




Soil gross N ammonification and nitrification from tropical to temperate forests in eastern China

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Abstract

1. Nitrogen (N) ammonification and nitrification are two primary microbial processes controlling the availability of soil ammonium (NH_4^+), a key nutrient for vegetative growth. The large-scale patterns of gross ammonification (GA) and gross nitrification (GN) rates represent soil microbial adaptations to different vegetative and environmental conditions. In this study, we investigated GA and GN rates in nine forest soils along a 3,700-km north–south transect in eastern China.
2. We used ^{15}N -labelling techniques, along with field experiments and laboratory incubations, to assess in situ and potential rates of the GA and GN. The mean in situ GA rate was $4.9 \pm 0.5 \text{ mg N kg}^{-1} \text{ day}^{-1}$, whereas the mean potential rate of GA was $32.0 \pm 8.6 \text{ mg N kg}^{-1} \text{ day}^{-1}$. The mean in situ GN rate was $1.7 \pm 0.3 \text{ mg N kg}^{-1} \text{ day}^{-1}$ (potential GN rate: $3.2 \pm 0.6 \text{ mg N kg}^{-1} \text{ day}^{-1}$). GA was significantly higher than GN along the transect, and there were high variations in GA and GN among different forests. Significant relationships were identified between meteorological factors (temperature and precipitation) and the GA and GN rates during the sampling month (August 2013). However, the mean GA rate in primary forest was significantly lower in the Huzhong (HZ), Dongling (DL), Taiyue (TY) and Dinghu (DH) sites compared with other sites, whereas with the exception of the Liangshui (LS) sampling site, the mean GN rate in primary and secondary forests showed the same trends. Significant differences in GA rates were found between primary and secondary forests at the LS and Changbai (CB) sites, and differences were detected in GN rate at the HZ, LS and Jiulian (JL) sites.
3. Structural equation modelling analysis suggested that soil N contents, microbial biomass N pool sizes and bacterial abundance are the primary determinants of the in situ rates of GA and GN. The strong control of edaphic factors on GA and GN indicates a need to improve soil N models with more explicit representation of edaphic factors and their control on soil N transformations.

KEYWORDS

ammonification, forest, microbe, nitrification, nitrogen, productivity, transect

1 | INTRODUCTION

Nitrogen (N) is one of the most important nutrients in terrestrial ecosystems (Vitousek & Howarth, 1991) and is subjected to competitive partitioning between plants and soil micro-organisms (Harrison, Bol, & Bardgett, 2007; Kuzyakov & Xu, 2013). Gross ammonification (GA) and gross nitrification (GN) rates are key soil microbial processes controlling the availability of ammonium (NH_4^+) in soils and thus the primary productivity of terrestrial ecosystems. Microbial ammonification is a key process in N cycling, as it defines the formation of NH_4^+ from organic matter, with ammonium being the preferred N form for plant and microbial metabolism and protein synthesis (Dannenmann et al., 2009). Microbial ammonification is also defined as N mineralization (Kirkham & Bartholomew, 1954). Nitrification is a key process converting NH_4^+ to nitrate in soils, and next to plant uptake, it represents the second largest sink of NH_4^+ (Butterbach-Bahl, Baggs, Dannenmann, Kiese, & Zechmeister-Boltenstern, 2013).

Soil GA and GN rates are primarily controlled by soil microbes and environmental factors, such as soil substrate quality and quantity, mean annual precipitation (MAP) and mean annual temperature (MAT), plant diversity and the composition of soil microbial communities (Grenon, Bradley, & Titus, 2004; Templer, Findlay, & Lovett, 2003; Xu, Zhou, & Shimizu, 2009). Mean annual precipitation and MAT have been found to substantially affect soil gross N transformations via different mechanisms (Emmett et al., 2004; Lukewille & Wright, 1997; Schmidt et al., 2004). For instance, higher MAT and MAP might stimulate N ammonification, as these conditions are favourable for soil microbes, whereas lower MAP might suppress ammonification as microbial communities are exposed to drought stress. In contrast, reduced MAP might promote soil ammonification or nitrification, as soil aeration might be improved (Dannenmann et al., 2009). Conflicting results have been obtained with regard to the effects of warming on ammonification; for example, some studies have detected stimulating effects (Larsen et al., 2011; Yin et al., 2013), whereas a few other studies have shown that warming can suppress ammonification (Beier et al., 2008) or that the temperature dependency of ammonification is not significant (Auyeung, Suseela, & Dukes, 2013). Drought impacts might be spatially heterogeneous; for instance, Larsen et al. (2011) and Emmett et al. (2004) found that drought decreased soil N ammonification rates in Danish heathland, whereas Breuer, Kiese, and Butterbach-Bahl (2002) and Niboyet et al. (2011) reported a large discrepancy in nitrification rates in an annual grassland ecosystem in the Jasper Ridge Global Change Experiment site (CA, USA). Other environmental factors have also been found to be of importance for N cycling processes; for example, a meta-analysis has indicated that GA is positively correlated with microbial biomass and soil C and N concentrations, whereas the soil C:N ratio exerts a negative effect on ammonification only after adjusting for differences in soil C (Booth, Stark, & Bastetter, 2005). Although several studies on ammonification/nitrification have been carried out, little is known regarding the responses of GA and GN rates to different environmental factors at a large scale (Booth et al., 2005).

Given the strong environmental controls on GA and GN rates and the spatial heterogeneity of environmental factors, large variations in

soil gross N transformations are expected across different ecosystem types (Baldos, Corre, & Veldkamp, 2015; Booth et al., 2005; Hart, 2006; Shaver et al., 2001). Furthermore, since climate change is likely to exert different effects on biogeochemical processes depending on factors such as forest types, which might be mostly synergistic or antagonistic rather than additive, comparative field studies at a large scale across different climate zones are urgently needed. However, spatial-temporal variations in soil GA and GN are poorly understood or explored, and few studies have investigated forests GA and GN rates at large scale. Moreover, studies comparing in situ measurements with laboratory-measured potential gross rates under standard conditions (temperature and moisture) are likely to enhance our mechanistic understanding of the control of N cycling across different ecosystems.

Here, using ^{15}N -labelling techniques for in situ experiments and laboratory incubation (using the growing season mean temperature and 55% soil water-holding capacity), we investigated the potential and in situ rates of GA and GN for nine paired forest sites (primary vs. secondary forests) from tropical forests to temperate forests in eastern China. We aimed to determine whether large-scale spatial patterns of soil gross N transformations exist and which environmental parameters are determinants for such patterns. Specifically, we set ourselves the following objectives: (1) to quantify the potential and in situ gross N turnover rates (GA and GN rates) at nine forest sites along a climatic gradient in eastern China; (2) to gain a mechanistic understanding of the environmental and biological controls of soil GA and GN rates along the transect; and (3) to determine differences in GA and GN between primary and secondary forest ecosystems along the transect.

