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RESEARCH ARTICLE

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Retention of available P in acid soils of tropical and subtropical evergreen broad-leaved forests

Abstract Precipitation of mineral phosphate is often recognized as a factor of limiting the availability of P in acidic soils of tropical and subtropical forests. For this paper, we studied the extractable P pools and their transformation rates in soils of a tropical evergreen forest at Xishuangbanna and a subtropical montane wet forest at the Ailao Mountains in order to understand the biogeochemical processes regulating P availability in acidic soils. The two forests differ in forest humus layer; it is deep in the Ailao forest while little is present in the Xishuangbanna forest. The extractable P pools by resin and sodium-bicarbonate decreased when soil organic carbon content was reduced. The lowest levels of extractable P pools occurred in the surface (0–10 cm) mineral soils of the Xishuangbanna forest. However, microbial P in the mineral soil of the Xishuangbanna forest was twice that in the Ailao forest. Potential rates of microbial P immobilization were greater than those of organic P mineralization in mineral soils for both forests. We suggest that microbial P immobilization plays an essential role in avoiding mineral P precipitation and retaining available P of plant in tropical acidic soils, whereas both floor mass accumulation and microbial P immobilization function benefit retaining plant available P in subtropical montane wet forests.

Keywords P microbial immobilization, P mineralization, P pools

1 Introduction

The available P by plant is commonly low in tropical and subtropical soils, which often limits ecosystem productivity in tropical forests. Orthophosphates in soil solution can react with the oxides and hydroxides of aluminum, iron and manganese to form water insoluble compounds when soil pH is $\leqslant 5$. This geochemical precipitation of plant available P can result in reduced rates of plant P absorption and eventually gross P mineralization (Chapin III et al., 2002). Soil microbes decompose organic P through excreting extracellular enzymes and immobilizing inorganic orthophosphates to avoid geochemical precipitation (Sun et al., 1993). Zou et al. (1995) demonstrated that this microbial P immobilization accounted for 23.2%–37.7% orthophosphates derived from both organic P mineralization and mineral P dissolution. Zhao and Lin (2001) showed that some microbes accumulate inorganic P in cells while mineralizing organic P. Microbes not only drive the mineralization of P, but also immobilize inorganic P to form an organic biomass of P or accumulate soluble inorganic P in their body fluids. Soil microbial biomass P serves as the most active P pool for plants (Mcgill and Cole, 1981; Brookes et al., 1984; Singh et al., 1989; Srivastava and Singh, 1991; Strivastava, 1992). Thus, soil microbial biomass of P and its cycling rates can impose a direct impact on forest ecosystem productivity (Vitousek and Farrington, 1997). With great potentials for mineral P precipitation in acidic tropical soils, the fact that tropical forests are among the most productive ecosystems on the planet suggests that microbial immobilization of soil solution orthophosphates may play a key role in retaining P for active biogeochemical cycling in tropical and subtropical forests (Olander and Vitousek, 2004, 2005).

Evergreen broad-leaved forests in tropical and subtropical montane areas often have acidic soils although they may differ in climate conditions and P transformation processes. Tropical soils often have thin humus layers on the soil surface due to the fast decomposition rates of organic materials under favorable climatic conditions. In contrast, soil humus layers can be relatively thick in subtropical montane forests due to the slower litter decomposition rates under the low temperature and dry conditions in winter and spring seasons. Among the factors controlling P biogeochemical transformations, such as climate conditions and plant species composition (Ou et al., 2005), the presence or absence of plant litter

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on the soil surface can also alter P biogeochemical cycling. For this paper, we compared P transformation processes in acidic soils from a tropical evergreen forest at Xishuangbanna and a subtropical montane wet evergreen broad-leaved forest at Ailao Mountains in Yunnan, China.

