

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

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

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Received: 26 October 2012 – Accepted: 26 October 2012 – Published: 8 November 2012

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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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

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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 CO₂ release from soils, which in return reinforces anthropogenic warming (Cox et al., 2000; Luo, 2007). Both climate models and satellite observations suggested
5 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.,
10 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;
15 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
20 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),
25 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,

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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
5 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;
10 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
15 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
20 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.

25 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

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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 $> 0.20 \text{ m}^3 \text{ m}^{-3}$, 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).

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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

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Table 3. Relationships of soil respiration (R , $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) with soil temperature (T , $^{\circ}\text{C}$) and soil moisture (M , % vol.) under different seasons and precipitation treatments at the DNR forests (parameter estimate \pm 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 \pm 0.1094	0.0268 \pm 0.0106 ^a	0.0421 \pm 0.0066 ^a	0.93
	AP	0.6572 \pm 0.0842	0.0017 \pm 0.0015 ^b	0.0720 \pm 0.0056 ^b	0.95
	DP	1.1751 \pm 0.1515	-0.0023 \pm 0.0021 ^b	0.0535 \pm 0.0058 ^a	0.89
MF	EP	0.4654 \pm 0.0952	0.0234 \pm 0.0099 ^a	0.0446 \pm 0.0067 ^a	0.95
	AP	0.6164 \pm 0.0587	0.0020 \pm 0.0011 ^b	0.0735 \pm 0.0038 ^b	0.98
	DP	1.0254 \pm 0.1427	-0.0008 \pm 0.0030 ^b	0.0577 \pm 0.0054 ^a	0.92
PF	EP	0.1366 \pm 0.0734	0.1146 \pm 0.0181 ^a	0.0039 \pm 0.0049 ^a	0.94
	AP	0.3894 \pm 0.0957	0.0184 \pm 0.0081 ^b	0.0502 \pm 0.0109 ^b	0.89
	DP	0.5085 \pm 0.1000	0.0105 \pm 0.0044 ^b	0.0583 \pm 0.0087 ^b	0.91
Dry season					
BF	EP	-0.0262 \pm 0.1219	0.0820 \pm 0.0106 ^a	0.0217 \pm 0.0056 ^a	0.86
	AP	0.5738 \pm 0.0602	0.0219 \pm 0.0039 ^b	0.0385 \pm 0.0038 ^b	0.93
	DP	0.6766 \pm 0.0878	0.0200 \pm 0.0055 ^b	0.0393 \pm 0.0050 ^b	0.89
MF	EP	-0.0598 \pm 0.0460	0.0837 \pm 0.0045 ^a	0.0163 \pm 0.0025 ^a	0.98
	AP	0.7602 \pm 0.1319	0.0206 \pm 0.0084 ^b	0.0338 \pm 0.0070 ^b	0.87
	DP	0.9674 \pm 0.0498	0.0051 \pm 0.0025 ^b	0.0388 \pm 0.0028 ^b	0.95
PF	EP	-0.0075 \pm 0.0204	0.1435 \pm 0.0184 ^a	-0.0054 \pm 0.0115 ^a	0.56
	AP	0.0682 \pm 0.1236	0.0820 \pm 0.0204 ^b	0.0315 \pm 0.0119 ^b	0.81
	DP	0.2084 \pm 0.1628	0.0772 \pm 0.0154 ^b	0.0292 \pm 0.0129 ^b	0.75