2 | MATERIALS AND METHODS

2.1 | Site description

Soil samples were collected from nine paired (primary versus secondary) forest ecosystems along the 3,700-km north-south transect of eastern China (NSTEC, Figure 1), a unique belt of vegetation zones reflecting a pronounced temperature and rainfall gradient (Table 1). We selected nine sampling sites representing different forest types: tropical forests (JF, Jianfeng; DH, Dinghu; JL, Jiulian), temperate/subtropical forests (SN, Shennong; TY, Taiyue; DL, Dongling) and temperate forests (CB, Changbai; LS, Liangshui; HZ, Huzhong). The growing season of the temperate forest ecosystems in the north of the transect lasts from approximately April to October, whereas the forest ecosystems investigated in the south of the transect are evergreen with a vegetation period covering the entire year. MAT at the sampling sites ranges from -0.30°C in LS to 20.90°C in DH, and MAP ranges from 481.60 in HZ to 2,449 mm in JF. The 18 forest ecosystems thus span a range of climates from temperate to tropical, and a range of forest types, including temperate forest and temperate, subtropical and tropical forest (Wang, He, Yu, & Yu, 2016). At each of the 18 forest sites, 10 plots ($10\text{ m} \times 10\text{ m}$) were randomly selected. All primary forest sites were located in national natural reserves in order to exclude possible anthropogenic disturbances. These natural reserves have relatively homogenous vegetation types that are representative

TABLE 1 Soil characteristics in different sampling sites ($M \pm SE$)

Sites	Forest type	ST (°C)	Pre (mm)	pH	SOM (g/kg)	Total N (%)	C/N	NH ₄ ⁺ (mg/kg)	NO ₃ ⁻ (mg/kg)
HZ	Primary	-4.40	481.60	4.79 \pm 0.07	7.27 \pm 0.18	0.31 \pm 0.02	15.85 \pm 0.70	8.35 \pm 0.37	4.22 \pm 0.21
	Secondary				15.49 \pm 1.33	0.68 \pm 0.07	20.61 \pm 0.58	9.64 \pm 1.22	4.60 \pm 0.30
LS	Primary	-0.30	676.00	5.41 \pm 0.01	11.87 \pm 1.23	0.46 \pm 0.04	16.85 \pm 1.04	10.98 \pm 1.35	5.06 \pm 0.41
	Secondary				13.17 \pm 0.89	0.46 \pm 0.05	19.72 \pm 0.56	11.32 \pm 1.25	5.16 \pm 0.39
CB	Primary	2.60	691.00	5.09 \pm 0.06	12.07 \pm 0.40	0.64 \pm 0.03	11.09 \pm 0.18	11.84 \pm 1.17	5.03 \pm 0.42
	Secondary				12.95 \pm 1.20	0.62 \pm 0.10	11.31 \pm 0.25	11.70 \pm 1.24	4.85 \pm 0.53
DL	Primary	4.80	539.10	5.68 \pm 0.04	6.81 \pm 0.11	0.31 \pm 0.01	12.48 \pm 0.07	11.99 \pm 1.13	4.66 \pm 0.59
	Secondary				5.08 \pm 0.24	0.24 \pm 0.01	13.78 \pm 0.19	10.93 \pm 0.96	4.61 \pm 0.57
TY	Primary	6.20	662.00	5.70 \pm 0.04	7.49 \pm 0.42	0.26 \pm 0.01	17.58 \pm 0.21	10.09 \pm 0.53	4.34 \pm 0.43
	Secondary				2.95 \pm 0.07	0.15 \pm 0.01	14.88 \pm 0.40	9.97 \pm 0.53	4.60 \pm 0.56
SN	Primary	10.60	1,330.00	5.84 \pm 0.002	6.61 \pm 0.34	0.38 \pm 0.01	11.11 \pm 0.25	9.66 \pm 0.32	4.80 \pm 0.58
	Secondary				7.33 \pm 0.11	0.41 \pm 0.01	15.41 \pm 0.72	10.26 \pm 0.42	5.64 \pm 0.64
JL	Primary	16.70	1,954.00	4.39 \pm 0.35	5.82 \pm 0.37	0.23 \pm 0.01	15.17 \pm 0.29	9.82 \pm 0.56	6.46 \pm 0.56
	Secondary				7.30 \pm 0.08	0.33 \pm 0.004	14.80 \pm 0.12	9.84 \pm 0.56	6.10 \pm 0.76
DH	Primary	20.90	1,927.00	4.11 \pm 0.20	5.06 \pm 0.14	0.18 \pm 0.10	15.93 \pm 0.22	9.73 \pm 0.57	5.84 \pm 0.87
	Secondary				5.83 \pm 0.59	0.24 \pm 0.01	17.26 \pm 0.34	9.50 \pm 0.62	5.24 \pm 0.97
JF	Primary	19.80	2,449.00	4.71 \pm 0.06	4.89 \pm 0.18	0.19 \pm 0.004	11.44 \pm 0.18	9.28 \pm 0.60	5.06 \pm 0.98
	Secondary				3.41 \pm 0.19	0.16 \pm 0.01	11.78 \pm 0.24	8.86 \pm 0.26	4.46 \pm 0.78

for each region. Detailed information regarding the selected forest ecosystems was provided by Xu et al. (2017). Secondary forest sites were located outside the primary forests and are subject to low anthropogenic disturbance. At these sites, we ensured that vegetation, soil type and slope were consistent with those sites identified in the natural reserves (Table 1).

2.2 | Field sampling and in situ incubation

Field sampling was conducted in July and August 2013. At each of the 10 plots within a forest site, we measured above-ground biomass and root biomass. Rates of soil GA and GN were measured in situ and under laboratory conditions using intact soil cores. Furthermore, we determined soil microbial biomass C (MBC) and N (MBN), the abundance of bacteria and fungi and other potentially relevant soil parameters, including soil pH, gravimetric soil moisture (SM), concentrations of soil ammonium (NH₄⁺) and nitrate (NO₃⁻), soil organic matter (SOM) and dissolved organic carbon (DOC).

