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RESEARCH ARTICLE

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Nitrification and denitrification in subalpine coniferous forests of different restoration stages in western Sichuan, China

Abstract Nitrification is the biological conversion of organic or inorganic nitrogen compounds from a reduced to a more oxidized state. Denitrification is generally referred to as the microbial reduction of nitrate to nitrite and further gaseous forms of nitric oxide, nitrous oxide and molecular nitrogen. They are functionally interconnected processes in the soil nitrogen cycle that are involved in the control of long-term nitrogen losses in ecosystems through nitrate leaching and gaseous N losses. In order to better understand how nitrification and denitrification change during the process of ecosystem restoration and how they are affected by various controlling factors, gross nitrification rates and denitrification rates were determined using the barometric process separation (BaPS) technique in subalpine coniferous forests of different restoration stages. The results showed that forest restoration stage had no significant effects on gross nitrification rates or denitrification rates (One-way ANOVA (analysis of variance), $p < 0.05$). There was no significant difference in the temperature coefficient (Q_{10}) for gross nitrification rate among all the forest sites (One-way ANOVA, $p < 0.05$). Gross nitrification rates were positively correlated with water content ($p < 0.05$), but not with soil pH, organic matter, total nitrogen, or C/N ratios. Denitrification rates in all the forest soils were low and not closely correlated with water content, soil pH, organic matter, or total nitrogen. Nevertheless, we found that C/N ratios obviously affected denitrification rates ($p < 0.05$). Results from this research suggest that gross nitrification is more responsible for the nitrogen loss from soils compared with denitrification.

Keywords gross nitrification, denitrification, barometric process separation (BaPS), subalpine coniferous forest

1 Introduction

Nitrification and denitrification are essential microbiological processes in soil nitrogen cycle, and are also involved in the control of long-term nitrogen losses in the ecosystem. At present, most studies on nitrification are mainly focused on net nitrification (Gosz, 1981; Robertson, 1982; Binkley and Hart, 1989; Venterea et al., 2003) instead of gross nitrification. Due to ignorance of the NO_3^{-1} assimilation in soil microbial communities, the net nitrification rates were greatly underestimated (Stark and Hart, 1997). Reports on nitrification and denitrification are rich in the agricultural ecosystem (Martin et al., 1993; Rochester et al., 1996; Shi and Norton, 2000; Schjønning et al., 2003), however, scarce in the forest ecosystem, especially on the dynamic process along restoration or succession of forest ecosystem (Davidson et al., 1992; Zou et al., 1992; Carmosini et al., 2002). Furthermore, there are obviously different results on the dynamic properties of nitrification along forest succession: Rice and Pancholy (1972) reported that nitrification decreased in the course of succession, Davidson et al. (1992) showed that the gross nitrification rates were not different between the young and old stages of forest succession, and Zou et al. (1992) concluded that the old-growth forest tended to have higher gross nitrification rates than the early-successional one after studying the forest soils in the Caribbean lowland in northeastern Costa Rica.

The subalpine coniferous forest is the main body of the forest vegetation in high altitude areas of western China, and is an ecological barrier of the eastern fringe from the Qinghai-Tibetan Plateau to the upper reaches of the Yangtze River (Liu, 2002), for it can regulate climate and prevent high-cold meadows from expanding in the forest areas, and it can prevent the arid valley vegetation from extending upwards. Unfortunately, since the 1940s, the primitive

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subalpine coniferous forests in this region had been clear-cut and were replaced by artificial forests as one of three biggest bases of timber of China.

Apparently, it is necessary to study the ecological function of nitrogen and to investigate the dynamics of nitrification and denitrification in subalpine coniferous forest during forest restoration, which can provide valuable information for the re-establishment of coniferous forest and building its regulation strategies. The object of this study was to study the dynamics of nitrification and denitrification in subalpine coniferous forest in different restoration stages by using the barometric process separation (BaPS) technique and to analyze the relationships between the dynamics of nitrification and denitrification in subalpine coniferous forest and environmental factors.

2 Study area

The study was conducted in the Miyaluo forest area, Li County, Sichuan Province (31°35′ N, 102°35′ E), which lay in the high mountain-canyon zone between the Qinghai-Tibetan Plateau and the Sichuan Basin. The climate is cool-temperate with mild wet summer and cold dry winter, dominated by the monsoon and mountainous topography. Mean annual temperature is 6°C to 12°C, annual accumulated temperature (⩾10°C) 1,200°C to 1,400°C, annual precipitation 600 mm to 1,100 mm, annual evaporation 1,000 mm to 1,900 mm. Brown earth is the main soil type (Wu et al., 2001).

