlated with

22   fine roots and rhizomorphs at W$_v$ but only with fine roots at H$_v$. We found a hysteresis loop for

23   seasonal R_s at W$_v$ where up to 86% difference in R_s was observed between increasing and

1   decreasing temperatures. We observed a pulse of R_s during a monsoon event equivalent to 100%

2   increase on mean annual value of R_s at both vegetation types. This pulse was associated with an

3   increase of fine root and rhizomorphs at W_v, but only of fine roots at H_v. R_s was decoupled from

4   soil temperature at the diel scale and we found a significant hysteresis effect at W_v but not at H_v.

5   The temperature-independent component of R_s was explained by variation in PAR and in

6   combination with the temperature-dependent component we were able to model the diel

7   hysteresis loops at W_v. In addition, the diel hysteresis was only present with higher vapor

8   pressure deficit values and moments of rhizomorph growth suggesting further biological controls

9   on R_s. We suggest that failure to account for possible hysteresis in R_s at diel and seasonal scales

10   may result in the over- or under-estimation of R_s depending on the shape and direction of the

11   loop. Further research is needed to fully understand the biophysical controls on the diel and

12   seasonal patterns of R_s and how plant types and dynamics of fine roots and rhizomorphs

13   influence these.

14

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10

2

3 **Table 1.** Pearson correlation coefficients between soil respiration, fine roots, rhizomorphs, soil

4 temperature, volumetric water content (VWC), vapor pressure deficit (VPD), and

5 photosynthtetically active radiation (PAR) at the woody vegetation (W_v) and the herbaceous

6 vegetation (H_v) sites. n = 59, * P < 0.05, *** P <0.001

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8

	Rs	Fine Roots	Rhizomorphs	Soil Temperature	VWC	VPD	PAR
Woody vegetation (W_v)							
Rs	1	**0.583*****	**0.393***	**0.871*****	**-0.405*****	**0.586*****	**0.685*****
Fine Roots		1	0.143	**0.277***	-0.01	0.109	0.218
Rhizomorphs			1	**0.537*****	**-0.510*****	**0.406*****	0.05
Soil Temperature				1	**-0.626*****	**0.774*****	**0.554*****
Soil Moisture					1	**-0.658*****	-0.075
VPD						1	**0.507*****
PAR							1
Herbaceous vegetation (H_v)							
Rs	1	**0.287***	0.072	**0.595*****	0.038	**0.320*****	**0.593*****
Fine Roots		1	0.072	**0.614*****	0.012	**0.330***	**0.790*****
Rhizomorphs			1	0.118	-0.045	0.043	0.034
Soil Temperature				1	**-0.630*****	**0.766*****	**0.638*****
Soil Moisture					1	**-0.708*****	-0.066
VPD						1	**0.442*****
PAR							1

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1 **Table 2.** Results of regression analyses relating soil respiration to soil water content and soil

2 temperature at the woody vegetation (W_v) and the herbaceous vegetation (H_v) sites. Model I has

3 the form $R_s = \beta_0\, e^{(\beta 1T)}$, Model II of $R_s = B_o e^{(B_1*T)} e^{(B_2*\theta)+(B_3*\theta^2)}$, and Model II of

4 $R_s = B_o e^{(B_1*T)} B_2 + (PAR + B_3)$.

5
6

Period	Model	Vegetation Type	β_0	β_1	β_2	β_3	r^2	P value	RMSE	AIC
Season	I									
		W_v	1.396	0.049	-	-	0.354	<0.0001	1.21	1444
		H_v	0.516	0.053	-	-	0.750	<0.0001	0.11	956
	II									
		W_v	0.193	0.089	22.149	-61.202	0.919	<0.0001	0.42	611
		H_v	0.168	0.059	22.095	-97.273	0.899	<0.0001	0.09	1205
Diel										
Phase I	III	W_v	0.002	0.614	1.791	0.001	0.734	<0.0001	0.009	-
	I	H_v	0.518	0.059	-	-	0.787	<0.0001	0.005	-
Phase II	I	W_v	2.008	0.042	-	-	0.812	<0.0001	0.003	-
	I	H_v	0.547	0.033	-	-	0.835	<0.0001	0.001	-
Phase III	III	W_v	1.943	0.034	0.855	0.001	0.941	<0.0001	0.019	-
	I	H_v	1.075	0.013	-	-	0.876	<0.0001	0.003	-
Phase IV	I	W_v	3.794	0.019	-	-	0.859	<0.0001	0.017	-
	I	H_v	1.509	0.013	-	-	0.673	<0.0001	0.004	-
Phase V	III	W_v	0.028	0.164	1.152	0.001	0.912	<0.0001	0.025	-
	I	H_v	0.662	0.25	-	-	0.894	<0.0001	0.005	-
Phase VI	III	W_v	0.002	0.745	1.505	0.001	0.846	<0.0001	0.008	-
	I	H_v	0.493	0.031	-	-	0.799	<0.0001	0.005	-

