Testing potassium limitation on soil microbial activity in a sub-tropical forest

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Abstract Because potassium (K) is a rock-derived essential element that can be depleted in highly-weathered tropical soils, K availability may limit some portion of soil microbial activity in tropical forest ecosystems. In this paper we tested if K limits microbial activity in the condition of sufficient labile C supply. An incubation experiment was performed using surface soil samples (0–10 cm depth) obtained from four permanent ecological research plots in a natural sub-tropical forest in southern China. Soil samples were taken in September 2016. Heterotrophic soil

respiration rates and microbial biomass were measured after the addition of glucose (both D and L) with and without K (potassium chloride). We did not observe any effects of K addition on soil microbial respiration, suggesting that K does not limit the microbial activity in the condition of sufficient labile C supply. The lack of microbial response to added K can be attributed to the high mobility of K in forest ecosystems, which may have provided sufficient K to microbes in our soil samples (already provided at the beginning of the incubation). However, at the present stage, we cannot conclude that K is not a limiting factor of soil microbial activity in other tropical forest ecosystems because of the heterogeneity of tropical forest ecosystems and few observations. The hypothesis needs to be tested in larger numbers of tropical forests.

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Introduction

For understanding ecosystem dynamics, it is essential to determine nutrients that limit biological processes, including soil microbial activity. Traditionally, in tropical forest ecosystems, soil microbial activity has been considered to be limited by P availability. This idea is based on several experimental results that P addition stimulated soil microbial respiration (Cleveland et al. 2002; Ilstedt and Singh 2005; Mori et al. 2010) and increased microbial biomass (Liu et al. 2012; Turner and Wright 2014). The low P availability in tropical soils due to deep weathering, chemical binds with aluminum (Al) and iron (Fe), and physico-chemical adsorption to Al and Fe (hydr) oxides (Cross and Schlesinger 1995) can explain the P shortage

for microbial activities in tropical soils (but see a review by Mori et al. 2018).

However, soil microbial activity in tropical forest soils may be limited not only by P but also by other nutrients. Recently, the traditional view of single-nutrient limitation is under re-consideration (Elser et al. 2007). Several studies suggested that biotic processes such as primary production may be co-limited by multiple nutrients (Davidson et al. 2007; Saito et al. 2008; Harpole et al. 2011; Bracken et al. 2015), especially in the community levels where several different kinds of species co-exist (Arrigo 2005; Danger et al. 2008). This can be also true in case of soil microbial activity. Different groups of microbes can be limited by different nutrients. Also, additions of different nutrients can alter microbial communities in different ways. In a nutrient-poor environment, native species are adapted to the situation. If additional nutrient was supplied, the originally-dominant species would be replaced by others which are better competitors in the new situation (Xun et al. 2015). Thus, it is plausible to hypothesize that multiple nutrients limit soil microbial activity. Nevertheless, few researchers have tested nutrient limitations on soil microbial activity in tropical forests, except for limitations of nitrogen (N) (Ilstedt and Singh 2005; Cleveland and Townsend 2006; Teklay et al. 2006; Gnakambary et al. 2008) and P (Cleveland et al. 2002; Ilstedt and Singh 2005; Cleveland and Townsend 2006; Liu et al. 2012; Mori et al. 2013b, 2016c, 2017) (but see a recent criticism by Mori et al. 2018).

Potassium (K), which is a major intracellular cation in all kinds of organisms including bacteria and fungi (Brown 1964; Weed et al. 1969), is a candidate to (co-)limit soil microbial activity in tropical forests, because K is an essential rock derived element that can be depleted in deeply-weathered tropical soils. The importance of K for primary production in tropical forests was reported by Wright et al. (2011) and Santiago et al. (2012), who demonstrated that K addition reduced fine-root biomass at the community level, reduced allocation to roots in seedlings, and increased seedling height growth rates in a Panamanian tropical forest. The stimulatory effects of K addition on plant growth were also reported in various types of ecosystems (see a review by Tripler et al. 2006). The role of K on litter decomposition was also tested in tropical forests (Kaspari et al. 2008; Powers and Salute 2011). Kaspari et al. (2008) demonstrated that decomposition of cellulose (filter paper) was stimulated by K addition in a Panamanian tropical forest, although effects through soil fauna were also included in the result. Meanwhile, litter decomposition was not affected by K addition either in the field (Kaspari et al. 2008) or the laboratory (Powers and Salute 2011). To our knowledge,

direct tests on the response of soil microbial activity to K addition are still rare.

