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Discussions

Effects of precipitation on soil respiration and its temperature/moisture sensitivity in three subtropical forests in Southern China

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Abstract

Both long-term observation data and model simulations suggest an increasing chance of serious drought in the dry season and extreme flood in the wet season in Southern China, yet little is known about how changes in precipitation pattern will affect soil respiration in the region. We conducted a field experiment to study the responses of soil respiration to precipitation manipulations – precipitation exclusion to mimic drought, double precipitation to simulate flood, and ambient precipitation (Abbr. EP, DP and AP, respectively) – in three subtropical forests in Southern China. The three forests include *Masson* pine forest (PF), coniferous and broadleaved mixed forest (MF) and monsoon evergreen broadleaved forest (BF). Our observations showed that altered precipitation can strongly influence soil respiration, not only through the well-known direct effects of soil moisture, but also by modification on both moisture and temperature sensitivity of soil respiration. In the dry season, soil respiration and its temperature sensitivity in the three forests showed rising trends with precipitation increase, and its moisture sensitivity showed an opposite trend. In the wet season, the EP treatment also decreased soil respiration and its temperature sensitivity, and enhanced moisture sensitivity in all three forests. Soil respiration under the DP treatment increased significantly in the PF only, and no significant change was found for either moisture or temperature sensitivity. However, the DP treatment in the MF and BF reduced temperature sensitivity significantly. Our results indicated that soil respiration would decrease in the three subtropical forests if soil moisture continues to decrease in the future. More rainfall in the wet season could have limited effect on the response of soil respiration to the rising of temperature in the BF and MF.

1 Introduction

As one of the largest carbon fluxes in terrestrial ecosystem, soil respiration has received renewed attention in recent decades due to the concerns over its potential feedback to future climate change (Trumbore, 1997; Valentini et al., 2000; Bond-Lamberty and Thompson, 2010). It is generally accepted that temperature rising would accelerate CO_2 release from soils, which in return reinforces anthropogenic warming (Cox et al., 2000; Luo, 2007). Both climate models and satellite observations suggested change in precipitation patterns in the warm climate (Easterling et al., 2000; IPCC, 2007; Allan and Soden, 2008). However, our studies of precipitation impacts on soil respiration have not generated a definite conclusion. Precipitation manipulation experiments showed variable effects on soil respiration largely depending on soil moisture conditions (Borken et al., 2006; Zhou et al.,. 2006; Scott et al., 2007; Davidson et al., 2008; van Straaten et al., 2010; Cleveland et al., 2010), and hence extensive research is necessary to make an accurate assessment of its global impacts.

Global and regional earth system modeling studies have indentified temperature and moisture as major factors regulating soil respiration in terrestrial ecosystems (Raich et al., 1995; Davidson et al., 1998; Reichstein et al., 2003; Gaumont-Guay et al., 2006; Heimann and Reichstein, 2008; Medvigy et al., 2010; Falloon et al., 2011). Traditional ecosystem modeling concept typically assumes temperature and moisture sensitivity of soil respiration to be constant during the year and with climate change (Davidson and Janssens, 2006; Kirschbaum, 2010; Falloon et al., 2011), but this hypothesis recently has been much challenged. Both experimental and modeling studies have shown that temperature sensitivity of soil respiration varied seasonally (Xu and Qi, 2001), and decreased with warming (Luo et al., 2001; Conant et al., 2008), which would weaken the positive feedback between the terrestrial carbon cycle and climate warming Several authors indicated that seasonal variation of temperature sensitivity was also associated with soil moisture (Xu and Qi, 2001; Curriel Yuste et al., 2003; Almagro et al., 2009), but the results were mostly based on the observations of seasonal variation, which may often be confounded by other factors such as temperature and phenological processes (Luo et al., 2001; Curriel Yuste et al., 2004; Wang et al., 2010). Direct evidences of the effects of precipitation on temperature sensitivity under precipitation manipulations are still lacking (Davidson et al., 2006; Jassal et al., 2008; Craine and Gelderman, 2011). Another crucial, but unresolved question is that whether soil moisture sensitivity varies during the year, or changes under different precipitation conditions Changes of moisture sensitivity could also lead to inaccurate estimation in ecosystem carbon cycling (Noormets et al., 2008). So far, only a few studies have attempted to study the soil moisture sensitivity change under climate change, particularly precipitation (Hui and Luo 2004; Liu et al., 2009; Misson et al., 2010).

While most studies of precipitation manipulation experiments were performed in tropical and temperate forests, little emphasis has focused on in subtropical forest ecosystems (Borken et al., 2006; Zhou et al., 2006; Scott et al., 2007; Davidson et al., 2008; van Straaten et al., 2010; Cleveland et al., 2010), and to our knowledge, there is no such information from China. Being favored by the subtropical monsoon, the climate in Southern China is abundant in heat, light, and water resources from April to September annually (Ding et al., 2001). Because of its unique climate regime, moist subtropical forests spread out in Southern China, and experience more pronounced dry season compared to the tropical forests. This strong seasonal variation of precipitation amount provides an excellent opportunity for studies of how soil respiration responds to altered precipitation influenced by soil moisture conditions. In addition, long-term observation records in Southern China showed that precipitation seasonal pattern and intensity varied drastically in the past three decades, and the forest soil moisture decreased significantly (Zhou et al., 2011). Model simulations in this region suggested an increasing chance of serious drought in the dry season and extreme flood in the wet season in the future (Zhou et al., 2011). We hypothesize that the changing precipitation pattern will have a significant impact on the soil carbon stock of subtropical forests in Southern China, but it has not been well studied.

