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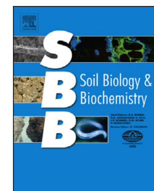

Carbon mineralization is promoted by phosphorus and reduced by nitrogen addition in the organic horizon of northern hardwood forests

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ABSTRACT

Limitations to the respiratory activity of heterotrophic soil microorganisms exert important controls of CO_2 efflux from soils. In the northeastern US, ecosystem nutrient status varies across the landscape and changes with forest succession following disturbance, likely impacting soil microbial processes regulating the transformation and emission of carbon (C). We tested whether nitrogen (N) or phosphorus (P) limit the mineralization of soil organic C (SOC) or that of added C sources in the Oe horizon of successional and mature northern hardwood forests in three locations in central New Hampshire, USA. Added N reduced mineralization of C from SOC and from added leaf litter and cellulose. Added P did not affect mineralization from SOC; however, it did enhance mineralization of litter- and cellulose- C in organic horizons from all forest locations. Added N increased microbial biomass N and K_2SO_4-extractable DON pools, but added P had no effect. Microbial biomass C increased with litter addition but did not respond to either nutrient. The direction of responses to added nutrients was consistent among sites and between forest ages. We conclude that in these organic horizons limitation by N promotes mineralization of C from SOC, whereas limitation by P constrains mineralization of C from new organic inputs. We also suggest that N suppresses respiration in these organic horizons either by relieving the N limitation of microbial biomass synthesis, or by slowing turnover of C through the microbial pool; concurrent measures of microbial growth and turnover are needed to resolve this question.

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1. Introduction

The activities of soil heterotrophs process plant-derived organic carbon (C), determining its pathway back to the atmosphere as CO_2 or into stabilized forms that could persist in soil pools for many years. The controls of microbial respiratory activity thus are of interest for understanding patterns of soil C storage, as well as nutrient mineralization, in different ecosystems. Evidence exists for nitrogen (N) limitation (Schimel and Weintraub, 2003; Meidute et al., 2008; Kamble and Bååth, 2014) and also for phosphorus (P) limitation (Cleveland et al., 2002, Cleveland and Townsend, 2006; Craine et al., 2007; Bradford et al., 2008) of microbial growth and activity in forest soils. While some evidence supports the idea that forest productivity and microbial respiration are limited by the same nutrient (Reed et al., 2011), this is not always the case and it remains generally unclear what determines patterns of limitation in individual ecosystems. Understanding nutrient limitation of respiratory activity is further complicated in some ecosystems by its dependence on the form of C (soil organic C (SOC) or new inputs of C) that is metabolized (Reed et al., 2011).

In this study we examined nutrient controls of microbial respiration, as part of efforts to understand nutrient limitation in northern hardwood forests (Vadeboncoeur, 2010; Fisk et al., 2014). These controls are of interest for understanding interactions between nutrient availability processes and soil C storage in response to ecosystem management or environmental change. In northeastern hardwood forests, acidic deposition has enriched soils with N and depleted essential cations, such as calcium (Ca) (Lawrence et al., 1995; Fenn et al., 1998; Likens et al., 1998; Aber et al., 2003), and potentially affected the availability of P via declining soil pH (Carreira et al., 2000; Fiorentino et al., 2003). Forest harvest also alters ecosystem nutrient status via nutrient removal and changes in recycling processes as vegetation recovers and matures (Fisk et al., 2002; McLauchlan et al., 2007; Milcu et al., 2011;

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Rastetter et al., 2013). These anthropogenic effects take place on a template of substantial landscape-level and regional variation in soils and microbial processes in these northern hardwood ecosystems (Johnson et al., 2000; Bohlen et al., 2001; Fisk and Fahey, 2001; Fisk et al., 2010).

Our goal in this study was to test whether N or P limit the mineralization of organic C in northern hardwood forest soils in the northeastern US, and whether effects differ in response to added C sources. We incorporated both spatial and successional sources of variation in our study to examine the generality of the microbial response to nutrient additions, by working in mid-successional and mature forests, and in three separate northern hardwood sites in central New Hampshire, USA. We focused on the surface organic horizon (Oe), where microbial processes can be crucial limiting steps in C transformations in these northern forest ecosystems because of the absence of vertical mixing by large decomposer organisms. Leaching and fungal translocation are the primary short-term means of downward vertical movement from surface horizons (Frey et al., 2003; Dittman et al., 2007). Most organic C of plant structural origin therefore decomposes in place, and is either mineralized to CO_2 or is transformed into dissolved forms or the humus of the Oa horizon. Thus, controls of respiratory processes in this horizon are crucial for understanding microbial contributions to patterns of soil C storage.