2 Materials and methods

2.1 Study area

The subtropical montane wet evergreen broad-leaved forest is located in Xujiabai (24°32′ N, 101°01′ E) of western Yunnan at an elevation of 2476 m. Annual mean precipitation is 1931 mm, annual mean temperature is 11.3°C (Zhang, 1983). July is the hottest month with a mean temperature of 15.6°C, while January is the coldest month with a mean temperature of 5.4°C. A pronounced wet-dry cycle divides the months into dry (from November to April) and wet (from May to October) periods. Annual mean relative air humidity reaches 86%. Tree density of the forest reaches 2,728 trees/hm^2, with a mean average height of 25 m and a mean diameter at breast height of 120 mm. Tree species are dominated by *Lithocarpus chintungensis*, *Rhododendron leptothrium*, *Vaccinium duclouxii*, *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Schima noronhae*, *Hartia sinensis*, *Manglietia insignis*, *Machilus viridis*, *Eriobtrya bengalensis*, *Lithocarpus hipovirides*, *Illiccium macranthum*, and *Ilex* sp. Understory vegetation is dominated by bamboo. Soil belongs to Alfisols with a pH of 5.0.

The tropical evergreen forest is located at Xishuangbanna (21°105′ N, 101°12′ E) with an elevation of 800–900 m. Mean annual precipitation is 1,557 mm, also with a strong wet–dry cycle (Shi and Zhu, 2003). Mean annual temperature reaches 21.5°C with the hottest month occurring in May (25.3°C) and the coldest month in January (15.5°C). Mean annual relative air humidity is 86%. Dominant tree species include *Castanopsis fleuryi*, *Aporusa yunnanensis*, *Schima wallichii*, *Castanopsis menkongensis*, *Lithocarpus truncates*, *Castanopsis argyrophylla*, *Castanopsis calathiformis*, *Wendlandia tinctoria*, *Engelhardtia roxburghiana*, *Cratoylon cochin-chinensis*, *Apodytes dimidiate*, *Linociera insignis*, *Millettia leptobotrya*, *Diospyros kaki* var. *sylvestris*, *Lithocarpus fenestratus*, *Syzygium* sp., *Ardisia* sp., *Olen rosea*, *Carcinia cowa*, *Glochidion lanceolarium*, and *Actinodaphne obovata.* Soil is Oxisols with a pH of 4.5.

2.2 Soil sampling

We took soil samples from the tropical evergreen forest and subtropical montane wet evergreen broad-leaved forest in August 2004. Five sampling sites were selected along a randomly located transect at 5 m intervals. At each sampling site, soil samples were taken from the humus horizon and 0–10 cm mineral layer. Humus horizon materials were collected from a 25 cm × 25 cm area and mineral soils were obtained with a soil corer of 5 cm in diameter. There were hardly any humus horizon materials for the tropical wet forest in Xishuangbanna, thus only mineral samples were obtained for the site. All samples were stored in zip-lock polyethylene bags at room temperature before being sieved (2 mm mesh size) and analyzed for labile P pools, potential P transformation rates, and acid phosphatase activities in the laboratory. Approximately 20 g of fresh soil from each sample were oven dried at 105°C for 24 h to determine field moisture content. All data are reported on an oven-dry soil basis.

2.3 Laboratory analyses

1) Resin-extractable effective inorganic P (P_i) (Zou et al., 1992, 1995): we weighed 1.75 g of field-moist soil into a 50 mL polyethylene bottle. A resin bag was placed into each bottle along with 30 mL of deionized water. Bottles were placed onto a shaker for 1 h at high speed. Resin bags and bottles were rinsed thoroughly with deionized water to remove soil particles. Resin bags were then extracted for 1 h with 30 mL of 0.5 mol/L HCl using the same bottles. The solution was then analyzed for resin-extractable P_i.