We conducted a precipitation manipulation experiment in subtropical forests in Southern China to study the responses of soil respiration to altered precipitation. We selected three common forests at the Dinghushan Nature Reserve (DNR), established three precipitation treatments in each forest, and measured soil respiration. Precipitation was controlled automatically through interception-redistribution systems to establish precipitation exclusion (EP), double precipitation (DP) treatments besides the ambient precipitation (AP) as a control (Borken et al., 2006; Zhou et al., 2006; Deng et al., 2012). Previous work in these forests has shown significant exponential relationships between soil respiration and soil temperature, and significant positive linear relationships between soil respiration and soil moisture even though soil moisture was relatively high in the region (Tang et al., 2006). However, precipitation manipulation with increased precipitation had no effects on soil respiration in the two of three forests (Deng et al., 2012). Thus, we suspected that such equal strong effects were due to high seasonal correlation between soil temperature and moisture. In this study, we focused on the seasonal responses of soil respiration and its temperature/moisture sensitivities to precipitation alterations. We hypothesized that:

1. The regulation of soil respiration by soil temperature and moisture in the three subtropical forests varied significantly in the wet season compared to that in the dry season. Particularly, we expected that the soil moisture sensitivity of soil respiration varied seasonally.
2. The responses of soil respiration to precipitation treatments also varied seasonally in the three forests.
3. Precipitation treatments would modify the moisture and/or temperature sensitivity of soil respiration in the three forests.

2 Materials and methods

2.1 Site description

This study was conducted at the Dinghushan Nature Reserve (DNR) located in the center of Guangdong Province in Southern China (112°13′39″–112°33′41″ E, 23°09′21″–23°11′30″ N). Climate in the region is typical south subtropical monsoon climate, with mean annual temperature of 21.4 °C, and total annual precipitation of 1956 mm, of which nearly 80 % falls in the hot–humid wet/rainy season (April–September) and 20 % in the dry season (October–March) (Wu et al., 1982). The bedrock is sandstone and shale. Soils are classified as oxisols with a pH of 4.0–4.9.

Three common subtropical forests (at elevations ranging from 150 to 300 m, less than 500 m from one another and facing the same slope direction) at the DNR were selected including a coniferous *Masson* pine forest (PF), a conifer and broadleaf mixed forest (MF), and an monsoon evergreen broadleaf forest (BF). The three forests were also representing forests in early-, mid-, and advanced-successional stages in the region (Peng and Wang, 1995). The PF (approximately 22 ha) originally planted by local people in the 1950s, was dominated by *Pinus massoniana* in the tree layer and *Baeckea frutescens*, *Rhodomyrtus tomenosa*, and *Dicranopteris linearis* in the shrub and herb layers. The MF (approximately 557 ha) was developed from artificial pine forest with a gradual invasion of some pioneer broadleaf species through natural succession. The upper canopy of the community is dominated by *Schima superba*, *Castanopsis chinensis*, and *Craibiodendron scleranthum var. kwangtungense*. Artificial disturbances have not occurred in the MF for about 100 yr. The BF (approximately 218 ha) located in the central area of the reserve was dominated by *Castanopsis chinensis*, *Cryptocarya concinna*, *Schima superba*, *Machilus chinensis* without any *Pinus massoniana*. No disturbance was recorded for the past 400 yr in the BF (Wang and Ma, 1982; Shen et al., 2001). Stand characteristics of the three forests have been reported in Deng et al. (2012).

2.2 Experimental design

We used a two-factor experimental design considering forest ecosystem type and precipitation treatment. At each forest site, a randomized block design was used with three blocks. In each block, three precipitation treatments were randomly arranged. From November 2006, precipitation in the precipitation exclusion (EP) plots was intercepted using transparent polyvinyl chloride (PVC) sheer roof (Borken et al., 2006) and was redistributed to the double precipitation (DP) plots using pipes similar to these used in

Zhou et al. (2006) and Deng et al. (2012). The control that received ambient precipitation (AP) was built next to these treatment plots in each forest. Each plot was 3 × 3 m^2 and the distance between plots was more than 1 m. In order to minimize the washing effect of double rainfall, the pipes in the DP plots were close to soil surface and their distance is only 5 cm. Around each EP plot, the thick PVC panels were inserted at the top 15 cm soil layer to prevent surface runoff and lateral movement of water from the outside surrounding soil. As precipitation interception roofs prevented litter-fall in the EP plots, we collected litter-fall after each measurement from nearby plots with the same area and evenly distributed to the EP plots after each measurement of soil respiration.

2.3 Soil respiration measurements

Five PVC soil collars (80 cm^2 in area and 5 cm in height) were permanently installed 3 cm into the soil in each plot in November 2006. The distance between adjacent collars was more than 50 cm. Soil respiration was measured three times a month in 2007 using a Li-6400 infrared gas analyzer (Li-COR, Inc., Lincoln, Nebraska, USA) connected to a Li-6400-09 soil respiration chamber (9.55 cm diameter) (Li-COR, Inc., Lincoln, Nebraska, USA). The measurements were made between 9:00 a.m. and 12:00 a.m. local time. Previous work at the DNR forests has demonstrated that soil respiration measured during this period was close to daily mean (Tang et al., 2006). Soil respiration was measured three times for each soil collar. Soil respiration in a treatment plot was calculated as the mean of five collar measurements (the measurement at five collars in a plot mostly differed by less than 5 % at any measurement period). Soil temperature at 5 cm below the soil surface was also monitored with a thermocouple sensor attached to the respiration chamber during the soil respiration measurement. Volumetric soil moisture of the top 5 cm soil layer was measured on five random locations within a treatment plot using a PMKit (ICT, Australia, see http://www.ictinternational.com.au/soils.htm), which consists of three amplitude domain reflectometry (ADR) moisture probes (MP406) and a data logger (MPM160 meter) (Deng et al., 2012).

2.4 Soil microbial biomass and fine root biomass measurements

To determine soil microbial biomass carbon, soil samples (0–20 cm depth) were collected in February, May, August and November of 2007, respectively. In each time, two samples of six cores (2.5 cm diameter) were randomly collected from each plot in the three forests. After removing roots and plant residues, the composited samples were immediately sieved through a 2-mm mesh sieve. The soil microbial biomass carbon was calculated using the fumigation–extraction method (Vance et al., 1987).