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Table A1. Relationships of soil respiration rate (R , $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) and soil temperature at 5 cm depth (T , $^{\circ}\text{C}$) [exponential equation $R = R_0\exp(bT)$] (parameter estimate \pm 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 \pm 0.1056	0.0586 \pm 0.0064	0.87
	AP	0.6769 \pm 0.0858	0.0746 \pm 0.0053	0.95
	DP	1.1487 \pm 0.1505	0.0511 \pm 0.0054	0.88
MF	EP	0.6199 \pm 0.0831	0.0624 \pm 0.0056	0.91
	AP	0.6564 \pm 0.0612	0.0754 \pm 0.0039	0.97
	DP	1.0053 \pm 0.1214	0.0572 \pm 0.0050	0.92
PF	EP	0.8042 \pm 0.3401	0.0194 \pm 0.0169	0.08
	AP	0.4190 \pm 0.1448	0.0761 \pm 0.0136	0.73
	DP	0.5188 \pm 0.1358	0.0747 \pm 0.0103	0.82
Dry season				
BF	EP	1.3226 \pm 0.3562	0.0099 \pm 0.0148	0.02
	AP	0.8427 \pm 0.1134	0.0466 \pm 0.0077	0.70
	DP	0.9193 \pm 0.1141	0.0487 \pm 0.0071	0.75
MF	EP	1.3687 \pm 0.4183	0.0044 \pm 0.0181	0.01
	AP	0.9274 \pm 0.1178	0.0407 \pm 0.0073	0.67
	DP	1.0236 \pm 0.0474	0.0420 \pm 0.0076	0.74
PF	EP	1.2596 \pm 0.4563	-0.0226 \pm 0.0193	0.08
	AP	0.6577 \pm 0.3624	0.0473 \pm 0.0284	0.14
	DP	0.7624 \pm 0.3799	0.0484 \pm 0.0260	0.17

15692

Table A2. Relationships of soil respiration (R , $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) and soil moisture of the top 5 cm soil layer (M , % vol.) (linear regression equation $R = a + cM$) (parameter estimate \pm 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

15693

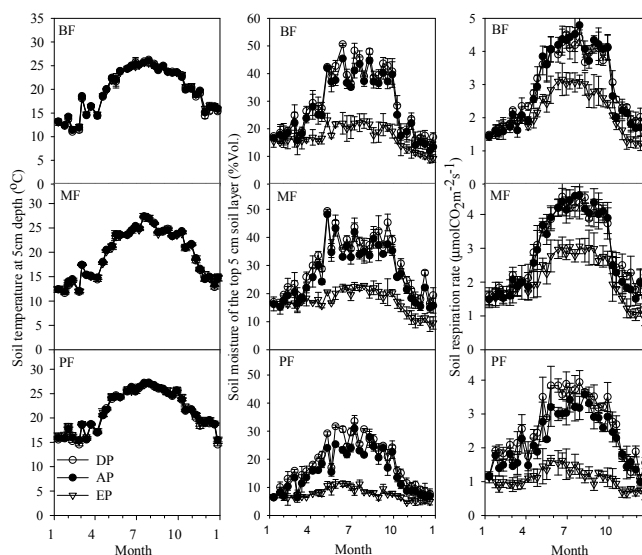


Fig. 1. Seasonal dynamics of soil temperature at 5 cm depth, soil moisture of the top 5 cm soil layer, and soil respiration rate under different precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests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

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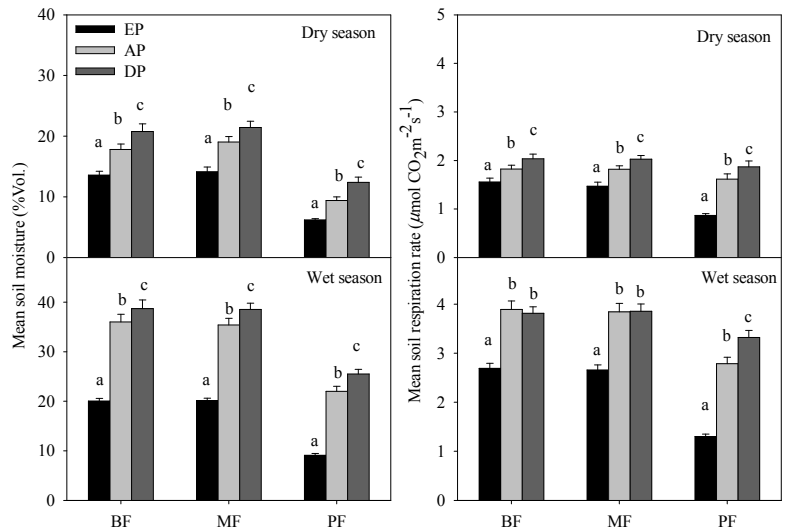


Fig. 2. Mean values of soil moisture and soil respiration rate in the dry season and in the wet season under different precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf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

