REGULAR ARTICLE

Effects of continuous drought stress on soil respiration in a tropical rainforest in southwest China

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Received: 21 October 2014 / Accepted: 15 May 2015 / Published online: 4 June 2015 © Springer International Publishing Switzerland 2015

Abstract

Background and aims Drought is predicted to have a profound impact on soil respiration. This study aimed to assess the effects of long-term precipitation decrease on soil respiration in a tropical rainforest.

Methods A precipitation reduction experiment was conducted in a tropical forest in southwest China at the beginning of 2011. Soil respiration and environmental parameters were measured monthly for three years.

Results The continuous precipitation reduction treatment did not affect the seasonal patterns of soil respiration, but it significantly increased soil respiration in the study plot during the rainy season, and the relationship between soil respiration and soil moisture differed in the control and reduction treatment in the rainy season. Compared with the net ecosystem exchange of carbon in this system, the increment of annual soil carbon emissions in the reduction treatment was considerable and should not be ignored.

Responsible Editor: Eric Paterson.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-015-2523-4) contains supplementary material, which is available to authorized users.

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X. Zhang · C. Wu University of Chinese Academy of Sciences, Beijing 100049, Conclusions Our results indicate that the responses of soil respiration to precipitation decrease may vary seasonally and the variation of volumetric water content in different seasons may be an important factor leading to the seasonal variation. The variation of soil moisture among different ecosystems as well as in different seasons should be taken into consideration when predicting the future response of soil respiration to drought globally.

Keywords Throughfall reduction \cdot Soil CO₂ efflux \cdot Soil water content \cdot Tropical rainforest

Introduction

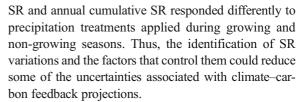
Climate-change scenarios indicate that extreme precipitation events and periods of extended drought will become more intense and frequent over tropical and subtropical regions (Kirtman et al. 2013). Regionally, CMIP5-based models suggest that southwest China will experience an extended drought period sometime before 2020 (Zhou and Xiao 2014). Decadal-scale observations in southern China show that dramatic variations in the seasonality and intensity of precipitation, as well as significant declines in forest soil moisture, have occurred in recent decades (Zhou et al. 2011). Climateinduced changes in precipitation patterns will directly impact the carbon budget of the terrestrial biosphere (Tian et al. 2000). Thus, an understanding of the carbon dynamic response of terrestrial ecosystems to drought is of fundamental importance for assessing the magnitude



of terrestrial CO_2 emission feedbacks to the atmosphere (van Straaten et al. 2010).

Soils store enormous quantities of organic carbon, and the CO₂ released from soils to the atmosphere via soil respiration (SR) is one of the most important fluxes in the global carbon cycle. Soil respiration, which represents the sum total of all soil metabolic processes that produce carbon dioxide, consists mainly of microbial respiration, root respiration, and faunal respiration (Singh and Gupta 1977). Soil respiration accounts for 60-90 % of total ecosystem respiration (Schimel et al. 2001; Raich et al. 2002) and exceeds anthropogenic CO₂ emissions 10-fold (Hanson et al. 2000; Kuzyakov 2006). Thus, the accumulation of carbon in soils can reduce atmospheric CO₂ concentrations and thereby mitigate climate change, whereas the release of soil carbon to the atmosphere can enhance climate change (Valentini et al. 2000).

