



Microbial P limitation in tropical forest soils could be overestimated: Insight from a sorption experiment and a meta-analysis

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ABSTRACT

The prevailing paradigm for soil microbial activity in tropical forests is that microbial activity is limited by phosphorus (P) availability, and thus exogenous P addition stimulates organic matter decomposition. This idea has been testified by studies demonstrating that experimental P addition accelerates soil respiration. Contrary to this conventional view, we hypothesize that the increased rates of soil microbial respiration could be due to the release of organic material from the surface of soil minerals when P is added, because P competes with organic C for binding sites in soil particles. Here we performed a sorption experiment in a tropical evergreen forest in southern China, where P addition had previously been reported to stimulate soil respiration but suppressed leaf litter decomposition. P addition to soils significantly increased dissolved organic carbon (DOC) content, which was extracted immediately after P addition and under a cold temperature where microbial activity was suppressed. This result can explain why P addition stimulated soil respiration but not litter decomposition in our study site. Namely, P addition abiotically elevated microbially-available C through the release of organic matter from the soil mineral surface. We also conducted a meta-analysis using data obtained in forest ecosystems, demonstrating that previous studies have consistently reported that P addition led to higher response ratios of soil microbial respiration than litter decomposition. Our findings suggest that the prevailing paradigm (i.e., soil microbial activity in tropical forests is limited by P availability) might require re-evaluation.

1. Introduction

In recent decades, nutrient inputs into ecosystems have been greatly altered by human activities (Gallardo and Schlesinger, 1994; Galloway et al., 2004). A complete understanding of nutrient limitation of soil microbial activity is essential for predicting global carbon (C) cycling as soil microbial activity plays an important role in the decomposition of C. Traditionally, soil microbial activity in tropical forests is considered to be limited by phosphorus (P) availability, and thus the addition of exogenous P stimulates organic matter decomposition. This traditional view has been justified by a number of studies which have demonstrated that the respiration rates of soil microbes increase with the experimental addition of P (Cleveland et al., 2002; Duah-Yentumi et al., 1998; Gnankambary et al., 2008; Ilstedt and Singh, 2005; Mori et al., 2013a, 2010b). These studies concluded that microbial activity in tropical forest

soils is P-limited.

However, Mori et al. (2018) suggested that the increased soil microbial respiration may be due to the release of organic matter from soil mineral surfaces, because P competes with organic C for binding sites on soil particles when added artificially (Guppy and Menzies, 2005; Kaiser and Zech, 1996; Ruttenberg and Sulak, 2011; Spohn et al., 2022; Spohn and Schleuss, 2019). The release of organic matter would increase the amount of resources available to soil microbes and stimulate microbial respiration (Cleveland et al., 2002). Thus, soil microbial activity may be predominantly C-limited, not P-limited (Mori et al., 2018; Spohn et al., 2022). If this is the case, the P-fertilization method that is commonly used to test microbial P-limitation would overestimate the impacts of P addition on the decomposition of soil organic matter, and thus the impacts of P addition on decomposition of soil organic matter associated with mineral soil may be larger than those on litter decomposition in the

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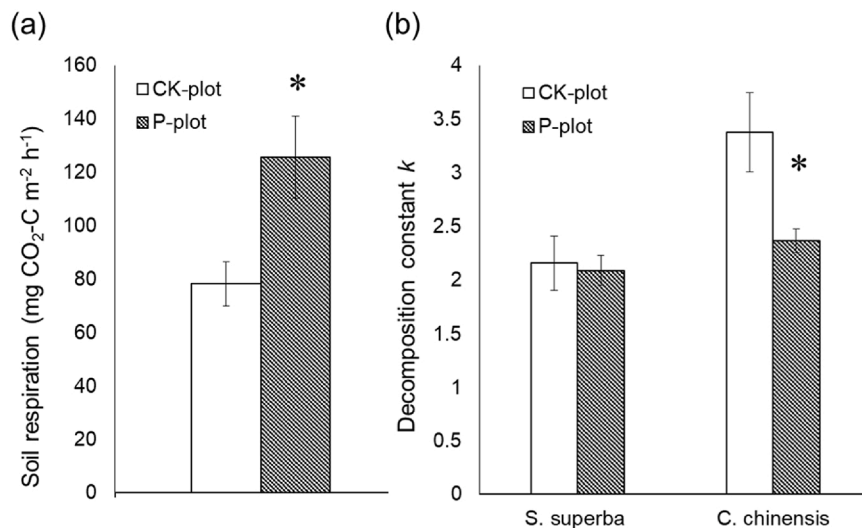


