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REGULAR ARTICLE

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

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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.
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 · Soil CO_2 efflux · Soil water content · 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). Climate-induced 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

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

Soils store enormous quantities of organic carbon, and the CO_2 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 CO_2 emissions 10-fold (Hanson et al. 2000; Kuzyakov 2006). Thus, the accumulation of carbon in soils can reduce atmospheric CO_2 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 CO_2 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 CO_2 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 SR and annual cumulative SR responded differently to precipitation treatments applied during growing and non-growing seasons. Thus, the identification of SR variations and the factors that control them could reduce some of the uncertainties associated with climate–carbon feedback projections.

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-m^2 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 (ΔTR) by determining the value of ΔTR as a proportion of annual NEE.

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

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

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:

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

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:

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

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 CO_2 fluxes and environmental factors between the control and reduction

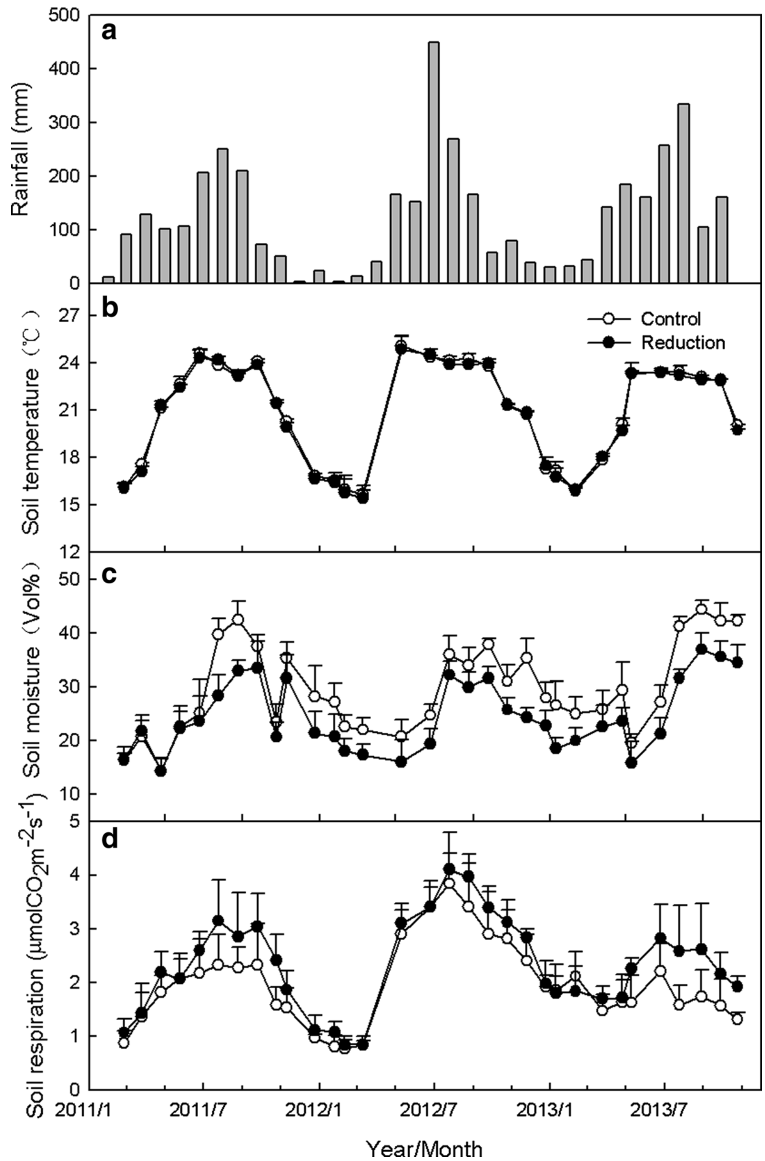

Fig. 1 Seasonal variations in (*a*) rainfall, (*b*) soil temperature (at 5 cm depth), (*c*) soil moisture (at 10 cm depth), and (d) soil respiration from February 2011 to October 2013. Data are the mean+SD (n=5)

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

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

Period	2011			2012			2013		
	SR	T	SWC	SR	T	SWC	SR	T	SWC
Dry season	0.56	1.21	0.03	1.96	0.33	9.37*	2.02	1.53	19.49**
Rainy season	9.85*	0.39	6.83*	5.43*	1.11	16.35**	24.97**	2.17	29.29**