Following plot selection, the plant community composition was recorded, which is described in detail in our previous publications (Wang, He, et al., 2016; Wang, Yu, He, & Xu, 2016). To investigate soil N transformations in the primary and secondary forest ecosystems, we sampled 720 (18 \times 10 \times 4) undisturbed soil cores, using stainless steel cylinders (diameter 5 cm, height 12 cm). At each plot, eight soil cores (two pairs of soil cores for in situ incubation and two pairs for laboratory incubation) were sampled at a 100 m distance between two soil cores. We selected two pairs of cylinders, one pair for Time 1 (T1, the beginning of incubation time) and the other for Time 2 (T2, 40 hr later for the end of incubation time). Two pairs of soil cores were transported

to the laboratory for labelling with ¹⁵N solution to measure GA and GN rates using the ¹⁵N pool dilution method (see below). After isotopic labelling, one pair of soil cores was transferred back to the field for incubation and the measurements of in situ rates, whereas the other pair was retained in the laboratory for incubation experiments. Detailed information on these procedures can be found in Wang, Chen, et al. (2016). There were two paired soil cores for quantifying GA and GN rates, which were labelled with ¹⁵NH₄⁺ and ¹⁵NO₃⁻, respectively. We also used another soil core to quantify gravimetric soil water content, organic extractable N, DOC, MBC and MBN and phospholipid fatty acid (PLFA) measurements. Annual and August precipitation and temperature data were obtained from meteorological stations adjacent to each of the nine different forest sites along the gradient.

2.3 | Measurement of the in situ rates of GA and GN

Intact soil cores were used to quantify GA and GN rates using the ¹⁵N pool dilution technique. Two soil cores were labelled with ¹⁵N-(NH₄)₂SO₄ solution for the quantification of GA rate, and another two soil cores were labelled with ¹⁵N-KNO₃ for determining GN rate. We used a multi-needle injector system consisting of 10 simultaneously operated syringes with custom-made side-port cannulas to achieve reproducible homogenous distribution of ¹⁵N label in the soil columns (described in detail by Wang, Chen, et al., 2016). In total, 2 mg N/kg dry soil of label was added, with a ¹⁵N enrichment of 30 atom%. Two paired soil cores were labelled immediately with ¹⁵NH₄⁺ and ¹⁵NO₃⁻, with one group (T1) being extracted immediately with 0.5 M K₂SO₄ solution using a soil/solution ratio of 1:2 (Dannenmann et al., 2009). The other group was subsequently incubated at a soil

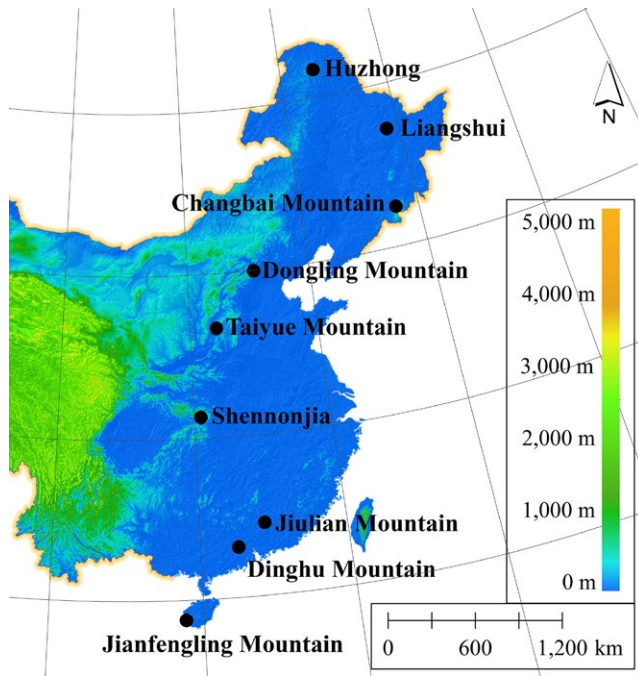


FIGURE 1 The map of sampling sites (cool temperate coniferous forest: Huzhong (HZ); warm temperate conifer broad-leaved mixed forest: Liangshui (LS), Changbai (CB); warm temperate deciduous broad-leaved forest: Dongling (DL), Taiyue (TY); subtropical evergreen broad-leaved forest: Shennong (SN), Jiulian (JL); subtropical monsoon evergreen broad-leaved forest: Dinghu (DH); tropical monsoon forest: Jianfeng (JF))

temperature close to the in situ soil temperature at 10:00 a.m. on the same day and was subsequently harvested 40 hr (T2) after isotopic labelling.

Soil extracts were immediately processed for diffusion of NH_4^+ and NO_3^- on acid filter traps as described by Dannenmann, Gasche, Ledebuhr, and Papen (2006). Filters were analysed for ^{15}N enrichment using elemental analyser-isotope ratio mass spectrometry analysis at the Nanjing Normal University. Extracted subsamples were brought back to the IBCAS laboratory for the analysis of NH_4^+ and NO_3^- concentrations. The equations provided by Kirkham and Bartholomew (1954) were used to calculate the rates of GA and GN. All soil samples were rewetted to c. 60% maximum water-holding capacity by adding or freeze drying soil to the respective amount of water. Soil samples were incubated in different chambers according to the average temperature of the growing seasons in corresponding sites.

2.4 | Measurement of potential GA and GN under experimental incubation

The ^{15}N pool dilution technique was also used to determine potential GA and GN rates as described in Wang, Dannenmann, Meier, and Butterbach-Bahl (2014). As in the field incubation, soil was labelled with either $^{15}\text{N}-(\text{NH}_4)_2\text{SO}_4$ or $^{15}\text{N}-\text{KNO}_3$ solution, with N being enriched at 30 atom% ^{15}N . Three millilitres of soil solution, equivalent to 2 mg N/kg soil, was added to 100 g^{-1} dry soil equivalent. For this, the $^{15}\text{N}-(\text{NH}_4)_2\text{SO}_4$ or $^{15}\text{N}-\text{KNO}_3$ solution was homogenously sprayed

on the soil and then the soil was mixed. After labelling, we extracted labelled soil with 60 mL of 0.5 M K_2SO_4 by rigorously shaking the soil solution (T1, the beginning of incubation time) for 0.5 hr using a reciprocal shaker and filtering through Whatman No. 1 filter papers (10.5 cm in diameter). This process was repeated after 40 hr (T2, the end of incubation time). Soil extracts were used for colorimetric determination of NH_4^+-N and NO_3^--N concentrations and ^{15}N enrichment in NH_4^+ and NO_3^- (Dannenmann et al., 2006; see above).

2.5 | Measurement of bacterial and fungal abundance

Phospholipid fatty acid analysis was used to measure soil microbial community diversity (Zhang, Wan, et al., 2015). This method allows a differentiation between bacteria and fungi (Amann, 1995). We extracted, fractionated and quantified PLFAs from fresh soils following the procedure described by Bossio and Scow (1998). Fresh soil samples equivalent to 8 g dry mass of soil were extracted for 2 hr by using a single-phase mixture containing a chloroform, methanol and phosphate buffer (1:2:0.8 v/v/v; detailed information can be found in Xu et al., 2017). It should be noted that GA, GN, NH_4^+ , NO_3^- , bacteria, fungi, N content and SOM are expressed on a mass basis (mg/kg).