Fig. 1. Effects of phosphorus (P) fertilization in the field on (a) soil respiration (Liu et al., 2012) and (b) decomposition of litter from *Schima superba* Chardn. & Champ. and *Castanopsis chinensis* Hance (Chen et al., 2013). P fertilization increased soil respiration rates, but had negative or no effects on litter decomposition. Soil respiration rates were averaged over three months (July to September 2009). Decomposition rates (*k*) were determined by running a single negative exponential model on 18 months of decomposition data. Con-plot, control plot without P fertilization; P-plot, treatment plot fertilized with 150 kg P·ha⁻¹·yr⁻¹ since Feb. 2007. Error bars indicate standard errors (SE). * *P* < 0.05 (ANOVA). Additional details can be found in Liu et al. (2012) and Chen et al. (2013).

organic layer of soil. Indeed, most of the studies reported stimulatory effects of P addition on soil microbial respiration in tropical ecosystems (Cleveland et al., 2002; Galicia and Garcia-Oliva, 2004; Mori et al., 2013b, 2013c), whereas studies on litter decomposition reported that P addition had neutral (Barantal et al., 2012; Cleveland et al., 2006; Davidson et al., 2004; McGroddy et al., 2004) or negative effects (Chen et al., 2013; Mori et al., 2015; Zheng et al., 2017).

Our earlier work also revealed that experimental P addition stimulated soil respiration in the field (Liu et al., 2012; Fig. 1) and suppressed leaf litter decomposition (Chen et al., 2013; Fig. 1). As discussed above, the difference in the impacts may be due to the abiotic increase in C availability following experimental P addition (Mori et al., 2018; Spohn et al., 2022), which might have a greater impact in mineral soil layers than in the organic layer since there are no minerals. In this study, we investigated whether P addition desorbs organic C from solid soil particles in the same tropical forest where we conducted previous work (Chen et al., 2013; Liu et al., 2012; Fig. 1). We also conducted a meta-analysis on the impacts of P fertilization on the decomposition of soil organic matter and litter. We hypothesized that the response ratio of soil microbial respiration to experimental P addition would be larger than that of litter decomposition.

2. Materials and methods

2.1. Site description

Our study was carried out in an old-growth monsoonal primary forest dominated by evergreen broadleaf trees, located in the Dinghushan Biosphere Reserve in the middle of Guangdong Province, southern China (112°10'E, 23°10'N). This region experiences a subtropical monsoon climate, and the soil consists of lateritic red earth (oxisols) formed from sandstone (Mo et al., 2003). The mean annual precipitation is 1927 mm; 75% of the rainfall occurs from March to August and only 6% occurs from December to February (Huang and Fan, 1982). The mean annual temperature is 21.0 °C; July is the warmest month (28.0 °C), and January is the coldest month (12.6 °C). Results from ¹⁴C analysis revealed that this forest has not been anthropogenically disturbed for 400 years (Shen et al., 1999). The dominant tree species in this forest are *Castanopsis chinensis*, *Schima superba*, *Cryptocarya chinensis* (Hance) Hemsl., *Cryptocarya concinna*, *Machilus chinensis* (Champ. Ex Benth.) Hemsl., and *Syzygium rehderianum* Merr. & Perry, whereas the understorey is dominated by *Calamus rhabdclidus* Burret, *Ardisia quinquegona* Bl., and *Hemigramma decurrens* (Hook.) Copel (Mo et al., 2003; Zhou et al., 2018). The characteristics of the study site are

Table 1
Characteristics of the study site.

Soil water pH	3.98 (0.02)
Soil organic matter (%)	7.3 (0.8)
Total N (mg g ⁻¹)	1.99 (0.18)
Total P (mg g ⁻¹)	0.49 (0.03)
Available P (mg kg ⁻¹)	2.2 (0.5)
Soil moisture (%)	22.6 (1.1)
Soil temperature (°C)	21.8 (0.36)
Stem density (tree ha ⁻²)	2267
Tree basal area (m ² ha ⁻²)	24.8

The site was previously surveyed in Feb. 2007. All data are from Liu et al. (2012). Values are expressed as means with standard errors in parentheses (n = 5). N, nitrogen; P, phosphorous.

summarized in Table 1.