The influence of SR on the net ecosystem exchange (NEE) of carbon between terrestrial ecosystems and the atmosphere, and the dependence of SR on temperature and precipitation, have attracted considerable interest on account of climate-related impacts (Davidson et al. 1998). Soil temperature (T_s) and soil water content (SWC) are important environmental factors affecting the production and emission of CO₂ from soils through their effects on soil redox dynamics (Edwards 1975; Silver et al. 1999; Hall et al. 2013), diffusion (Millingt and Shearer 1971; Davidson and Trumbore 1995; Schwendenmann and Veldkamp 2006), root and microbial activity (Stevenson 1956; Linn and Doran 1984; Skopp et al. 1990; Bouskill et al. 2013), and nutrient availability (Birch 1958; Van Schreven 1967; Keith et al. 1997; Townsend et al. 2011; Wood and Silver 2012). Both laboratory and field experiments have shown that rising temperatures stimulate CO₂ release from soils, which in return reinforces global warming (Luo 2007; Balser and Wixon 2009; Wood and Silver 2012; Wood et al. 2012). However, precipitation manipulation experiments have shown that the effects of precipitation on SR are variable and ecosystem-dependent (Borken et al. 2006; Zhou et al. 2006; Sotta et al. 2007; Davidson et al. 2008; Cleveland et al. 2010; van Straaten et al. 2010, 2011; Jiang et al. 2013), indicating the complexity of the SR response to soil moisture. In addition, soil moisture can vary widely even at seasonal scales and within a single ecosystem, resulting in a seasonal dependence of the SR response to rainfall variations. Suseela and Dukes (2013) found that both



In the present study, we conducted a precipitation reduction experiment in a tropical rainforest in southwest China to determine: (1) the long-term effects of drought on soil respiration and the dependence of soil respiration on environmental parameters, and (2) the effects of changes in SR on carbon cycling.

Materials and methods

Study site

The experiment was conducted in a tropical rainforest in Xishuangbanna, southwest China (101°16′E; 21°55′N; 568 m above sea level). The average height of the canopy is over 35 m. The annual mean temperature is 21.7 °C, with a maximum monthly temperature of 25.7 °C for the hottest month (June) and a monthly minimum of 15.9 °C for the coldest month (January) (Liu et al. 2005). Xishuangbanna, which is located at the northern edge of tropical Southwest Asia, has a strongly seasonal climate that is dominated by the South Asian monsoon. Annual precipitation averages 1487 mm, of which approximately 87 % occurs during the May–October rainy season (Tan et al. 2010).

The soil at the study site is an oxisol derived from sandstone, with a 2–5 cm depth of litter and a 1–3 cm depth of humus. The organic matter content of mineral soil (0–20 cm depth) is about 20 g kg⁻¹. The tree species are dominated by *Barringtonia macrostachya*, *Haomalium laoticum*, *Horsfieldia tetratepala*, *Myeristica yunnanensis*, *Pometia tomentosa*, and *Terminalia myriocarpa* (Cao et al. 1996).

Experimental design

To investigate the influence of precipitation on soil respiration under conditions drier than those normally experienced, an artificial drought was created in January 2011 using a precipitation reduction treatment. The experiment consisted of two treatments: a control treatment with ambient precipitation and a precipitation reduction treatment with partial throughfall exclusion.



Each treatment was applied to five 100-m² plots. In the precipitation reduction plots, throughfall was intercepted by transparent polyvinyl chloride (PVC) sheets that covered ~50 % of the ground area and remained in place for the duration of the experiment. The control plots were situated adjacent to the precipitation reduction plots, separated by a buffer distance of 15 m. All plots were trenched around their borders to a depth of 1.5 m to prevent surface run-off and lateral movement of water from the surrounding soil. To avoid disturbance to litter fall from the precipitation-interception roofs, litter fall on the roofs was collected and evenly redistributed across the surface of the plots one week before each measurement of soil respiration.

Soil respiration

Soil respiration was measured monthly from February 2011 to October 2013 using a Li-6400 infrared gas analyser (Li-COR, Lincoln, NE, USA) connected to a Li-6400-09 soil respiration chamber (9.5 cm diameter) (Li-COR). All the PVC collars (diameter of 10.4 cm and height of 7.0 cm) were permanently installed in the forest floor to a depth of ~4 cm. Soil respiration in the control plot and reduction plot was calculated as the mean value of five plots. Measurements were made between 09:00 and 12:00 (local time) to represent soil respiration during that day (Sha et al. 2005). To ensure the measurement stability of the instrument, soil respiration was measured at least three times for each soil collar and take the average as the measured value.