Turner and Wright (2014) reported P addition but not K addition increased microbial biomass C in a tropical lowland forest in Panama. They suggested that microbial biomass was limited by P, and that K was less important in the forest. However, to understand whether K limits microbial activity, it is essential to test the effects of K addition on microbial respiration, not only on microbial biomass. Recent review suggested that the response of soil microbial biomass to nutrient addition cannot necessarily identify a limiting nutrient (Mori et al. 2018). This is because standing microbial biomass is not always an indicator of microbial activity. For example, boreal and temperate forest soils have much larger amount of microbial biomass compared with tropical forest soils, where microbial activity is higher (Xu et al. 2013). In mountain ecosystems, soils at higher elevations support greater microbial biomass than do lower areas (Wagai et al. 2011). These facts indicate that a higher microbial activity, which leads to a quicker soil organic matter decomposition, can result in less standing microbial biomass. Therefore only measuring microbial biomass might incorrectly identify the limiting nutrients of soil microbial activity. Indeed, Mori et al. (2016b) demonstrated that soil respiration and microbial biomass responded in contrasting ways to exogenous nutrient addition.

We conducted an incubation experiment to examine the effects of K addition on soil microbial respiration as well as soil microbial biomass. According to the copiotrophic hypothesis (Ramirez et al. 2012), nutrient addition can reduce soil microbial respiration by suppressing recalcitrant organic matter decomposition because of the microbial community shift from more oligotrophic to more copiotrophic conditions. In our experiment, labile C was simultaneously added to provide sufficient C and to reduce the impacts of nutrient addition on any microbial community shift and accompanying changes in recalcitrant C decomposition. Although the addition of a limiting nutrient can suppress organic matter decomposition by reducing microbial mining of the limiting nutrient from organic matter (Craine et al. 2007), this is not a case for K because K does not combine with organic C. Thus, our incubation experiment with and without K addition provided us an opportunity to test whether K limits microbial activity in the condition of sufficient labile C supply.

Materials and methods

Study site and soil sampling

The experiment was conducted at a research site in the Shimentai National Nature Reserve (24°22′–24°31′N, 113°05′–113°31′E), Guangdong Province, southern China. The climate is subtropical monsoon with wet and dry seasons. Mean temperature is 20.8 °C and mean annual rainfall is 1700 mm (Shi et al. 2016). The vegetation type at the study site was broadleaved evergreen forest that was around 50 years old at the time of the study. The dominant canopy tree species were *Cryptocarya concinna*, *Schima superba*, *Machilus chinensis*, *Castanea henryi* (Skan) Rehd., and *Engelhardtia roxburghiana*. Basic characteristics of the forest stand are presented in Table 1. The soil type in the study site was latosolic red clay-loam soil.

We took soil samples (0–10 cm depth) from four permanent ecological research plots, after removing litter layers. The radius for each circular plot was 17 m, having an area of 907 m². In each plot, soil samples were taken from six randomly-selected points, by using a soil core (4 cm diameter). The six cores were composited and passed through a 2-mm sieve after fine roots and organic matter were removed. Basic soil chemical properties are presented in Table 2. Exchangeable K⁺, Ca²⁺, Mg²⁺, and Na⁺ contents were determined after extraction with 1 N ammonium acetate at pH 7. Exchangeable Al³⁺ was extracted by 1-M KCl. Soil pH(H₂O) was measured using a soil to water ratio of 1:2.5. Exchangeable cations and soil pH(H₂O) were determined by using air-dry soil. Dissolved and microbial forms of C and N were determined using fresh soils with the same methods described later.

Incubation

Soil samples with 20 g oven-dry equivalent weight were placed in 700 mL-plastic bottles with lids equipped with a CO₂ analyzer (GMP43, Vaisala). For dissolved organic matter (both C and N) and microbial biomass analysis, 5 g samples were placed in 50 mL bottles. We provided C to both control and K-added soils in the form of glucose (1.2 mg g⁻¹) (Ilstedt and Singh 2005; Mori et al. 2013a) because no C was provided by the litter layer or root

exudates in the incubation experiment. Potassium was added in the form of KCl (Wright et al. 2011) at 0.1 mg g⁻¹. The soil water content was adjusted to 42% (mass%). The samples were incubated for 142.6 h at 20 °C in the dark. At the start of the incubation, all bottles were covered with polyethylene plastic wrap to prevent water evaporation (Mori et al. 2016a).