2.2. Long-term fertilization experiment

A long-term P fertilization experiment was initiated in 2007 (Liu et al., 2012), and five treatment (P-plot) and five control (Con-plot) plots were established. Each plot had an area of 5 × 5 m and was separated from other plots by 5 m buffer strips. Monosodium phosphate (NaH₂PO₄) solution (15 g P·m⁻²·yr⁻¹) mixed with 5 L of water was sprayed below the tree canopy using a backpack sprayer to add P to the treatment plots (Liu et al., 2012). Our experimental design, including plot size and fertilizer dosage, were in the same range of the protocol of a similar fertilization experiment in Costa Rica (Cleveland and Townsend, 2006). In 2016, we established four new Con-plots, where the possibility of fertilizer contamination was completely ruled out. This was done because four of the five old Con-plots were suspected to be slightly contaminated by fertilization. These new Con-plots were established in a row next to the old plots.

2.3. Soil and dissolved organic matter sampling

Surface soil samples (0–10 cm) were collected in October 2016, after removing the organic layer. We took six soil cores (3-cm inner diameter) from each of five Con-plots (four new plots and one old plot). In each plot the six cores were combined into a single composite sample, roots were removed and soil passed through a 2-mm mesh sieve and mixed well. Leaf litter was collected from the unfertilized area to extract dissolved organic matter (DOM). We mixed 150 g of litter with 1500 mL deionized water for 24 h, and extracted DOM by filtering the mixture through a 0.45-μm membrane filter (Merida, USA). The DOM contained

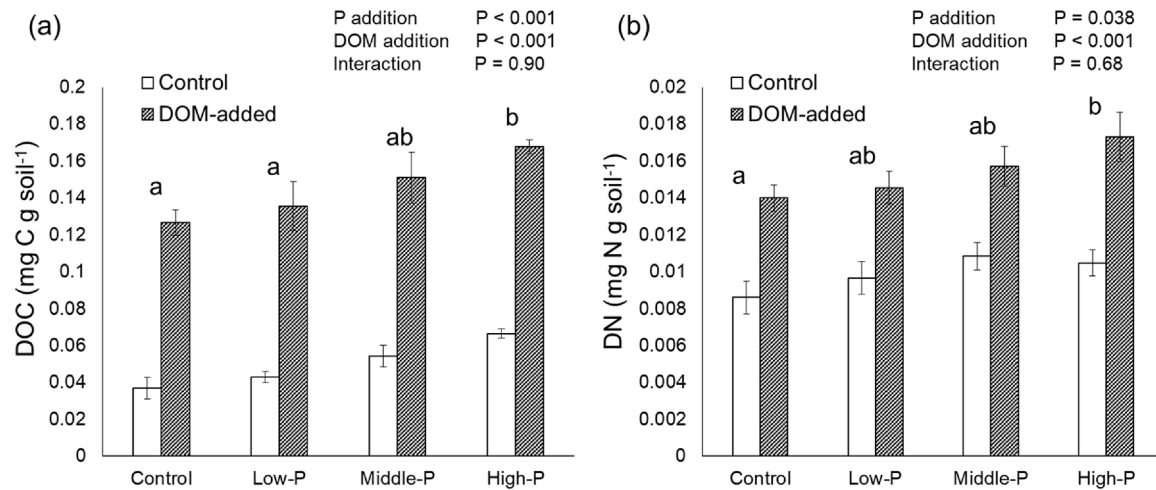


Fig. 2. Effects of phosphorus (P) addition on water-extracted (a) dissolved organic carbon (DOC) and (b) dissolved nitrogen (DN) in the presence and absence of additional dissolved organic matter (DOM). The *P*-values from two-way ANOVA are listed for each treatment. Different lowercase letters represent significant differences among P-fertilization treatments ($P < 0.05$, Tukey's post-hoc test). Error bars indicate SE.

327.6 mg C per L and 19.83 mg N per L.

2.4. Sorption experiment

We tested the effect of P addition on water-extracted DOC contents in the soil from the Con-plots with and without additional DOM. Five g of soil (oven-dry equivalent) was shaken with monopotassium phosphate (KH_2PO_4 ; 0, 20, 100, or 500 $\mu\text{g P g soil}^{-1}$) and DOM (0 or 3 ML) for 10 min in a designated section of the experimental room surrounded by glass walls and maintained at its maximum cooling capacity using an air conditioner. Subsequently, the soil sample was promptly subjected to centrifugation immediately after the end of the shaking. During the waiting time for the centrifugation, samples were put in a refrigerator at 4 °C to prevent microbial decomposition (note that not all tubes can be centrifuged at the same time). Subsequently, samples were filtered through 0.45- μm membrane filters immediately after the end of the centrifugation. Since microbial activity continues at temperatures as low as 4 degrees (Pietikäinen et al., 2005), the filtration was done immediately. The filtration process took 11 h in total due to the relatively long filtering time for each sample, which may have resulted in some DOM decomposition even at 4 degrees. Nevertheless, we believe that even in the event of decomposition at 4 degrees, the rates of decomposition should be higher in the DOM extracted from P-added soils compared to the P-unamended control. Consequently, under these circumstances, the obtained results offer a more robust validation of our hypothesis, which posits that DOM contents extracted from P-added soils should demonstrate higher values. Since P addition slightly decreased soil pH (\pm standard error) from 3.84 ± 0.03 – 3.66 ± 0.06 (measured using 5 g fresh soil samples taken from five old Con-plots in 2020 with and without KH_2PO_4 (500 $\mu\text{g P per g fresh soil}$)), our result could be partly due to changes in soil pH.