Environmental monitoring

Monthly measurements of volumetric soil water content were undertaken simultaneously with SR measurements at four random locations in each plot, using a portable time domain reflectometer (MP-KIT; Beijing Channel, Beijing, China). Soil temperature in the upper 5 cm was monitored using a digital thermometer (6310; Spectrum, IL, USA). A previous study in this region showed that soil temperature at a depth of 5 cm in mineral soil had a closer relationship with soil respiration than did temperatures at other depths (Sha et al. 2005); thus, the soil temperature at a depth of 5 cm was chosen as the temperature index for measuring the effect of temperature on soil respiration.

Data processing and analysis

We calculated annual, rainy season (May–October) and dry season (November–April) cumulative respiration (TR) using the method proposed by Sha et al. (2005). Our measurements were assumed to represent the daily average soil respiration rate. We then multiplied the corrected daily flux by the number of days in that month and calculated the cumulative flux over the entire year, as well as during the rainy and dry seasons. To evaluate the effects of precipitation reduction on the carbon cycle, we analysed the cumulative incremental soil respiration (Δ TR) by determining the value of Δ TR as a proportion of annual NEE.

We used the exponential function to explore the relationship between soil temperature and SR, as follows:

$$SR = a \cdot \exp(b \cdot T) \tag{1}$$

where T (°C) is the soil temperature at 5 cm depth, the coefficient a is the intercept of SR when the temperature is zero (i.e., the basal respiration rate), and the coefficient b is the temperature sensitivity of SR.

To assess the effect of moisture on SR we fitted SR and volumetric soil water content using a quadratic least squares regression as follows:

$$SR = y_0 + a \cdot x + b \cdot x^2 \tag{2}$$

where x is the volumetric soil water content in the top 10 cm of soil, and y_0 , a, and b are constants.

At the present site, T_s and SWC showed similar seasonal variations (Fig. 1). Considering their interaction effect on soil CO_2 effluxes, we also fitted SR using a two-factor regression model (Qi and Xu 2001) as follows:

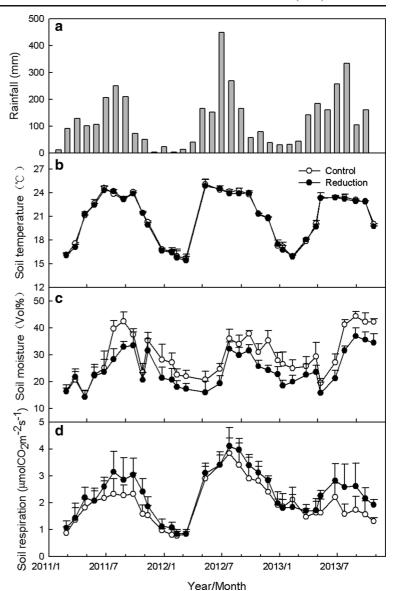
$$SR = a \cdot \exp(b \cdot T) \cdot W^c \tag{3}$$

where a is the model intercept; b is the coefficient of temperature sensitivity; c is the coefficient of water sensitivity; T (°C) is soil temperature at 5 cm depth; and W (%) is soil water content. Coefficients were estimated from the above model by non-linear regression using the Dynamic Fit Wizard in Sigmaplot 12 (Systat Inc., Point Richmond, CA, USA).

Repeated measures ANOVA analysis using SPSS 13.0 (SPSS Inc., Chicago, IL, USA) was performed to test for significant differences in mean CO₂ fluxes and environmental factors between the control and reduction



Fig. 1 Seasonal variations in (*a*) rainfall, (*b*) soil temperature (at 5 cm depth), (*c*) soil moisture (at 10 cm depth), and (d) soil respiration from February 2011 to October 2013. Data are the mean+SD (*n*=5)



plots for various periods. A value of p<0.05 was taken to indicate a significant difference.

Results

Soil temperature and soil moisture

There were strong seasonal variations of precipitation throughout the three years, with intensive precipitation occurring from May to October (Fig. 1a). The annual precipitation amount was 1240.9, 1466.4, and

1679.2 mm in 2011, 2012, and 2013, respectively. The maximum of monthly precipitation occurred in July 2012 (Fig. 1a), which reached 449.7 mm and accounted for 30.7 % of the annual precipitation.

