



## Nitrogen and phosphorus supply controls soil organic carbon mineralization in tropical topsoil and subsoil



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### ABSTRACT

Nitrogen (N) deposition to soils is globally rising, but its effect on soil organic carbon (SOC) turnover is still uncertain. Moreover, common theories of stoichiometric decomposition and microbial N mining predict opposing effects of N supply on SOC turnover. We hypothesized that the effect of N deposition on SOC turnover depends on initial soil nutrient conditions. Thus, we sampled tropical forests and rubber gardens with pronounced gradients of nutrient availability from the topsoil to the deep subsoil (up to 400 cm) and measured substrate-induced respiration (SIR) for 30 days in four treatments (C, CN, CP, CNP additions). A natural <sup>13</sup>C abundance approach was conducted to quantify priming effects (PE) of the added C on SOC mineralization. For this purpose we assessed the <sup>13</sup>CO<sub>2</sub> isotope composition after adding a C4 sugar to the C3 soil; to correct for isotopic fractionation a treatment with C3 sugar additions served as control. We found that nutrient additions to topsoil did neither alter cumulative CO<sub>2</sub> release within 30 days (SIR<sub>acc</sub>) nor PE (PE = 1.6, i.e., sugar additions raised the release of SOC-derived CO<sub>2</sub> by a factor of 1.6). In the upper subsoil (30–100 cm), however, both CN and CP additions increased SIR<sub>acc</sub> (by 239% and 92%, respectively) and the PE (PE = 5.2 and 3.3, respectively) relative to the treatments that received C only (PE = 1.7), while CNP additions revealed the largest increase of SIR<sub>acc</sub> (267%) and PE (PE = 6.0). In the deep subsoil (> 130 cm depth), only the CNP addition consistently increased SIR<sub>acc</sub> (by 871%) and PE (PE = 5.2) relative to only C additions (PE = 2.0). We conclude that microbial activity was not limited by nutrients in the topsoil but was co-limited by both N and P in the subsoil. The results imply that microbes mine nutrients from previously unavailable pools under the conditions that 1) deficiency actually exists, 2) co-limitation is alleviated, and 3) nutrient reserves are present. Yet, as opposed to microbial nutrient mining theories, we showed that the subsoil PE is highest when nutrient supply matches microbial demand. As a result also N deposition might exert variable effects on SOC turnover in tropical soils: it might have no effect in nutrient-rich topsoils and in co-limited subsoils without P reserves but might increase SOC turnover in co-limited subsoils with potentially acquirable P reserves.

### 1. Introduction

Tropical forests cover about 12% of the global land surface (Townsend et al., 2011) but account for 30% of the global soil organic carbon (SOC) stocks (Jobbágy and Jackson, 2000). Several studies suggest that more than half of this SOC reservoir is stored in the subsoil (below 20 or 30 cm depth) and that considerable proportions are even located below 2 m depth (Batjes, 1996; Jobbágy and Jackson, 2000). Given this quantitative importance, tropical forest soils including the subsoil play a key role in regulating the global carbon (C) cycle and small changes in the soil C balance might have large impacts on

atmospheric CO<sub>2</sub> concentrations (see also Heimann and Reichstein, 2008).

Due to its quantitative importance, the fate of the tropical soil carbon stock under global change is of critical relevance. Global change induces, among others, massive changes in carbon and nutrient supply to soils. Warming and increasing atmospheric CO<sub>2</sub> concentrations are supposed to increase plant productivity, thereby increasing above-ground litter input, root-exudate inputs (Heimann and Reichstein, 2008; Yin et al., 2013), and subsoil fine-root biomass (Leppälammikujansuu et al., 2013; Norby et al., 2004). Further, nitrogen (N) is increasingly deposited from the atmosphere to soils as a result of fossil

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fuel combustion and fertilizer production (Galloway et al., 2004; Hietz et al., 2011; Vitousek et al., 1997), which enhances the availability of N in soils globally.

It is well known that the input of fresh and easily degradable C stimulates the decomposition of pre-existing soil organic matter (SOM, Derrien et al., 2014; Fontaine et al., 2004), especially in subsoils (Fontaine et al., 2007; Karhu et al., 2016). This reaction is known as positive priming effect (Kuzyakov, 2010). Thus, an elevated input of fresh and easily degradable C, e.g., from increasing root-exudate inputs and root biomass, could probably increase the decomposition of old SOC and affect total SOC stocks (Fontaine et al., 2004). But the mechanisms controlling priming effects remain poorly understood. It has long been recognized that N and P play a crucial role in regulating the priming effect (Chen et al., 2014; Dijkstra et al., 2013; Fontaine et al., 2011); but despite decades of research, the intensity and direction of nutrient effects on SOC turnover is still controversially debated (Chen et al., 2014).

The conceptual understanding of nutrient effects on SOC mineralization traditionally follows Liebig's Law of the Minimum (Liebig, 1842) or stoichiometric decomposition theories (Hessen et al., 2004). According to these concepts, microbial activity is constrained by the scarcest nutrient and an addition of the most rate-limiting nutrient increases SOC-mineralization. Thus, SOC mineralization rates might be highest when nutrient contents match microbial demand. Indeed, many studies report increasing SOM turnover after nutrient additions, or, in turn, that SOM turnover is limited in nutrient-deficient soils (Allen and Schlesinger, 2004; Cleveland and Townsend, 2006; Conde et al., 2005). According to these concepts, it is reasonable to speculate that N-deposition might accelerate SOC mineralization.

