Lability of C in temperate forest soils: Assessing the role of nitrogen addition and tree species composition

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ABSTRACT

Understanding how atmospheric nitrogen (N) deposition affects carbon (C) stabilization in forest soils has become an important focus as humans continue to alter global C and N cycles. Recent reviews have found a positive effect of increased N inputs on C stabilization in soils of temperate forest ecosystems. However, there is still uncertainty about the role and magnitude of the effect of chronic N inputs on forest soil C sequestration and how different tree species can modulate this effect. We evaluated the response of soil C lability to experimental N additions across plots with different dominant tree species (*Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Tsuga canadensis* and *Quercus rubra*). We used a 14-year N addition experiment with a single-species, paired-plot design, and several measurements to estimate C lability, including soil laboratory incubations and density fractionation. Our two principal measures of C lability showed statistically significant interactive effects of N treatment and tree species composition: soils from maple (*Acer*) stands showed the greatest effect of added N on the light fraction mass in the mineral horizon (a 69% increase), and soils from beech (*Fagus*) stands showed the greatest N effect on potentially mineralizable C (a 23% decrease). Decreases in soil decomposition and respiration rates in organic and mineral horizons in response to N addition across all five species suggest a significant suppression of C mineralization, particularly in the first few weeks of the incubation, with the strongest responses in beech and oak (*Quercus*) stands. Our results confirm that increased N additions significantly reduce soil organic matter decomposition rates and the lability of soil C for some tree species, and indicate that mechanisms other than organo-mineral associations could play an important role in the stabilization of C in these soils. Further, our research illustrates the need to consider varying responses among different tree species when predicting future consequences of N inputs on soil C storage.

1. Introduction

Increases in nitrogen (N) deposition and atmospheric CO_2 are two of the largest anthropogenic environmental perturbations (Galloway et al., 2008; IPCC, 2007). As human activities continue to dramatically alter the carbon (C) and N cycles, understanding the interactions between these two elements has become an imperative task (Gruber and Galloway, 2008; Liu and Greaver, 2010).

Identifying the controls on C and N cycling and storage in soils is crucial for building accurate biogeochemical models and projections of future climate change scenarios (Neff et al., 2002; Kaye et al., 2003; Durán et al., 2013). One important topic of recent research is the extent to which N deposition enhances C stabilization in forest ecosystems (e.g. see Sutton et al., 2008; Janssens et al., 2010). It is known that N additions may influence C storage in forests through aboveground effects on plant growth and litter production (e.g., Townsend et al., 1996; Solberg et al., 2009; Thomas et al., 2010; Davidson et al., 2012). Recently, however, the importance of soil as the largest terrestrial C reservoir (Chapin et al., 2012; Dungait et al., 2012) and a primary sink for added N in many forest

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ecosystems (Nadelhoffer et al., 1999; Templer et al., 2012) has stimulated interest in studies focused on the belowground coupling of N and C storage (Neff et al., 2002; Zak et al., 2008; Janssens et al., 2010). Recent reviews of this topic have found N addition to frequently affect various aspects of soil C cycling in temperate forests (Nave et al., 2009; Janssens et al., 2010; Liu and Greaver, 2010; Prescott, 2010). Some studies suggest that N addition increases C storage through reductions in litter decomposition, soil respiration and microbial biomass (see Knorr et al., 2005; Treseder, 2008; Hobbie et al., 2012), inhibition of microbial enzymes that degrade lignin (Fog, 1988; DeForest et al., 2004) or changes in the chemical and physical stabilization of organic matter (Berg and Matzner, 1997; Neff et al., 2002). However, some studies have shown that the effects of added N on C cycling can be transient (Bowden et al., 2004; Hagedorn et al., 2012), or highly heterogeneous (Pregitzer et al., 2008; Janssens et al., 2010), while other studies have not found a significant effect of N addition on soil C storage (Lovett and Goodale, 2011). Thus the role and magnitude of effect of chronic N input on forest soil C pools and stabilization remains uncertain. Even more uncertain is to what extent different tree species may control the effect of the added N on the stabilization of C in soil. While some studies have suggested that tree species can play an important role in determining the effect of added N on soil C cycling based on their litter quality and recalcitrance (Janssens et al., 2010; Waldrop et al., 2004; Lovett et al., 2013), most of the N addition studies on natural ecosystems have been done in mixed-species plots (but see Lovett et al., 2013).

The stability of soil organic matter, defined as its tendency to resist further transformation or degradation (Sollins et al., 1996), can be influenced by the biological and physicochemical properties of the soil environment (Schmidt et al., 2011; Dungait et al., 2012), but also by the chemical quality of the substrate itself, its physical protection (e.g. formation of aggregates) and its associations with clay surfaces and other minerals (von Lutzow et al., 2006; Filley et al., 2008). The organic matter pool with high resistance to being transformed or degraded is called the stable pool, whereas the pool with low resistance to transformation/degradation is considered labile. No single analytical method is yet able to isolate fractions of organic matter associated with all the different forms of stability (Kaye et al., 2003). As an alternative, applying multiple methods independently to the same soils with a clear understanding of their operational and interpretation limitations provides complementary insights on C stability and help identify the mechanisms that promote it (Crow et al., 2007).