CO₂ flux measurement

CO₂ fluxes were measured at 8, 24.3, 36, 48.3, 60, 72.3, 84, 108.2, and 142.6 h after the start of the incubation. After the polyethylene plastic wrap was removed, the upper air of the plastic bottles was mixed well so that the accumulated CO₂ was removed. CO₂ fluxes were measured by monitoring the changes in CO₂ concentrations after the closure of lid equipped with a CO₂ analyzer (GMP43, Vaisala). We recorded the changes in CO₂ concentration 13 times during 6–7 min measurements. The recording started several minutes after the closure of the lids so that the disturbance by the manipulation was minimized. Gas fluxes were determined by linear regression model. The R value of regression line for every gas flux measurement was higher than 0.9 (more than 75% of the R values were higher than 0.99).

Soil chemical and microbial properties

At the end of the incubation, dissolved organic carbon (DOC) and dissolved N (DN) in the soil were extracted by adding 50 ml of 0.5 mol/L K₂SO₄ and shaking for 60 min. DOC and DN were analyzed by a total organic C analyzer (TOC-V_{CHN} analyzer, SHIMADZU, Kyoto, Japan). Soil microbial biomass C (MBC) and N (MBN) were determined by using the chloroform fumigation extraction method (Vance et al. 1987). Incubated soils were exposed to CHCl₃ vapor for 24 h in a vacuum desiccator. After residual CHCl₃ was removed, fumigated soils were shaken with 50 ml of 0.5 mol/L K₂SO₄ for 60 min and DOC and DN were extracted. Soil MBC and MBN contents were calculated from the differences between the fumigated and un-fumigated samples using a conversion factor of 0.45 (Jenkinson et al. 2004).

Table 1 Basic characteristics of the study site

Stand density ^a (tree ha ⁻¹)	Mean DBH ^a (cm)	Mean tree height ^a (m)	Litter layer (g m ⁻²)	Fine root (0–10 cm depth) (g m ⁻²)
818	18.6	13.8	403	396

^aData cited from Zhang et al. (2015). Samples for litter layer data and fine root data were collected simultaneously with the soil samples for the present incubation experiment

Table 2 Basic chemical properties of the soil sample used for the incubation experiment

pH(H ₂ O)	DOC ($\mu\text{g g}^{-1}$)	DN ($\mu\text{g g}^{-1}$)	MBC ($\mu\text{g g}^{-1}$)	MBN ($\mu\text{g g}^{-1}$)	K ⁺ (mmol kg ⁻¹)	Ca ²⁺ (mmol kg ⁻¹)	Mg ²⁺ (mmol kg ⁻¹)	Na ⁺ (mmol kg ⁻¹)	Al ³⁺ (mmol kg ⁻¹)
3.69 (0.02)	150 (16.8)	12.3 (2.4)	301.1 (39.4)	94.6 (13.6)	0.86 (0.63)	0.36 (0.1)	0.37 (0.03)	0.24 (0.01)	22.4 (2)

DOC is dissolved organic carbon, DN is dissolved nitrogen, MBC is microbial biomass carbon, MBN is microbial biomass nitrogen. Mean values are shown with standard error

Statistical analysis and calculations

Statistical analysis was performed using the Excel software package (version 2013; Microsoft Corp.; Redmond, WA, USA) with statistical add-in software (Excel statistics version 2015 and its updates; Social Survey Research Information Co., Ltd.; Tokyo, Japan). The level of significance was examined by two-way repeated ANOVA (K addition versus sampling time) for CO₂ fluxes and paired t test for cumulative CO₂ emissions and soil properties, assuming the normality and homoscedasticity of the data.

The cumulative CO₂ emissions were estimated using the linear trapezoidal method (Mori et al. 2013c). The CO₂ fluxes at 0 h were estimated as the crossing point of the y-axis and the line connecting fluxes of 8 h and 24.3 h in the figure (Fig. 1). If the estimated flux was lower than zero, we assumed the flux at 0 h was zero. The timing of extraction of DOC and DN (at 142.0 h) differed slightly from that of gas sampling (at 142.6 h), but we assumed the error was ignorable.

Fig. 1 Effects of K addition (0.1 mg g⁻¹) on soil microbial respiration. Error bars represent standard errors ($n = 4$). P values indicate the statistical significance using two-way repeated ANOVA

Results and discussion

In contrast with the copiotrophic hypothesis, we did not observe any effects of K addition on soil microbial activity. Potassium addition had no effects either on CO₂ fluxes ($P = 0.86$, two-way repeated ANOVA, Fig. 1) or on cumulative CO₂ emissions during the incubation period (0.53 ± 0.05 and 0.55 ± 0.04 mg C g soil⁻¹ in control and K-added soil, respectively, $P = 0.31$, paired t-test). Microbial biomass and dissolved forms of C and N were also unaffected by addition of K ($P > 0.05$, paired t-test, Fig. 2). These results suggest that at our study site K did not limit soil microbial activity in the condition of sufficient labile C supply.

