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Soil nitrogen conservation mechanisms in a pristine south Chilean *Nothofagus* forest ecosystem

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Abstract

A ^{15}N tracing study was carried out to identify microbial and abiotic nitrogen (N) transformations in a south Chilean *Nothofagus betuloides* forest soil which is characterized by low N inputs and absence of human disturbance. Gross N transformation rates were quantified with a ^{15}N tracing model in combination with a Markov chain Monte Carlo sampling algorithm for parameter estimation. The ^{15}N tracing model included five different N pools (ammonium (NH_4^+), nitrate (NO_3^-), labile (N_{lab}) and recalcitrant (N_{rec}) soil organic matter and adsorbed NH_4^+), and ten gross N transformation rates. The N dynamics in the *N. betuloides* ecosystem are characterized by low net but high gross mineralization rates. Mineralization in this soil was dominated by turnover of N_{lab}, while immobilization of NH_4^+ predominantly entered the N_{rec} pool. A fast exchange between the NH_4^+ and the adsorbed NH_4^+ pool was observed, possibly via physical adsorption on and release from clay lattices, providing an effective buffer for NH_4^+. Moreover, high NH_4^+ immobilization rates into the N_{rec} pool ensure a sustained ecosystem productivity. Nitrate, the most mobile form of N in the system, is characterized by a slow turnover and was produced in roughly equal amounts from NH_4^+ oxidation and organic N oxidation. More than 86% of the NO_3^- produced was immediately consumed again. This study showed for the first time that dissimilatory nitrate reduction to ammonium (DNRA) was almost exclusively (>99%) responsible for NO_3^- consumption. DNRA rather than NO_3^- immobilization ensures that NO_3^- is transformed into another available N form. DNRA may therefore be a widespread N retention mechanism in ecosystems that are N-limited and receive high rainfalls.

Keywords: Unpolluted old-growth forest; *Nothofagus betuloides*; Andisol; ^{15}N tracing model; Functional soil organic matter (SOM) pools; N retention; Dissimilatory nitrate reduction to ammonium (DNRA); Nitrification; Heterotrophic nitrification; Dissolved organic nitrogen (DON)

1. Introduction

According to Odum (1969), ecosystem succession culminates in stabilized systems which are characterized by closed biogeochemical cycles and a high capacity for nutrient retention. Vitousek and Reiners (1975) examined Odum's hypothesis in more detail and came to the conclusion that nutrient retention in ecosystems is directly linked to the net ecosystem productivity (NEP). While this hypothesis provides a general mechanism for the control of nutrient losses, it does not explain how specific microbial and abiotic retention mechanisms develop during ecosystem succession. Nitrogen (N) is one of the key elements for biomass growth, thus, N-limited and natural ecosystems need to conserve the available N and minimize losses via gaseous N production and/or leaching, in particular in parts of the world where atmospheric N deposition is low and rainfall rates are high. The key N transformation processes that need to be understood are those related to the production and consumption of nitrate (NO_3^-), the most mobile form of N in most ecosystems. Vitousek et al. (1979) showed that soil disturbance and anthropogenic impacts lead to NO_3^- built up and accelerated N losses.

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Therefore, it can be expected that internal N dynamics in N-limited ecosystems are optimized to retain NO_3^- in the system and keep concentrations low. Possible mechanisms are low NH_4^+ oxidation rates and high NO_3^- immobilization (Vitousek et al., 1979) but without negatively affecting the ecosystem productivity. Stark and Hart (1997) observed surprisingly high rates of NO_3^- built up in undisturbed forest soils which were counterbalanced by high NO_3^- immobilization rates. However, NO_3^- that is immobilized by the soil organic matter (SOM) is only available after re-mineralization. Therefore, processes such as dissimilatory nitrate reduction to ammonium (DNRA) would be ideal to reduce the NO_3^- concentrations and at the same time keep the N in an available form (Silver et al., 2005). However, due to its strict anoxic nature it is often assumed that DNRA either plays no role or only a negligible role in aerobic top soils (Tiedje, 1988). Ammonium (NH_4^+) is generally less mobile than NO_3^- but high NH_4^+ availability in the ecosystem might support NH_4^+ oxidation and subsequent NO_3^- buildup. High NH_4^+ concentrations typically occur after soil disturbance when mineralization activities are enhanced (Vitousek and Reiners, 1975). Moreover, the rate of NH_4^+ oxidation is an indicator of N availability that increases with the level of anthropogenic influence (Schimel and Bennett, 2004). To control the availability of NH_4^+ and subsequent nitrification in an ecosystem, immobilization of NH_4^+ and adsorption and release of NH_4^+ with cation exchange sites might play an important role, in particular in soils which are characterized by high organic matter and high clay contents (Brady and Weil, 2002).