2.6 | Statistics

Differences in GA, GN, MBC/N, bacterial, fungal and N contents and SOM were assessed using a one-way ANOVA. The effects of forest type on the examined parameters were analysed using a two-factorial ANOVA with treatment (in situ incubation and laboratory incubation) and site (nine sampling sites) as factors ($n = 6$ replicated measurements per sampling day and treatment). Pearson's correlation coefficients were calculated to identify relationships between N turnover rates and microbial diversity, as well as other soil characteristics. In order to determine significant differences between primary forest and secondary forest at each sampling site, a one-way ANOVA with Fisher's least significant difference test for independent samples was performed. Statistical analyses were conducted using SAS 8.0.

3 | RESULTS

3.1 | Variation in in situ GA and GN between primary and secondary forests

Significant differences in GA and GN were found between the primary and secondary forests at two sites: LS ($p < .05$; Figure 2) and Chang Bai Mountain (CB; $p < .01$, Figure 3). At the LA site, GA in the primary forest was significantly higher by 46.5% than that in the secondary forest ($7.53 \pm 0.82 \text{ mg kg}^{-1} \text{ day}^{-1}$ vs. $4.03 \pm 1.07 \text{ mg kg}^{-1} \text{ day}^{-1}$), whereas at the CB site, GA in the primary forest was significantly lower by 37.8% than that in the secondary forest ($5.28 \pm 0.95 \text{ mg kg}^{-1} \text{ day}^{-1}$ vs. $8.48 \pm 0.32 \text{ mg kg}^{-1} \text{ day}^{-1}$). At other sampling sites, there were no significant differences in GA rates between primary and secondary forests ($p > .05$). However, the

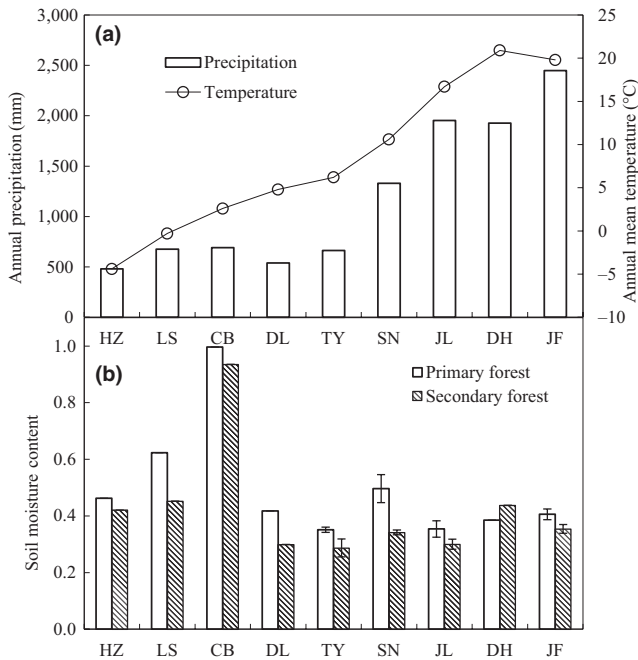


FIGURE 2 Mean annual precipitation (MAP) and temperature (MAT) for the nine forest ecosystems (site abbreviations: JF, Jianfeng; DH, Dinghu; JL, Jiulian; SN, Shennong; TY, Taiyue; DL, Dongling; CB, Changbai; LS, Liangshui; HZ, Huzhong)

differences in GN rates between primary and secondary forests varied across sites. For example, GN rate was significantly lower in primary forest than that in secondary forest for the HZ ($p < .001$) and JL Mountain ($p < .01$) sites, whereas GN rate was significantly higher in primary forest than in secondary forest sites for the LS site ($p < .05$, Figure 3). At other sampling sites, there were no significant differences in GN rates between primary and secondary forests ($p > .05$).

3.2 | Variation in potential GA and GN between primary and secondary forests

Potential soil GA rates between primary (48.63 ± 8.12 to 156.42 ± 11.27 $\text{mg kg}^{-1} \text{day}^{-1}$) and secondary (2.46 ± 0.50 to 55.36 ± 9.28 $\text{mg kg}^{-1} \text{day}^{-1}$) forest ecosystems showed different patterns along the transect (Figure 4). Potential GA rates were significantly higher only in the secondary forest compared with those observed for primary forests at the HZ and JL sites ($p < .05$, Figure 4). However, there were no significant differences in potential GA rates between primary and secondary forests at the DL site. At the other six sites (LS, CB, TY, SN, DH and JF), the potential GA rate was significantly higher in the soils of primary forest ($p < .05$, Figure 3) than in the soils of secondary forest. For all sites, we detected no significant differences in potential GN rates between primary and secondary forests.

3.3 | Ratio of in situ to potential rates of GA and GN along the transect

There were no significant differences in the ratio of in situ to potential rates of soil GA (c. 0.41) between primary forest and secondary forests

across all nine sites ($p > .05$, Figure 5). For the ratio of in situ to potential rates of GN, significant differences were found between primary and secondary forests in HZ, CB and JL sites ($p < .0001$, Figure 5). The ratio of in situ to potential rates for GN was significantly higher in secondary forest than in primary forest ($p < .05$). In DL, SN and JF, the ratios of in situ to potential rates of GA and GN were c. 1, indicating the small limitation effect of environmental factors on N processes. For the other ecosystems, considerably lower ratios indicated that the N processes of N transformations were readily affected by changes in global warming or precipitation patterns in northern forests.

3.4 | Biotic and abiotic controls on GA and GN

Both GA and GN are controlled by biotic and abiotic factors. GA was positively correlated with total soil N concentration (Table 2, Figure 6), reflecting the importance of substrate availability in regulating inorganic N production. Microbial biomass N was also significantly correlated with GA and GN rates (Table 2). As with microbial biomass, there was a significant negative relationship between the soil C:N ratio and GA and GN rates (Table 2, $p < .001$). With an increase in the C:N ratio, there was a significant decrease in the GA rates in secondary forest ($R^2 = .11$, $p = .007$, Table 2). Furthermore, GN rates were negatively correlated with the C:N ratio in primary forests ($R^2 = .34$, $p < .001$, Table 2), although we could detect no differences between primary and secondary forest sites. Positive relationships between GN rates and N content and MBN, bacterial quantity, soil N and SOC were found for both primary and secondary forest sites (Table 2, Figure 6).

