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Effects of precipitation on soil acid phosphatase activity in three successional forests in Southern China

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Abstract

Phosphorus (P) is often a limiting nutrient for plant growth in tropical and subtropical forests. Global climate change has led to alterations in precipitation in the recent years, which inevitably influences P cycling. Soil acid phosphatase plays a vital role in controlling P mineralization, and its activity reflects the capacity of P supply to ecosystems. In order to study the effects of precipitation on soil acid phosphatase activity, an experiment of precipitation treatments (no precipitation, natural precipitation and doubled precipitation) in three forests of early-, mid- and advanced-successional stages in Southern China was carried out. Results showed that driven by seasonality of precipitation, changes in soil acid phosphatase activities coincided with the seasonal climate pattern, with significantly higher values in the wet season than in the dry season. Soil acid phosphatase activities were closely linked to forest successional stages, with enhanced values in the later stages of forest succession. In the dry season, soil acid phosphatase activities in the three forests showed a rising trend with increasing precipitation treatments. In the wet season, no precipitation treatment depressed soil acid phosphatase activity, while doubled precipitation treatment exerted no positive effects on it, and even significantly lowered it in the advanced forest. These indicate the potential transformation rate of organic P might be more dependent on water in the dry season than in the wet season. The negative responses of soil acid phosphatase activity to precipitation suggest that P supply in subtropical ecosystems might be reduced if there was a drought in a whole year or more rainfall in the wet season in the future. NP, no precipitation; Control, natural precipitation; DP, double precipitation.

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1 Introduction

Phosphorus (P) limitation to forest primary productivity and other ecosystem processes is widespread in tropical forests (Attiwill and Adams, 1993). Apart from the weathering of parent material in soils, P input is reliant on the mineralization of soil organic matter.

5 Phosphatases, originating from fungi, bacteria and root exudates, catalyze the hydrolysis of ester bonds between phosphate and carbon compounds in organic substrates to enhance P availability to ecosystems (Turner and Haygarth, 2005). These enzymes therefore play an important role in maintaining and controlling the rate of P cycling in forest ecosystems. Of the phosphatases, acid phosphatase is predominant in forest
10 soils due to their pH optima (Juma and Tabatabai, 1988). Its activity can be considered as a good predictor of the organic P mineralization potential and biological activity of soils (Speir and Ross, 1978; Dick and Tabatabai, 1993; Krämer and Green, 2000). Acid phosphatase activity has been applied in several studies to evaluate P limitation in forest ecosystems (Schneider et al., 2001; Gress et al., 2007).

15 Acid phosphatase activity is correlated with the conditions of soil and vegetation (Ho, 1979; Herbien and Neal, 1990; Krämer and Green, 2000). It can be affected by changes of different related factors such as plant species (Ushio et al., 2010), litter quality (Conn and Dighton, 2000), carbon dioxide increase (Moscatelli et al., 2005), nitrogen (N) addition (Carreira et al., 2000; Wang, Q. K. et al., 2008), soil N availability
20 (Olander and Vitousek, 2000), soil P availability (Chen et al., 2003b) and soil temperature and moisture (Krämer and Green, 2000). However, fewer investigations describe the responses of acid phosphatase activity to changes in precipitation in forest ecosystems.

25 Climate changes to global precipitation (Houghton et al., 2001) have potential to greatly influence P cycling dynamics, since soil moisture is a key factor of controlling P availability in soils through several processes, including affecting mineralization processes, influencing P demand for plant growth and impacting microbial activity (Leiros et al., 1999; Raghothama, 1999; Grierson and Adams, 2000; Sardans et al., 2007). In

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season than that in the dry season; (2) soil acid phosphatase activity would be greater in the later stages of forest succession and exhibit different responses to precipitation treatments depending on forest types; (3) precipitation treatments would have different patterns of effects on soil acid phosphatase activity in the dry and wet seasons due to the uneven distribution of seasonal rainfall within a year.

