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Soil gross nitrogen transformations along a secondary succession transect in the north subtropical forest ecosystem of southwest China

Jing Wang [a], Yi Cheng [b], Jin-bo Zhang [a,c,d,e,*], Christoph Müller [f,g], Zu-cong Cai [a,c,d,e]

[a] School of Geography Sciences, Nanjing Normal University, Nanjing 210023, China
[b] State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210008, China
[c] Jiangsu Center for Collaborative Innovation in Geographical Information Resource Development and Application, China
[d] Key Laboratory of Virtual Geographical Environment (VGE), Ministry of Education, Nanjing Normal University, China
[e] Jiangsu Provincial Key Laboratory of Materials Cycling and Pollution Control, China
[f] Department of Plant Ecology, Justus-Liebig University Giessen, Heinrich-Buff-Ring 26, 35392 Giessen, Germany
[g] School of Biology and Environmental Science and Earth Institute, University College Dublin, Belfield, Ireland

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ABSTRACT

Soil nitrogen (N) transformations in forest soils play a vital role in plant N availability. However, the effect on soil N dynamics of forest succession remains largely unknown. A ^{15}N tracing study was conducted in situ to investigate gross N transformation rates along a secondary succession transect (grassland GL, coniferous forest CF, coniferous-broad-leaved mixed forest CBF, broad-leaved forest BF, natural broad-leaved forest NF) under a north subtropical monsoon climate. Gross N mineralization and NH_4^+ immobilization rates were significantly higher in the BF soil than in the NF, CBF, GL and CF soils, although no significant differences were found among the latter four soils. Gross NO_3^- immobilization rates in the GL and CF soils were negligible, and were significantly lower than those in the three late succession stage soils. In all soils, NO_3^- was produced almost exclusively by heterotrophic nitrification. The ratio of the gross NO_3^- immobilization rate to the gross nitrification rate was significantly lower in the GL and CF soils than in the other three soils, indicating a higher NO_3^- retention capacity in the three late successional stage soils. The combination of higher gross N mineralization, NH_4^+ and NO_3^- immobilization turnover and higher NO_3^- retention promotes a faster N turnover, resulting in greater N availability and N retention capacity in the late successional stages. Such results also suggested that during succession, internal N cycles adapt and develop mechanisms (i.e. increasing soil organic C and N concentration) in response to soil–plant interactions that enhance the soil N supply and N retention.

1. Introduction

Native ecosystems (e.g. grassland, forests) in subtropical regions are commonly unfertilized, and thus the soil N supply plays a vital role in supplying sufficient N for plant growth. The supply of soil N is largely controlled by microbially-mediated N transformation processes, which are influenced by many factors, such as the quantity and quality of soil organic matter, the composition and diversity of the microbial community, and pH (Stevenson and Cole, 1999; Compton and Boone, 2002; Templer et al., 2003; Grenon et al., 2004). All these factors can be affected by vegetation succession because of the differences in the quantity and quality of above- and below-ground litter input to the soil, which in turn might cause changes in soil microbial communities and N transformations during vegetation succession (Merilä et al., 2002; Nave et al., 2014). However, very few studies have investigated N dynamics during succession.

Vegetation succession can recover degraded soil properties and maintain soil fertility (Aweto, 1981). A chronosequence of the vegetation change along the succession could offer an opportunity to study the interrelationship between vegetation succession and microbial processes affecting N availability to plants. However, to date, net N mineralization and nitrification rates have been determined mainly during succession (White, 1986; Klingensmith and Van Cleve, 1993; Van Cleve et al., 1993; Yan et al., 2009). Considering that net N transformation rates represent only the sum of interacting processes, to gain a mechanistic understanding, it is important to unravel the complexity of interdependent N transformations by looking at the individual gross N transformation rates (Hart et al., 1994; Booth et al., 2005). Several studies have indicated that plant species and their spatial distribution have a profound impact on soil gross N transformation dynamics (Van Cleve et al., 1991; Schimel et al., 1998; Sotta et al., 2008). During succession, changes in plant species, the spatial distribution of plants and associated soil properties can affect gross N transformation rates. However,

* Corresponding author at: School of Geography Sciences, Nanjing Normal University, Nanjing 210023, China.
E-mail address: zhangjinbo@njnu.edu.cn (J. Zhang).