7
8

9 The best-fit model parameters ($\beta_0, \beta_1, \beta_2,$ and β_3) are reported for each model together with the squared

10 coefficient of regression (r^2), the root mean squared error (RMSE) and the Akaike Information Criterion

11 (AIC; for the seasonal estimates). T is temperature (°C) at 8 cm depth, θ is volumetric water content (m^{-3}

12 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}).

13 Model parameters were estimated using the Levenberg–Marquardt method.

List of figures

Fig. 1. Daily mean of climate variables at the James Reserve during 2006 including (A) mean soil temperature in the 0-16 cm layer, (B) mean soil volumetric water content (VWC) in the 0-16 cm layer, and (C) vapor pressure deficit (VPD). Solid line represents woody vegetation and dashed line represents the herbaceous vegetation. Vertical dashed lines divide the Phases of study (I to VI) according to changes in soil moisture and temperature (see Results). DOY means day of the year during 2006. Phase IV represents a monsoon event.

Fig. 2. Length of (A) fine roots and (B) rhizomorphs at the woody and herbaceous areas during the Phases of the studied year (see Fig. 1). Error bars represent standard deviations of the mean. * *P*<0.05, *** *P*<0.001.

Fig. 3. Comparisons between soil respiration values from the gradient method and from the chamber method using a soil respiration system (LI-8100) with woody vegetation (A) and scatter herbaceous vegetation (B). Each circle represents the average of 18 measurements associated with locations of minirhizotron tubes within each vegetation type.

Fig. 4. Seasonal course of daily mean soil respiration with (A) woody vegetation and (B) herbaceous vegetation at the James Reserve. Each "Node" represents a sampling point within two transects at each site (see Methods). Daily mean of soil respiration at (C) woody vegetation and (D) herbaceous vegetation generated from values of all nodes at each site. Roman numbers indicate phases of the study (see Fig. 1). DOY means day of the year during 2006.

1

2   **Fig. 5.** Relationship between daily mean soil respiration and daily soil temperature at 8 cm depth

3   at (A) woody vegetation and (B) herbaceous vegetation. Open circles represent increasing

4   temperatures and black circles decreasing temperatures during the year of 2006. Solid line

5   represents the best fit of an exponential equation (see Table 1).

6

7   **Fig. 6.** Diel patterns of soil respiration and soil temperature at 8 cm depth with woody vegetation

8   (●) and herbaceous vegetation (▲). Open circles indicate increasing temperatures during the

9   day under woody vegetation. The arrows indicate the direction of the hysteresis effect, and time

10   in parenthesis indicates maximum soil respiration rates. Letters indicate different phases during

11   2006: (A) Phase I, (B) Phase II, (C) Phase III, (D) Phase IV, (E) Phase V, and (F) Phase VI (see