2) $NaHCO_3$-extractable P_i and organic P (P_o) (Srivastava, 1992; Zou et al., 1995): we followed the method of Bowman and Cole (1978) to estimate $NaHCO_3$-extractable P_i and P_o. We weighed 1.75 g of field-moist soil into a 50 mL polyethylene bottle. Each bottle received 30 mL of 0.5 mol/L $NaHCO_3$ (pH = 8.5). Bottles were shaken for 30 min at high speed. The extract was filtered and then analyzed for $NaHCO_3$-extractable P_i. A subsample (5 mL) of this filtrate was further oxidized with acidified ammonium persulfate before analysis for P concentration (U.S. Environmental Protection Agency, 1979; Zou, 1995). Differences in P concentrations between the oxidized and non-oxidized extracts give an estimate of $NaHCO_3$-extractable P_o.

3) Microbial biomass of P: we used the chloroform fumigation procedure to estimate the soil microbial biomass of P (Brookes et al., 1982). We weighed 10 g field-moist soil into a 100 mL polyethylene bottle. There were two subsamples: one was incubated in a chamber with water as a control, another was fumigated before incubation. Both were kept in incubators for 24 h before they were shaken with 40 mL Bray-1 solution on the a shaker for 30 min, then filtered. Filtrates were analyzed for the microbial biomass of P.

4) Potential transformation rates of P: the irradiation-autoclaving-incubation procedure of Zou et al. (1992, 1995) was used to examine potential transformation rates of P. Three treatments were applied to soil subsamples of 2.5 g fresh weight each: control, irradiation only, and irradiation plus autoclaving. We irradiated samples with ^{60}Co for a total of 30 kGy at room temperature (25°C). Soils of each subsample were then moved into a 150 mL flask. One of the irradiated subsamples was subsequently autoclaved (120°C, 2.12 MPa) for 5 min. Toluene (0.5 mL) was added to each of the irradiated and irradiated–autoclaved soils to maintain sterile conditions. Anion-exchange bags (each containing 1 g of

201 × 7 anion exchange resin in nylon netting) were added along with 50 mL of deionized water to each flask. All flasks were covered with pledget and then incubated on a shaker at a speed of 100 rev/min for 24 h. Resin bags were analyzed for P content as described above.

Irradiation and autoclaving treatments may affect resin-extractable P pools by releasing microbial P, but Zou et al. (1992, 1995) detected no significant effect of these treatments, thus the correction factors were taken as zero. P transformations were calculated using the following equations:

$$P_{\mathrm{gm}} = (P_{\mathrm{r}} - P_{\mathrm{ra}})/t$$

$$P_{\mathrm{im}} = (P_{\mathrm{r}} - P_{\mathrm{c}})/t$$

$$P_{\mathrm{ns}} = P_{\mathrm{ra}}/t$$

where P_c is the resin-extractable P (mg/kg soil) for the control samples, P_r for the irradiated samples, and P_{ra} for the irradiated and autoclaved samples; P_{gm} is gross P mineralization rate (mg/kg); P_{ns} is the net P solubilization rate; P_{im} is the microbial P immobilization rate; t is the incubation period in day (s) (in this study $t = 1$).

5) Phosphatase activity (Zhou, 1987): we weighed 1 g of field-moist soil into a 50 mL flask, 0.5 mL toluene was placed in the flask to restrain microbial growth, 15 min later, we added 10 mL acetate buffer with pH = 5.0. There were three subsamples, one was added with 10 mL water as the control, the other two subsamples were added with 10 mL 6.75 g/L disodium phenyl phosphate. All of the flasks were incubated at 37°C for 24 h. We then filtered the mixture in 100 mL flasks, and used spectrophotometry to analyze the content of hydroxybenzene at 578 nm. Phosphatase activity was shown as mg phenol/(g · day).

6) Preparation for anion exchange resin bags: equivalent to 1 g of 201 × 7 anion exchange resin (Experiment Factory of Yunnan Normal University, Kunming, China) in Cl^- form enclosed in nylon netting. P concentrations in resin extract solution were determined using the Barry colorimetric method in a spectrophotometer. P concentration was shown as mg/kg. Data were statistically analyzed by one-way ANOVA (SPSS 11.0).