2.5. Statistics

The impacts of P fertilization on DOC and DN contents were tested by analysis of variance (ANOVA), assuming a normal distribution of the model residuals. R version 3.4.4 was used for every statistical analysis (R Core Team, 2018). ANOVA and multiple comparisons were performed using the *aov* and *TukeyHSD* functions, respectively.

2.6. Meta-analysis

On May 21, 2023, we collected publications reporting the impact of P

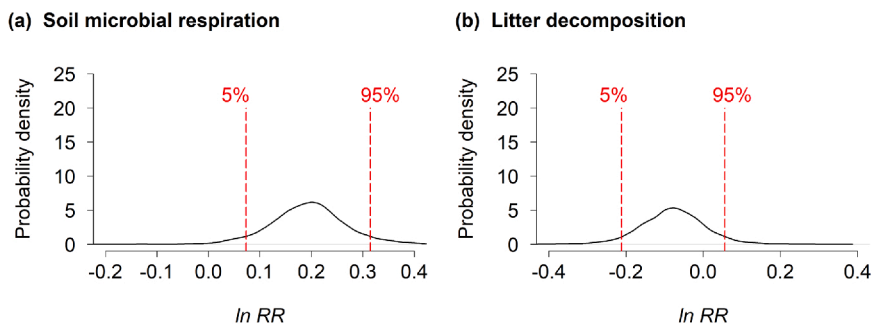
fertilization on the decomposition of both litter and soil organic matter at the same study site. Literature was searched by using Web of Science with the combination of the following key words: ("microbial respiration" OR "heterotrophic soil respiration" OR "soil organic matter decomposition" OR "decomposition of soil organic matter" OR "SOM decomposition" OR "decomposition of SOM") AND ("litter bag" OR "litter decomposition") AND ("phosph* add*" OR "P add*" OR "phosph* elevat*" OR "P elevat*" OR "phosph* fertiliz*" OR "P fertiliz*" OR "phosph* appl*" OR "P appl*" OR "phosph* enrich*" OR "P enrich*"). The literature search was complemented using other search engines such as Google and Google Scholar. We set the following criteria for data collection. (i) Studies conducted in streams, wetlands, or mangroves were not included, as the focus was on terrestrial ecosystems without submerged environments. (ii) Studies with field measurements of soil respiration data were excluded, as increased litter production (Liu et al., 2012) and the stimulatory effect of P fertilization on root respiration (Mori et al., 2013c) can overestimate the organic matter decomposition in P-fertilized soil. (iii) Studies on the effects of simultaneous additions of C and P on microbial respiration were excluded, because we are unable to separate the P effects on CO_2 emissions derived from added C and those derived from the decomposition of soil organic matter (Nottingham et al., 2015). (iv) Data on soil microbial respiration from incubation experiments using soil taken from P-fertilized and unfertilized sites were excluded, because organic matter content could have been affected by fertilization in the field and different at the beginning of the incubation study (for example, organic matter in P-fertilized soils is already decomposed quickly, and thus contains less amount of organic matter at the beginning of incubation). (v) Experiments that mixed soil and litter were excluded. If data were only reported in figures, the means were extracted using DataThief (<https://datathief.org/>). For studies with multiple sampling dates, we considered this repetition to be dependent (Mori, 2017), and only used the measurements corresponding to the latest sampling period. If multiple experiments performed in different sites were reported by one article, each of them was considered as an independent study.

The response ratio (RR) of soil microbial respiration or litter decomposition was calculated as follows:

$$\text{RR of soil microbial respiration} = \text{SR}_p / \text{SR}_c \quad (1)$$

$$\text{RR of litter decomposition} = \text{ML}_p / \text{ML}_c \quad (2)$$

where SR_p is the rate of soil microbial respiration in soil with added P, SR_c is rate of soil microbial respiration in control soil, ML_p is litter mass loss (ratio) (or carbon dioxide [CO_2] emissions during decomposition)



decomposition.

when P is added, and ML_c is litter mass loss when no P is added (control).