12   Fig. 1 for details).

13

1   **Fig. 1**. Climate variables
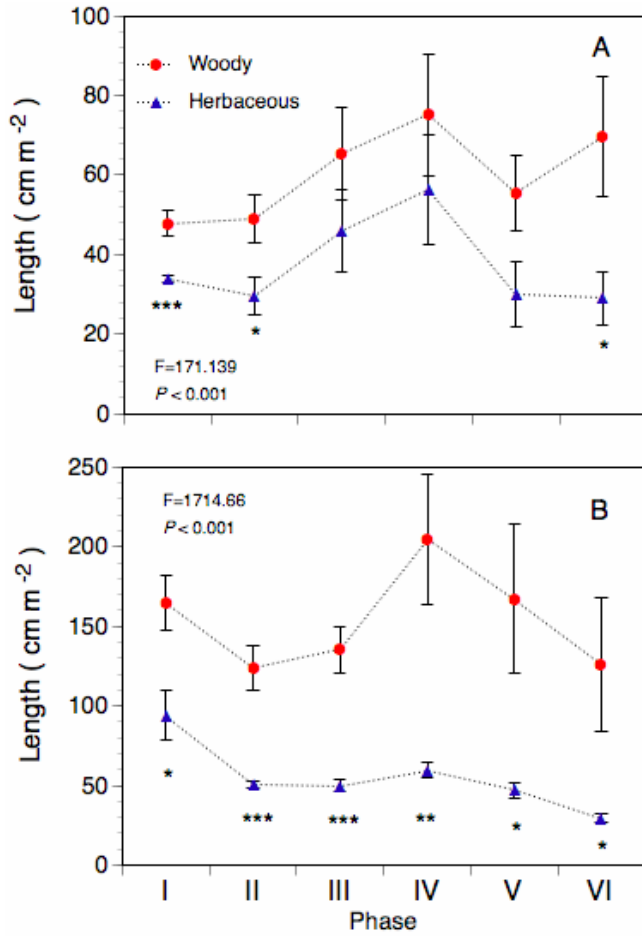
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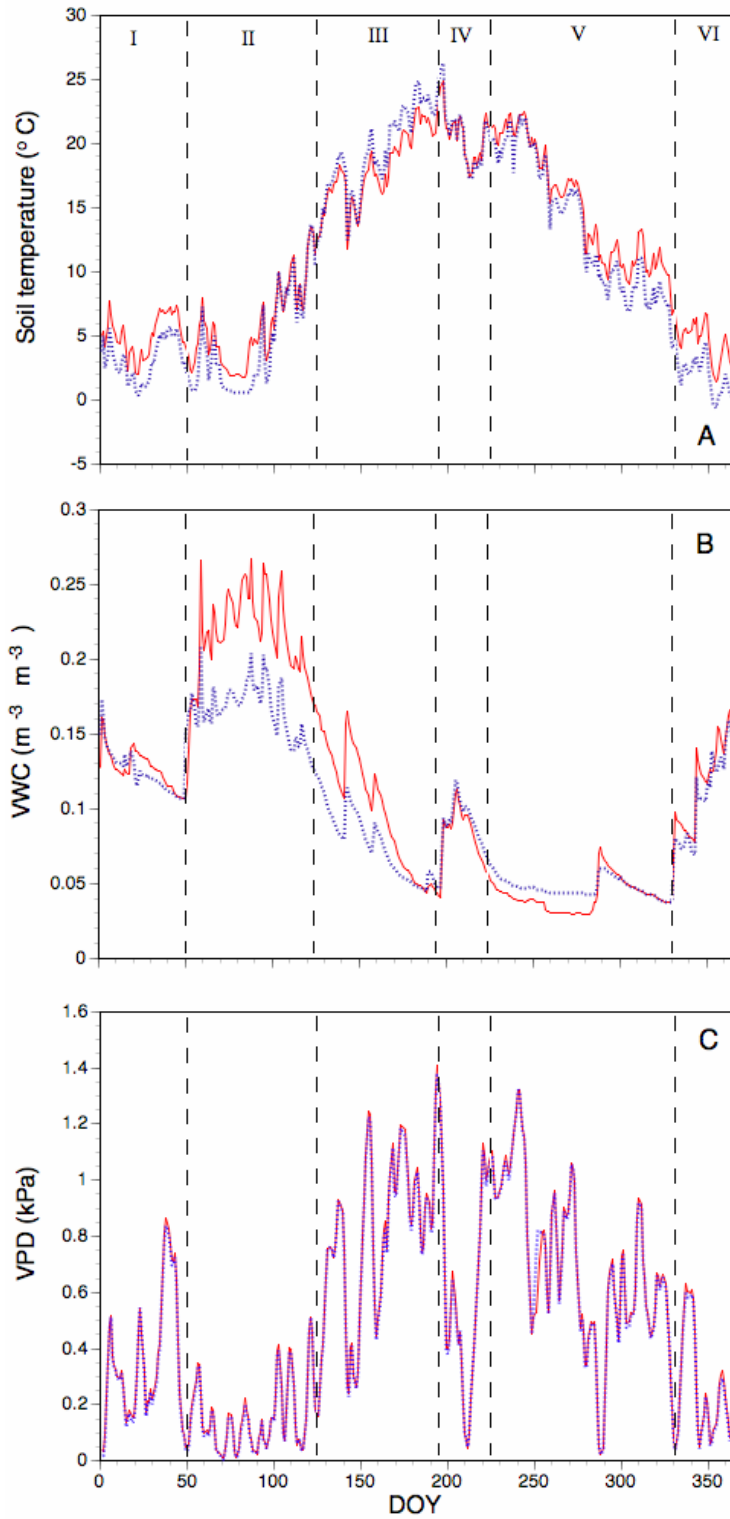
3   **Fig. 2.** Root and rhizomorph length