3 Results

3.1 P pools

Labile P pools differed significantly between the two forests; resin-extractable P_i and $NaHCO_3$-extractable P_i and P_o were highest in humus materials of the Ailao forest, and lowest in surface mineral soils of the Xishuangbanna forest. Resin-extractable P_i and $NaHCO_3$-extractable P_i in humus materials of the Ailao forest was 6–7 times greater than that in the surface mineral soil of Ailao mountain, and more than ten times that of surface mineral soils from the Xishuangbanna forest. $NaHCO_3$-extractable P_o in humus materials of the Ailao forest was 2–3 times that of the mineral soils in the Ailao forest, and 6–7 times that of mineral soils from the Xishuangbanna forest. Microbial biomass P pool in mineral soils of the Xishuangbanna forest, which had the lowest soluble P_i pools, was twice greater than that of mineral soils from the Ailao forest. Ratios of microbial biomass P pools to soluble P_i pools were 1.2–13 in all forest soils (Fig. 1, Table 1).

3.2 Potential P transformation rates

P transformation rates were significantly different in the soils of the two forests. Humus materials of the Ailao forest had the higher rates. Rates of P_{ns} in mineral soils of the Ailao forest were higher than those in the mineral soils of the Xishuangbanna forest. Rate of P_{im} was higher than that of P_{gm} in both forests. In the mineral soils of the Ailao forest, rates of P_{ns} were higher than those of P_{gm}, and the opposite was seen in the humus materials of the Ailao forest and the mineral soils of the Xishuangbanna forest. Proportion of P_{im} flux to available P fluxes (net dissolution of mineral P and

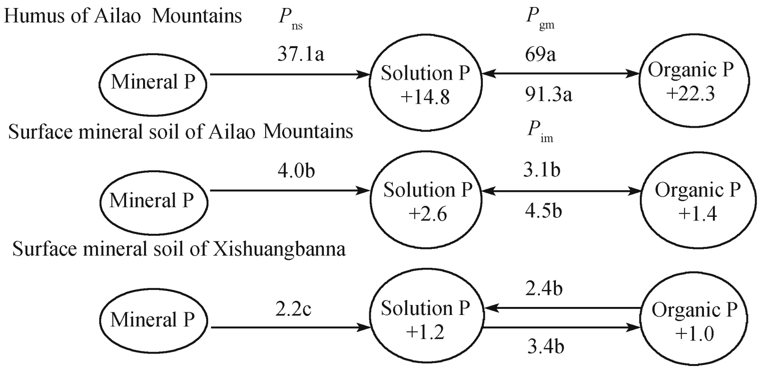

Fig. 1 Phosphorus transformations in humus and 0–10 cm mineral soil in forests of Ailao Mountains and Xishuangbanna: P_{ns} = net phosphorus solubilization rate, P_{gm} = gross phosphorus mineralization rate, P_{im} = microbial phosphorus immobilization rate; changes in solution $P = P_{ns} + P_{gm} - P_{im}$, changes in organic $P = P_{gm} - P_{im}$ (mg/(kg · day))
Note: different letters indicate significant difference among the three soil types ($\alpha = 0.05$).

Table 1 Soil P pools: resin-extractable inorganic P (P_i), NaHCO$_3$-extractable P_i and organic P (P_o), microbial biomass P (P_m) (unit: mg·kg^{-1})

Soil samples	Resin-extractable P_i	Microbial biomass P_m	NaHCO$_3$-extractable P	
			P_i	P_o
Humus of the Ailao Mountain forest	15.8(2.4)^a	180.9(12.7)^a	10.4(0.8)^a	130.3(13.9)^a
Surface mineral soil of the Ailao Mountain forest	2.4(0.1)^b	2.6(2.7)^c	2.4(0.5)^b	45.3(7.5)^b
Surface mineral soil of the Xishuangbanna forest	1.2(0.1)^c	5.2(5.5)^b	0.8(0.15)^c	20.1(1.9)^c

Standard errors are in the parentheses; letters showed the significant differences among the data ($\alpha = 0.05$).

mineralization of organic P) in mineral soils of the Xishuangbanna forest was 74%, higher than 63% of that for mineral soils of the Ailao forest. Potential turnover time of NaHCO$_3$-extractable organic P (P_o/P_{im}) was less than one day in two forest soils.