4 | DISCUSSION

4.1 | Spatial pattern and environmental controls of soil gross N transformations in different forest ecosystems

Our results showed that there were significant differences between in situ and potential soil GA and GN rates among different forest ecosystems. However, no apparent latitudinal pattern was detected. Instead, our data show that in soils with lower C:N ratios and higher organic and mineral N pools, there are higher rates of GA and GN. This finding is consistent with the results of studies in adjacent native forest in China (Zhang, Zhu, Cai, & Müller, 2011). Thus, together with the results of previous studies, our data indicate that the possible influence of climate gradients might be masked by the large spatial heterogeneity in gross N turnover in forest ecosystems (Burton, Chen, Xu, & Ghadiri, 2007). With regard to the magnitudes of GA and GN, Zhao, Cai, and Xu (2015) reported rates of GA and GN of $5.00 \text{ mg kg}^{-1} \text{day}^{-1}$ and up to $2.19 \text{ mg kg}^{-1} \text{day}^{-1}$, respectively, for subtropical forests in China. A further study by Zeng et al. (2014) has found comparably high rates, that is, GN rates of 4, 5.3 and $6 \text{ mg kg}^{-1} \text{day}^{-1}$ in coniferous, deciduous and evergreen broad-leaved forests in northern China, respectively. These observations are further confirmed in our study on GA and GN across nine different forest ecosystems in China, in which we recorded GA rates

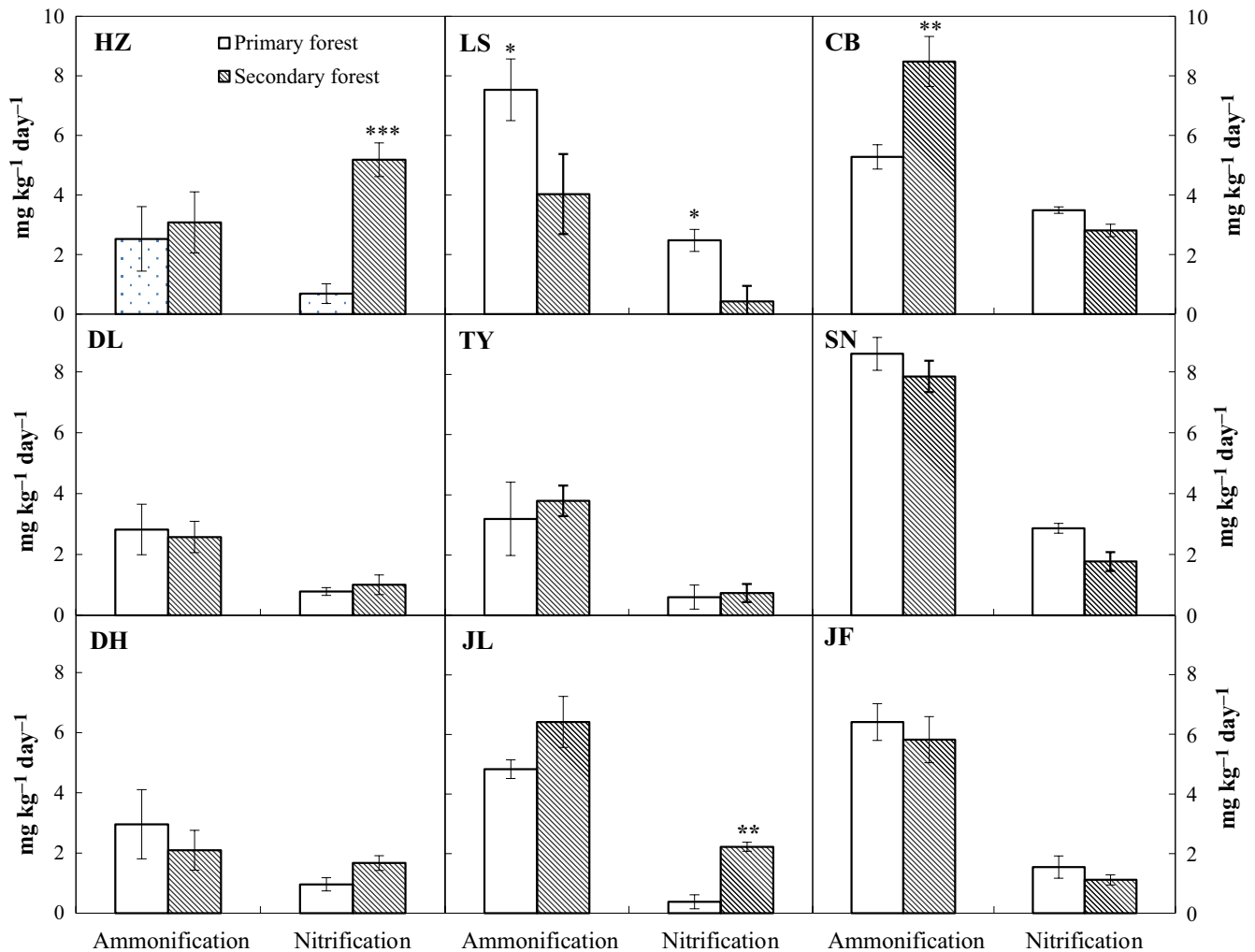


FIGURE 3 The in situ rates of gross ammonification and nitrification in different forest types (site abbreviations: JF, Jianfeng; DH, Dinghu; JL, Jiulian; SN, Shennong; TY, Taiyue; DL, Dongling; CB, Changbai; LS, Liangshui; HZ, Huzhong) *, **, *** indicates difference at the significance level of $p = .05$, $p = .01$, $p = .001$

ranging from 2.5 to 8.6 mg kg⁻¹ day⁻¹, and GN rates in the range of 0.6–3.49 mg kg⁻¹ day⁻¹.

In addition to soil properties such as C:N ratio, soil microbial diversity (Xu et al., 2017) was also found to control GA and GN rates in our forest ecosystem study sites. This is also confirmed by our study, as differences in soil N form and MBN content among the different forests were mirrored by GA and GN rates. In our study, GA was primarily affected by the soil C:N ratio in coniferous forests, but by soil pH in deciduous forests, whereas GA rates in subtropical evergreen forests were closely related to total C and N, NH₄⁺-N, DON and MBN contents (Table 2, Figure 6). Combined with the correlations between N transformations and soil properties, these findings suggest that soil C and N contents, as well as changes in MBC and MBN, are the principal factors contributing to the observed significant differences in gross soil N transformation rates across our nine sampling sites.