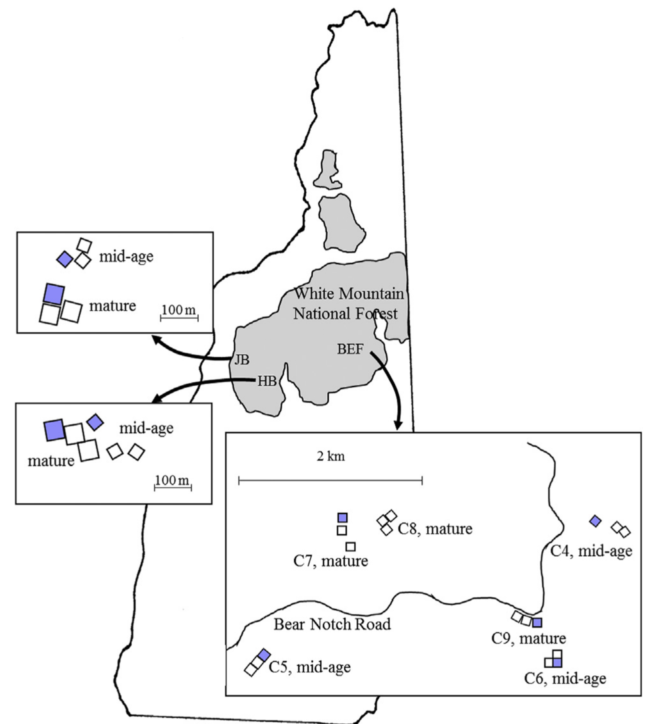

Fig. 1. Locations of the Bartlett Experimental Forest (BEF), Hubbard Brook Experimental Forest (HB), and Jeffers Brook sites (JB) within the White Mountain National Forest, NH, USA. Plot layouts are shown within each site; plots sizes are not to scale in the BEF. One composite sample was analyzed from each plot. Samples from shaded plots were used for the litter and nutrient addition experiments (C8 was not included); samples from shaded plots in C9 and C4 were used for the cellulose and glucose addition experiment.

2. Materials and methods

2.1. Study sites and sample collection

We studied northern hardwood forests in three sites in central to southeast New Hampshire, USA (Fig. 1). Three mid-age (30–36 yrs since clearcut) stands and three mature (>100 yrs old) stands were in the Bartlett Experimental Forest (BEF; 44°2–4′N, 71°9–19′W; elevation 250–500 m). One mid-age and one mature stand were in the Hubbard Brook Experimental Forest (HBEF; 43°56′N, 71°44′W; elevation 500 m), and one mid-age and one mature stand were in the Jeffers Brook forest (JB; 44° 02′ N, 71° 53′ W; elevation 730 m). Soils are mostly spodosols (typic and aquic haplorthods) that developed in glacial till derived from granitic rock at BEF, from a mix of granitic rock and mica schist at HBEF, and from amphibolite at JB. The mature forest is generally dominated by American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), and sugar maple (*Acer saccharum* Marsh.), with some ash (*Fraxinus americana* L), red maple (*Acer rubrum* L), and white birch (*Betula papyrifera* Marsh.). The mid-age stands originated following clearcut harvest and forest composition is typical of early-successional hardwood forests of the region, with pin cherry (*Prunus pensylvanica* L.f), white birch, yellow birch, red maple, and American beech common in the overstory. In each forest stand we sampled soils in three 50 × 50 m plots, except for the mid-age plots at JB and HBEF, which were 30 × 30 m. At BEF, these were the same plots as described in Naples and Fisk (2010).

Multiple soil cores (approximately 30; 2 cm diam) were collected from each plot in early June, 2008. The Oe horizon was separated from the underlying Oa by visual criteria in the field. We identified Oe as the layer of decayed organic matter that was of recognizable plant origin or was fibrous and reddish to dark brown. We separated this from the non-fibrous amorphous organic matter of the Oa that was closer to black in color, had a smooth or greasy consistency, and sometimes contained mineral flecks. Oe samples were pooled into one composite sample per plot. Soils were stored at approximately 4 °C prior to processing (within one week) and then were homogenized gently by hand to remove roots and coarse fragments and to facilitate uniform subsampling.

2.2. Mineralization and microbial biomass

We quantified C mineralization, N mineralization, and microbial biomass C (MBC) and N (MBN) in laboratory incubations of all samples (3 plots per stand × 10 stands). From each sample, an "initial" subsample (10 g fresh mass; 4–5 g dry mass) was shaken in 100 mL 2 M KCl, allowed to settle for approximately 16 h, and filtered through Whatman #1 filter paper. A second subsample was incubated for 21 d at 20–23 °C in a canning jar. After incubation, soil in each jar was further divided into 3 subsamples. One subsample of incubated soil ("final") was extracted in 2 M KCl in the same manner as the initial subsample. We used a phenolate-hypochlorite method to quantify NH_4^+ (method 351.2, US EPA 1983) and a cadmium reduction method to quantify NO_3^- (method 353.2, US EPA 1983) in extracts. Net N mineralization potential was estimated as the difference in extractable $NH_4^+ + NO_3^-$ between final and initial extracts.

The remaining subsamples of incubated soil were subjected to the chloroform-fumigation extraction method (Brookes et al., 1985) to quantify MBC and MBN. One subsample was shaken in 0.5 M K_2SO_4 for 30 min and filtered immediately through Whatman #42 paper. The other subsample was fumigated with chloroform for 3 d in a humid desiccator, and then extracted in the same manner. For N analysis, extracts were subjected to persulfate digestion and NO_3^- in digests was quantified using the above cadmium reduction method. Carbon in extracts was quantified using a Schimadzu TOC analyzer. MBC and MBN were estimated as the difference between fumigated and unfumigated extracts, corrected with a K_c of 0.45 for C and a K_n of 0.54 for N (Brookes et al., 1985; Vance et al., 1987).

We estimated C mineralization by quantifying CO_2 evolved from soils throughout the 21 d incubation. Glass scintillation vials

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