2 Materials and methods

2.1 Site description

This study was carried out in the DBR ($23^{\circ}09'21''$ N– $23^{\circ}11'30''$ N, $112^{\circ}30'39''$ E– $112^{\circ}33'41''$ E), located in the central part of Guangdong province, South China. DBR is the first natural reserve in China with an area of 1133 ha. The reserve is characterized by a typical subtropical monsoon humid climate with an annual average relative humidity of 80%. The mean annual temperature is 21°C , with a minimum monthly average temperature at 12.6°C in January and a maximum one at 28°C in July. The annual average precipitation of 1927 mm has a distinct seasonal pattern, with about 80% of it falling from April to September (wet-warm season) and 20% occurring from October to March (dry-cool season). The bedrock is sandstone and shale. Soils are classified in the ultisol group and udult subgroup according to USDA soil classification system (Buol et al., 2003).

In the DBR, key vegetation types consist of MPF, MF and MEBF, and they represent a sequence of natural successional stages, from pioneer community (MPF), transition community (MF) to regional climax vegetation (MEBF). MPF, belonging to the first stage of the successional processes, occurs in the periphery of the reserve at an elevation of about 200 m. It was planted in the 1950s. The dominant species in MPF is *Pinus massoniana* Lamb. (Brown et al., 1995). The MF is distributed between the core area and periphery of the reserve at an elevation of about 200–300 m. It originated from MPF planted in the 1930s. Due to a gradual invasion of some pioneer broadleaf species

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through natural succession, the plant composition in MF had greatly changed. Dominant species in the canopy layer of MF are *P. massoniana*, *Schima superba* Gardn. et Champ, *Castanopsis chinensis* Hance, and *Craibiodendron scleranthum* var. *kwangtungense* (S. Y. Hu) Judd. If sufficient time was allowed, MF is believed to develop into

5 MEBF (Wang and Ma, 1982). MEBF is distributed in the core area of the reserve at an elevation varying from 200 to 300 m. It has been undisturbed for more than 400 years (Zhou, G. Y. et al., 2006). Major species in MEBF include *C. chinensis*, *Machilus chinensis* (Champ. ex Benth.) Hemsl., *S. superba*, *Cryptocarya chinensis* (Hance) Hemsl., *Syzygium rehderianum* Merr. et Perry in the canopy and sub-canopy layers.

10 2.2 Experiment design

The precipitation experiment was started within the three forests in December 2006. Three precipitation treatments consisted of no precipitation (NP), natural precipitation (control) and doubled precipitation (DP). Each treatment was replicated three times. In each forest, we selected the plots with similar slope aspect, slope degree, slope position

15 and community structure in order to minimize the heterogeneity among them. Each plot had a dimension of 3 m × 3 m, and the distance between plots was more than 1 m. Precipitation was intercepted in the NP plots using polyvinyl chloride (PVC) sheer roof and was redistributed to the DP plots (Borken et al., 2006; Zhou, X. H. et al., 2006). The control plot receiving natural precipitation was built beside these treatment plots.

20 Around each NP plot, the thick PVC plates were inserted into grounds at 15 cm deep to prevent surface runoff and lateral movement of water from the surrounding soil. The litter falling on precipitation interception roofs of NP plots was removed manually and periodically sprinkled on soils below the plates (Chen et al., 2010). Soil moisture of the top 5 cm soil layer, determined as volumetric soil water content (%), cm^3/cm^3 , was measured on five random locations within a plot using a PMKit (Tang et al., 2006) twice a month throughout the experiment.

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2.3 Soil sampling

We conducted soil sampling in February (the dry season) and June (the wet season) 2009. For each plot, we collected soil samples from 0–20 cm mineral soils after removal of the litter layer. Six soil cores (2.5 cm in diameter) were randomly taken and evenly combined to one sample in each plot. Soil samples were put in sealed plastic bags and immediately taken to the laboratory. Each sample was passed through a 2 mm sieve after removing roots, stones and other impurities. We divided each sample into two aliquots. One aliquot was air dried for analysis of related soil chemical properties. The other one was kept without drying at 4 °C until analysis of acid phosphatase activity was conducted. The measurement procedures of soil acid phosphatase activity were completed within 28 days.