Soil temperature varied seasonally, from a minimum of 13.6 °C in May to a maximum of 26.3 °C in December, with no significant difference between the control and reduction plot throughout the study period (Fig. 1b; Table S1; Table 1; P > 0.05). Volumetric soil water content in both treatments displayed similarly strong seasonal variations (Fig. 1c). At the onset of the study period, SWC was not significantly different between



0.56

9.85*

Dry season

Rainy season

19.49**

29.29**

1.53

2.17

 Seasons

 Period
 2011
 2012
 2013

 SR
 T
 SWC
 SR
 T
 SWC

0.33

1.11

1.96

5.43*

9.37*

16.35**

Table 1 Effects of precipitation reduction treatment on soil respiration (SR), soil temperature (T), and soil water content (SWC) in different seasons

Numbers are F values. Stars indicate the level of significance (*=P<0.05, **=P<0.01)

0.03

6.83*

1.21

0.39

the plots assigned to drought and ambient conditions (Fig. 1c; Table 1; P > 0.05). From the early rainy season (June 2011), SWC began to diverge between two treatments (Fig. 1c). Soil in the reduction plot was significantly drier than that in the control plot (Table 1; Table S1; P < 0.05). As time went on, the effect of throughfall decrease on SWC became more distinct (Table 1; P < 0.01). However, the effect of throughfall decrease on SWC varied between rainy and dry seasons (Fig. 1c). During the rainy season, SWC in the control treatment ranged from 23.4 to 42.5 %, and in the precipitation reduction treatment from 19.3 to 36.9 %. During the dry season, SWC ranged from 11.4 to 34.8 % in the control and from 10.9 to 29.6 % in the precipitation reduction treatment.

Soil respiration

Generally, soil CO_2 efflux followed a similar seasonal pattern to that of T_s , ranging from a minimum of 0.64 µmol m⁻² s⁻¹ in February to a maximum of 4.19 µmol m⁻² s⁻¹ in August in the control plots (Fig. 1d). In both treatments, SR in the rainy season

was higher than that in the dry season (Fig. 1d; Table S1). Through the observation period, SR was strongly influenced by precipitation treatment, and varied among seasons. Averaged across the entire study period, the precipitation reduction treatment significantly increased the mean SR by 0.31 μ mol m⁻² s⁻¹ (Table S1; P < 0.01). In the rainy season, the SR in the precipitation reduction treatment was 0.51 µmol m⁻² s⁻¹ higher than that in the control treatment (P<0.01), while the increase was $0.11 \mu \text{mol m}^{-2} \text{ s}^{-1}$ in the dry season (P>0.05). Fluxes of CO₂ were not significantly different between the control and reduction treatment at the beginning of the study period (Fig. 1d; Table 1; P > 0.05), but diverged during the early rainy season (Fig. 1d). During the dry season, CO₂ efflux in the precipitation reduction treatment did not differ (P>0.05) from the control treatment throughout the three years; however, during the rainy seasons CO₂ efflux from the precipitation reduction treatment was significantly higher than the control treatment (Fig. 1d; Table 1; P < 0.05). During the three-year period, the annual average soil CO₂ efflux measured in the control was 15.8 % higher than that in the precipitation reduction treatment, being 22.3 and

2.02

24.97**

Fig. 2 Cumulated soil CO_2 efflux (a) annually, (b) in rainy season and (c) in dry season. Different letters (a and b) indicate significant differences between control and reduction treatments. Bars represent means+SD (n=5)

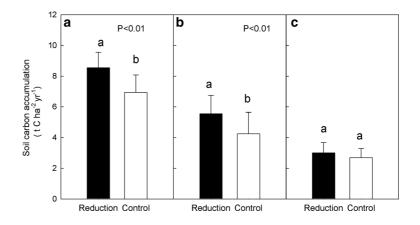




Table 2 Variation of soil respiration accumulation (TR) between control and reduction treatments

	△TR (t C ha-1 yr-1)	△TR/TR (%)	△TR/NEE (%)
2011	1.67	28.61	99.69
2012	1.39	16.39	82.91
2013	1.62	31.69	96.20

5.6 % higher in the rainy season and dry season, respectively (Table S1).