In this area, the subalpine coniferous plantations were composed of 20-, 30-, 40- and 60-year-old spruce forests established by artificial regeneration on the cut-over area of fir forest in Minjiang. The community structure varied greatly among different plantation forests. Generally, only few species, such as *Picea asperata* and *Picea likangensis* var. *balfouriana*, dominated the tree layer. Most shrub layer was harvested, except *Smilax stans* and *Berberis* spp., which were still found. The herb layer consisted of *Adiantum davidii*, *Carpesium macrocephalum* etc. (Wu et al., 2001). Litter reserves increased greatly with the increase of forest age, then decreased, the maximum value (26.6×10^3 kg/hm^2) was observed in the 40 year-old forest (Pang et al., 2004).

The series of natural forest succession was composed of coniferous broad-leaved forest and natural coniferous forest. Natural coniferous forest showed obvious vertical stratification, and the tree layer was occupied by *Picea asperata*, *Picea likangensis* var. *balfouriana*, *Larix potaninii* and *Picea wilsonii.* There were a few species, including *Rubus aurantiacus*, *Pruns tatsienensis* and *Lonicfra nervosa*, appearing in the shrub layer. In the herb layer, the dominant species were *Pseudocystopteris subtriangultare* and *Cacalia roborowskii*. In coniferous broad-leaved forest, species richness or abundance was lower than that in the natural coniferous forest, and the main tree species were *Betula* spp. and *Picea likiangensis* var. *balfouriana* (Shi et al., 1988). Litter reserves were 19.20×10^3 kg/hm^2 and 12.5×10^3 kg/hm^2 in coniferous broad-leaved forest and natural coniferous forest respectively (Pang et al., 2004).

3 Materials and methods

3.1 Sample collection

Six forest sites (the 20-, 30-, 40- and 60-year-old spruce artificial forests, coniferous broad-leaved forest and natural coniferous forest) were selected with similar environmental conditions, such as altitude, slope and exposure. Then, three plots (1.5 m × 1.5 m) were established randomly between trees at each forest site. Soil samples were taken from these plots at a depth of 0–20 cm using double-rings method (A larger metal ring was driven into the soil around each small ring so that the two formed concentric circles. The pair was removed, and the soil between the two rings was collected to analyze their physical and chemical properties), three random replicates per plot. The sampling has been done in September 2003.

3.2 Physical and chemical analysis

We adopted the National Standard Methods of China to measure soil water content, soil organic matter (SOM), total nitrogen (N), and soil pH. Soil water content was measured with the gravimetric method (GB7833-87); SOM with the potassium-dichromate method (GB9834-88); total N with the copper sulfate-selenium powder diffusion method (GB7848-87), and soil pH (water) with the potentiometric method (GB7859-87).

3.3 Determination of nitrification and denitrification rates

Gross nitrification rates and denitrification rates were determined using the BaPS technique. Three intact soil samples that were taken with soil sampling rings (height ⩽ 40.5 mm, outside diameter ⩽ 60 mm) from the same plot were placed into the borings inside the incubation container simultaneously, and the lid with sensor fittings and thermostat were put on the container to adjust to the desired temperature. After the system has reached temperature stability for at least half an hour, a defined volume of gas was drawn out of the headspace to test air tightness, then configuration parameters were entered and the settings for the measurement were selected. The incubation time for the soil samples in the closed system was 12 h. Gross nitrification rate and denitrification rate were calculated via evaluation with delta values or evaluation with regression straight line. BaPS is a new simple approach to determine gross nitrification rates and denitrification rates in soils. By using BaPS, many traditional problems using other methods can be overcome, such as destruction of the original structure of the soil or addition of labeled substrates to the soil as in the Isotope technique and underestimation of denitrification due to scavenging of intermediate nitric oxide generated by acetylene inhibition technique. Statistical analysis revealed that the mean values of nitrification rates obtained using BaPS and the isotope technique in well-aerated soils were not significantly different (Ingwersen et al., 1999; Breuer et al., 2002; Kiese et al., 2002).

3.4 Temperature coefficient estimation

The Arrhenius equation could effectively calculate the influence of temperature on rate constants for most chemical reactions and many biological reactions (Bailey and Ollis, 1986; Levenspiel, 1972). For nitrification and denitrification, the temperature coefficients (Q_{10}) were determined b using the Arrhenius equation:

$Q_{10\text{nitrification}} = \text{nitrification rate } (T+10)/ \text{ nitrification rate } (T)$

$Q_{10\text{denitrification}} = \text{denitrification rate } (T+10)/ \text{ denitrification rate } (T)$

3.5 Statistical analysis

All statistical analyses were performed with SPSS 10.0. One-way ANOVA was used to compare gross nitrification rates, denitrification rates and Q_{10} values for gross nitrification in subalpine coniferous forests of different restoration stages (since denitrification rates were close to the detection limit in these soil samples, One-way ANOVA was not used to compare Q_{10} values for denitrification). Linear regression was used to determine whether there was any linear relationship between gross nitrification rates or denitrification rates and soil water content or pH values. Bivariate correlation was used to determine the effects of SOM, total N or C/N ratios on gross nitrification rates or denitrification rates.