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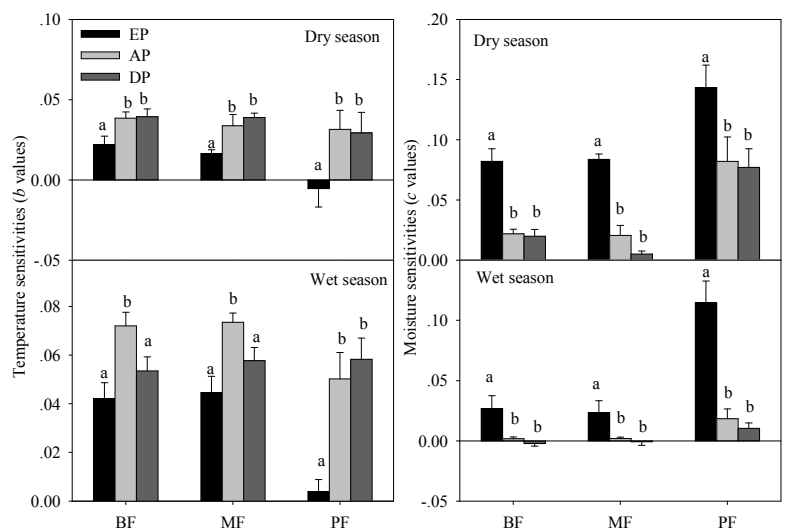


Fig. 3. Temperature and moisture sensitivities (*c* and *b* values) in the dry season and in the wet season under different precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf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

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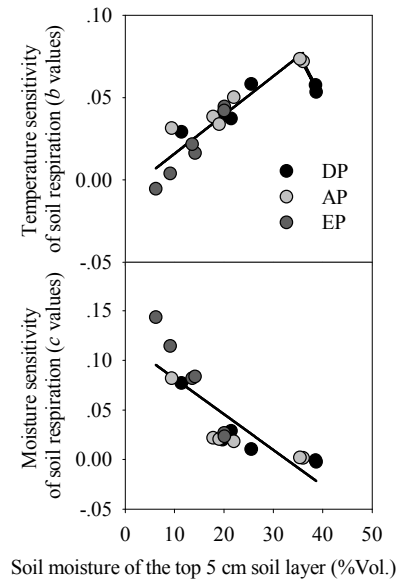


Fig. 4. Relationships of seasonal soil moistures at the DNR forests with moisture sensitivities (*c* values), and temperature sensitivities (*b* values), respectively. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. *c* and *b* values were listed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

15697

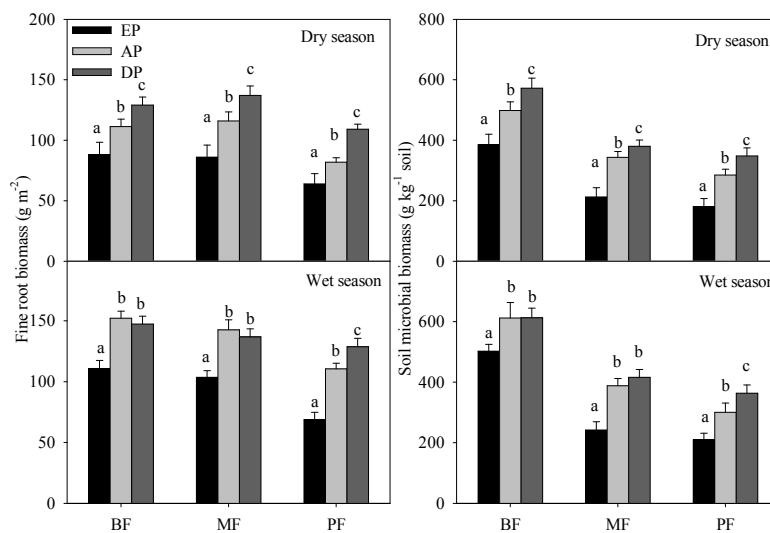


Fig. 5. Mean values of fine root biomass and soil microbial biomass in the dry season and in the wet season under different precipitation treatments at the DNR forests. The treatments are: EP = precipitation exclusion, AP = ambient precipitation, DP = double precipitation. The forests are: BF = broadleaf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

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