Nitrogen and phosphorus constrain labile and stable carbon turnover in lowland tropical forest soils

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ABSTRACT

Tropical forests contain a large stock of soil carbon, but the factors that constrain its mineralization remain poorly understood. Microorganisms, when stimulated by the presence of new inputs of labile organic carbon, can mineralize ('prime') soil organic matter to acquire nutrients. We used stable carbon isotopes to assess how nutrient demand and soil properties constrain mineralization of added labile (sucrose) carbon and pre-existing (primed) soil carbon in tropical forest soils. In a series of lowland tropical forest soils from Panama, we found that the mineralization of fresh labile carbon was accelerated foremost by phosphorus addition, whereas the mineralization of pre-existing soil carbon was constrained foremost by nitrogen addition. However, there was variation in the relative importance of these nutrients in different soils and the largest effects on the acceleration of sucrose metabolism and constraint of priming occurred following the addition of nitrogen and phosphorus together. The respiration responses due to sucrose or primed soil carbon mineralization were reduced at pH below 4.8 and above 6.0. We conclude that in these tropical forest soils, phosphorus availability is more important in promoting microbial mineralization of sucrose carbon, whereas nitrogen availability is more important in constraining the priming of pre-existing soil organic carbon. This response likely arises because nitrogen is more closely coupled to organic matter cycling, whereas phosphorus is abundant in both organic and inorganic forms. These results suggest that the greatest impact of priming on soil carbon stocks will occur in moderately acidic tropical forest soils of low nitrogen availability. Given long-term changes in both atmospheric carbon dioxide and nitrogen deposition, the impact of priming effects on soil carbon in tropical forest soils may be partially constrained by the abundance of nitrogen.

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1. Introduction

The large amounts of carbon (C) stored in tropical forest soils is affected by anthropogenic alteration of the global cycles of C and nitrogen (N) (Dixon et al., 1994; Phillips et al., 2008; Hietz et al., 2011; Sayer et al., 2011), yet whether tropical forest soils become a source or sink of atmospheric C remains a major uncertainty in global change models (Friedlingstein et al., 2006). The outcome will depend in part on the direction and magnitude of priming effects, which determine the balance between fresh C stabilized in soil and pre-existing C lost from soil. Priming is regulated by microbial demand for energy and nutrients (Fontaine et al., 2007; Kuzyakov, 2010). Increasing input of labile C to soil from leaf litter, fine roots and root exudates under a CO_2 enriched atmosphere can induce positive priming effects (Langley et al., 2009; Sayer et al., 2011), which feed-back positively on atmospheric CO_2, with important consequences for global climate. In contrast, increasing input of N has been shown to induce negative priming effects and reduce soil CO_2 efflux (Blagodatskaya et al., 2007; Janssens et al., 2010). Despite the large perturbations in C and nutrient cycles in tropical forests (Phillips et al., 2008; Hietz et al., 2011) we lack a mechanistic understanding of priming effects in tropical forest soils, which is required urgently if we are to predict the stability of the 209 Pg C they contain (Pan et al., 2013).

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Priming effects are changes in the turnover of soil organic matter following addition of C or nutrients to soil, which either promote or retard microbial mineralization of soil organic C by altering microbial demand for energy and nutrients (Fontaine et al., 2007; Kuzyakov, 2010). For example, positive priming (loss of soil C) may occur when a fresh input of labile organic C increases microbial demand for mineral nutrients and provides the necessary energy to acquire these nutrients from soil organic matter. Consequently, C contained within soil organic matter is liberated, metabolized and released as 'primed' CO_2. In contrast, negative priming (conservation of soil C) may occur when an input of mineral nutrients reduces microbial mineralization of organic matter, due to reduced 'mining' for organic nutrients (Blagodatskaya et al., 2007). Thus, natural organic matter inputs (containing both C and nutrients) could induce either positive or negative priming effects, dependent on their elemental stoichiometry (Kuzyakov, 2010). Studies in moderately-weathered temperate soils suggest that priming is driven by microbial demand for N from soil organic matter and will therefore be greatest in N-poor soils (Blagodatskaya and Kuzyakov, 2008; Langley et al., 2009). However, the nutrient that stimulates priming may differ for strongly-weathered tropical soils, in which the availability of phosphorus (P) often limits decomposition processes (Cleveland et al., 2002; Cleveland and Townsend, 2006; Kaspari et al., 2008).

Despite the large potential impacts of priming on the tropical forest C cycle, the extent to which different nutrients regulate priming in tropical forest soils remains unknown. In particular, no distinction has been made between potential nutrient limitation of different C pools (e.g. fresh input of soluble C and soil organic matter). Phosphorus, rather than N, limits microbial metabolism of fresh plant-derived C in strongly-weathered tropical soils (Cleveland et al., 2002; Kaspari et al., 2008), despite being abundant in organic forms in these soils (Turner and Engelbrecht, 2011). However, microorganisms can overcome P limitation by acquiring P from organic compounds when provided with sufficient energy, such as following input of labile C (Olander and Vitousek, 2004; Nottingham et al., 2011).

