Catena 172 (2019) 285–294

Contents lists available at ScienceDirect

Catena

journal homepage: www.elsevier.com/locate/catena

Soil C:N ratio is the main driver of soil $\delta^{15}N$ in cold and N-limited eastern Canadian forests

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ARTICLE INFO

Keywords:
Soil N
$\delta^{15}N$
C:N ratio
Forest soils

ABSTRACT

Significant relationships have been observed between soil N isotopic natural abundance ($\delta^{15}N$) and both climate and soil characteristics across a large range of ecosystems over the globe, suggesting strong and consistent effects of these variables on N cycling. However, whether the strength and the nature of these relationships vary at regional scales and with soil depth is less documented, especially in northern cold and N-limited forest ecosystems. In this study, we analyzed $\delta^{15}N$ in soil horizons at 21 forest sites in eastern Quebec along a gradient of concomitant decreasing N deposition and temperature (MAAT) and increasing precipitation (MAP). We hypothesized that both soil $\delta^{15}N$ and the magnitude of increase in soil $\delta^{15}N$ would decrease along this gradient, in accordance with relationships reported at a global scale. The data show an increase in $\delta^{15}N$ with soil depth, although it remained constant or sharply decreased between the B- and the C-horizon at most sites. The natural abundance of ^{15}N in the forest floor (FF), in the B-horizon and in the C-horizon averaged 2.2 ± 0.9‰, 6.2 ± 1.2‰ and 4.9 ± 2.0‰, respectively while total soil profile $\delta^{15}N$ ranged from 3.8‰ to 7.4‰. Contrary to our hypothesis, soil $\delta^{15}N$ was poorly correlated with climate, vegetation and most soil metrics. As a consequence, there was no spatial gradient in soil $\delta^{15}N$ values and in the magnitude of increase in $\delta^{15}N$ with soil depth across the study area. Soil C:N ratio was the only variable significantly correlated with soil $\delta^{15}N$. Multivariate models including the C:N ratio explained 47%, 60% and 36% of the inter-sites $\delta^{15}N$ variation in B-horizon, C-horizon and total soil, respectively. In contrast with global scale studies, which have reported higher soil $\delta^{15}N$ at sites with low soil C:N ratio, the relationship between these two variables was positive across the study area. The possible influence of ecto-myccorhizal association on this pattern is discussed. Overall, our data show that soil $\delta^{15}N$ is controlled by complex mechanisms influenced by several variables with potential antagonist effects. Climate and most soil metrics appear to have no direct influence in the cold and N-limited forest ecosystems studied here and soil C:N ratio can affect soil $\delta^{15}N$ in an opposite manner to what has been commonly observed.

1. Introduction

Nitrogen (N) cycle in forest ecosystems has been the focus of many researches in the last decades partly because of its important direct influence on primary productivity and its potential control on carbon (C) cycle and climate change. N is actually an important limiting factor for vegetation growth, especially in cold temperate and boreal forests, where N addition significantly increases primary productivity and C sequestration (Schulte-Uebbing and de Vries, 2018). An increase in N availability is therefore expected to enhance the terrestrial C sink and to mitigate climate change. Most soil organic N is located in mineral horizons in temperate and boreal forests (Marty et al., 2017), in a form that is not directly available to the vegetation. Changes in climate and vegetation are nevertheless expected to impact these N pools and may release inorganic N in the soil solution (Melillo et al., 2011; Quan et al., 2014). Whether this will impact vegetation growth and C sequestration is still uncertain as N retention widely varies among ecosystem types, vegetation growth forms and soil characteristics (Templer et al., 2012).

Abbreviations: MAAT, Mean Annual Air Temperature; MAST, Mean Annual Soil Temperature; MAP, Mean Annual Precipitation; PET, Potential Evapo-Transpiration; Pc, Percentage of conifers in the canopy; Phwd, Percentage of hardwoods in the canopy; pH_{FF}, pH in H_2O of the forest floor; pH_B, pH in H_2O of the B horizon; N-NO_3 (d), annual NO_3 deposition from the atmosphere

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https://doi.org/10.1016/j.catena.2018.08.029
Received 1 May 2018; Received in revised form 28 July 2018; Accepted 27 August 2018
0341-8162/

In cold N-limited ecosystems such as northern temperate and boreal forests, N leaching is nevertheless generally low due to N deposition interception by canopy and forest understory, rapid microbial immobilization, root uptake and efficient internal recycling (Gundale et al., 2014, 2011; Houle et al., 2014; Nadelhoffer et al., 1999; Rennenberg et al., 2009).