Across all sites, soil GA rates were higher than soil GN rates. This indicates that nitrification is limited even under optimal conditions (Dannenmann et al., 2006). The low GN rates under low pH conditions indicate that soil acidity is a major factor controlling the nitrification

process (Dannenmann et al., 2006; Zhang, Cai, Zhu, Yang, & Müller, 2013). Comparable higher rates of GN have been reported in studies analysing microbial N turnover in the temperate grasslands of Inner Mongolia, China (Holst et al., 2007; Wu et al., 2011). These authors explained the high rates found in their studies in terms of the occurrence of heterotrophic nitrification, which involves the direct oxidation of reduced organic N compounds to nitrite or nitrate (Huygens et al., 2008; Zhang, Müller, & Cai, 2015). Heterotrophic nitrification has also been found to be a significant and even dominant process of nitrate production in some forest ecosystems (Burton et al., 2007; Grenon et al., 2004; Koyama, Kavanagh, & Stephan, 2010; Pedersen, Dunkin, & Firestone, 1999), as well as in a range of more acidic grassland ecosystems (Cookson et al., 2006; Huygens et al., 2008; Rutting et al., 2008).

4.2 | Soil N pools control GA and GN rates in forest ecosystems along the transect

Several studies have indicated that soil gross N transformation rates are forest type-dependent; however, the underlying mechanisms

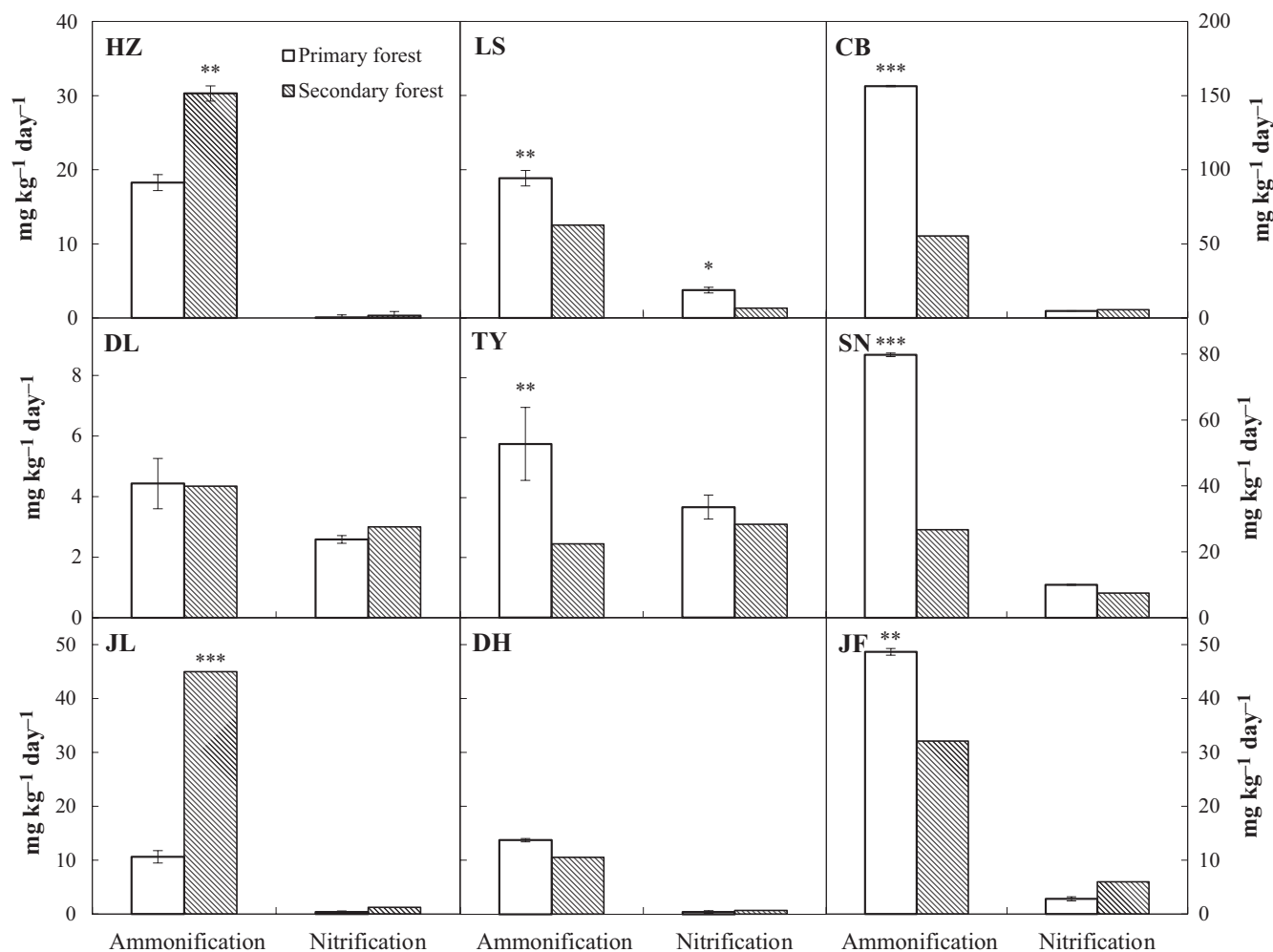


FIGURE 4 Potential rates of gross ammonification and nitrification in different forest types measured in laboratory (site abbreviations: JF, Jianfeng; DH, Dinghu; JL, Jiulian; SN, Shennong; TY, Taiyue; DL, Dongling; CB, Changbai; LS, Liangshui; HZ, Huzhong). *, **, *** indicates difference at the significance level of $p = .05$, $p = .01$, $p = .001$

have yet to be clarified (Zhang et al., 2013, 2016). The present study shows that across a wide range of forest ecosystems, soil GA and GN rates are positively correlated with the soil active N pool (MBN) and soil total N pool, which is consistent with the findings of a previous comprehensive meta-analysis (Booth et al., 2005). In addition, we found that the soil C:N ratio is significantly negatively correlated with GA rates, suggesting that SOM also plays an important role in regulating ammonification to some extent, through its influence on microbial biomass and activity (Zhang, Wan, et al., 2015). Interestingly, GN rates were significantly the lowest at the DL and TY sites, that is, those sites where not only MBN, bacterial quantity and soil total N contents were low, but which also showed significant relationships between GN rates and these parameters ($p < .05$). This observation is consistent with the positive correlation between GN and microbial biomass reported by Baldos et al. (2015). The highest GN rates in the present study were detected at sites in the subtropics, where we also recorded a higher soil total organic N pool. The rate of nitrification remained low even though the rate of ammonification was twice that of nitrification. This result is in agreement with the findings of other studies, which have indicated that the NO_3^- immobilization process can

function independently of NH_4^+ concentration (Dannenmann et al., 2006; Zhang et al., 2011).