Recent studies questioned the simple view on this relationship and propose a non Liebig's world of multiple nutrient limitations with synergistic interactions between nutrient cycles (Kaspari et al., 2008; Townsend et al., 2011; Vitousek et al., 2010). This paradigm change was triggered by recent findings that the addition of various nutrients stimulates C-mineralization even when applied individually (Kaspari et al., 2008). The theory of microbial N mining (Craine et al., 2007) even predicts higher SOC mineralization rates in N-deficient soils than in N-rich soils. According to this theory, input of fresh and labile C increases the demand of microorganisms for N and provides energy for the breakdown of SOM, which contains the required N. The release of N from SOM enables the microbes to mineralize the labile C and, in addition, enhances mineralization of C compounds contained within the decomposed SOM (i.e., primed C). Indeed, several studies report that positive priming effects are more pronounced in N-deficient than in N-rich soils (Blagodatskaya and Kuzyakov, 2008; Fontaine et al., 2011), or, in turn, that high N supply to formerly N-deficient soils decreases SOC mineralization rates (Blagodatskaya et al., 2007; Janssens et al., 2010; Meyer et al., 2017; Poelau et al., 2016b). As a consequence, the priming effect has increasingly been interpreted as a response of microbes to nutrient deficiency (Murphy et al., 2015). According to this theory, and dependent on initial soil nutritional status, it seems reasonable to assume that N deposition might preserve SOC.

While the concept of nutrient mining was originally developed for N acquisition strategies, it is still debated whether similar processes also apply to P, i.e., microbial P mining. Several studies reported that the microbial need for P induces the production of phosphatase enzymes that promotes by catalysis release of required P from organic or inorganic pools (Liu et al., 2014; Nottingham et al., 2012; Olander and Vitousek, 2004). Yet, whether this P acquisition is coupled to increasing SOM turnover is questionable especially because P is not necessarily associated with recalcitrant C (Craine et al., 2007; Milcu et al., 2011). However, an understanding of P acquisition strategies in the context of increasing N deposition is important especially in tropical soils for at least two reasons. First, tropical forest soils exhibit generally poor nutrient supply (Vitousek and Sanford, 1986); especially phosphorus (P) is frequently deficient in highly weathered tropical soils (Cleveland et al.,

2002; Duah-Yentumi et al., 1998) because it is strongly bound to iron and/or aluminum oxides (Vitousek and Sanford, 1986; Walker and Syers, 1976). Second, also N limitation of the microbial community or even co-limitation by both N and P were reported to occur in tropical soils (Ilstedt and Singh, 2005; Teklay et al., 2006) but N deficiency is increasingly alleviated by N deposition. This may strengthen the importance of P as most limiting nutrient in tropical forests (Vitousek et al., 2010). Thus, the effect of N deposition on SOC turnover might be coupled to P acquisition strategies.

Altogether, the effect of nutrients on SOC mineralization is still not fully understood. The contrasting results from previous studies suggest that N deposition might have variable effects on SOM turnover and that no universal response exists. Here, we aimed at mimicking the effects of N deposition on SOC mineralization by a single N addition. While this does not reflect continuous N deposition with different N species, it allows elucidating the response of microorganisms to sudden inputs of elevated N supply. In particular, this study aims at investigating the effect of N addition on SOC mineralization in soils of tropical forests and rubber garden with large gradients of inherent nutrient (N and P) supply ranging from nutrient-rich topsoils to nutrient-poor deep subsoils. We hypothesize that soil nutrient conditions determine microbial mining strategies, which, in turn, regulate priming of SOC mineralization. We further assume that the change in N and P mining strategies upon N addition determines whether SOC mineralization decreases, increases, or remains unaffected as compared to the original soil. To answer these hypotheses, we conducted substrate-induced respiration measurements (SIR) with labile C additions (i.e., glucose) for 30 days in four treatments (C, CN, CP, and CNP treatment). Measurements of  $^{13}\text{C}$  in evolved  $\text{CO}_2$  after adding a C4 sugar enabled us to distinguish sugar from pre-existing SOC derived  $\text{CO}_2$ , i.e., to quantify the priming effect. As the focus of this study was to investigate the effect of N and P supply on SOC turnover in different depths of soil, we concentrated on the analyses of vertical gradients with in the soil profiles rather than assessing spatial differences across land use types.

## 2. Material and methods

### 2.1. Study area and soil sampling

The study area was located close to Keluin (1°08'57" N, 112°15'37" E), a hamlet in the district of Batang Lupar in the province of West Kalimantan, Indonesia. The climate was tropical with an average temperature of 26.7 °C and a mean annual precipitation of 4231 mm (data recorded at Putussibau, a town located approximately 80 km east of Keluin, <https://de.climate-data.org>). The altitude of the study site ranged between 70 and 150 m above sea level. The surrounding area was covered by secondary forests and rubber gardens (Indonesian: *kebun karet*), the latter have been established after converting traditionally cultivated land (i.e., *ladang* cropping, a sequence of forest burning, crop cultivation, and fallow, Labrière et al., 2015). The rubber gardens are characterized by minimal management practices from smallholders, which include weeding and management of paths (Lawrence, 1996). Besides rubber trees, other tree species grew as result of natural regeneration and because of targeted planting. Soils were Acrisols having haptic, leptic, and stagnic properties with textures ranging between clay and silt (WRB, 2007). The mean contents of SOC and total N have been summarized in Table 1. The soils were acidic and revealed slightly but significantly increasing pH values with increasing depth (Table 1).

Three investigated sites were covered by secondary forests (F1, F2, F3), and other three sites by recently (< 8 years ago) established rubber gardens (R1, R2, R3, see Fig. S1 for spatial information on the sampling design). As sites belonged to different owners, we considered them as independent field replicates. At each of the 6 sampling sites, one soil profile was investigated. One topsoil sample was taken at each soil profile from 0 to 20 cm depth. Below 20 cm, one soil sample was

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