Anthropogenic activities have resulted in increased N depositions in many regions of the world, which can potentially alter ecosystem C and N cycling process and ecosystem functioning such as increased productivity and C sequestration (Berg and Matzner, 1997; Vitousek et al., 1997, 2002; Matson et al., 2002). However, when N inputs exceed the demand or storage capacity, N losses via leaching or gaseous emissions may occur (Aber et al., 1989). To understand, model and predict the anthropogenic influence on ecosystem N cycling and how ecosystems functioned before any anthropogenic influence, investigations in unpolluted mature ecosystems may provide us with valuable baseline information (Hedin et al., 1995). One of the last areas in the world where N pollution is almost nonexistent is in remote Southern Hemisphere locations such as in temperate *Nothofagus* forests of South Chile. Studies by Perakis and Hedin (2001) indicated that these ecosystems are characterized by a tight N cycling with high retention of inorganic N into recalcitrant SOM and are therefore in line with the trends expected by Odum (1969) to occur in mature ecosystems.

Nitrogen-15 tracing studies represent the current "state-of-the-art" technique to identify simultaneously occurring gross N transformation rates and to obtain quantitative information on N pathways in ecosystems (Mary et al., 1998; Müller et al., 2007). Tracing models are used for data analysis, which contain all important N pools and N transformations of the particular ecosystem. Parameters in those models are simultaneously determined with optimization algorithms. In this study, we use a Markov chain Monte Carlo (MCMC) algorithm that has been developed to estimate parameters in complex ^{15}N models (Müller et al., 2007). The main advantage of ^{15}N tracing models over the commonly used dilution technique (Stark and Hart, 1997; Perakis and Hedin, 2001; Booth et al., 2005) is that simultaneous estimation can be made of many N transformations such as pool specific mineralization and immobilization rates or DNRA. Stark and Hart (1997) were only able to attribute NO_3^- consumption to immobilization but not to DNRA, which we hypothesize to be important in unpolluted ecosystems. Since the publication of the current N mineralization paradigm by Schimel and Bennett (2004), studies have shown that this paradigm lacks the important pathway of organic N oxidation to NO_3^- (heterotrophic nitrification) (Cookson et al., 2006). The study here provides a unique opportunity to further refine the postulated N paradigm by evaluating the importance of DNRA in an ecosystem that is characterized by high precipitation and is therefore suitable for this process.

In this paper, we present results from a ^{15}N tracing study with soil from an unpolluted old-growth South Chilean *Nothofagus betuloides* mountain forest ecosystem. The aim of this study was to identify nitrogen conservation mechanisms and therefore to gain a mechanistic understanding of N dynamics in natural ecosystems. We propose ecosystem state variables that can be used to evaluate the influence of anthropogenic alterations on ecosystem N dynamics.

2. Materials and methods

2.1. Study site

The study site is located in the Andean mountain range, Antillanca, southern Chile (40°47′S, 72°12′W). The average annual temperature is 4.5 °C, while mean annual precipitation amounts to about 7000 mm. The site is located at 900 m a.s.l. The vegetation is characterized as a *N. betuloides* forest type (Donoso, 1981) with an average tree age of 325 years, a stand density of 865 trees ha^{-1}, a mean tree height of 23 m, and a canopy cover of 69%. The overstorey is constituted of *N. betuloides* and *Saxegothaea conspicua* (9 m height). The understorey (3–5 m height) is dominated by *Podocarpus nubigena*, *S. conspicua* and *Myrceugenia chrisocarpha* with a cover of 15%. The lower understorey (2–4 m height) is comprised of *Chusquea argentina*, and *Chusquea montana* with a cover of 90%. The dominant species in the scrub stratum (<2 m) are *C. Montana*, *Blechnum magellanicum*, *Pernettya mucronata*, *Desfontainea spinosa*, *Myrceugenia planipes*, and *M. chrisocarpha* (Godoy et al., 2001). Total annual bulk N deposition equals 11.8 N kg ha^{-1}, from which 8.2 kg N ha^{-1} is in the form of dissolved organic nitrogen