The available K content at our study site (0.86 ± 0.10 mmol kg⁻¹, Table 2) was lower than a tropical lowland forest in Panama ($1.4\text{--}3.4$ mmol kg⁻¹), secondary forests and monoculture plantations in Indonesia ($2\text{--}5$ mmol kg⁻¹) (Yamashita et al. 2008), and a dry evergreen forest in Thailand ($5.4\text{--}11.9$ mmol kg⁻¹) (Yamashita et al. 2011). The values were in the range of 71 different forests in the Amazonian basin ($0.3\text{--}2.4$ mmol kg⁻¹, Quesada et al. 2010). Therefore, we assume that soil microbes in many tropical forest ecosystems are not limited by K availability. Indeed, our results are consistent with a report by Turner and Wright (2014), who suggested that K did not limit the microbial biomass in a lowland tropical forest in Panama (but note that a response of microbial biomass to nutrient addition does not necessarily indicate a nutrient limitation of microbial activity). At the same research site in Panama, Kaspari et al. (2008) reported that K addition had no effects on leaf-litter decomposition. In a laboratory microcosm experiment, Powers and Salute (2011) demonstrated that K addition had no impacts on decomposition of two types of leaf litter taken from tropical dry forest trees. These reports all support the idea that K is not a limiting factor of microbial activity in soil and/or litter. However, at the present stage, we cannot conclude absolutely that K is not a limiting factor of soil microbial activity in tropical forest ecosystems, because of the heterogeneity of tropical forest ecosystems and few observations. The hypothesis needs to be tested in larger numbers of tropical forests. Now we are

Fig. 2 Effects of K addition on **a** DOC, **b** DN, **c** MBN, and **d** MBC contents at the end of incubation. *DOC* dissolved organic carbon, *DN* dissolved nitrogen, *MBC* microbial biomass carbon, *MBN* microbial biomass nitrogen. No significant differences were detected among control and K-added soils for each property ($P > 0.05$, $n = 4$, paired t test)

trying to test this question in various types of tropical forests.

The lack of microbial response to added K in our study site can be attributed to physical and chemical characteristics of K in forest ecosystems, which may have provided sufficient K to microbes in our soil samples (already provided at the beginning of the incubation). It is well known that K has high mobility in the soil compared with other nutrients (Sayer and Tanner 2010). In addition, K is readily leached from organic matter. Recent research reported that 100% of K was water-extracted from leaf litter (Schreeg et al. 2013). Due to the high mobility of K in forest ecosystems, microbes might easily re-use K from organic matter (Tobon et al. 2004). This direct pathway contrasts with the indirect pathways for uptake of N and P, both of which require various kinds of enzymes to be converted to available forms (Marklein and Houlton 2012; Kitayama 2013; Turner and Wright 2014).

The high mobility of K would also enable plants to easily access K, but research has clearly shown a stimulatory effect of K on primary production in tropical forests (Wright et al. 2011; Santiago et al. 2012). If microbes in tropical forest soils are not limited by K but plants are, the

difference could have a practical meaning. For example, in tree plantations in the tropics, K fertilization has potential to elevate C sequestration by trees without accelerating the loss of soil C via soil respiration. The contrasting responses to K addition can be explained by the following two possibilities: (i) microbes compete more aggressively for K than do plants; and (ii) microbes require less K than do plants. Further research will be needed to clarify these possibilities.

Although we demonstrated that K did not stimulate soil microbial activity in our laboratory experiment, the incubation might contain some limitations. Since we provided C in the form of glucose (Duah-Yentumi et al. 1998; Ilstedt and Singh 2005; Gnankambary et al. 2008; Mori et al. 2013a), stimulatory effects of K addition on several microbial groups might have been masked in our experimental setup. It is possible that K addition stimulates cellulose decomposers if cellulose (instead of glucose) is supplied. Kaspari et al. (2008) reported cellulose decomposition was stimulated in K-fertilized plots. It is also possible that our results were biased to identify a nutrient limitation of copiotrophic microbes rather than one of oligotrophs: copiotrophs become stronger in a resource-

rich conditions. Additional incubation experiments are needed to test the effects of K addition on soil respiration with amendments of various forms of C including cellulose and recalcitrant organic matter. Despite its limitations, the present study demonstrated that K addition did not stimulate soil microbial activity when labile C was amended.

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