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

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 μmol 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 μmol m^{-2} s^{-1} in the dry season ($P>0.05$). Fluxes of CO_2 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, CO_2 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 CO_2 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 CO_2 efflux measured in the control was 15.8 % higher than that in the precipitation reduction treatment, being 22.3 and

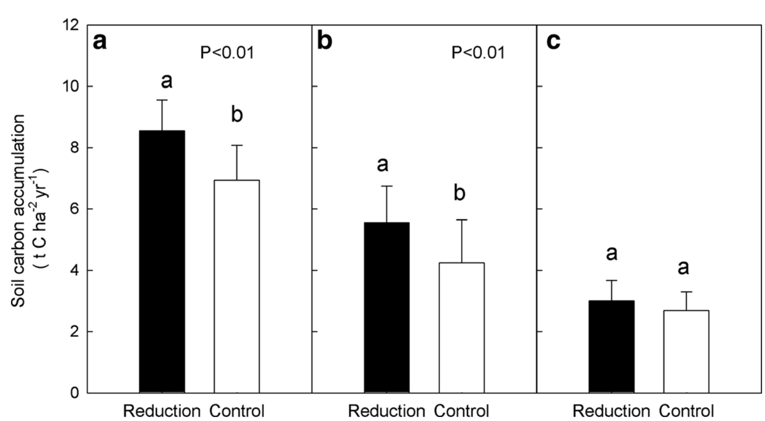

Fig. 2 Cumulated soil CO_2 efflux (*a*) annually, (*b*) in rainy season and (*c*) in dry season. Different letters (*a* and *b*) indicate significant differences between control and reduction treatments. Bars represent means+SD (*n*=5)

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 O_2 (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 CO_2 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 (*=$P<0.05$, **=$P<0.01$)

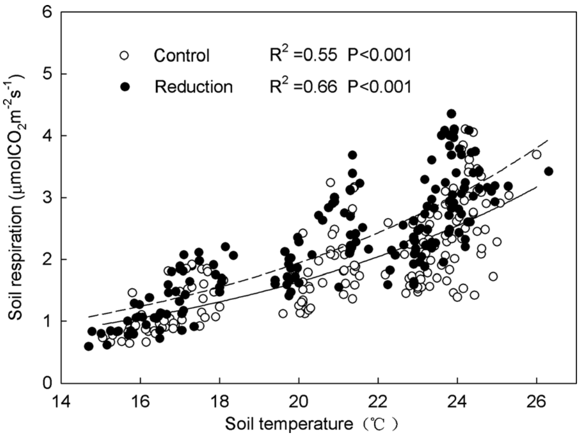

Fig. 3 Exponential relationship between soil respiration and soil temperature (February 2011–October 2013) in control and reduction treatments

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 CO_2 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 CO_2 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 CO_2 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 CO_2 (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)

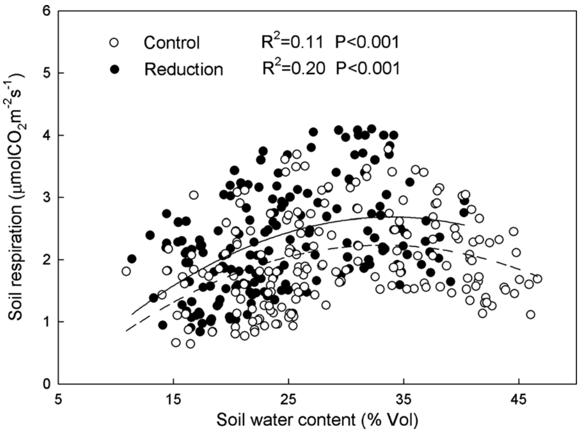

Fig. 4 Quadratic relationship between soil respiration and soil moisture (February 2011–October 2013) in control and reduction treatments

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 m^3/m^3; in the case of sandy soils in tropical forests, this tipping point was reduced to ~0.22 m^3/m^3. And precipitation decrease in some cases can possibly mitigate the super-saturated state in the soil and induce an increase of SR. In our site, with an oxisol soil derived from sandstone, the tipping point was ~0.30–0.33 m^3/m^3, which was closer to the range of clay soils. For most studies where precipitation reduction decrease SR, the maximum of volumetric water content in the control treatment was usually below the tipping point (Cattanio et al. 2002; Borken et al. 2006; Sotta et al. 2007; Suseela et al. 2012); thus, CO_2 emissions tended to decrease under precipitation reduction treatment.