2.4 Soil chemical properties and acid phosphatase activity measurements

Gravimetric soil moisture was determined from mass loss after drying for 24 h at 105 °C. Soil pH was measured in a deionized water suspension using glass electrodes at a ratio of 25 ml water to 10 g soil (Liu et al., 1996). Total carbon (C) was determined by dichromate oxidation before titration with a Fe^{2+} solution (Liu et al., 1996). Total N was measured by semimicro-Kjeldahl digestion followed by steam distillation and final titration of ammonium (Liu et al., 1996). Total P was determined colorimetrically after digestion (Liu et al., 1996). Available P was extracted with a solution containing 0.03 M NH_4F and 0.025 M HCl (Liu et al., 1996).

Soil acid phosphatase activity was measured using *para*-nitrophenyl phosphate (*p*-NPP) as an orthophosphate monoester analogue substrate. We used the method of Schneider et al. (2000) based on the original one of Tabatabai and Bremner (1969). We took 1 g of fresh soil (<2 mm) in a 100 ml Erlenmeyer flask, added 4 ml of modified universal buffer (pH 6.5) and 1 ml of 100 mM *p*-NPP substrate dissolved in the buffer, and swirled lightly the flask for a few seconds to mix the contents. The flask was then sealed and incubated at 30 °C for 30 min. After incubation, we immediately placed the

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flask on ice and then added 1 ml of 2 M CaCl_2 and 4 ml of 0.2 M NaOH to terminate the reaction and extract the *para*-nitrophenol (*p*-NP) formed. The sample was diluted with 90 ml of deionized water and then filtered through Whatman-42 filter paper. Absorbance of released *p*-NP was determined spectrophotometrically at 400 nm. Four replicates including one blank were used for each soil sample. For the blank, *p*-NPP was added after (instead of before) the incubation. The acid phosphatase activity was expressed as μmol *p*-NP per gram dry soil and incubation time (μmol *p*-NP $\text{g}^{-1} \text{h}^{-1}$).

2.5 Statistical analysis

Data analyses were carried out with SPSS 11.5 for windows. We applied the *T*-test for independent samples to analyze differences between the dry and wet seasons for soil moisture, soil chemical properties and soil acid phosphatase activity in the three forests. We used ANOVA followed by Tukey multiple comparison test to study: (1) the differences among the controls of three forests for soil moisture, soil chemical properties and soil acid phosphatase activity; (2) the effects of precipitation intensity on soil moisture, soil chemical properties and soil acid phosphatase activity among the treatments for each season separated. In addition, Pearson correlation coefficients were performed to show the relationships between soil chemical properties and acid phosphatase activity. For all statistical tests, we chose the probability level to reject the null hypothesis to be inferior or equal to 0.05 unless otherwise stated.

20 3 Results

3.1 Soil moisture

Soil was dry from October to March of the next year (the dry season) and became wet from April to September (the wet season) (Fig. 1), but the difference in soil moisture between the two seasons was significant only in MPF ($P < 0.01$). In controls, the

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3.3 Soil acid phosphatase activity

In all cases, the wet season showed significantly higher soil acid phosphatase activities than the dry season ($P < 0.01$). On average, the value of soil acid phosphatase activity in the wet season was 1.33 times greater than in the dry season. In the two seasons, the controls of MEBF and MF exhibited significantly higher soil acid phosphatase activities than that of MPF ($P < 0.01$ for both), and the difference between MEBF and MF was not significant. The mean values of soil acid phosphatase activity in the two seasons were $4.89 \mu\text{mol } p\text{-NP g}^{-1} \text{ h}^{-1}$ for MPF, $12.41 \mu\text{mol } p\text{-NP g}^{-1} \text{ h}^{-1}$ for MF and $12.29 \mu\text{mol } p\text{-NP g}^{-1} \text{ h}^{-1}$ for MEBF, respectively.