To measure fine root biomass (diameter $\leq$ 3 mm), we also collected randomly soil corns (0–20 cm depth) in February 2007 using a 10 cm diameter stainless–steel corer, and three more times in April, August and October of 2007, respectively. In each time, two samples were randomly collected from each plot in the three forests. The fine roots were separated by washing and sieving, dried at 60 °C for 48 h and weighed.

2.5 Statistical analysis

Soil respiration and soil temperature in a plot were calculated as the means of five collar measurements. Soil moisture was calculated as the mean of five measurements at random locations in a plot. We used repeated measure Analysis of Variance (ANOVA) to test the differences in soil respiration rate, soil temperature and soil moisture among forests, precipitation treatments, and seasons. Tukey multiple comparison test (HSD) was conducted if significant effects of forest ecosystem types, precipitation treatments or seasons were found.

Previous work at the DNR as well as this study have demonstrated that soil respiration increases exponentially with soil temperature and linearly with soil moisture (Tang et al., 2006; Deng et al., 2010, 2012). Thus, we first developed the relationship between soil respiration (R) and soil temperature (T) with an exponential function [$R = a\exp(bT)$] and the relationship between soil respiration and soil moisture (M) with a linear regression mode ($R = a + cM$). Considering that soil temperature and moisture may interactively regulate soil respiration, we further fit soil respiration (R) with soil temperature (T) and soil moisture (M) together using $R = (a + cM)\exp(bT)$, where a is parameter related to basal soil respiration when both $T = 0$ and $M = 0$; b and c are parameters related to the temperature and moisture sensitivities of soil respiration, respectively. Similar models were also developed for individual season in each forest. We then used t-test to determine the difference of temperature and moisture sensitivities between seasons and among precipitation treatments. All data analyses were carried out using the SAS software (SAS Institute Inc., Cary, NC, USA).

Results

2.6 Soil temperature and soil moisture

Among the three forests, soil in the PF was significantly warmer than those in the other two forests ($p < 0.05$). No significant difference in soil temperature was found between MF and BF ($p > 0.05$). In all the three forests, soil temperature in the dry season was significantly lower than those in the wet season ($p < 0.05$) (Fig. 1). The mean values of soil temperature in the wet season were 24.7, 23.2 and 23.2 °C for the PF, MF and BF, respectively. Mean soil temperature in the dry season were 18.7, 16.4 and 16.3 °C for the PF, MF and BF, respectively. Precipitation treatments did not significantly change soil temperature in all three forests (Tables 1 and 2).

Among the three forests, soil in the PF was significantly dryer than those in the MF and BF ($p < 0.05$). No significant difference in annual mean soil moisture was found between MF and BF ($p > 0.05$). Soil moisture under the AP treatment also displayed a strong seasonal variation in all three forests ($p < 0.05$) (Fig. 1). The mean values of soil moisture in the wet season were 22.0 % vol. for PF, 35.4 % vol. for MF and 36.0 % vol. for BF, respectively. The mean values of soil moisture in the dry season were 9.4 % vol. for PF, 19.0 % vol. for MF and 17.8 % vol. for BF, respectively. Soil moisture was significantly influenced by precipitation treatments (Table 1). Compared to the controls, soil moisture decreased under the EP treatments by about 58.6 % for PF, 43.2 % for MF and 44.4 % for BF, respectively, in the wet season, and about 34.0 % for PF, 25.7 % for MF and 23.8 % for BF, respectively, in the dry season (Table 2). The soil moisture increased under the DP treatment by approximately 3 % vol. in all three forests, compared to the controls (Table 2).

2.7 Soil respiration

Among the three forest ecosystems, soil respiration was significantly greater in the BF and MF than those in the PF ($p < 0.05$). There were no significant differences of soil respiration between the BF and the MF ($p > 0.05$). In all three forests, soil respiration in the wet season was significantly higher than those in the dry season ($p < 0.05$) (Fig. 1). In the controls, mean soil respiration in the wet season was 2.79, 3.85 and 3.89 μmol CO_2 m^{-2} s^{-1} in the PF, MF and BF, respectively, and in the dry season was 1.62, 1.82 and 1.83 μmol CO_2 m^{-2} s^{-1} in the PF, MF and BF, respectively.

Soil respiration was influenced significantly by precipitation treatments, and varied among the three forests and seasons (Table 1). In the BF and MF, annual mean soil respiration was not significantly different between the DP and AP plots (Table 2). Only in the PF, soil respiration increased by 18.0 % under the DP treatment (Table 2). The EP treatment decreased the soil respiration significantly in all three forests (Table 2). Annual mean soil respiration rates under the EP treatment decreased by 25.9 %, 27.2 %, and 50.9 % in the BF, MF, and PF, respectively (Table 2). Soil respiration in the dry season increased significantly with increasing precipitation treatments in all three forests (Fig. 2). In the wet season, soil respiration was decreased by the EP treatment in all three forests (Fig. 2). However, the DP treatment increased soil respiration by 19.2 % in the PF only (Fig. 2).

2.8 Relationships of soil respiration with soil temperature and moisture

In this study, soil respiration showed exponential relationships with soil temperature in all three forests ($p < 0.001$ for all). Significant positive linear relationships between soil respiration and soil moisture were also found in all three forests ($p < 0.001$ for all). By analyzing subsets of data within the wet and dry seasons, we found that soil respiration in the wet season showed an exponential relationship with soil temperature, and a positive linear relationship with soil moisture in the PF (Tables A1 and A2). In the MF and BF, soil respiration had an exponential relationship with soil temperature only. No significant relationship between soil respiration and soil moisture was found (Tables A1 and A2). In the dry season, soil respiration showed an exponential relationship with soil temperature, and a positive linear relationship with soil moisture in the MF and BF (Tables A1 and A2). In the PF, soil respiration showed a positive linear relationship with soil moisture only, and no significant relationship between soil respiration and soil temperature was found (Tables A1 and A2). Model fits using the mixed function in $R = (a + cM)\exp(bT)$ showed that temperature sensitivities of soil respiration in the wet season were significantly higher than those in the dry season in all three forests ($p < 0.05$) (Table 3), but moisture sensitivities showed an opposite trend ($p < 0.05$) (Table 3). No significant difference of the moisture sensitivities in PF was found between the wet season and the dry season ($p > 0.05$) (Table 3).