4 Results and discussion

4.1 Changes of nitrification and denitrification rates in subalpine coniferous forests of different restoration stages

Gross nitrification rates varied between 83.94 and 246.85 μg N /(kg·h) in subalpine coniferous forests of different restoration stages. For denitrification rates, the observed maximum value was 82.33 μg N /(kg·h) in 30 year-old plantation forest closing to the detection limit of BaPS. There were no significant differences among all forest sites in gross nitrification or denitrification ($p < 0.05$) (Fig. 1).

Rice and Pancholy (1972), who determined the numbers of *Nitrosomonas* and *Nitrobacter*, reported that nitrification decreased during the course of forest succession. Nevertheless, recent studies have shown that heterotrophic microorgamisms are also responsible for heterotrophic nitrification in forest soils besides these autotrophic bacteria, and furthermore, heterotrophic nitrification may be the dominant process for NO_3^- formation in some acidic coniferous soils (Killham, 1990; Duggin et al., 1991; Papen and von Berg, 1998). Bremner and McCarty (1988) also suspected Rice and Pancholy's hypotheses (1972) after studying the inhibition of nitrification. Zou et al. (1992) concluded that old-growth forests tended to have higher gross nitrification rates compared with early-successional forests, but high-intensity artificial disturbance was practiced in their study site, which could lead to the change of inner and outer environments of the ecosystem, the loss of nutrient materials from the system and the variation of community structure and function. Our results were consistent with those reported by Davidson et al. (1992), that there were similar gross nitrification rates in different stages of coniferous forest restoration or succession, which revealed that the microbial environment for nitrification had not been significantly altered in the course of forest restoration or succession.

For the soil nitrate pool, gross nitrification is the production process; and consumption processes include denitrification, microbial immobilization, leaching, and plant uptaking. Our results showed that there were no significant differences among all forest sites in gross nitrification or denitrification. In addition, Davidson et al. (1992) found that in spite of similar gross nitrification rates, the net nitrification rates were lower in the old forest than those in the young forest. Above results suggested that the higher rates of microbial immobilization or assimilation of nitrate occurred in the late-successional forest soil, which would lead to less nitrate leaching losses from soil (Stark and Hart, 1997). The low denitrification rates in subalpine coniferous forests of

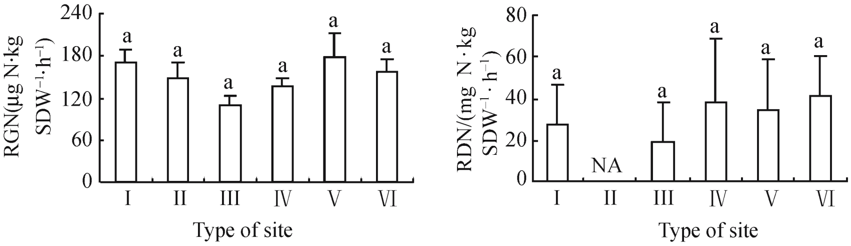


Fig. 1 Variation of gross nitrification rates and denitrification rates in subalpine coniferous forests of different restoration stages

I: 20-year-old spruce plantation
II: 30-year-old spruce plantation
III: 40-year-old spruce plantation
IV: 60-year-old spruce plantation
V: Natural coniferous forest
VI: Coniferous broadleaved forest
RGN: Gross nitrification rate
RDN: Denitrification rate
NA: Not application
Bars with the same letter are not significantly different ($p < 0.05$)

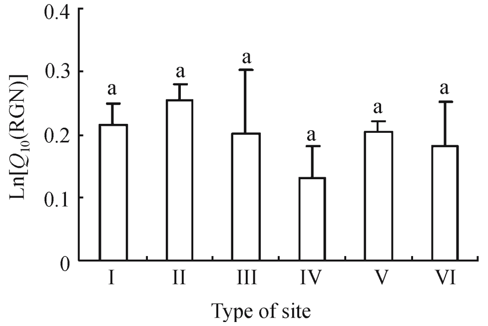
different restoration stages were consistent with the results from other studies (Groffman and Tiedje, 1989; Martikainen and de Boer, 1993; Mummey et al., 1994), which indicated that denitrification played a less important role in nitrogen losses from the subalpine coniferous forest soil in contrast to gross nitrification.