The responses of soil acid phosphatase activity to precipitation varied with seasons and forests (Fig. 2). In the dry season, increasing precipitation treatments exerted positive impacts on soil acid phosphatase activities in the three forests (Fig. 2a). For MPF, DP treatment significantly increased soil acid phosphatase activity when compared with NP treatment and control ($P < 0.01$ for both), and the difference between NP treatment and control was not significant. For MF, soil acid phosphatase activity in NP treatment was around 21% and 23% lower than control and DP treatment, respectively. As for MEBF, although the differences among treatments were not remarkable, soil acid phosphatase activity showed a positive response to increasing precipitation. The values were in this order: $8.70 \mu\text{mol } p\text{-NP g}^{-1} \text{ h}^{-1}$ for NP treatment $< 9.77 \mu\text{mol } p\text{-NP g}^{-1} \text{ h}^{-1}$ for control $< 10.54 \mu\text{mol } p\text{-NP g}^{-1} \text{ h}^{-1}$ for DP treatment. In the wet season, soil acid phosphatase activities were all significantly lowered by NP treatments in the three forests ($P < 0.01$ for all) (Fig. 2b). However, they were not stimulated by DP treatments in both MPF and MF, and it was even significantly depressed by DP treatment in MEBF. Among the three forests, the responses of soil acid phosphatase activity to precipitation treatments were the most pronounced in MEBF. The differences among the three treatments in MEBF all came up to significant levels.

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3.4 Relationships between soil chemical properties and soil acid phosphatase activity

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In the two seasons, soil acid phosphatase activity had a significantly negative correlation with soil pH, whereas it had significantly positive correlations with total C, total N and total P. A significantly negative relationship between soil acid phosphatase activity and available P was monitored in the wet season, while no obvious relationship between them was found in the dry season (Table 2).

4 Discussion

4.1 Soil acid phosphatase activity in the dry and wet seasons

Phosphatases are inducible enzymes regulated by end-product inhibition. Plant roots and microbes will increase the excretion of phosphatases into soils when available P dose not meet their demands (Goldstein et al., 1988). It is expected that soil acid phosphatase activity would be clearly greater in the wet season than in the dry season in our experiment, a seasonal pattern observed previously by Grierson and Adams (2000). Actually, in the wet season, plants grow fast, and microbial biomass is always high (Table 3) (Deng et al., 2011). This increasing enzyme activity would respond to meet the increasing P demand by plant and microbe growth in the wet season. Since heavy rain in the wet season often leads to nutrient loss, low available P detected in the wet season (Table 1) further intensifies the competition for P in ecosystems in the growing season. On the contrary, dry season is the least biologically active period. Moreover, soil available P was relatively high (Table 1) to meet the biological demands because of the accumulation of nutrients released from litter decomposition and low soil nutrient diffusion (Xia et al., 1997). The fact that a significantly negative correlation between soil acid phosphatase activity and available P was found only in the wet season but not in the dry season indicates that soil acid phosphatase activity is



more dependent on soil available P in the growing season than in the least biologically active season (dry season).

4.2 Effects of forest succession on soil acid phosphatase activity in the controls

- 5 The values of soil acid phosphatase activity in the three forests of DBR fell in the range observed in previous studies of other acidic forest soils (Pang and Kolenko, 1986; Schneider et al., 2000; Trasar-Cepeda et al., 2000; Dinesh et al., 2004). That MF and MEBF exhibited higher soil acid phosphatase activities than MPF indicates that soil acid phosphatase activity is correlated with forest succession. This evidence might also
10 reflect an enhanced biological P limitation in the later successional forests since soil acid phosphatase activity is a prevailing indicator of the degree in P limitation (Turner et al., 2002). This was partly supported by Mo et al. (2000), suggesting that P was possibly one of the factors limiting the plant productivity in the mature forest of the DBR.
- 15 The reason for the differences of soil acid phosphatase activity among the three forests could be explained by the distinction in soil nutrient status and vegetation conditions (Harrison, 1983; Ushio et al., 2010). Our results also showed that soil chemical properties had close relationships with soil acid phosphatase activity (Table 2), which was also partly confirmed by other studies (Schneider et al., 2000; Turner and Haygarth, 2005; Chen et al., 2003a, 2008), indicating that the better soil nutrient condition,
20 the higher soil acid phosphatase activity would be. In the DBR, soil nutrient condition in MF was comparable with that in MEBF despite their different successional stages, but they were both superior to that in MPF (Table 1). The results reinforce the idea that soil acid phosphatase activity is strongly dependent on forest types. With progressive forest succession (MPF→MF→MEBF), plant community developed from almost monospecific with only occasional broad-leaved tree species to rich and diversiform species. The biomass, litterfall production (Table 4) and litter decomposition rate (Mo et al., 2006), which were very important in balancing loss and removal of P from mineral