3.3 Activity of acid phosphatase

Acid phosphatase activities differed between the two soil layers in the Ailao forest and between the two forests. Phosphatase activity in humus materials of the Ailao forest was 47.4 mg phenol/(g·day), which was twice that of its surface mineral soil, four times that in the mineral soils of the Xishuangbanna forest (Fig. 2).

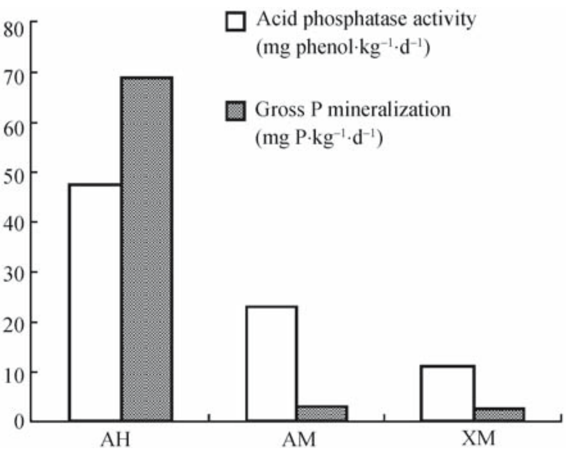

Fig. 2 Acid phosphatase activity and gross phosphorus mineralization rate in the Ailao Mountain and Xishuangbanna forest: AH, humus of the Ailao Mountain forest; AM, surface mineral soil of the Ailao Mountain forest; XM, surface mineral soil of the Xishuangbanna forest

4 Discussion

Mineralization of organic P in soil is the main resource of available P for plants in natural ecosystems. Orthophosphate in water solution has more than one fate; they can either be taken up by plants, immobilized by microbes, or precipitated with cations, oxides or hydroxides of aluminum and iron to form insoluble phosphate minerals. Greater potentials for microbial immobilization than organic P mineralization suggest a mechanism to retain plant-available P in soils. To the opposite, greater P mineralization than P immobilization may lead to net precipitation of orthophosphate, thus it is beneficial to reduce plant-available P levels in soils. In the Ailao forest, a large fraction of P was stored in the floor mass due to the slow decomposition of plant litter. Furthermore, potential rates of microbial P immobilization are greater than those of organic P mineralization. These two mechanisms function together to minimize the formation of insoluble inorganic P and retain plant available P in active pools. In the tropical forest of Xishuangbanna, microbial biomass P pool in the mineral soil was relatively high as compared with that in the Ailao forest and microbial P immobilization was also greater than organic P mineralization, but there was almost no existence of a humus layer. Percentage of P_{im} rates to P supply rates (net solubilization of mineral P plus mineralization of organic P) in the mineral soils of Xishuangbanna was 74%, higher than 63% in the mineral soils of the Ailao forest. Floor mass of the Ailao and Xishuangbanna forests were 34.71 t/hm^2 (Qiu and Xie, 1998) and 7.16 t/hm^{2*} respectively. Thus, high microbial biomass P and high rates of microbial immobilization both serve to retain plant available P in active pools and avoid massive P mineral precipitation in tropical Oxisols of Xishuangbanna.

Ailao forest soil is developed under mild temperature and moisture climate conditions. The pH values of humus and surface mineral soils were 4.5 and 4.2 respectively. Under the hot and moist climate conditions, the soils in Xishuangbanna forest were developed into Oxisols with soil pH of 4.5, and the processes of plant litter decomposition were rapid. There was almost no humus layer existing above the mineral soil. High soil pH suggests high P_{ns} rates in acidic soil with pH$<$5.5 (Chapin III et al., 2002). Although the pH value of Xishuangbanna surface mineral soil was higher than that of Ailao forest, P_{ns} was higher in the mineral soil of the Ailao forest than that in the Xishuangbanna forest (Fig. 1). This might be partially due to the lower total P content in the mineral soils of Xishuangbanna forest than that in the Ailao forest (Table 2). Furthermore, organic chelates might play an important role in enhancing P solubility (Zou et al., 1995). High content of organic matter in Ailao mineral soil could enhance mineral P solubilization through chelating the hydroxides and oxides of aluminum and iron.