The analysis of ^{15}N natural abundance in the vegetation and soil is a powerful tool to study N dynamics in ecosystems and can provide insightful information regarding N cycling (Högberg, 1997; Koba et al., 2003). Several studies have for instance highlighted the link between soil $\delta^{15}N$ and N retention (Pardo et al., 2006, 2007a, 2007b; Templer et al., 2012), gaseous N losses (Houlton et al., 2006), N availability and the type and the degree of mycorrhizal association (Craine et al., 2009; Hobbie and Ouimette, 2009; Mayor et al., 2012). There is a large range in soil $\delta^{15}N$ (from ~ -4 to $+15$‰) among ecosystems on a global scale with generally higher $\delta^{15}N$ in both hot and dry ecosystems than in cold and wet ecosystems (Amundson et al., 2003; Craine et al., 2015; Díaz et al., 2016). Globally, soil $\delta^{15}N$ is negatively correlated with mean annual precipitation (MAP) and positively correlated with mean annual air temperature (MAAT), suggesting a direct influence of climate on N cycling (Amundson et al., 2003). However, some soil characteristics such as C and clay concentrations covary with climate, and when these variables are accounted for, soil $\delta^{15}N$ show no consistent trends along global climate gradients, suggesting that the direct impact of climate on soil $\delta^{15}N$ may be limited and is probably mediated by soil properties (Craine et al., 2015). However, different patterns have been observed at a regional scale. For instance, a study in southern Patagonia's forests has found that climatic variables were a better predictor of soil $\delta^{15}N$ than soil characteristics (Peri et al., 2011). The relationship between soil $\delta^{15}N$ and MAAT has also been shown to change along a climatic gradient within the inner Mongolian grasslands (Cheng et al., 2009), suggesting that ecosystem's characteristics can counteract the effect of climate. These contrasted patterns probably result from the counteracting effects of several factors involved in the determination of soil $\delta^{15}N$ such as the N loss mechanisms (e.g., denitrification, ammonia volatilization), N sources (e.g., N deposition, N_2 fixation), the type and the density of mycorrhizal fungi in the soil and mixing of soil N among different layers by bioturbation (Hobbie and Ouimette, 2009). Conflicting results among studies may also result from sampling method, especially the depth at which soils samples are collected. There is actually an increase in $\delta^{15}N$ with soil depth in various ecosystem types, which reflects a change in the composition and turnover rate of SOM (Gebauer et al., 1994; Högberg et al., 1996; Marty et al., 2011; Nadelhoffer and Fry, 1988). To our knowledge, whether the relationship between $\delta^{15}N$ and climatic variables changes with soil depth is unknown. In addition, how the magnitude and the pattern of $\delta^{15}N$ increase with soil depth vary along climatic and vegetation gradients are not well documented.

In the present study, we measured $\delta^{15}N$ in the bulk of both organic (FF) and mineral soil horizons at 21 forest sites distributed throughout a wide area of south Quebec, Canada. The study area is characterized by decreasing temperature and nitrate deposition (Fig. 1a and c), and increasing precipitation and proportion of coniferous species from southwest to north-east (Fig. 1b and d). Previous studies in the region have shown that the vegetation is the main driver of $\delta^{13}C$ enrichment with soil depth and of the distribution of C and N within the soil profile (Marty et al., 2015a). In contrast, soil C and N stocks were more influenced by MAP and MAAT (Marty et al., 2015b; Marty et al., 2017). In the present study, we tested the relationship between soil $\delta^{15}N$ and several climatic, ecological and edaphic variables with simple and multiple regression analyses. Our goal was to assess the influence of these biophysical variables i) on soil $\delta^{15}N$ at different soil depth; and ii) on the pattern and the magnitude of the increase in $\delta^{15}N$ with soil depth in this cold and N-limited ecosystem. Since several studies have reported higher foliar and soil $\delta^{15}N$ in deciduous-dominated stands than in coniferous-dominated stands, and an increase in foliar $\delta^{15}N$ with N