We also tested whether soil moisture and/or temperature sensitivities of soil respiration varied under precipitation treatments. In all three forests, the EP treatment significantly reduced temperature sensitivities of soil respiration, and increased soil moisture sensitivities in both the wet season and dry season (Fig. 3). The DP treatment in the wet season significantly decreased the temperature sensitivities in the BF and MF (Fig. 3). In the dry season, there was no significant difference of temperature and moisture sensitivity of soil respiration between the DP and AP treatments in all three forests (Fig. 3). Irrespective of forest types, we further found that seasonal moisture sensitivity showed a negative relationship with soil moisture, and that seasonal temperature sensitivity peaked at intermediate soil water content and declined under both wetter and drier conditions (Fig. 4).

2.9 Soil microbial biomass and fine root biomass

Among the three forest ecosystems, fine root biomass was significantly greater in the BF and MF than those in PF (Table 2). There were no significant differences of soil respiration between the BF and MF ($p > 0.05$). In all three forests, the fine root biomass was higher in the wet season than those in the dry season (Fig. 5). Only in the PF, however, the season difference of the fine root biomass was significant ($p < 0.05$). The soil microbial biomass was greatest in the BF, compared to that in the MF and PF (Table 2). In all three forests, soil microbial biomass was significantly higher in the wet season than those in the dry season ($p < 0.05$) (Fig. 5).

Both soil microbial biomass and fine root biomass were significantly influenced by precipitation treatments, and varied among the three forests and seasons (Table 1). In the wet season, the DP treatment increased fine root biomass and soil microbial biomass by 16.5 % and 20.9 %, respectively, in the PF (Fig. 5). The EP treatment decreased fine root biomass and soil microbial biomass in all three forests (Fig. 5, Table 2). In the dry season, both fine root biomass and soil microbial biomass showed significant increasing trend with increasing precipitation treatments in the three forests (Fig. 5).

3 Discussion

3.1 Environmental controls over soil respiration varied seasonally

Similar to that reported in Tang et al. (2006), on annual, soil respiration in this study showed exponential relationships with soil temperature in all three forests ($p < 0.001$ for all). Significant positive linear relationships between soil respiration and soil moisture were also found in all three forests ($p < 0.001$ for all). Such equally strong effects of soil temperature and soil moisture on soil respiration were likely due to a strong seasonal correlation between soil temperature and soil moisture ($p < 0.001$). However, analyzing subsets of data with the wet and dry seasons, we found that soil temperature and moisture controlled soil respiration differently in the wet seasons compared to that in the dry seasons in the three forests. In the MF and BF, soil respiration in the dry season showed a positive linear relationship with soil moisture (Table A2). Similar result was also found in an oak–hickory stand, where soil respiration depended on only soil temperature when soil moisture was $> 0.20\,\mathrm{m^3\,m^{-3}}$, and on both soil temperature and moisture when the soil was dry (Palmroth et al., 2005; Almagro et al., 2009). Soil respiration in the PF had positive linear relationships with soil moisture in both the wet season and the dry season, but depended on soil temperature in the wet season only (Table A1). This was consistent with the result from a temperate maritime pine forest, where water became the only limiting factor for soil respiration variations when soil moisture decreased to less than 15 % (Curriel Yuste et al., 2003). These results suggested that modeling predication of soil respiration with seasonal varying parameters may be more accurate than those with constant parameters.

3.2 Effects of precipitation treatments on soil respiration

In the past three decades, precipitation seasonal pattern and intensity in the region varied drastically, and soil moisture in forests decreased significantly (Zhou et al., 2011). Our results showed soil respiration was responsive to precipitation, but the response patterns were nonlinear in the three forests – significant decreases in soil respiration under the EP treatment, but no or small increase under the DP treatment on annual (Table 2). Moreover, we found that the effects of the DP treatment on soil respiration varied seasonally in the MF and BF (Fig. 2). These results strongly supported our model study in the BF and MF, where soil moisture affects soil respiration significantly in the dry season only (Tables A1 and A2). Previous studies on the temporal effect of precipitation manipulation experiments on soil respiration had also shown variable results during the year (Asencio et al., 2007; Chou et al., 2008; van Straaten et al., 2010).

Soil moisture can influence soil respiration mainly by altering root respiration and soil microbial decomposition (Davidson et al., 2000; Joffre et al., 20003; Williams, 2007). We did find that the fine root and soil microbial biomass increased significantly under the DP treatment in the dry season, but not increased in the wet season in the MF and BF (Fig. 5). Soil respiration in the PF showed a positively linear relationship with soil moisture in both wet season and dry season (Tables A1 and A2). The DP treatment in PF increased the fine root and soil microbial biomass significantly throughout the year (Fig. 5), and increased the soil respiration accordingly (Fig. 2). On the contrary, the EP treatment significantly decreased fine root and soil microbial biomass in both wet and dry seasons (Fig. 5), thus soil respiration in the EP plots decreased significantly throughout the year in all three forests (Fig. 2).

3.3 Effects of precipitation treatments on soil temperature and moisture sensitivities

The magnitude of soil respiration feedback to climate change depends largely on soil temperature and moisture sensitivities. Our results confirmed precipitation changes influenced soil temperature sensitivity of soil respiration. We found soil temperature sensitivity reduced significantly under the EP treatment in all three forests (Fig. 3). One of the reasons for the lower temperature sensitivity was that drought reduces contact among the substrate, the extracellular enzymes and the microbes involved in decomposition (Jassal et al., 2008). The EP treatment significantly reduced soil microbial biomass in all three forests (Fig. 5 and Table 2). Another reason was that drought could reduce substrate supply (Davidson et al., 2006) by a decrease in photosynthesis (Harper et al., 2005; Jassal et al., 2008), which decreases translocation of recent photosynthates to rhizosphere (Hogberg et al., 2001; Bhupinderpal-Singh et al., 2003). Significant decreases of fine root biomass were also revealed in our EP plots across all three forests (Fig. 5 and Table 2).