Soil respiration accumulation

Drought significantly increased annual cumulative SR compared with ambient conditions (Fig. 2; Table S1; P<0.01), although this effect varied with the season. Averaged across the observation period, soil respiration accumulation in the reduction treatment annually was 23.38 % higher than that in the control treatment; during the rainy season, drought increased cumulative SR by 30.59 % compared with ambient conditions (Table S1). No significant effects were recorded for the cumulative SR in the dry season (P>0.05). Precipitation reduction treatment increased annual cumulative SR by an average of 1.62 t C ha⁻¹ yr⁻¹ throughout the three years. As the mean annual NEE of the rainforest in Xishuangbanna is 1.68 t C ha⁻¹ yr⁻¹ (Zhang et al. 2010), the increment of soil carbon emissions from reduction treatment is equivalent to an average of 92.93 % of the annual NEE (Table 2).

Modelling the effects of T_s and SWC on SR

The correlation between SR and T_s was significant in both treatments (Table 3, Fig. 3, P<0.01); T_s explained 55 and 66 % of variation in SR in the control and

precipitation reduction treatments, respectively. In addition, T_s was a better predictor of SR during the dry season than during the rainy season, in both treatments (Table 3). A significant parabolic relationship between SR and SWC was observed in both treatments (Table 4, Fig. 4, P<0.01), although SWC explained only 11 and 20 % of the variation in SR in the control and precipitation reduction treatments, respectively.

Because soil temperature and moisture levels tend to co-vary, we applied a two-factor regression model to determine the relative dependence of SR on the two variables (Table 5, Fig. 5, P<0.01). During the dry season, the model showed a positive correlation between SR and SWC both in the control and precipitation reduction treatment; however, during the rainy season, the relationship between SR and moisture differed in the control and the reduction treatment. Soil respiration in the control treatment had a negative relationship with moisture and that SR in the reduction treatment had a positive relationship with SWC (Table 5, P<0.01).

Discussion

Effects of precipitation reduction treatment on soil respiration

It is widely assumed that soil moisture influences SR directly through physiological processes of roots and microorganisms (Stevenson 1956; Linn and Doran 1984;), and indirectly via diffusion of substrates and O₂ (Birch 1958; Van Schreven 1967; Millingt and Shearer 1971; Davidson and Trumbore 1995), and on this basis, a decrease in precipitation levels is expected to suppress soil CO₂ emissions. Consistent with this expectation, many precipitation reduction experiments have shown that SR decreases with decreasing moisture levels (Cattanio et al. 2002; Borken et al. 2006; Suseela

Table 3 Relationships of soil respiration (SR) and soil temperature (T) using a exponential function (SR= $a \cdot \exp(b \cdot T)$) under different seasons and precipitation treatments (February 2011–October 2013)

Period	Control	Reduction
Annual	SR=0.18e ^{0.110T} , r ² =0.55**	SR=0.21e ^{0.112T} , r ² =0.66**
Rainy season	SR=0.10e ^{0.135T} , r ² =0.31**	SR=0.28e ^{0.099T} , r ² =0.30**
Dry season	SR=0.17e ^{0.114T} , r ² =0.53**	SR=0.19e ^{0.117T} , r ² =0.58**

 r^2 is the coefficient of determination. Stars indicate the level of significance (*=P<0.05, **=P<0.01)



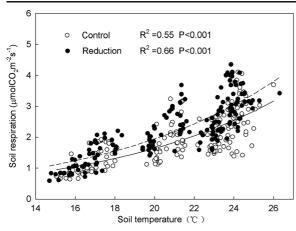


Fig. 3 Exponential relationship between soil respiration and soil temperature (February 2011–October 2013) in control and reduction treatments

et al. 2012; Jiang et al. 2013). In the present study, we found that experimental drought significantly increased soil respiration in the rainy season, but had no significant impact on soil respiration in the dry season.