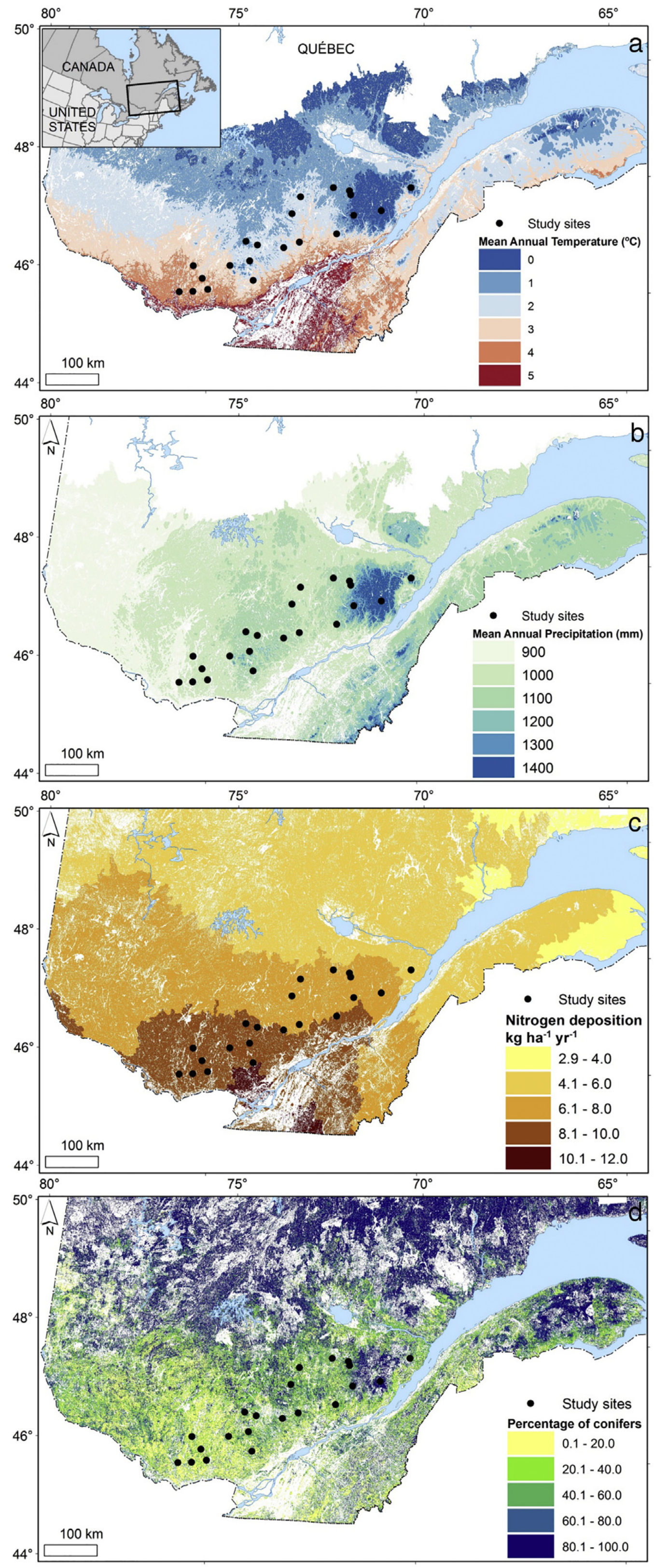

Fig. 1. Changes in mean annual air temperature (a), mean annual precipitation (b), mean annual nitrate deposition (c) and the percentage of conifers (d) throughout the study area. Dots indicate the 21 studied sites.

deposition (Pardo et al., 2007a, 2007b), we hypothesized there would be a decrease in soil $\delta^{15}N$ along the increase in MAP and the percentage of conifers, and the decrease in MAAT and nitrate deposition from the