We also found that the DP treatments in the wet season reduced temperature sensitivities in the BF and MF (Fig. 3). This might be related to the decreases in soil aeration and soil oxygen concentration due to high soil moisture (Cleveland et al., 2010). Due to the subtropical monsoon climate, forests at the DNR receive abundant of heat, light, and water resources in the wet season (from April to September) (Tang et al., 2006). Soil respiration response to temperature in these moist forests is often limited by soil oxygen concentration and nutrients during the wet season (Yan et al., 2009; Deng et al., 2011). In the PF, where soil moisture was still relatively low even in the wet season, enhanced soil moisture due to the DP treatment might have no effect on soil aeration and soil oxygen concentration, and hence did not change temperature sensitivity. Our results in Fig. 4 supported the hypothesis reported by Davidson and Janssens (2006) that temperature sensitivity of soil respiration peaked at intermediate soil water content, and declined under both wetter and drier conditions.

Our results demonstrated that altered precipitation could also modify soil moisture sensitivity of soil respiration. The moisture sensitivity of soil respiration in all three forests enhanced significantly under the EP treatments (Fig. 3). Irrespective of forest types, we further found that soil moisture sensitivity showed a negative relationship with soil moisture (Fig. 4). To our knowledge, this is the first field study to examine the alterations of moisture sensitivity under climate change, particularly precipitation. Many studies have also shown that, when soil moisture was within a site-specific threshold, soil temperature is typically a reliable predictor of soil respiration. In the presence of a drought, soil respiration is more sensitive to soil moisture than soil temperature (e.g. Moncrieff and Fang, 1999; Xu and Qi, 2001; Curriel Yuste et al., 2003; Davidson et al., 2006). These findings could have potential implications for climate-carbon modeling, as uncertainty remains regarding environmental controls over soil respiration. While much controversy surrounds the effect of warming on the temperature sensitivity of soil respiration (e.g. Luo et al., 2001; Conant et al., 2008; Reth et al., 2009), our results highlighted the relative importance of soil moisture and seasonal variation in determining the responses of soil respiration to not only soil temperature, but also to soil moisture. Lower temperature sensitivity indicated that soil respiration would have limited response to climate warming. High moisture sensitivity under drought condition indicated that soil respiration would decrease more strongly if soil moisture continues to reduce. Ecosystem modeling that does not include this change in soil temperature and soil moisture sensitivities with soil moisture or seasonal variations may produce misleading conclusions (Heimann and Reichstein, 2008; Medvigy et al., 2010; Falloon et al., 2011).

4 Conclusions

Using a precipitation manipulation field experiment, we found that soil respiration in subtropical forests was responsive to precipitation, but the response pattern was non-linear depending on either seasons or soil moisture conditions. Precipitation alteration could modify both temperature and moisture sensitivities of soil respiration, which strongly contrasted with traditional ecosystem modeling concept where temperature and moisture sensitivities are often assumed to be constant. Considering drastic variation of precipitation intensity and seasonal pattern in subtropical China (Zhou et al., 2011), the contrasting seasonal responses of soil respiration to precipitation and the shifts of moisture and temperature sensitivities of soil respiration may have large impacts on subtropical forest ecosystem carbon cycling and feedback on climate change. Our results indicated that soil respiration would decrease in the subtropical forests if soil moisture continues to decrease in the future. More rainfall in the wet season could have limited effect on the response of soil respiration to climate warming.

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Table 1. Significances of the effects of forest type, precipitation treatment, season and their interactions on soil respiration rate, soil temperature, and soil moisture at the Dinghushan Nature Reserve, China. Numbers are F-values. Stars indicate the level of significance ($^{*} = P < 0.05$, $^{**} = P < 0.01$).

Source	Soil respiration	Soil temperature	Soil moisture
Forest	90.39^{**}	45.99^{**}	584.99^{**}
Treatment	204.28^{**}	0.15	663.33^{**}
Forest × Treatment	6.39^{**}	0.13	2.10
Season	972.46^{**}	1173.16^{**}	1907.69^{**}
Forest × Season	23.76^{**}	3.64^{*}	21.64^{**}
Treatment × Season	35.17^{**}	0.76	168.19^{**}
Forest × Treatment × Season	0.87	0.12	0.32

Table 2. Soil temperature at 5 cm depth, soil moisture of the top 5 cm soil layer, soil respiration rate, fine root biomass and soil microbial biomass under ambient precipitation (AP), precipitation exclusion (EP) and double precipitation (DP) treatments from the broadleaf forest (BF), the mixed forest (MF) and the pine forest (PF) (mean ± standard error). Mean values in each forest within a row with different letter have significant treatment differences at α = 0.05 level.

