Opposing effects of nitrogen and phosphorus on soil microbial metabolism and the implications for soil carbon storage

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ARTICLE INFO

ABSTRACT

Nitrogen (N) and phosphorus (P) availability plays a crucial role for carbon cycling in terrestrial ecosystems. However, the effect of nutrient supply on soil organic matter decomposition and microbial metabolism is generally not well understood. In this study, we incubated soils with three contrasting nutrient regimes from each of three Swedish long-term agricultural experiments (>45 years, 7—30% clay), namely an unfertilised control (0NPK), high P but no N fertilisation (PK_{0N}) and high N but no P fertilisation (N_{0PK}). In the laboratory, we amended all soils with no fertiliser or with N, P and N + P, with and without glucose, and monitored CO_2 and heat production over five hours. Significant effects of the treatments were observed when nutrients were added in combination with glucose. Averaged over all field treatments, Glucose + N addition reduced CO_2 and heat production by 14% and 14%, respectively, compared with glucose addition alone, while glucose + P addition increased CO_2 and heat production by 17% and 9%, respectively. Similar results were found comparing the contrasting long-term field-treatments: PK_{0N} showed higher glucose-induced CO_2 and heat production per unit SOC than 0NPK, while both variables were suppressed in N_{0PK}-fertilised soils. Basal respiration per unit soil organic carbon (SOC) proved to be linked to long-term losses in SOC stocks, which were highest in the PK_{0N}-fertilised plots at all three sites. Combined analyses of field and laboratory treatments revealed that the suppressing effect of laboratory N-addition on respiration only occurred in N-deficient soils, which clearly indicates that long-term N-addition alleviated N-mining. In conclusion, N and P showed opposing effects on the microbial metabolic processes, including respiration. The observed effects were similar in the short- and long-term and across different sites, which suggests that direct physiological controls of nutrients on microbial metabolism strongly regulate SOC turnover. Short-term nutrient effects were only observed in combination with a labile C source and the N-effect was restricted to N-deficient soils. Therefore, we conclude that those findings might be more important for nutrient-poor but carbon-rich ecosystems exposed to sudden nutrient inputs in comparison with nutrient rich and relatively carbon poor agricultural systems.

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1. Introduction

Soil nutrients influence CO_2 exchange between terrestrial biosphere and atmosphere, which is one of the major fluxes in the global carbon cycle (Reed et al., 2011). Today, the amount of anthropogenic nitrogen (N) annually applied to the biosphere (~150 Tg yr^{-1}) is 10-fold higher than 100 years ago (Schlesinger, 2009; Ramirez et al., 2012). The response of net primary production to nutrient supply has been extensively studied, while nutrient effects on plant litter and soil organic carbon (SOC) decomposition are less well understood (Craine et al., 2007; Schlesinger, 2009; Reed et al., 2011). This hampers the ability to accurately predict net ecosystem responses to nutrient additions. However, with rising pressure on global land resources due to increasing food demand and climate change (Trostle, 2010), as well as rising deposition of nutrients in natural ecosystems (Bragazza et al., 2006), we need to further our understanding of the effect of nutrients on SOC decomposition.

The majority of studies investigating nutrient effects on SOC decomposition focused primarily on nitrogen (N) and the reported effects varied widely. Positive effects on SOC decomposition and thus potentially negative effects on SOC stocks have been explained by *basic stoichiometric decomposition theory* (Craine et al., 2007), which predicts that microbial activity is driven by the microbial demand for resources, with an optimal C:N:P ratio of 60:7:1 (Cleveland and Liptzin, 2007). It implies that decomposition is maximised when material undergoing decomposition contains this C to nutrient ratio. Several studies have shown that N addition leads to an increase in heterotrophic respiration (Melillo et al., 1982; Dilly, 2001; Milcu et al., 2011). However, the opposite, i.e. reduced heterotrophic respiration after N addition has also been observed, which is usually explained with 'nutrient mining' (Schimel and Weintraub, 2003; Craine et al., 2007). According to this theory, the nutrients needed for biosynthesis are acquired by decomposing more recalcitrant organic matter using energy from labile, nutrient-poor C sources, and this mechanism occurs primarily under nutrient-limiting conditions. This process obtains nutrients at high C costs leads to low microbial C use efficiency (CUE), i.e. a high rate of respiration per unit substrate assimilation and thus to less C being retained in the soil per unit C input. Both, a decrease in SOC decomposition after N addition (Ammann et al., 2007; Griepentrog et al., 2014) and (ii) an increase in stabilisation of plant litter (Kirkby et al., 2014; Poeplau et al., 2015b) have been observed. Recently, Murphy et al. (2015) showed that organic matter decomposed due to priming had a C:N ratio of 5, while the organic matter decomposed during basal respiration had a C:N ratio of 20, which indicates that i) microorganisms have the ability for compound-specific mining and ii) mining can trigger priming. However, since the opposite effect of N addition has also been observed, the mechanism of N-mining cannot be generalised and constitutes a major uncertainty in predicting ecosystem responses to N addition.