Available P pools (resin-extractable P_i and NaHCO$_3$-extractable $P_{i(o)}$) in mineral soils of the Ailao forest were higher than those in mineral soils of the Xishuangbanna

Table 2 Soil physical and chemical properties in the Ailaoshan and Xishuangbanna evergreen broad-leaved forests of Yunnan, China

Soil samples	pH	Water content /%	Organic carbon $/(\mathrm{g\cdot kg^{-1}})$	Total N $/(\mathrm{g\cdot kg^{-1}})$	Total P $/(\mathrm{g\cdot kg^{-1}})$	Exchangeable cations			
						Na $/(\mathrm{mg\cdot kg^{-1}})$	K $/(\mathrm{mg\cdot kg^{-1}})$	Mg $/(\mathrm{mg\cdot kg^{-1}})$	Ca $/(\mathrm{mg\cdot kg^{-1}})$
Humus of the Ailao Mountain forest	4.5	72	304	18	1.18	0.25	0.96	2.45	5.43
Surface mineral soil of the Ailao Mountain forest	4.2	58	116	7	0.82	0.19	0.22	0.70	0.59
Surface mineral soil of the Xishuangbanna forest	4.5	50	68	1.6	0.26	0.13	0.18	0.25	0.64

forest. The available P pools in the humus materials of the Ailao forest were higher than those of mineral soils in both forests. These differences in extractable P pools suggest higher P availability in the Ailao forest than in the Xishuangbanna forest. However, forest productivity does not differ between the two forests (Zhang, 1983; Shi and Zhu, 2003). This coincided with the same P_{gm} rates between the two forests (Fig. 1), which suggests that P pool sizes alone cannot reflect P availability in acidic soils and that P_{gm} rates are better indices to reflect soil P availability than available P pools.

The altered soil pH in buffer solution for measuring acid phosphatase activity might have contributed to the lack of correlation between acid phosphatase activity and P_{gm} rates (Rojo et al., 1990; Antibus et al., 1992). Zou et al. (1995) thought that buffer $\mathrm{pH} = 5.0$ is unlikely to alter substantially the pattern of acid phosphatase activity in acidic soils. The absence of correlation between phosphatase activity and P_{gm} rates suggests that organic P mineralization is not limited by enzyme activity. Acid phosphatase activity in mineral soils of the Ailao forest was higher than that in the Xishuangbanna forest, but both mineral soils had almost the same P_{gm} rates (Fig. 2). In contrast, the high acid phosphatase activity coincided with the high P_{gm} rates in humus materials of the Ailao forest, suggesting a different mechanism that regulated the relationship between phosphatase activity and P_{gm} rates. Clay colloids were suggested to limit phosphatase activity (Zhao et al., 2003), and this limitation shall be even more pronounced in the Oxisols of the Xishuangbanna forest than the Alfisols of the Ailao forest. Thus, possible mechanisms for the lack of correlation between phosphatase activity and P_{gm} rates include: 1) the two forests differ in the quality and quantity of organic P, and high levels of microbial P in the Xishuangbanna mineral soil can elevate P_{gm} rates; 2) resins inhibited the formation of iron and aluminum phosphate (colloids) through the removal of orthophosphates in soil solution, resulting in an increased phosphatase activity during the incubation for obtaining P_{gm} rates; 3) soil solution and the mixing by shaker during the laboratory incubation promoted the inhibition of clay colloids to phosphatase activity as compared with its influence under field conditions where both orthophosphates and clay colloids are relatively immobile.

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