We calculated the probability distribution of natural log-transformed response ratios ($lnRR$) of both soil microbial respiration and litter decomposition in the framework of Bayesian statistics, with uniform priors and the collected literature data, assuming normal distribution of $lnRR$. The Hamiltonian Monte Carlo algorithm implemented in RStan (Stan Development Team 2020; ver. 2.21.0) was used. Following Mori et al. (2022), the default setting with 2000 iterations was used for the calculation. If the 5th to 95th percentiles of the posterior distribution do not contain zero, the $lnRR$ was evaluated as significantly different from zero. R ver. 4.1.1 (R Core Team, 2021) with the “rstan” library was used for the analysis.

3. Results and discussion

The sorption experiment demonstrated that P addition abiotically elevated the availability of C and N. P addition to the soil in Con-plots significantly increased DOC and DN content (Fig. 2) which were extracted immediately after P addition under cool temperatures where microbial activity was suppressed. This result indicated that P addition could potentially explain stimulated soil respiration previously reported in these soils (Liu et al., 2012). Namely, stimulated soil respiration in our previous study (Liu et al., 2012) could be observed because P addition abiotically elevated C availability via detachment of organic matter from soil mineral surfaces. This hypothetical mechanism can also explain the contradictory results of our earlier work, i.e., P fertilization stimulated soil respiration but suppressed (or had no effects on) leaf litter decomposition (Fig. 1), better than the conventional explanation, because if the soil microbes were P-limited as the prevailing paradigm suggests, P fertilization would increase both soil respiration and litter decomposition rates. Recently, Spohn and Schleuss (2019) demonstrated that inorganic P detached organic compounds from mineral soils and accelerated the respiration of soil microbes even in P-rich soils. It strongly supported our idea, because in the P-rich soils, it was unlikely that the added P accelerated soil microbial respiration through alleviating the P-shortage of soil microbes. Thus, we suggest that the abiotic elevation of C availability specifically occurring in soils could have caused the contrast effects of P fertilization on soil respiration (Liu et al., 2012) and litter decomposition (Chen et al., 2013) in our study site (or the abiotic increase in C availability following experimental P addition could be greater in soils than in litter layers without mineral soils). Our hypothesis may be confirmed by additional works such as multiple-regression analysis testing whether the increase of P availability or release of DOC better explains stimulation of soil microbial respiration. Nevertheless, it should be noted that the stimulated soil respiration in our study site (Fig. 1a) may be partly explained by increased litter production (Liu et al., 2012), which elevates C substrates, and stimulated root respiration rates, which were reported to contribute to stimulated soil respiration by P fertilization (Mori et al., 2013c).

Fig. 3. Posterior distribution of natural log-transformed response ratios ($lnRR$) of (a) soil microbial respiration and (b) litter decomposition in the framework of Bayesian statistics. Uniform priors and data from ten study sites were used: three tropical montane forests in Hawaii reported by Hobbie and Vitousek (2000) and Reed et al. (2011), a tropical rain forest in Costa Rica reported by Cleveland et al. (2006, 2002), a tropical tree plantation in Indonesia reported by Mori et al. (2010a, 2015), two tropical tree plantations in Thailand reported by Mori et al. (2016, 2023), a birch forest in northern Sweden reported by Hartley et al. (2010), and two European beech forests reported by Spohn and Schleuss (2019). The 5–95th percentile posterior distribution of $lnRR$ of soil microbial respiration did not overlap with those of litter

The meta-analysis also supported our hypothesis, by demonstrating that other studies have also reported that P fertilization had contrasting effects on soil microbial respiration and litter decomposition (Fig. 3). The 5–100th percentile posterior distribution of $lnRR$ of soil microbial respiration were larger than zero, indicating that P fertilization stimulated soil respiration (Fig. 3a). On the other hand, P fertilization was not observed to influence litter decomposition rates, as indicated by the 5–95th percentile posterior distribution of $lnRR$ of litter decomposition overlapping with zero (Fig. 3b). Furthermore, the 5–95th percentile posterior distribution of $lnRR$ of soil microbial respiration did not overlap with those of litter decomposition, indicating that the impact of P fertilization on soil microbial respiration was larger than that on litter decomposition. Thus, the contrasting response of soil microbial respiration and litter decomposition to P addition may be a common phenomenon.

In conclusion, together with the previous studies, we suggest that the impact of P addition on soil microbial respiration may be overestimated, through the abiotic elevation of C availability by P addition. Our findings suggest that the prevailing paradigm that soil microbial activity in tropical forests is limited by P availability might require re-evaluation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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