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**

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 CO_2 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

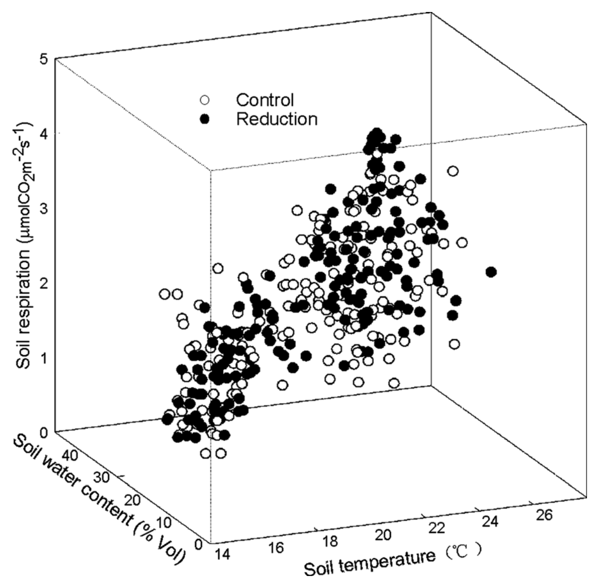

Fig. 5 The interactive effect of soil temperature and soil moisture on soil respiration (February 2011–October 2013) in control and reduction treatments

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.

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References

Balser TC, Wixon DL (2009) Investigating biological control over soil carbon temperature sensitivity. Glob Chang Biol 15: 2935–2949

Birch H (1958) The effect of soil drying on humus decomposition and nitrogen availability. Plant Soil 10:9–31

Borken W, Savage K, Davidson EA, Trumbore SE (2006) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. Glob Chang Biol 12:177–193

Bouma TJ, Bryla DR (2000) On the assessment of root and soil respiration for soils of different textures: interactions with soil moisture contents and soil CO_2 concentrations. Plant Soil 227:215–221

Bouskill NJ, Lim HC, Borglin S, Salve R, Wood TE, Silver WL, Brodie EL (2013) Pre-exposure to drought increases the resistance of tropical forest soil bacterial communities to extended drought. Isme J 7:384–394

Cao M, Zhang J, Feng Z, Deng J, Deng X (1996) Tree species composition of a seasonal rain forest in Xishuangbanna, southwest China. Trop Ecol 37:183–192

Cattanio JH, Davidson EA, Nepstad DC, Verchot LV, Ackerman IL (2002) Unexpected results of a pilot throughfall exclusion experiment on soil emissions of CO_2, CH_4, N_2O, and NO in eastern Amazonia. Biol Fertil Soils 36:102–108

Chambers JQ, Tribuzy ES, Toledo LC, Crispim BF, Higuchi N, Jd S, Araujo AC, Kruijt B, Nobre AD, Trumbore SE (2004) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. Ecol Appl 14:72–88

Cleveland CC, Wieder WR, Reed SC, Townsend AR (2010) Experimental drought in a tropical rain forest increases soil carbon dioxide losses to the atmosphere. Ecology 91:2313–2323

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–187

Davidson EA, Trumbore SE (1995) Gas diffusivity and production of CO_2 in deep soils of the eastern Amazon. Tellus Ser B Chem Phys Meteorol 47:550–565

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Glob Chang Biol 4:217–227

Davidson EA, Nepstad DC, Ishida FY, Brando PM (2008) Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. Glob Chang Biol 14:2582–2590

Edwards NT (1975) Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest. Soil Sci Soc Am J 39:361–365

Hall SJ, McDowell WH, Silver WL (2013) When wet gets wetter: decoupling of moisture, redox biogeochemistry, and greenhouse gas fluxes in a humid tropical forest soil. Ecosystems 16:576–589

Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48:115–146

Jassal RS, Black TA, Novak MD, Gaumont-Guay D, Nesic Z (2008) Effect of soil water stress on soil respiration and its temperature sensitivity in an 18-year-old temperate Douglas-fir stand. Glob Chang Biol 14:1305–1318