4.3 | Climatic factors affect soil GA and GN rates in forest ecosystems along the transect

Less favourable climatic conditions (precipitation and temperature) have been shown to contribute to increased or decreased soil gross N ammonification (Baldos et al., 2015; Wang, Chen, et al., 2016). Although we identified significant relationships between actual soil temperature or moisture and GA and GN rates in primary and secondary forest soils along the transect, we were unable to detect a general climate effect. The lack of an overall climate response of GA and GN in our study is in contrast to the results presented by Shaw and Harte (2001), who reported that soil GA and GN rates across different sub-alpine forest ecosystems were controlled by climatic factors, such as precipitation and temperature. Furthermore, at a regional scale, significant relationships between N ammonification rates and soil temperature/precipitation within the same plant community ecosystem have been demonstrated (Koyama et al., 2010; Wang et al., 2011;

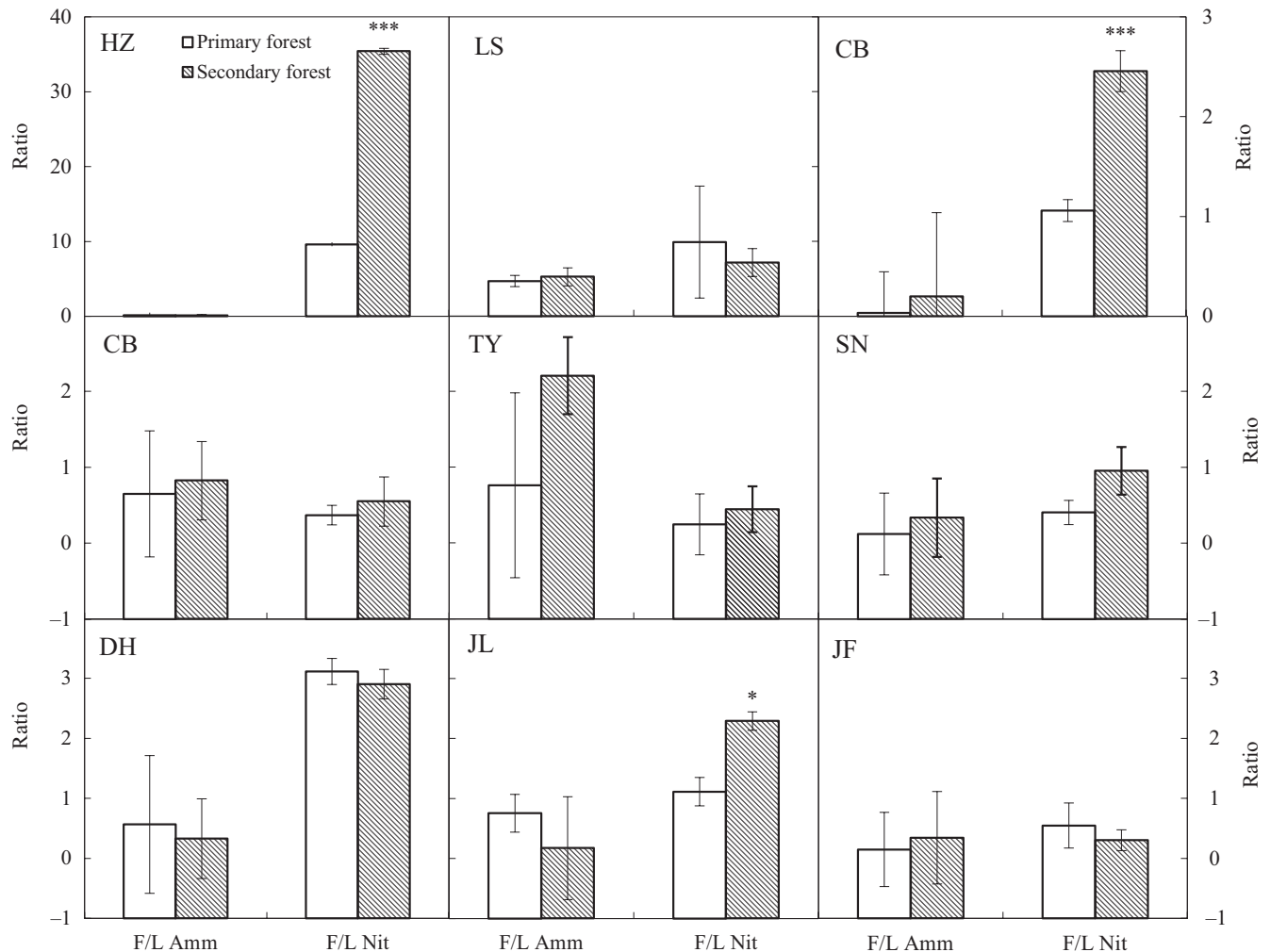


FIGURE 5 The ratio of in situ measurements to potential rates of gross ammonification and nitrification for nine forest ecosystems (different letters represent different sampling sites; site abbreviations: JF, Jianfeng; DH, Dinghu; JL, Jiulian; SN, Shennong; TY, Taiyue; DL, Dongling; CB, Changbai; LS, Liangshui; HZ, Huzhong; *** indicates difference at the significance level of $p = .05$)

Wang, Wan, Xing, Zhang, & Han, 2006; Zhang et al., 2016). Generally, the important role of soil organic carbon and substrate availability for the regulation of N ammonification is well accepted (Booth et al., 2005; Cheng, Wang, & Wang, 2014) and confirmed by the findings of the present study. Different forest litter produces different organic substrates, and the effects of soil characteristics on N ammonification were greater than those of precipitation and temperature at a large scale. This indicates that although climate change induced by increasing temperature and changes in precipitation patterns may directly affect soil enzyme activities via changes in soil temperature and moisture, it is more likely to affect these activities by increasing the availability of labile carbon substrates.

The laboratory incubation experiment performed in the present study showed that soil potential GA and GN rates gradually increase with increasing SM below the field water-holding capacity, confirming the previous results of Bengtson, Falkengren-Grerup, and Bengtsson (2005). Additionally, Mathieu, Milloux, Bizouard, and Andreux (2006) found that potential GA rates were higher under saturated conditions than under unsaturated conditions in an arable soil, and Burton et al.