Both nitrification and denitrificaton determined the nitrogen losses form forest soil. Generally, nutrient mechanisms of ecosystems tend to be more effective and nutrient cycle to be more closed from open system in the development stages of forest ecosystems. It seems as if the results of our study do not support this view. Furthermore, there is a piece of evidence that late-successional species prefer ammonium over nitrate as a nitrogen source (Gosz, 1981; Kronzucker et al., 1997). Thus, we inferred that the most valuable ecological process could be firstly enhanced or accelerated in the development of ecosystems, such as nitrogen mineralization in soil nitrogen cycle. Davidson et al. (1992) found that gross mineralization rates in the old forest (above 100-year-old) were two to three times as high as gross mineralization rates in the 10-year-old mixed-conifer plantation. For nutrient mechanisms of forest ecosystems, in the course of restoration or succession, compared with closed nutrient cycle, the more effective mechanisms should be emphasized.

For the result of no significant differences among all forest sites in gross nitrification or denitrification, environmental heterogeneity within each coniferous forest site was also the reason besides those mentioned above, therefore further study was necessary.

4.2 Q_{10} values for gross nitrification

The Q_{10} values (at 11.5°C to 21.5°C) for gross nitrification rates varied from 1.1 to 2.5 in subalpine coniferous forests of different restoration stages. There were no significant differences in the Q_{10} values among all forest sites ($p < 0.05$) (Fig. 2).



I–VI, RGN: see Fig. 1

Fig. 2 Variation of Q_{10} for gross nitrification in subalpine coniferous forests of different restoration stages

It is well known that nitrification in soil is a microbial process and restricted at excessively high or low temperatures. Breuer et al. (2002) reported that gross nitrification was positively correlated to the increase of soil temperature in the Australian tropical rain-forest soils, nitrification activity increased in average 1.17 mg/(m^2·h), and the Q_{10} value was 3.60 at 14°C to 24°C. Ingwersen et al. (1999) studied gross nitrification in a temperate spruce forest soil and found that gross nitrification rates obviously increased with the increasing temperature between 5°C and 25°C, and the Q_{10} value was 4.13 at 15°C to 25°C. In our study, the Q_{10} values for gross nitrification rates at 11.5°C to 21.5°C varied from 1.1 to 2.5. The Q_{10} value defined the temperature dependence or sensitivity to temperature change of soil nitrification, thus these data suggested that variations in topographic positions or community types could alter the temperature dependence of gross nitrification in soil. However, obviously subalpine coniferous forest restoration or succession did not affect the temperature dependence of gross nitrification in current studies.

4.3 Relationships between soil nitrification or denitrification rates and soil water content

Soil water content in our study showed great variation, ranging from 27% to 64%. There was a statistically significant positive relationship between gross nitrification and soil water content ($p < 0.05$). However, no evident relationship was found between denitrification and soil water content ($p < 0.05$) (Fig. 3).

Breuer et al. (2002) found that gross nitrification rates clearly decreased with the increase of soil water content, an explanation for which might be the appearance or extension of anaerobic micro-sites because of restricted O_2 diffusion into the soil at higher soil water contents. In our study, the result of a positive relationship between gross nitrification and soil water content agreed with those of other studies, suggesting that microbial activity increased with the increase of soil water content only within a certain range of water content (Stark and Firestone, 1995; Ingwersen et al., 1999). Denitrification is generally considered as an anaerobic microbial process. Since reductase activities are inhibited by oxygen under aerobic conditions, denitrification is evidently regulated by soil water content and pore space. Weier et al. (1993) reported that denitrification rates increased with the increase of water filled pore space (WFPS). In the present study, no significant relationship between denitrification and soil water content might be associated with denitrification rates that were close to the detection limit.

4.4 Relationships between soil nitrification or denitrification rates and soil pH

All the forest soils in our study site are acid with a pH (water) range of 5.33 to 6.44. As shown in Fig. 4, there were no significant linear relationships between gross nitrification or denitrification and soil pH ($p < 0.05$).