Jiang H, Deng Q, Zhou G, Hui D, Zhang D, Liu S, Chu G, Li J (2013) Responses of soil respiration and its temperature/moisture sensitivity to precipitation in three subtropical forests in southern China. Biogeosciences 10:3963–3982

Jones CD, Cox P, Huntingford C (2003) Uncertainty in climate-carbon-cycle projections associated with the sensitivity of soil respiration to temperature. Tellus Ser B Chem Phys Meteorol 55:642–648

Keith H, Jacobsen KL, Raison RJ (1997) Effects of soil phosphorus availability, temperature and moisture on soil respiration in Eucalyptus pauciflora forest. Plant Soil 190:127–141

Kirtman B, Power SB, Adedoyin JA, Boer GJ, Bojariu R, Camilloni I, Doblas-Reyes FJ, Fiore AM, Kimoto M, Meehl GA, Prather M, Sarr A, Schär C, Sutton R, van Oldenborgh GJ, Vecchi G, Wang HJ (2013) Near-term climate change: projections and predictability. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 953–1028

Kuzyakov Y (2006) Sources of CO_2 efflux from soil and review of partitioning methods. Soil Biol Biochem 38:425–448

Linn D, Doran J (1984) Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. Soil Sci Soc Am J 48:1267–1272

Liu WH, Zhang YP, Li HM, Liu YH (2005) Fog drip and its relation to groundwater in the tropical seasonal rain forest of Xishuangbanna, Southwest China: a preliminary study. Water Res 39:787–794

Londo AJ, Messina MG, Schoenholtz SH (1999) Forest harvesting effects on soil temperature, moisture, and respiration in a bottomland hardwood forest. Soil Sci Soc Am J 63:637–644

Luo YQ (2007) Terrestrial carbon-cycle feedback to climate warming. Annu Rev Ecol Evol Syst 38:683–712

Millingt RJ, Shearer RC (1971) Diffusion in aggregated porous media. Soil Sci 111:372–378

Qi Y, Xu M (2001) Separating the effects of moisture and temperature on soil CO_2 efflux in a coniferous forest in the Sierra Nevada mountains. Plant Soil 237:15–23

Raich JW, Potter CS, Bhagawati D (2002) Interannual variability in global soil respiration, 1980–94. Glob Chang Biol 8:800–812

Schimel DS, House JI, Hibbard KA, Bousquet P, Ciais P, Peylin P, Braswell BH, Apps MJ, Baker D, Bondeau A, Canadell J, Churkina G, Cramer W, Denning AS, Field CB, Friedlingstein P, Goodale C, Heimann M, Houghton RA, Melillo JM, Moore B, Murdiyarso D, Noble I, Pacala SW, Prentice IC, Raupach MR, Rayner PJ, Scholes RJ, Steffen WL, Wirth C (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414: 169–172

Schwendenmann L, Veldkamp E (2006) Long-term CO_2 production from deeply weathered soils of a tropical rain forest: evidence for a potential positive feedback to climate warming. Glob Chang Biol 12:1878–1893

Schwendenmann L, Veldkamp E, Moser G, Holscher D, Kohler M, Clough Y, Anas I, Djajakirana G, Erasmi S, Hertel D, Leitner D, Leuschner C, Michalzik B, Propastin P, Tjoa A, Tscharntke T, van Straaten O (2010) Effects of an experimental drought on the functioning of a cacao agroforestry system, Sulawesi, Indonesia. Glob Chang Biol 16:1515–1530

Sha LQ, Zheng Z, Tang JW, Wang YH, Zhang YP, Cao M, Wang R, Liu GG, Wang YS, Sun Y (2005) Soil respiration in tropical seasonal rain forest in Xishuangbanna, SW China. Sci China Ser D Earth Sci 48:189–197

Silver WL, Lugo AE, Keller M (1999) Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. Biogeochemistry 44:301–328

Singh JS, Gupta SR (1977) Plant decomposition and soil respiration in terrestrial ecosystems. Bot Rev 43:499–528

Skopp J, Jawson MD, Doran JW (1990) Steady-state aerobic microbial activity as a function of soil water content. Soil Sci Soc Am J 54:1619–1625