(2007) also reported higher rates under aerobic than under anaerobic incubation in soils covered by forest and hoop pine plantation. Increases in labile organic C and N concentrations resulting from the lysis of dead microbial cells could increase gross N ammonification rates by increasing SM content (Borken & Matzner, 2009). Previous studies have reported that the relationship between SM content and N ammonification differs in different soils and that dry soil has an adverse on N ammonification (Paul et al., 2003; Rosenkranz et al., 2010) as substrate diffusion becomes limiting (Wang, Chen, et al., 2016). Drying below a certain threshold, which is soil texture-dependent, generally decreases microbial activity, as can be observed by a decrease in heterotrophic respiration under lower SM content (Cheng, Wang, et al., 2014). However, most studies have failed to demonstrate a general relationship between in situ SM content and ammonification rates across soil types, because of differences in factors such as microbial community composition, porosity, organic matter content, pH and temperature (Paul et al., 2003; Wang, Zhang, Müller, & Cai, 2017; Zhang et al., 2013). Similarly, Saetre and Stark (2005) found that GA and GN rates were sensitive to SM changes in boreal forest soils,

TABLE 2 Pearson's correlation coefficients for the collected soil parameters as calculated for the dataset at the level single organic layer (0–10 cm). Significant Pearson's coefficient is boldface, and asterisks indicate the level of statistical significance

	GA	GN	Bacterial	Fungi	F/B	Precipitation	Temperature	MBC	MBN	MBC/MBN	NH ₄	NO ₃	N%	C/N	DON
GA															
GN	0.08*														
Bacterial	0.09**	0.074**													
Fungi	0.078**	0.104***	0.0004												
F/B	-0.14***	-0.13***	-0.079*	0.73***											
Precipitation	0.02	0.02	0.03	0.012	0.011										
Temperature	0.002	0.07**	0.055*	0.04*	0.06*	0.87***									
MBC	0.005	0.07**	0.05*	0.09**	0.19***	0.22	0.51***								
MBN	0.24***	0.14***	0.28***	0.04*	0.14***	0.14***	0.26***	0.22***							
MBC/MBN	0.006	0.03	0	0.09**	0.13***	0.12***	0.33***	0.77***	0.009						
NH ₄	0.08**	0.006	0.99	0.002	0.0006	0.17***	0.09*	0.004	0.03	0.01					
NO ₃	0.08**	0.004	0.001	0.0002	0.006	0.09**	0.103***	0.05*	0.02	0.04*	0.004				
N%	0.067**	0.41***	0.23***	0.12***	0.24***	0.23***	0.35***	0.34***	0.41***	0.15***	0.03	0.02			
C/N	-0.11***	-0.34***	-0.2***	0.05*	0.03	0.07**	0.08**	0.17***	0.1**	0.3***	0.14***	0.006	0.01		
DON	0.064**	0.03	0.11***	0.0006	0.01	0.1*	0.1*	0.05*	0.02	0.09**	0.09**	0.01	0.004	0.18***	
pH	0.035	0.0003	0.0001	0.0008	0	0.3***	0.21***	0.009	0.07**	0.09**	0.0005	0.01	0.02	0.01	0.005

p* < .05, *p* < .01, ****p* < .001.

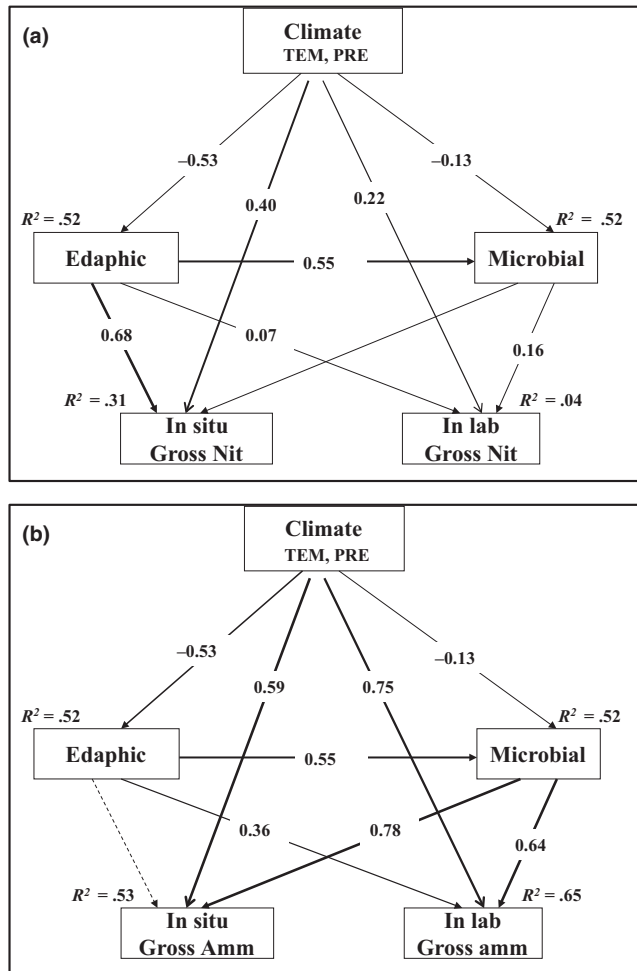


FIGURE 6 Structure equation model (SEM) analysis of the effects of climate (temperature and precipitation) on in situ and in laboratory gross ammonification (a) and nitrification (b) rates via pathways of edaphic and microbes in nine forest ecosystems

which was also confirmed at the boreal forest sites investigated in the present study.

5 | CONCLUSION

Using a ^{15}N -labelling technique, we investigated N cycling (ammonification and nitrification) in nine forest soils along a 3,700-km NSTEC. We determined the rates of GA and GN along the transect and examined their controlling factors. GA was significantly higher than GN along the transect, and there were high variations in GA and GN among different forests. Significant relationships were detected between actual temperature and precipitation and the GA and GN rates. Significant differences in GA were detected between primary and secondary forests, and soil N content, MBN pool sizes and bacterial abundance were identified as factors controlling potential and in situ rates of GA and GN rates. The strong control of edaphic factors on GA and GN indicates a need to improve soil N models with more explicit representation of edaphic factors and their control on soil nitrogen transformations.

This study represents the first attempt to simultaneously investigate potential and in situ soil gross N transformations from tropical to temperate forests across a 3,700-km transect in China. As nitrogen cycling and its regulation of carbon cycling have been incorporated into Earth system models in recent years, this large-scale study is valuable in two respects. First, the spatial variations in GA and GN and their controlling factors advance our understanding of N cycling in forest ecosystems and the mechanistic controls; second, the dataset and information obtained in this study could be used as an important foundation for modelling and predicting N cycling under a changing climate.

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AUTHORS' CONTRIBUTIONS

C.W., N.H., S.N., G.Y. and X.H. conceived the ideas and designed methodology; N.W., J.Z. and Y.L. collected the data; C.W. and N.W. analysed the data; C.W., X.X. and N.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. For data sharing or any other questions, please contact Dr. N. P. He.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.6nq0d> (Wang, Zhang, et al., 2017).

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