Many other studies have reported varying responses of SR to a decrease in precipitation. For example, Davidson et al. (2008) found that precipitation reduction had no effect on CO₂ fluxes, and that the dominant effect of precipitation reduction on soil processes was enhanced soil aeration, which transiently affected greenhouse gas production and consumption. Another study in a lowland rainforest in Amazon showed that precipitation reduction treatment reduced CO₂ fluxes over a period of two years (Sotta et al. 2007). And they suspected that different components of SR responded differently as drought continued. Van Straaten et al. (2011) also found that CO₂ emissions decreased when precipitation reduced in a tropical forest in Indonesia, and that increase in concentration of dissolved organic carbon was the major reason for SR decrease. Based on tropical rainforest studies in Costa Rica, Cleveland et al. (2010) reported that precipitation reduction resulted in increased SR. The authors hypothesized that precipitation reductions in tropical rainforests increase CO_2 fluxes to the atmosphere via the soil response to elevated concentrations of dissolved organic matter or increased soil O_2 availability. Suseela et al. (2012) reported that CO_2 fluxes decreased with drought, not only through well-known direct effects, but also by altering the apparent temperature sensitivity of SR.

Our results showed that the influence of drought on SR depends on a variety of factors and is seasonally dependent, with SR being less sensitive to drought in the dry season. This result is possibly related to the concurrence of both low soil temperatures and low soil moisture during the dry season. On one hand, lowered soil temperatures act to decrease soil respiration by reducing the rates of microbial decomposition, root respiration and the diffusion of enzymes and substrates (Jassal et al. 2008); on the other hand, at our study site, precipitation during the dry season is usually <17 % of the yearly total; consequently, soil moisture levels in the precipitation reduction treatment will be less affected. However, during the rainy season, SR levels increased significantly under conditions of precipitation reduction. We hypothesize that during the rainy season, T_s was not a limiting factor on SR, and that soil moisture levels in the control plot were generally higher than the field capacity, which may have reduced air-filled porosity in the soil to low levels, thus reducing SR by restricting microbial activity or reducing the diffusion of CO₂ (Silver et al. 1999). Under precipitation reduction conditions, SWC rarely reached the field capacity, and moisture levels were within the range required for optimal microbial and root activities. The results of the quadratic model and the two-factor regression model support this hypothesis. As showed in Fig. 4, SR tended to decrease when SWC was >35 %, and in the rainy season SR was negatively correlated with SWC in the

Table 4 Relationships of soil respiration (SR) and soil water content (W) of the top 10 cm soil using a quadratic function (SR= $y_0+a\cdot x+b\cdot x^2$) under different seasons and precipitation treatments (February 2011–October 2013)

Period	Control	Reduction
Annual	SR=-0.83+0.18 W-0.003 W ² , r ² =0.11**	SR=-0.87+0.21 W-0.003 W ² , r ² =0.20**
Rainy season	SR=-1.06+0.25 W-0.004 W ² , r ² =0.19**	SR=-0.85+0.29 W-0.005 W ² , r ² =0.12**
Dry season	SR=1.62-0.04 W+0.002 W ² , r ² =0.16**	SR=3.31-0.21 W+0.006 W ² , r ² =0.12**

 r^2 is the coefficient of determination. Stars indicate the level of significance (*=P<0.05, **=P<0.01)



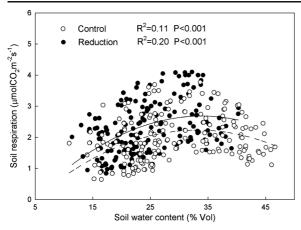


Fig. 4 Quadratic relationship between soil respiration and soil moisture (February 2011–October 2013) in control and reduction treatments

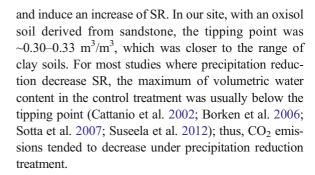
control treatment; however, in the precipitation reduction treatment, SR was positively correlated with soil moisture (Table 5).