Sotta ED, Veldkamp E, Schwendenmann L, Guimaraes BR, Paixao RK, Ruivo M, Da Costa ACL, Meir P (2007) Effects of an induced drought on soil carbon dioxide (CO_2) efflux and soil CO_2 production in an Eastern Amazonian rainforest, Brazil. Glob Chang Biol 13: 2218–2229

Stevenson I (1956) Some observations on the microbial activity in remoistened air-dried soils. Plant Soil 8:170–182

Suseela V, Dukes JS (2013) The responses of soil and rhizosphere respiration to simulated climatic changes vary by season. Ecology 94:403–413

Suseela V, Conant RT, Wallenstein MD, Dukes JS (2012) Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. Glob Chang Biol 18:336–348

Tan ZH, Zhang YP, Yu GR, Sha LQ, Tang JW, Deng XB, Song QH (2010) Carbon balance of a primary tropical seasonal rain forest. J Geophys Res 115:D00h26. doi:10.1029/2009JD012913

Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich J, Moore B, Vorosmarty CJ (2000) Climatic and biotic controls on annual carbon storage in Amazonian ecosystems. Glob Ecol Biogeogr 9:315–335

Townsend AR, Cleveland CC, Houlton BZ, Alden CB, White JWC (2011) Multi-element regulation of the tropical forest carbon cycle. Front Ecol Environ 9:9–17

Valentini R, Matteucci G, Dolman AJ, Schulze ED, Rebmann C, Moors EJ, Granier A, Gross P, Jensen NO, Pilegaard K, Lindroth A, Grelle A, Bernhofer C, Grunwald T, Aubinet M, Ceulemans R, Kowalski AS, Vesala T, Rannik U, Berbigier P, Loustau D, Guomundsson J, Thorgeirsson H, Ibrom A, Morgenstern K, Clement R, Moncrieff J, Montagnani L, Minerbi S, Jarvis PG (2000) Respiration as the main determinant of carbon balance in European forests. Nature 404:861–865

Van Schreven D (1967) The effect of intermittent drying and wetting of a calcareous soil on carbon and nitrogen mineralization. Plant Soil 26:14–32

van Straaten O, Veldkamp E, Kohler M, Anas I (2010) Spatial and temporal effects of drought on soil CO_2 efflux in a cacao agroforestry system in Sulawesi, Indonesia. Biogeosciences 7:1223–1235

van Straaten O, Veldkamp E, Corre MD (2011) Simulated drought reduces soil CO_2 efflux and production in a tropical forest in Sulawesi, Indonesia. Ecosphere 2, art119

Wood TE, Silver WL (2012) Strong spatial variability in trace gasdynamics following experimental drought in a humid tropical forest. Glob Biogeochem Cycles 26:12. doi:10.1029/2010gb004014

Wood TE, Cavaleri MA, Reed SC (2012) Tropical forest carbon balance in a warmer world: a critical review spanning microbial- to ecosystem-scale processes. Biol Rev 87:912–927

Wood TE, Detto M, Silver WL (2013) Sensitivity of Soil Respiration to Variability in Soil Moisture and Temperature in a Humid Tropical Forest. Plos One 8:7. doi:10.1371/journal.pone.0080965

Yan J, Zhang Y, Yu G, Zhou G, Zhang L, Li K, Tan Z, Sha L (2013) Seasonal and inter-annual variations in net ecosystem exchange of two old-growth forests in southern China. Agric For Meteorol 182:257–265

Zhang YP, Tan ZH, Song QH, Yu GR, Sun XM (2010) Respiration controls the unexpected seasonal pattern of carbon flux in an Asian tropical rain forest. Atmos Environ 44:3886–3893

Zhou XH, Xiao ZN (2014) Climate projection over yunnan province and the surrounding regions based on CMIP5 data. Climatic Environ Res 19:601–613 (in Chinese with English abstract)

Zhou XH, Sherry RA, An Y, Wallace LL, Luo YQ (2006) Main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux in a grassland ecosystem. Glob Biogeochem Cycles 20, GB1003

Zhou GY, Wei XH, Wu YP, Liu SG, Huang YH, Yan JH, Zhang DQ, Zhang QM, Liu JX, Meng Z, Wang CL, Chu GW, Liu SZ, Tang XL, Liu XD (2011) Quantifying the hydrological responses to climate change in an intact forested small watershed in Southern China. Glob Chang Biol 17:3736–3746