On the basis of studies in agricultural systems, nitrification was considered to be a process mediated solely by autotrophic bacteria and restricted to soils with neutral to slightly alkaline pH, since NO_2 oxidizers limited the accumulation of

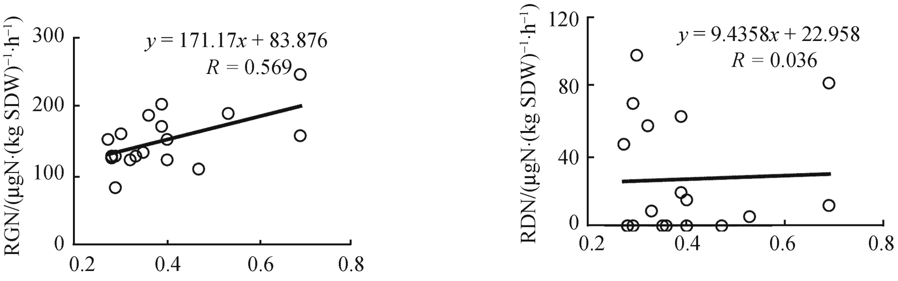


Fig. 3 Relationship between soil water content and gross nitrification rate or denitrification rate

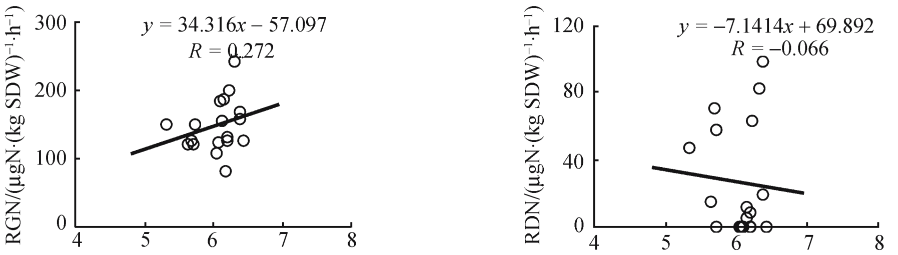


Fig. 4 Relationship between soil pH value and gross nitrification rate or denitrification rate RGN, RDN: See Fig. 1

nitrite in acidic conditions (Hankison and Schmidt, 1988; Laanbroek and Woldendrop, 1995). Our results and those reported recently showed that nitrification could also occur in acid soil (de Boer et al., 1992; Martikainen and de Boer, 1993), which could be explained if heterotrophic microorganisms were responsible or autotrophic nitrifiers were adapted to acidic conditions (Duggin et al., 1991; de Boer et al., 1992; Martikainen and de Boer, 1993). Although soil pH may locally be an important regulator of nitrification, it is not generally a good predictor of regional differences (Robertson, 1982). We found that soil pH did not obviously affect the gross nitrification rates in the current study, which might be related to shifts, at different pH values, in the relative significance of different types of nitrifying microorganisms, acid-tolerant versus acid-sensitive nitrifiers or heterotrophic microorganisms versus autotrophic nitrifiers (Berg et al., 1997). It has been reported that the most optimum soil pH given for denitrification seems to lie in the range from 6 and 8 (Paul and Clark, 1989) and denitrification is inhibited by acid conditions (Blackmer and Bremner, 1978). The low denitrification rates determined in the current study could be due to small populations of denitrifying microorganisms protected in microsites with neutral pH or due to denitrifying microorganisms with low pH optima (Nägele and Conrad, 1990).

4.5 Soil organic matter, total N and C/N ratios

Though high SOM content was found in the 40 year-old spruce plantation forest, coniferous broad-leaved forest and natural coniferous forest, bivariate correlations showed that there was no significant correlation between gross nitrification rates and SOM. There were also no significant correlations between gross nitrification and total N or C/N ratios ($p < 0.05$). Denitrification rates in forest soil were not closely correlated with SOM and total N ($p < 0.05$), but was tightly correlated with C/N ratios ($p < 0.05$) (Table 1).

Table 1 Respective correlation coefficients of gross nitrification rates or denitrification rates with organic matter, total nitrogen or C/N ratios

Correlation coefficient	Organic matter	Total N	C/N ratios
Gross nitrification rates	0.257	0.143	0.600
Denitrification rates	0.029	−0.543	0.829*

* the significant correlation is marked with an asterisk ($p < 0.05$).

The earlier research has been done by Verchot et al. (2002) and found gross nitrification was not significantly correlated with any soil parameter such as total carbon, total nitrogen and C/N ratios in the Yellowstone National Park. The results above suggested that gross nitrification was relatively conservative compared with net nitrification (Stark and Hart, 1997). In general, denitrification is carried out by heterotrophic microorganisms. Ecological factors such as the availability of organic matter, nitrogen content and C/N ratios are usually able to affect soil denitrification rates. According to current study, denitrification rates were not closely correlated with SOM or total N, but correlated with C/N ratios. Our results were consistent with those reported by Menyailo and Huwe (1999), indicating that C/N ratios played a more important role in regulating soil denitrification rates in contrast to SOM and total N.

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