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how the soil gross N cycling adapts and changes in response to forest ecosystem succession is largely unknown.

In this study, the successional stages of forest development after human-induced destruction of a native forest ecosystem was investigated on a successional gradient in the northern side of the east-west main channel in the Samachang area, which lies in the midland of Yunnan province. The succession of forest vegetation starts with grassland (GL), followed by coniferous forest (CF), coniferous-broad-leaved mixed forest (CBF) and secondary broad-leaved forest (BF) towards an almost natural broad-leaved (NF) forest. A general observation is that the decomposition of C and N is slower in CF soils than in broad-leaved forest soils, mainly because of the lower chemical quality of the litter produced by coniferous tree species (Reich et al., 2005). Zhang et al. (2011a, 2011b) also found that gross N mineralization and NH_4^+ rates were much higher in BF soil than in coniferous forest soil. Thus, it can be expected that increasing abundance of broad-leaved tree species along the succession would result in enhanced gross N mineralization and NH_4^+ immobilization rates.

The objective of this study was to characterize the gross N transformation rates and the composition of soil microbial communities along a secondary succession transect under a north subtropical monsoon climate. Specific gross N transformation rates were determined using numerical ^{15}N tracing techniques and the determination of the composition of soil microbial communities was carried out by phospholipid fatty acids (PLFA) analysis.

2. Materials and methods

2.1. Study site and soil samples

The study was conducted along a secondary successional transect (from GL to NF) in Mouding County of the Chuxiong Autonomous Prefecture, Yunnan Province, China (N25°15′, E101°27′). The sites were located in Samachang village, which lies in the midland of Yunnan province, with a total area 253 ha and an elevation of 2100–2200 m, which originally was covered in evergreen broad-leaved forest. The mean annual precipitation is approximately 760 mm (30-year average) and the mean annual temperature is 14.1 °C (30-year average). The soil is classified as a Pup-Orthic Entisol in the Chinese soil taxonomy and as a Eutric Regosol in the Food and Agriculture Organization of the United Nations (FAO) soil classification, originating from purple shale. The climate, parent soil material, slope and soil type were similar in the studied sites. However, the natural forest was almost completely destroyed by excessive logging in the 1950s. After that, these sites regenerated naturally after seeding of the native species of *Pinus yunnanensis* at different times, mainly in 1955, 1971 and 1987, respectively. Before planting, grass (dominated by *Imperata cyliadrica*) and shrubs were the dominant vegetation. Thus, the different secondary forest ecosystems, dominated by *P. yunnanensis*, *Cyclobalanopsis glaucoides* and *Keteleeria evelyniana*, respectively, developed because of the different sowing times. In this study (note, the age of the ecosystems refer to the time of soil sampling), 8-year old *grassland* (dominated by *I. cyliadrica*) and shrubland (GL), 23-year old *coniferous forest* (CF), 39-year old semi-natural *coniferous-broad-leaved mixed forest* (CBF), 55-year old natural *secondary evergreen broadleaved forest* (BF), 260-year old *natural broad-leaved forest* (NF) (which was not destroyed in the 1950s because of the protection for the temple regions) were investigated. The approach of space-for-time substitution was used in the present study. The climate, parent soil material, slope and soil type were similar; therefore, these sites reflect the different conditions imposed by the successional stage, which was also considered the main driver influencing soil gross N transformation dynamics.

Surface soil (0–20 cm) samples were collected from the five sites in January 2010. For each forest site, three plots (10 m × 10 m) were selected. From each plot, three cores were taken from the A horizon (0–20 cm), and pooled together to form a composite sample. After collection, soils were immediately sieved (2 mm) and stored at 4 °C. The soil properties are presented in Table 1.

2.2. PLFA analyses

Microbial biomass was estimated as total extractable PLFA. PLFA profiles were analyzed to determine the microbial community composition. Briefly, lipids were extracted from 0.5-g soil samples using the modified Bligh and Dyer method (Bligh and Dyer, 1959; Yao et al., 2006). Fatty acids extracted from soil microorganisms were quantified and identified automatically using the MIDI Sherlock software (MIDI, Newark, DE, USA). The abundances of individual fatty acid methylesters were expressed as mole percentages. The nomenclature of the fatty acids followed that used by Frostegård et al. (1993).