A similar mining mechanism for P has not been reported. Craine et al. (2007) found N- but no P-mining in a leaf litter decomposition experiment, where P addition was instead found to increase SOC mineralisation. It is not clear why N- but not P-mining should occur and which conditions trigger mining. P effects on SOC cycling are generally not well studied. However, in the past years several studies reported an increase in heterotrophic respiration after P addition, mostly in P-limited forest soils (Cleveland and Townsend, 2006; Reed et al., 2011; Liu et al., 2013). Recently, Poeplau et al. (2016) reported a significant net decrease in SOC stocks after long-term PK but no N fertilisation (PK_{0N}) compared with unfertilised control soils in Swedish agricultural long-term experiments, although net primary production was positively affected by PK_{0N} fertilisation. This questioned the paradigm that SOC build-up is directly proportional to C input (Christopher and Lal, 2007; Kätterer et al., 2012). Poeplau et al. (2016) suggested four different mechanisms that are potentially involved, of which stimulated heterotrophic respiration was hypothesised to be the major cause. Since the relative importance of each mechanism is not known, controlled experiments are, however, needed in this research area. Two other recent studies (Cleveland et al., 2006; Fisk et al., 2015) showed opposing effects of short-term N and P addition in combination with different labile C sources on CO_2 production. Both studies were not able to entirely explain their observations, while Hartman and Richardson (2013) hypothesised that N limits microbial biomass synthesis and P limits metabolism.

Carbon dioxide (CO_2) is the end product of microbial decomposition of organic material. However, microbial metabolism consists of many concurrent anabolic and catabolic reactions. Measuring the heat efflux (Q) from soil samples with isothermal calorimetry quantifies the net balance of all catabolic (energy releasing) and anabolic (energy consuming) reactions (Herrmann et al., 2014). Such a 'microbial energetics' approach has been found to provide complementary insights on microbial metabolism in comparison with determination of CO_2 production alone. Complete oxidation of carbon to CO_2 is the process which releases maximum heat, while other catabolic processes referred to as "incomplete decomposition" release less heat. Most obviously, not only heterotrophic respiration, but the entire microbial metabolism should be affected by nutrient availability, yet this has not been investigated comprehensively in a soil system context. The calorespirometric ratio, i.e. the ratio of heat production (R_Q) to CO_2 production (R_{CO2}), can be of use as an indirect indicator of microbial C use efficiency (Hansen et al., 2004; Herrmann et al., 2014) with a lower heat dissipation per unit CO_2 indicating that less energy is lost from the system. Lower heat dissipation may be the result from an increase in anabolic reactions, such as biosynthesis, and/or more "incomplete decomposition" in relation to CO_2 respiration. Herrmann and Bölscher (2015) developed a high-throughput method whereby heat and CO_2 production can be determined simultaneously in soil samples without any methodological bias. In the present study we used this approach in order to advance understanding of how major soil nutrients influence microbial metabolism and SOC cycling. Short- and long-term effects of contrasting N and P availability for soil microorganisms were evaluated on: i) CO_2 production, ii) heat production and iii) calorespirometric ratio in three contrasting agricultural soils from long-term field experiments. We expected nutrient additions to increase total microbial metabolism, but also to foster anabolism (biosynthesis) over catabolism (decay) and thus to decrease heat dissipation per unit CO_2 or increase CUE. We had the following hypothesis: 1. Short-term nutrient addition of N and P will significantly alter microbial metabolism; 2. The patterns observed after short-term nutrient additions are reflected in significantly different microbial metabolism between the long-term contrasting fertiliser treatments; 3. The obtained results can explain long-term SOC stock dynamics in the investigated experiments (Poeplau et al., 2016).

2. Materials and methods

2.1. Study sites and soil sampling

In March 2015, we sampled three out of 12 sites of the meta-replicated (same experimental design at all sites) Swedish long-term soil fertility experiments established during the period 1957–1969 (Carlgren and Mattsson, 2001). These experiments were established to study the effect of mineral and organic fertiliser application on soil fertility-related properties. In total, they consist of 16 combinations of mineral fertiliser (NPK) including four different N levels and four different PK levels, which are compared in two different crop rotations (with or without manure applications). In this study we only investigated soils from the rotation without manure addition. All treatments are replicated (n = 2) and randomised in a split-block design. Five experiments are located in southern Sweden, five in central Sweden and two in northern Sweden. In this study, we sampled two central sites (Högåsa, Bjertorp) and one southern site (Ekebo), which are described in detail elsewhere (Kirchmann et al., 1999, 2005). A summary of basic soil properties is provided in Table 1. We selected these field experiments in order to obtain a large gradient in soil texture (7–30% clay) and we sampled three contrasting combinations of NPK: i) no NPK (0NPK); ii) no PK but highest N level (N_{0PK}); and iii) no N but highest PK level (PK_{0N}). The highest N and PK levels provide on average 200 kg N, 45 kg P and 120 kg K ha^{-1} $year^{-1}$ at the southern site (Ekebo) and 125 kg N, 45 kg P and 120 kg K at the central Swedish sites (Högåsa, Bjertorp). Five soil cores (8 cm diameter) were taken randomly in each plot to a depth of 20 cm and pooled