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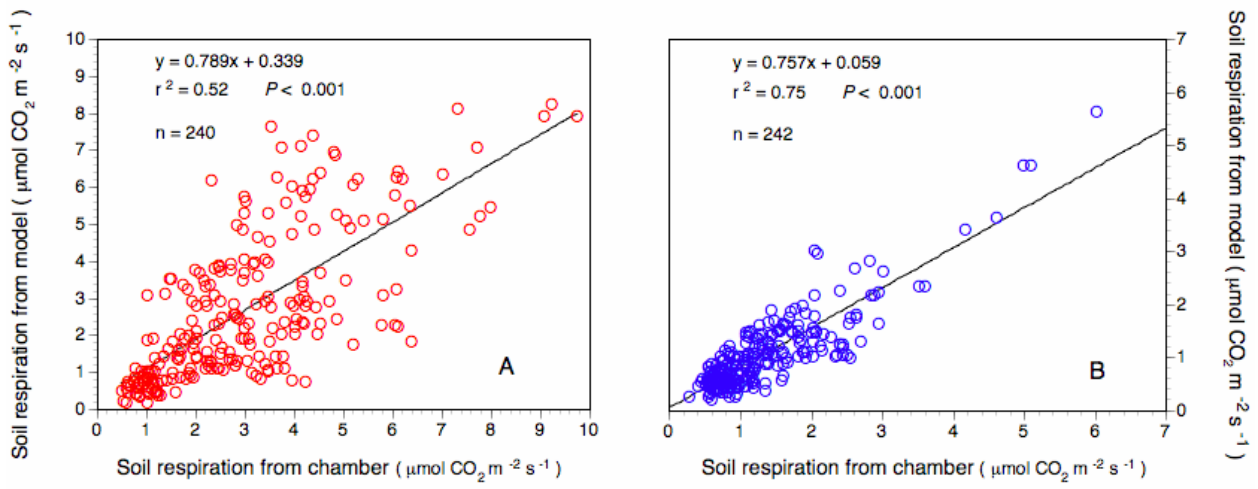
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4 **Fig. 3.** Soil respiration model validation
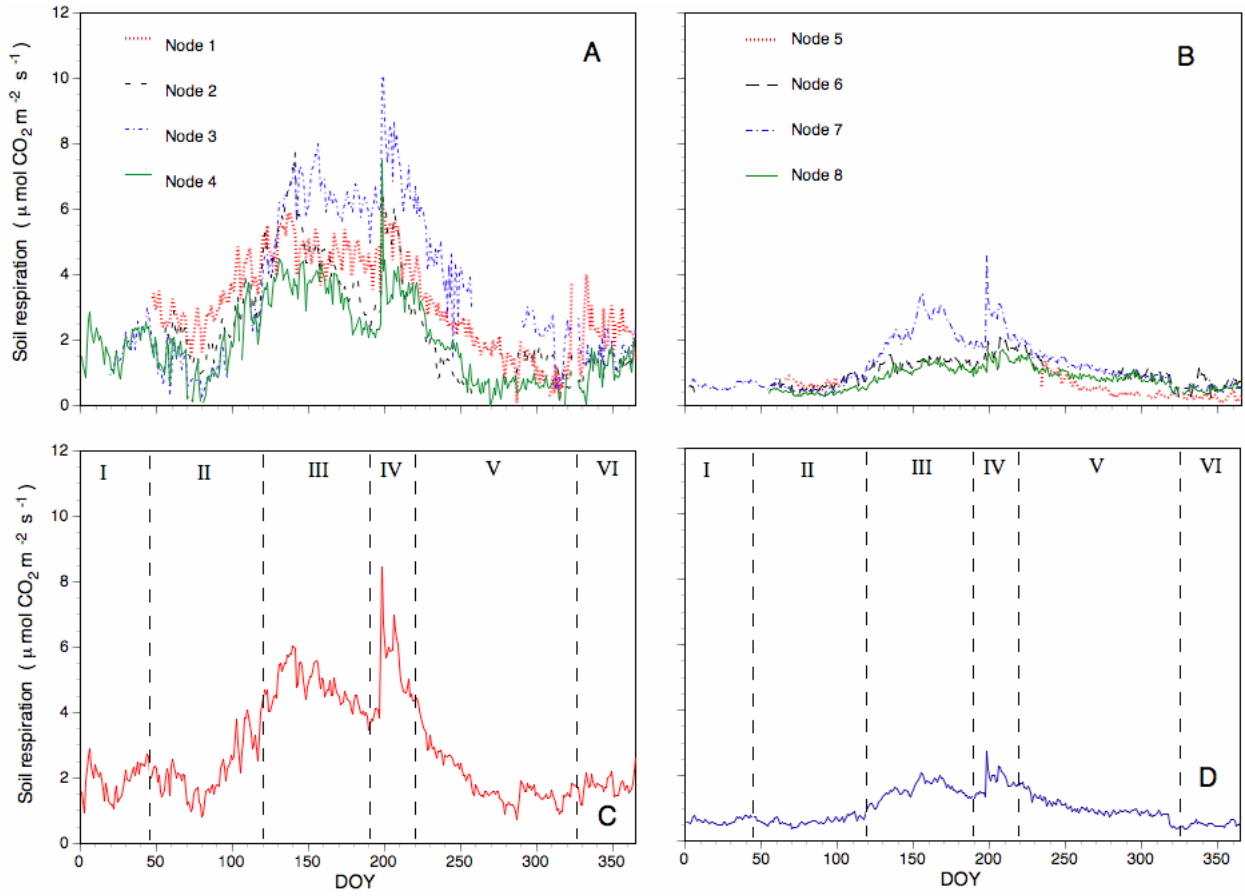