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soil by plant uptake and microbial activity (Chen et al., 2000, 2003a), exhibited an increasing tendency with progressive successional stages. The biomass of fine root and microbe (Table 3), associating with the production of soil acid phosphatase, were also enhanced with forest succession.

4.3 Effects of precipitation treatments on soil acid phosphatase activity

Phosphatases are involved in hydrolyzing organic P into inorganic P, and their activities are important in affecting soil P availability. In the dry season, our results showed that increasing precipitation treatments had positive effects on soil acid phosphatase activity, especially in MPF and MF. The increased soil acid phosphatase activity would facilitate the acquisition of available P to plant and mitigate P limitation. Zhou and Yan (2001) studying in this area stated that owing to moderate solar radiation input in dry season, plant growth potential still kept high and demanded for moderate water, but less rainfall in the season could not meet the need. Increased precipitation input, directly inducing the enhancement of soil moisture, was conducive to the release of organic P to ecosystems and, consequently, had an indirect benefit to plant growths. We observed that precipitation treatments did not affect total P (Table 1), and the available P was not correlated with soil acid phosphatase activity (Table 2). These results indicate that changes in soil acid phosphatase activity might be more dependent on soil moisture and less a consequence of an effect of changes in the substrate and end-production of soil phosphatase. Therefore, more rainfall occurring in this season would be helpful to promote forest productivity potential, especially for the early stages of forest succession.

However, the amount of water requirement varies with forest types. In MPF, our results showed that soil acid phosphatase activity was only greatly enhanced by DP treatment, demonstrating that water was a key limited factor in controlling the P cycling due to its own quite low soil moisture (Fig. 1). As a transition community MF, the evidence that soil acid phosphatase activity was only pronouncedly depressed by NP implies that water in MF is not as important as that in MPF because of its relatively high soil



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moisture. As a regional climax community MEBF, it had a wholesome self-regulating mechanism and a high capability of resisting outside interference, thus, precipitation treatments did not markedly influence soil acid phosphatase activity.

In the wet season, soil acid phosphatase activities in three forests exhibited different patterns in responses to precipitation treatments. That NP treatment had a clearly negative effect on soil acid phosphatase activity was consistent with the results reported in other literatures, representing that phosphatase activity was well correlated with soil water availability (Krämer and Green, 2000; Sardans and Penuelas, 2005, Sardans et al., 2008). The decrease in soil acid phosphatase activity produced by drought might result in a reduction of P supply to plants and further aggravate the pressure of P limitation in this region in the long time. Apart from the decrease in soil moisture, the increasing acidity of soil accompanied by the prolonged drought condition (Table 1) was the most probable mechanism involved in the reduction of soil acid phosphatase activity. Previous studies have reported that a low soil pH value could cause a reduction in soil microbial biomass (Baath et al., 1980; Wang, H. et al., 2008). This was confirmed by Deng et al. (2011), showing that soil microbial biomass was significantly depressed by NP treatments in the three forests (Table 3). A considerable risk of aluminum toxicity also likely appeared in a relatively low soil pH, which would inhibit plant root growth and nutrient absorption (Liu, 2000). These factors would greatly go against acid phosphatase since it is closely bound up with microbe, root growth and plant demand for P (Tarañdar and Claassen, 1988).