Variable	Broadleaf forest (BF)			Mixed forest (MF)			Pine forest (PF)		
	EP	AP	DP	EP	AP	DP	EP	AP	DP
Soil temperature (°C)	19.92^{a} ± 0.77	19.87^{a} ± 0.78	19.77^{a} ± 0.82	19.76^{a} ± 0.82	19.82^{a} ± 0.83	19.66^{a} ± 0.85	22.02^{a} ± 0.65	21.85^{a} ± 0.67	21.69^{a} ± 0.69
Soil moisture (% vol.)	16.91^{a} ± 0.69	27.05^{b} ± 1.79	29.36^{c} ± 1.93	17.21^{a} ± 0.68	27.45^{b} ± 1.62	30.24^{c} ± 1.67	7.75^{a} ± 0.33	16.02^{b} ± 1.24	18.82^{c} ± 1.41
Soil respiration (μmol CO_2 m^{-2} s^{-1})	2.14^{a} ± 0.12	2.89^{b} ± 0.20	2.95^{b} ± 0.17	2.08^{a} ± 0.12	2.86^{b} ± 0.20	2.97^{b} ± 0.17	1.10^{a} ± 0.05	2.24^{b} ± 0.13	2.64^{c} ± 0.16
Fine root biomass (g m^{-2})	99.52^{a} ± 8.69	139.23^{b} ± 4.92	138.31^{b} ± 4.82	94.89^{a} ± 9.27	131.83^{b} ± 5.73	131.90^{b} ± 4.41	66.42^{a} ± 5.22	101.21^{b} ± 5.00	124.90^{c} ± 4.47
Soil microbial biomass (g kg^{-1} soil)	448.32^{a} ± 21.39	558.57^{b} ± 24.83	594.78^{b} ± 31.78	218.40^{a} ± 19.58	371.37^{b} ± 21.12	402.71^{b} ± 19.60	194.40^{a} ± 16.99	293.33^{b} ± 22.70	355.41^{c} ± 19.16

Table 3. Relationships of soil respiration (R, μmol CO$_2$ m^{-2} s^{-1}) with soil temperature (T, °C) and soil moisture (M, % vol.) under different seasons and precipitation treatments at the DNR forests (parameter estimate ± standard error). The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf forest, MF = mixed forest, PF = pine forest. R^2 is the determination of coefficient. Different letters in each forest within a column denote significant difference ($p < 0.05$) among precipitation treatments. Numbers in bold indicate the level of function fitting is significant ($p < 0.05$).

Forests	Treatments	*a*	*c*	*b*	R^2
Wet season					
BF	EP	0.4723 ± 0.1094	0.0268 ± 0.0106^a	0.0421 ± 0.0066^a	**0.93**
	AP	0.6572 ± 0.0842	0.0017 ± 0.0015^b	0.0720 ± 0.0056^b	**0.95**
	DP	1.1751 ± 0.1515	−0.0023 ± 0.0021^b	0.0535 ± 0.0058^a	**0.89**
MF	EP	0.4654 ± 0.0952	0.0234 ± 0.0099^a	0.0446 ± 0.0067^a	**0.95**
	AP	0.6164 ± 0.0587	0.0020 ± 0.0011^b	0.0735 ± 0.0038^b	**0.98**
	DP	1.0254 ± 0.1427	−0.0008 ± 0.0030^b	0.0577 ± 0.0054^a	**0.92**
PF	EP	0.1366 ± 0.0734	0.1146 ± 0.0181^a	0.0039 ± 0.0049^a	**0.94**
	AP	0.3894 ± 0.0957	0.0184 ± 0.0081^b	0.0502 ± 0.0109^b	**0.89**
	DP	0.5085 ± 0.1000	0.0105 ± 0.0044^b	0.0583 ± 0.0087^b	**0.91**
Dry season					
BF	EP	−0.0262 ± 0.1219	0.0820 ± 0.0106^a	0.0217 ± 0.0056^a	**0.86**
	AP	0.5738 ± 0.0602	0.0219 ± 0.0039^b	0.0385 ± 0.0038^b	**0.93**
	DP	0.6766 ± 0.0878	0.0200 ± 0.0055^b	0.0393 ± 0.0050^b	**0.89**
MF	EP	−0.0598 ± 0.0460	0.0837 ± 0.0045^a	0.0163 ± 0.0025^a	**0.98**
	AP	0.7602 ± 0.1319	0.0206 ± 0.0084^b	0.0338 ± 0.0070^b	**0.87**
	DP	0.9674 ± 0.0498	0.0051 ± 0.0025^b	0.0388 ± 0.0028^b	**0.95**
PF	EP	−0.0075 ± 0.0204	0.1435 ± 0.0184^a	−0.0054 ± 0.0115^a	**0.56**
	AP	0.0682 ± 0.1236	0.0820 ± 0.0204^b	0.0315 ± 0.0119^b	**0.81**
	DP	0.2084 ± 0.1628	0.0772 ± 0.0154^b	0.0292 ± 0.0129^b	**0.75**

Table A1. Relationships of soil respiration rate (R, µmol CO$_2$ m^{-2} s^{-1}) and soil temperature at 5 cm depth (T, °C) [exponential equation $R = R_0 \exp(bT)$] (parameter estimate ± standard error) under different seasons and precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf forest, MF = mixed forest, PF = pine forest. R^2 is the determination of coefficient. Numbers in bold indicate the level of function fitting is significant ($p < 0.05$).

Forests	Treatments	R_0	b	R^2
Wet season				
BF	EP	0.6837 ± 0.1056	0.0586 ± 0.0064	**0.87**
	AP	0.6769 ± 0.0858	0.0746 ± 0.0053	**0.95**
	DP	1.1487 ± 0.1505	0.0511 ± 0.0054	**0.88**
MF	EP	0.6199 ± 0.0831	0.0624 ± 0.0056	**0.91**
	AP	0.6564 ± 0.0612	0.0754 ± 0.0039	**0.97**
	DP	1.0053 ± 0.1214	0.0572 ± 0.0050	**0.92**
PF	EP	0.8042 ± 0.3401	0.0194 ± 0.0169	0.08
	AP	0.4190 ± 0.1448	0.0761 ± 0.0136	**0.73**
	DP	0.5188 ± 0.1358	0.0747 ± 0.0103	**0.82**
Dry season				
BF	EP	1.3226 ± 0.3562	0.0099 ± 0.0148	0.02
	AP	0.8427 ± 0.1134	0.0466 ± 0.0077	**0.70**
	DP	0.9193 ± 0.1141	0.0487 ± 0.0071	**0.75**
MF	EP	1.3687 ± 0.4183	0.0044 ± 0.0181	0.01
	AP	0.9274 ± 0.1178	0.0407 ± 0.0073	**0.67**
	DP	1.0236 ± 0.0474	0.0420 ± 0.0076	**0.74**
PF	EP	1.2596 ± 0.4563	−0.0226 ± 0.0193	0.08
	AP	0.6577 ± 0.3624	0.0473 ± 0.0284	0.14
	DP	0.7624 ± 0.3799	0.0484 ± 0.0260	0.17

Table A2. Relationships of soil respiration (R, µmol CO$_2$ m^{-2} s^{-1}) and soil moisture of the top 5 cm soil layer (M, % vol.) (linear regression equation$R = a + cM$) (parameter estimate ± standard error) under different seasons and precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf forest, MF = mixed forest, PF = pine forest. R^2 is the determination of coefficient. Numbers in bold indicate the level of function fitting is significant ($p < 0.05$).