The main goal of our study was to estimate the extent to which the lability of C is influenced by elevated N inputs and modulated by tree species composition in temperate forests. Temperate forest ecosystems contain approximately 10% of global soil C stocks, and most terrestrial C sequestration at mid-latitudes in the Northern Hemisphere occurs in seasonal montane forest ecosystems such as the one studied here (Rasmussen et al., 2006; Monson et al., 2006). There is therefore a strong need to assess how N input and tree species influence C lability in these systems.

To achieve our goal we separated the total soil C stock into labile and stable pools using two different approaches of soil fractionation: a density fractionation and a microbial fractionation. Density fractionation is widely used to separate organic matter into labile and stable fractions (Crow et al., 2007). However, this technique separates soil fractions only based on the extent to which organic matter is associated with minerals. Microbial fractionation, on the other hand, takes into account all mechanisms that play a role in the protection of the organic matter as it lets microbes determine what is decomposable and what is not (Kaye et al., 2002). Earlier work in our single-species plots showed an increase in the organic soil C storage after 6 years of N additions with differences in direction and magnitude of the N

treatment effect among species (Lovett et al., 2013). Based on this finding, we hypothesized that N addition enhances C storage in soil by reducing C lability, and that plots occupied by different species may differ in the extent to which the N-induced decrease in soil C lability is expressed due to known differences in their litter chemistry. Because added N has been shown to reduce lignin degradation (Carreiro et al., 2000; Waldrop et al., 2004; Weand et al., 2010) we specifically hypothesized that the N addition would reduce C lability more in species with high-lignin litter (e.g., *Quercus, Fagus and Betula*—oak, beech, and birch) than in species with low-lignin litter (e.g., maple).

2. Methods

2.1. Site description

This study is part of a larger project that assesses the role of tree species and N addition in mediating ecosystem nutrient cycling and C storage in northern hardwood forests of the Catskill Mountains, New York (e.g., Lovett et al., 2004; Templer et al., 2005; Hancock et al., 2008; Christenson et al., 2009; Lovett et al., 2013). The Catskill Mountains are an area of flat-topped mountains and deeply incised valleys encompassing about 5000 km^2 in southeastern New York State. The bedrock in the highest elevations (>500 m) is relatively homogeneous, consisting primarily of flat-lying sandstones, shales and conglomerates of Devonian age (Stoddard and Murdoch, 1991), and is overlain by glacial till of variable depth (Rich, 1934). Soils of this region are classified as Lithic Dystrochrepts (Loamy, skeletal, mixed, mesic). Upland soils in this region are typically shallow, with an organic horizon (Oe + Oa) of approximately 2–12 cm depth, generally no A horizon, and a B horizon of variable depth averaging ~50 cm (Johnson, 2013). These soils are moderately to somewhat excessively well drained and are formed on glacial till derived from sandstone, siltstone and shale (Tornes, 1979). The Slide Mountain weather station at 808 m in the central Catskills has a mean annual temperature of 4.3 °C (January mean = −8.5 °C, July mean = 16.7 °C) and a mean annual precipitation of 153 cm, about 20% of which falls as snow. In the last decade, annual average wet N deposition (including NO_3^- and NH_4^+) and dry deposition (including HNO_3 vapor and particulate NO_3^- and NH_4^+) have averaged 5.9 kg N ha^{-1} y^{-1}, and 3.1 kg N ha^{-1} y^{-1}, respectively, for a total annual average N deposition of 9.0 kg N ha^{-1} y^{-1} (NADP wet deposition data from http://nadp.sws.uiuc.edu/data/ntndata.aspx, site NY 68; CASTNet dry deposition data from http://epa.gov/castnet/, site CAT175). This estimate of N deposition must be considered approximate as the models used to estimate dry deposition are not well suited to such complex terrain, and atmospheric deposition varies considerably across mountain landscapes (Weathers et al., 2000, 2006).

Forests of the Catskill Mountains are dominated by northern hardwood forests (McIntosh, 1972). We studied five of the most dominant tree species in the region: sugar maple (*Acer saccharum* Marsh), American beech (*Fagus grandifolia* Ehrh), yellow birch (*Betula alleghaniensis* Britton), eastern hemlock (*Tsuga canadensis* (L.) Carr) and northern red oak (*Quercus rubra* L.). These five species have been shown to differ in their leaf litter quality and recalcitrance (C:N, lignin, tannins) (see Lovett et al., 2004; Templer et al., 2005; Lovett et al., 2013), ranging from relatively labile in the case of sugar maple and yellow birch to recalcitrant in the case of American beech, eastern hemlock and red oak (Weand et al., 2010). For brevity, henceforth we will refer to these species as maple, beech, birch, hemlock, and oak, respectively.

2.2. Plot design and description

For each species we chose six pairs of monospecific plots (12 m diameter) located throughout the central Catskills in a region of