Nevertheless, in the wet season, no positive effects and even some negative effects of DP treatments on soil acid phosphatase activity were detected in the three forests. These indicate that water brought by natural rainfall is sufficient for plant growths because of large rainfall occurring in the wet season, and that more water has no competitive advantage under enhanced P demands in the growing season. The results also imply that some other factors become more important to impact soil acid phosphatase activity than water. High N content in the rainfall of this area was observed in previous studies (Zhou and Yan, 2001; Fang et al., 2008) resulting from the increasing industrial

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and agricultural activities. The fact that doubled rainfall brought about more available N input into ecosystems might account for the reduction of soil acid phosphatase activity, especially in MEBF. Excessive available N input would result in a nutrient imbalance, which is deleterious to microbial growth that requires balanced nutrient proportions (Kupperman, 1999), and eventually influence soil acid phosphatase activity. As for MEBF, Mo et al. (2006) stated that this forest was likely N saturated due to both long-term high atmospheric N deposition in this region (Zhou and Yan, 2001) and self-accumulation in the mature forest (Vitousek, 1982, 1984). Soil available N was relatively higher in MEBF than those in MPF and MF (Table 4). More N input produced by increased precipitation is detrimental to MEBF and, as a result, has a significant negative on soil acid phosphatase activity, which would further intensify P deficiency relative to the increasing N availability.

5 Conclusions

Driven by the seasonality of precipitation, soil acid phosphatase activities presented an obvious seasonal pattern, with high values in the wet season and low ones in the dry season, which corresponded to the most biological activity and lower soil available P in the growing season. Forest succession strongly influenced soil acid phosphatase activities, with the smallest values in MPF, followed by MF and MEBF. These suggest that soil acid phosphatase activity is closely related to forest types, and that the requirements for P by ecosystems might be enhanced in the later stages of forest succession. Our results also show that a reasonable distribution of water plays a critical role in controlling the rate of P cycling in subtropical forest soils. In the dry season, the results exhibited a tendency of increased soil acid phosphatase activities with elevating precipitation treatments in the three forests, which implies soil water content might be more important to relieve the stress of P limitation in this region. In the wet season, drought was adverse to soil acid phosphatase activities within the three forests, demonstrating that ecosystems would involve in further P limitation if there is a decrease in soil water

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content. However, DP treatments exerted little effects on soil acid phosphatase activity except for that in MEBF, showing clearly negative effects on it. These effects indicate that factors rather than water primarily might affect soil acid phosphatase activity in the growing season. The negative effects on soil acid phosphatase activity suggest that if drought throughout the year or more rainfall in the wet season happened in the further, P supply might be further decreased, and this would be detrimental to plant growth in the subtropical forests.

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Table 2. Pearson correlation coefficients between soil chemical properties and soil acid phosphatase activity at Dinghushan Biosphere Reserve.

		Pearson correlation coefficients				
Time		pH	Total C	Total N	Total P	Available P
Dry season	Soil acid phosphatase activity	−0.753*	0.851*	0.657*	0.584*	0.018
Wet season		−0.513*	0.567*	0.822*	0.686*	−0.731*

* Significant at $P < 0.01$.

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Time	Treatment	MPF	MF	MEBF
Dry season	NP	156c	175b	311b
	Control	279b	384a	451a
	DP	368a	411a	456a
Wet season	NP	287b	347c	483b
	Control	442a	527b	711a
	DP	542a	697a	705a

Data in the table cited from Deng et al. (2011).



Table 4. Relevant factors related to soil acid phosphatase activity in three forests of Dinghushan Biosphere Reserve. MPF, *Masson* pine forest; MF, coniferous and broad-leaved mixed forest; MEBF, monsoon evergreen broad-leaved forest.

Forest	MPF	MF	MEBF
Biomass (Mg C ha^{-1})	40.6	116.2	147.8
Litterfall production ($\text{g m}^{-2} \text{ year}^{-1}$)	356	861	849
Fine root biomass (Mg C ha^{-1})*	1.9	2.8	4.9
Soil available N (mg kg^{-1})	6.24	6.22	14.77

* Fine root biomass refers to root biomass in 0–20 cm depth of soils. Data in table cited from Fang et al. (2004), Peng and Zhang (1994), Tang et al. (2006), Wen et al. (1998), and Zhou et al. (2007).