Forests	Treatments	a	b	R^2
Wet season				
BF	EP	−0.6482 ± 0.2479	0.1682 ± 0.0248	**0.74**
	AP	1.4607 ± 0.8362	0.0675 ± 0.0229	0.30
	DP	2.5073 ± 0.6997	0.0335 ± 0.0177	0.18
MF	EP	−0.8731 ± 0.4567	0.1758 ± 0.0226	**0.79**
	AP	1.4781 ± 0.9550	0.0669 ± 0.0267	0.28
	DP	1.9409 ± 1.0366	0.0498 ± 0.0266	0.18
PF	EP	0.1316 ± 0.0799	0.1284 ± 0.0087	**0.93**
	AP	−0.6482 ± 0.2479	0.1682 ± 0.0248	**0.74**
	DP	1.4607 ± 0.8362	0.0675 ± 0.0229	0.30
Dry season				
BF	EP	0.1226 ± 0.2360	0.1056 ± 0.0171	**0.72**
	AP	0.8289 ± 0.3192	0.0559 ± 0.0176	**0.40**
	DP	0.8056 ± 0.3928	0.0624 ± 0.0195	**0.41**
MF	EP	−0.0131 ± 0.1226	0.1049 ± 0.0085	**0.91**
	AP	0.6237 ± 0.2462	0.0628 ± 0.0127	**0.62**
	DP	1.1528 ± 0.3307	0.0408 ± 0.0151	**0.53**
PF	EP	0.0010 ± 0.1627	0.1325 ± 0.0260	**0.65**
	AP	0.1226 ± 0.2360	0.1056 ± 0.0171	**0.72**
	DP	0.8289 ± 0.3192	0.0559 ± 0.0176	**0.40**

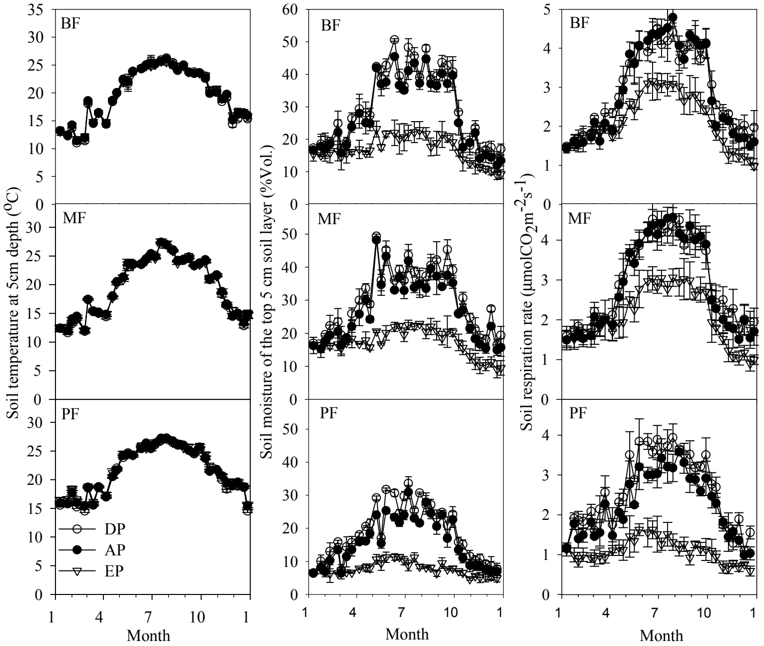

Fig. 1. Seasonal dynamics of soil temperature at 5 cm depth, soil moisture of the top 5 cm soil layer, and soil respiration rate under different precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf forest, MF = mixed forest, PF = pine forest. Error bars are standard deviations.

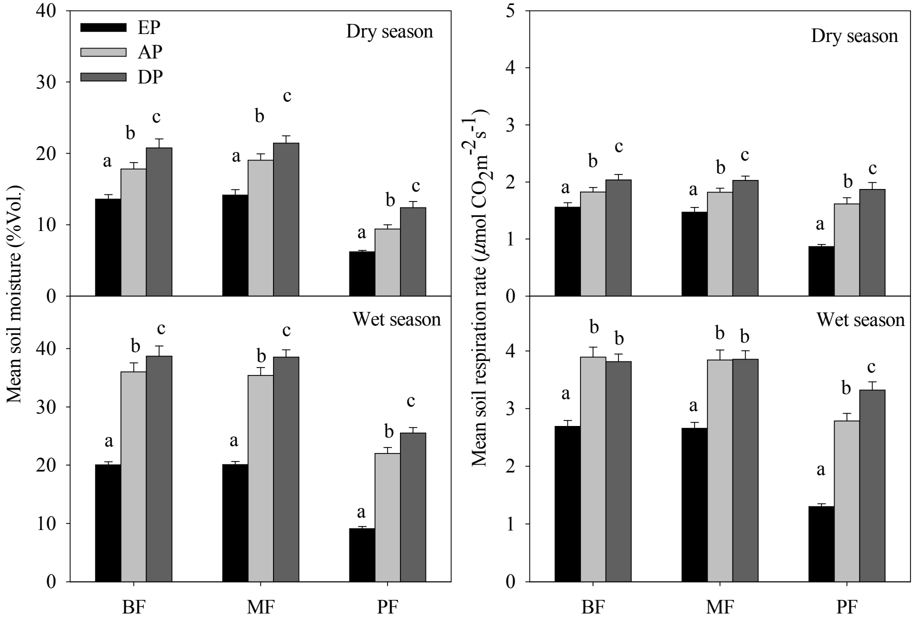

Fig. 2. Mean values of soil moisture and soil respiration rate in the dry season and in the wet season under different precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf forest, MF = mixed forest, PF = pine forest. Error bars are standard errors.