The fatty acids i12:0, i13:0, i14:0, i15:0, a15:0, i16:0, i17:0, 17:0cy, 18:lm7c and 19:0cy were chosen to represent bacterial PLFAs. The unsaturated PLFAs 18:1ω9, 18:2 ω6,9 and 18:3ω6 were used as indicators of fungal biomass. The monoenoic and cyclopropane unsaturated PLFAs 10Me16:0, 10Me17:0, 10Me18:0, i12:0, i13:0, i14:0, i15:0, a15:0, i16:0, a16:0, i17:0 and a17:0 were chosen to represent gram-positive bacteria (G^+). Finally, the branched, saturated PLFAs 3OH 11:0, 3OH i11:0, 12:0, 3OH 12:0, 3OH 13:0, 14:0, 3OH 15:0, 3OH i15:0, 16:0, 2OH 16:1, 3OH i16:0, 16:1 ω5, 16:1 ω7, 17:0, 3OH i17:0, 18:1 ω5, 18:1 w6, 18:1 ω7, cy17:0, cy19:0 and 11Me18:1ω7 were chosen to represent gram-negative bacteria (G^-).

2.3. ^{15}N tracing experiment

A field ^{15}N tracing experiment was conducted to study gross N transformation rates during 140 h of in situ incubation. The subsample used for the in situ study was passed through a 2 mm sieve immediately after collection at each site. The fresh, sieved soil (100 g oven-dry) was then added to incubation cylinders and the bottom of the cylinder (4.7 cm diameter × 7.3 cm long) was sealed immediately. The bulk density of the soil in the cylinder corresponded to field conditions at each site. All soil cores were pre-incubated for 24 h at field temperatures before ^{15}N tracer addition. There were two NH_4NO_3 treatments (each with three replicates). In one treatment, the ammonium was labeled ($^{15}NH_4NO_3$), and in the other, the nitrate was labeled ($NH_4^{15}NO_3$). Each was labeled with ^{15}N at 99.2 atom% excess by adding 1.5 mL of the $^{15}NH_4NO_3$ or $NH_4^{15}NO_3$ solution to each of the soil cores at a rate of 2 μg NH_4^+–N g^{-1} soil and 2 μg NO_3^-–N g^{-1} soil. Such N addition might

Table 1
Soil properties (0–20 cm) from five different successional stage soils (mean ± SD).

	Total N (g N kg^{-1})	Organic C (g C kg^{-1})	C/N	NH_4^+ (mg N kg^{-1})	NO_3^- (mg N kg^{-1})	pH	Water-stable macro-aggregates (%)
GL	0.7 (0.3)^a	13.9 (3.5)^a	19.8 (5.9)^a	3.5 (0.6)^a	2.0 (0.5)^a	5.0 (0.1)^a	37.2 (7.7)^a
CF	0.9 (0.2)^a	19.5 (4.2)^a	23.8 (0.5)^a	2.9 (1.1)^a	1.9 (0.4)^a	5.0 (0.2)^a	44.2 (3.4)^a
CBF	1.3 (0.1)^a	26.4 (1.9)^a	27.9 (0.8)^a	2.7 (0.6)^a	1.4 (0.1)^a	4.8 (0.1)^a	46.7 (3.0)^a
BF	1.4 (0.1)^a	28.1 (1.2)^a	24.9 (3.9)^a	2.2 (0.1)^a	1.9 (0.2)^a	4.7 (0.2)^a	54.8 (2.7)^b
NF	2.5 (0.7)^b	68.8 (24.2)^b	32.8 (8.1)^b	12 (4.8)^b	1.9 (0.6)^a	4.4 (0.1)^b	60.2 (2.2)^c

GL, grassland; CF, coniferous forest; CBF, coniferous and broad-leaved mixed forest; BF, secondary broad-leaved forest; NF, natural secondary broad-leaved forest. Different letters within the same column denote significant differences for different successional stages ($P < 0.05$).