Many previous studies have reported a similar quadratic relationship between soil respiration and soil moisture (Londo et al. 1999; Bouma and Bryla 2000; Chambers et al. 2004; Sha et al. 2005; Schwendenmann and Veldkamp 2006; Schwendenmann et al. 2010). Wood et al. (2013) found that there was a "tipping point" of the positive effect of soil moisture on CO_2 efflux on clay soils, with relative volumetric soil moisture levels of ~0.35–0.45 m³/m³; in the case of sandy soils in tropical forests, this tipping point was reduced to ~0.22 m³/m³. And precipitation decrease in some cases can possibly mitigate the super-saturated state in the soil

Table 5 The interactive effect of soil temperature (T) and soil water content (W) on soil respiration (SR) (February 2011–October 2013) using a two-factor regression model (SR=a exp (b T) W^c)

Period	Treatment	a	b	c	r ²
Annual	Control	0.20	0.11	-0.04	0.55**
	Exclusion	0.16	0.11	0.09	0.67**
Rainy season	Control	0.14	0.13	-0.06	0.32**
	Exclusion	0.20	0.10	0.07	0.31**
Dry season	Control	0.08	0.12	0.24	0.56**
	Exclusion	0.10	0.12	0.20	0.59**

 $[\]rm r^2$ is the coefficient of determination. Stars indicate the level of significance (*=P<0.05, **=P<0.01)



Effects of precipitation reduction treatment on ecosystem carbon balance

An increase in soil CO₂ emissions can weaken the C sink strength of terrestrial ecosystems and even change them into C sources (Cox et al. 2000; Jones et al. 2003). Our results showed that the precipitation reduction treatment significantly increased annual cumulative SR throughout the three-year period, both annually and during the rainy season, and the increment of soil respiration accumulation was not negligible compared with the annual soil respiration accumulation. Previous studies in the same region have shown that the ecosystem was a weak carbon sink, as determined by both eddy covariance and biometric methods (Tan et al. 2010). In addition, the seasonal variation in NEE was driven

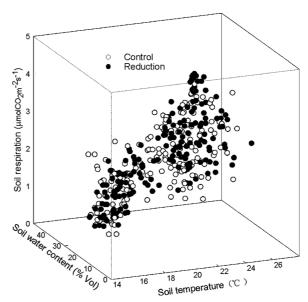


Fig. 5 The interactive effect of soil temperature and soil moisture on soil respiration (February 2011–October 2013) in control and reduction treatments



mainly by variations in monthly ecosystem respiration (Zhang et al. 2010; Yan et al. 2013). At an inter-annual scale, annual NEE varied with annual rainfall from year to year. Therefore, annual rainfall may be a fundamental driver of annual carbon sequestration in tropical forests in southern China. Under the assumption that photosynthesis in this system being constant, the weak carbon sink in this forest could be offset by the increment of cumulative soil respiration due to drought stress. Based on these previous results, combined with those of the present study, we speculate that long-term drought can weaken the carbon sink in the studied tropical forest ecosystem due to the increase in soil respiration.

Conclusion

This study reports the effects of continuous drought on soil respiration in a tropical rainforest in southwest China. Over the three years of the study period, T_s showed no difference between two treatments, while SWC decreased significantly in the precipitation reduction treatment, especially during the rainy season. Soil respiration increased significantly both annually and in the rainy season, and the relationship between SR and SWC differed in the control and reduction treatment in the rainy season. Compared with the net ecosystem exchange of carbon in this system, the increment of annual soil carbon emissions in the reduction treatment was considerable and should not be ignored. Our results indicate that the responses of soil respiration to precipitation decrease may vary seasonally and the variation of volumetric water content in different seasons may be an important factor leading to the seasonal SR variation. The variation of soil moisture among different ecosystems as well as in different seasons should be taken into consideration when predicting the future response of soil respiration to drought globally.

Acknowledgments We thank two anonymous reviewers, Wenjun Zhou and Jing Zhu for comments and assistance in improving this manuscript. We also appreciate the members of the Global Change Ecology Group for their assistance with the collection of field data. This project was supported by the National Natural Science Foundation of China (NSFC) (U1202234, 41271056, 41071071), the "Strategic Priority Research Program" of the Chinese Academy of Sciences (XDA05050601, XDA05050206) and the CAS 135 project (XTBG-F01). This work was also supported by Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies and the Biogeochemistry Laboratory of the Public Technology Service Center of XTBG.

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