Microbial P acquisition has been suggested to occur through two mechanisms, which are not mutually exclusive: 'biochemical mineralization' through extracellular hydrolysis of organic P esters stabilized to, but not bound within, organic matter and 'biological mineralization' through the oxidation of organic matter to release P (McGill and Cole, 1981). Support for biochemical mineralization as a dominant mechanism comes from converging or diverging ratios of C:organic P during soil development (McGill and Cole, 1981), although a significant role of biological mineralization is suggested by experiments that demonstrate coupled cycling of organic P and C. For example, in an experiment using dual labelled phosphate monoesters (^{14}C and ^{33}P) the release of ^{33}P appeared to occur as a consequence of ^{14}C uptake (Spohn and Kuzyakov, 2013). Evidence for biological P mineralization in tropical forests comes from marked reductions in both soil organic C and P following litter removal (Vincent et al. 2010) and increased mineralization of C from organic matter alongside increased activity of phospho-monoesterase following sucrose addition, which suggested a relationship between the release of soil organic C and hydrolysis of simple monoester-linked organic phosphates (Nottingham et al., 2011). If microbial metabolism of C in strongly-weathered tropical soils is indeed limited by P and if microbial mineralization of organic C and organic P are closely coupled, then priming in these soils may occur due to microbial acquisition of P rather than N.

Physicochemical soil properties, in addition to the availability of N or P, may also influence priming. If priming is a response to microbial nutrient demand alone then a direct relationship between soil fertility and priming would be expected. However, this was not found in study of temperate soils (Hamer and Marschner, 2005) or tropical soils (Nottingham et al., 2011). Priming might also depend on microbial demand for cations during decomposition (Kaspari et al. 2008), on soil mineralogy (Rasmussen et al. 2007), abundance and stability of soil C, or soil pH (Blagodatskaya and Kuzyakov, 2008). However, our understanding of how these properties influence priming is limited because there have been insufficient studies on contrasting soils.

To assess the influence of N and P addition on soil organic C among different tropical forest soils, we conducted manipulative laboratory experiments on a series of eleven tropical forest soils with a wide range of soil properties, including total C (28.1–104.0 g C kg^{-1}), total N (2.14–8.94 g N kg^{-1}), total P (74–1650 mg kg^{-1}), and pH (3.9–6.8) (Table 1 and S1). By manipulating N or P with sucrose additions, we tested the hypothesis that priming effects following a labile C addition are determined by microbial N or P limitation in tropical forest soils. By studying a range of soils we were able to investigate the relationships between priming and soil physical, chemical and biological properties. Our overall aim was to determine the factors that regulate microbial metabolism of soil organic C following an input of labile C in tropical forest soils.

2. Materials and methods

2.1. Study sites

Soil was collected from 11 lowland tropical forest plots in the Center for Tropical Forest Science (CTFS) network in the Republic of Panama, between February and May 2008. The network spans a rainfall gradient that ranges from <1800 mm yr^{-1} on the Pacific coast to >4000 mm yr^{-1} on the Atlantic coast, which is correlated to an increase in soil moisture during the dry season and a decrease in dry season length (Turner and Engelbrecht, 2011). The sites include secondary, mature secondary and old growth primary lowland forest (Pyke et al., 2001) (elevation 10–410 m a.s.l.) growing on soils with a range of properties derived from a series of geological substrates (Table 1). Further detail on the geology and soils is available elsewhere (Dieter et al., 2010; Turner and Engelbrecht, 2011).

2.2. Experimental design

Soils were sampled from the top 10 cm at 25 systematically distributed locations within each 1 ha plot using a 2.5 cm diameter soil corer. Although the same priming mechanisms would apply to surface and deeper soils alike, we used surface soils because they are more likely to give rise to priming under field conditions (Fontaine et al., 2007; Salome et al., 2010). Within 24 h of collection, the 25 soil cores collected from each plot were pooled, sieved (<2 mm), weighed into pots (each contained 50 g dry weight), adjusted to 60% water holding capacity and then incubated at constant moisture and 22 °C for 10 days before experimental treatments began. Sub-samples for each soil type were analyzed for chemical properties (see Supplementary information).

The incubation experiment had a partial factorial randomized block design, with three replicates of each of six treatments: (i) soil only (CTL), (ii) N and P addition (+NP), (iii) sucrose addition (+C), (iv) sucrose and N addition (+CN), (v) sucrose and P addition (+CP), (vi) sucrose, N and P addition (+CNP). Therefore, we had 11 soils × 6 treatments × 3 replicates = 198 sample incubations in total. Carbon additions were 1 mg C g^{-1} soil in the form of sucrose derived from C_4 sugar cane; therefore we used the natural abundance difference in δ^{13}C between C_4 plants and C_3 soils to determine the