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1   **Fig. 4.** Seasonal patterns of soil respiration
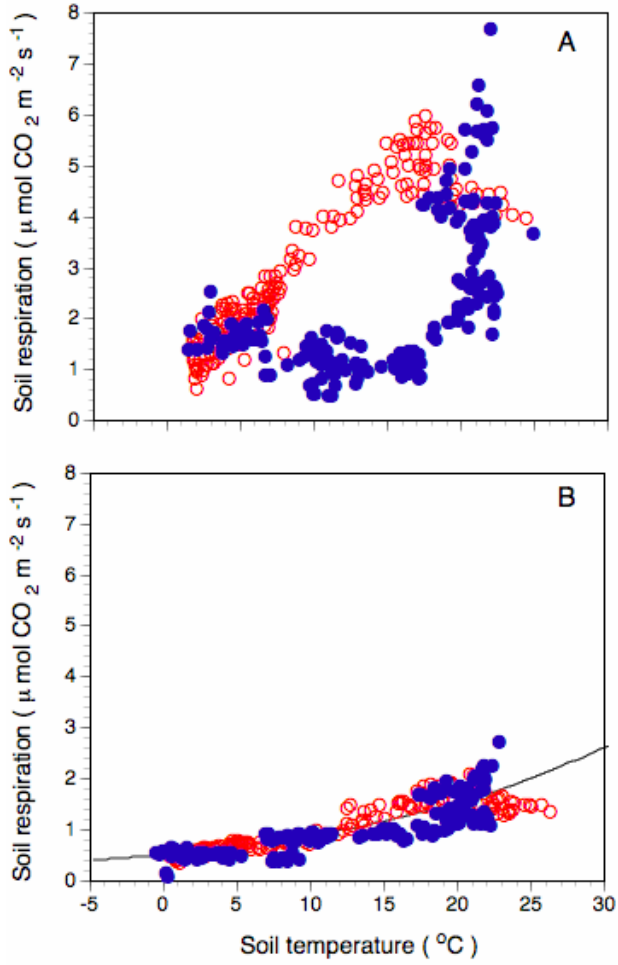
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1   **Fig. 5** Seasonal soil respiration and soil temperature
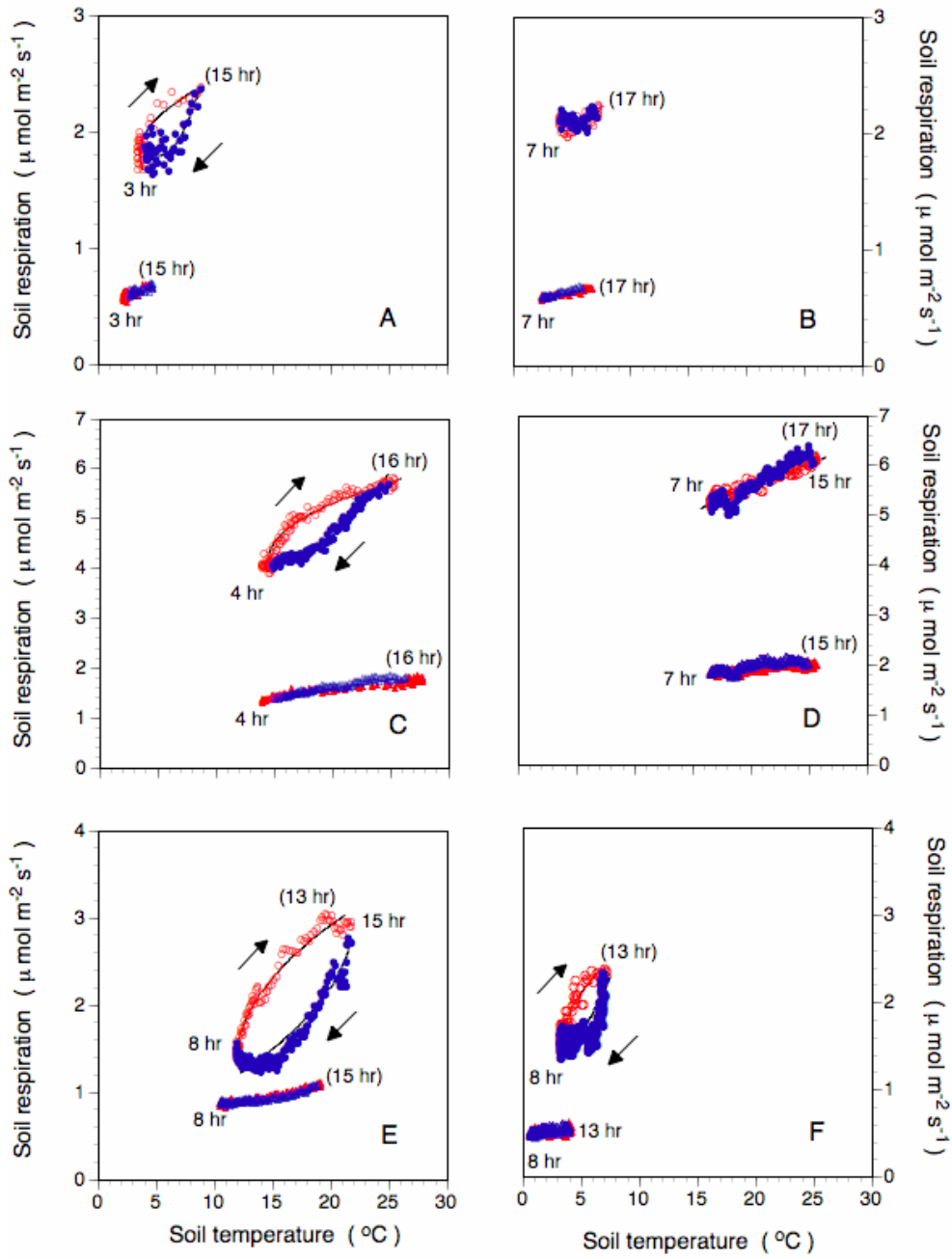
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Fig. 6. Diel patterns of soil respiration and soil temperature