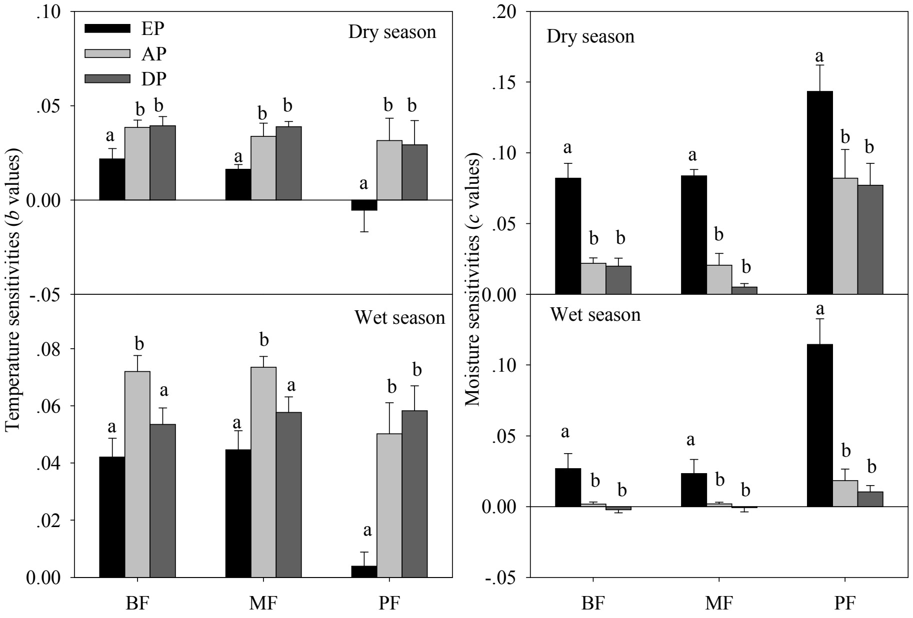

Fig. 3. Temperature and moisture sensitivities (*c* and *b* values) in the dry season and in the wet season under different precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf forest, MF = mixed forest, PF = pine forest. Error bars are standard errors. *c* and *b* values were listed in Table 3.

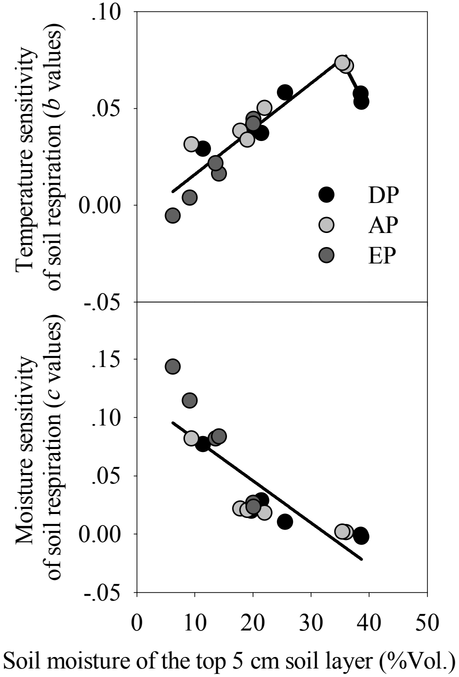

Fig. 4. Relationships of seasonal soil moistures at the DNR forests with moisture sensitivities, and temperature sensitivities (*c* and *b* values), respectively. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. *c* and *b* values were listed in Table 3.

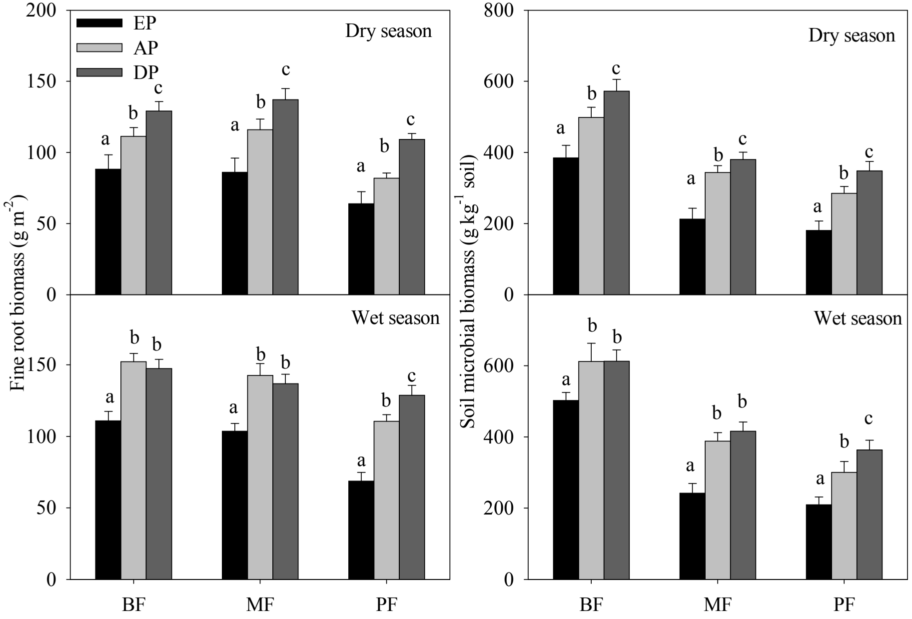

Fig. 5. Mean values of fine root biomass and soil microbial biomass in the dry season and in the wet season under different precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf forest, MF = mixed forest, PF = pine forest. Error bars are standard errors.