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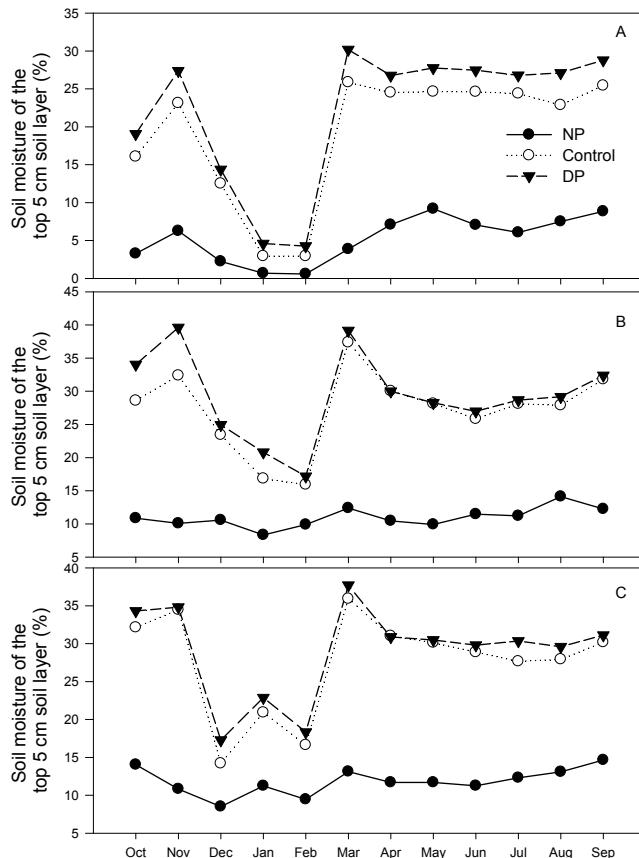


Fig. 1. Seasonal dynamics of soil moisture of the top 5 cm soil layer under different precipitation treatments from October 2008 to September 2009 in *Masson* pine forest (**A**), coniferous and broad-leaved mixed forest (**B**) and monsoon evergreen broad-leaved forest (**C**) of Dinghushan Biosphere Reserve. NP, no precipitation; Control, natural precipitation; DP, double precipitation.

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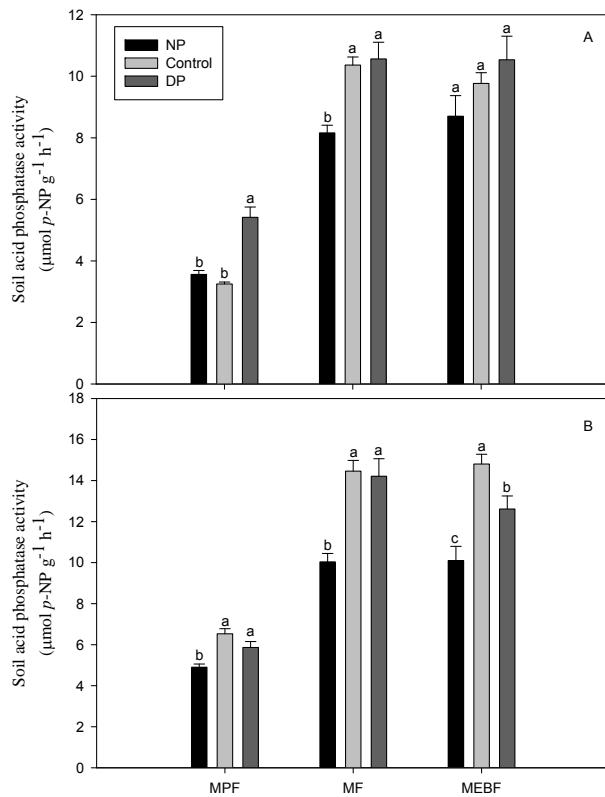


Fig. 2. Soil acid phosphatase activity in the dry (**A**) and wet (**B**) seasons under different precipitation treatments in 0–20 cm mineral soils of three forests at Dinghushan Biosphere Reserve. Error bars represent standard errors. Different lowercase letters denote significant differences between treatments at $P < 0.05$. MPF, *Masson* pine forest; MF, coniferous and broad-leaved mixed forest; MEBF, monsoon evergreen broad-leaved forest. NP, no precipitation; Control, natural precipitation; DP, double precipitation.

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