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Unexpected malformations in
Xenopus tropicalis



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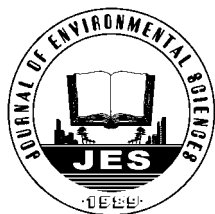
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Effects of temperature change and tree species composition on N₂O and NO emissions in acidic forest soils of subtropical China

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ABSTRACT

Tree species and temperature change arising from seasonal variation or global warming are two important factors influencing N₂O and NO emissions from forest soils. However, few studies have examined the effects of temperatures (5–35°C) on the emissions of forest soil N₂O and NO in typical subtropical region. A short-term laboratory experiment was carried out to investigate the influence of temperature changes (5–35°C) on soil N₂O and NO emissions under aerobic conditions in two contrasting (broad-leaved and coniferous) subtropical acidic forest types in China. The results showed that the temporal pattern of N₂O and NO emissions between the three lower temperatures (5°C, 15°C, and 25°C) and 35°C was significantly different for both broad-leaved and coniferous forest soils. The effects of temperature on soil N₂O and NO emission rates varied between broad-leaved and coniferous forest soils. Both N₂O and NO emissions increased exponentially with an increase in temperature in the broad-leaved forest soil. However, N₂O and NO emissions in the coniferous forest soil were not sensitive to temperature change between 5°C and 25°C. N₂O and NO emission rates were significantly higher in the broad-leaved forest soil as compared with the coniferous forest soil at all incubation temperatures except 5°C. These results suggest that the broad-leaved forest could contribute more N₂O and NO emissions than the coniferous forest for most of the year in the subtropical region of China.

Introduction

Nitrous oxide (N₂O) is a potent greenhouse gas involved in global warming and nitric oxide (NO) is a precursor of tropospheric ozone which contributes to the greenhouse effect (Bouwman, 1990; Williams et al., 1992). About 57% of the global atmospheric N₂O originates from the soil (Mosier and Kroeze, 1998). Although abiotic processes (e.g., chemodenitrification) may account for a small portion of total soil derived N₂O and NO, the biological processes of nitrification and denitrification are believed to

be the predominant sources of N₂O and NO emission in soils (Firestone and Davidson, 1989; Williams et al., 1992; Wrage et al., 2001).

Soil temperature has long been recognized as a key factor that influences N₂O and NO emissions. It has been shown that both N₂O and NO emissions increase exponentially with an increase in temperature in most temperate forest soils (Schindlbacher et al., 2004; Pilegaard et al., 2006; Schauffler et al., 2010). This is due to the fact that rates of enzymatic processes generally increase exponentially with temperature, as long as other factors (e.g., substrate or moisture availability) are not limiting (Meixner and Yang, 2006). Surprisingly, high N₂O emissions at low temperatures have also been found

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during the freezing and thawing cycles of boreal and temperate regions as well (Teepe et al., 2001; Koponen and Martikainen, 2004). Subtropical and tropical forest soils have been acknowledged to represent significant sources of N₂O and NO emissions (Davidson and Kinglerlee, 1997; Breuer et al., 2000; Prather and Ehhlalt, 2001; Werner et al., 2007); however, little research has been carried out to investigate the effects of temperature change on N₂O and NO emissions in forest soils from subtropical regions.

Coniferous and broad-leaved forests are typical floras of subtropical and tropical regions. It might be expected that both N₂O and NO emissions are different between the coniferous and broad-leaved forest soils, due to the differences in soil environments, microflora, as well as litter properties in these types of forests (Binkley and Giardina, 1998). Many studies on soil N₂O and NO emissions in temperate regions have shown that N₂O emissions were significantly higher in deciduous forests as compared to coniferous forest soils, while NO emissions were significantly lower in deciduous forests than coniferous forest soils (Butterbach-Bahl et al., 1997, 2001, 2002; Gasche and Papan, 1999; Ambus et al., 2006; Pilegaard et al., 2006). In contrast to temperate forests that are characterized as being naturally N-limited (Hall and Matson, 1999; Matson et al., 2002), subtropical and tropical forests are more typically phosphorus (P) limited, and the soils are often highly acidic with low base cation concentrations (Vitousek and Sanford, 1986; Matson et al., 2002; Hall and Matson, 2003). The effect of tree species on soil N₂O and NO emissions between the temperate and subtropical and tropical forests may also be a factor and it is not clear whether the effect of soil temperature on N₂O and NO emissions depends on the particular tree species. The level of N₂O and NO emissions at different soil temperatures may also vary between different tree species, as they may provide different environmental conditions for nitrogen oxide emissions. Therefore, the comparison of the differences in soil N₂O and NO emissions between tree species under various soil temperatures could more accurately predict the impacts of temperature change arising from seasonal variation or global warming on soil N₂O and NO emissions in subtropical forests.

The objectives of this study were to investigate the influence of soil temperature change (5–35°C) on soil N₂O and NO emissions in two contrasting (broad-leaved vs. coniferous) subtropical forests in China. It was hypothesized that an increase in temperature would stimulate soil N transformations and thus N₂O and NO emissions, but

such effects would vary between the tree species due to differences in intrinsic biological properties of the plants.

1 Materials and methods

1.1 Site description and soil analyses

The study sites were located in Yingtan City, Jiangxi Province, China (28°23'N, 117°02'E), and were characterized by a typical subtropical monsoon climate and had four distinct seasons. The mean annual precipitation was approximately 1788 mm (30-year average), approximately 50% of which occurs from April to June. The mean annual temperature was 17.6°C with the minimum and maximum monthly average temperature of 5.6°C in January and 29.3°C in July (30-year average), respectively.

Two forest soils from different forest types were selected for this study: (1) one was taken from natural secondary coniferous forests (abbreviated as CF) (about 60 years), dominated by *Pinus massoniana* Lamb; (2) the other was from natural secondary evergreen broad-leaved forests (BF) (about 60 years), dominated by *Cinnamomum camphora* L. For each forest type, the soils were collected from three different sites (> 1000 m apart) as three spatial replications. The soils within two forests were classified as hapludults according to USA soil taxonomy and based on various chemical and physical properties (Table 1). In four representative 100 m × 100 m plots in each site, four grids (about 4 m × 4 m) were randomly staked out. From each grid, the O horizon was removed and three cores were taken from the mineral horizon (0–20 cm). The fresh soil samples were pooled to form a composite sample and sieved (2 mm mesh), and subsequently split into two subsamples. One subsample was stored at 4°C for incubation studies and the other was air-dried to determine the chemical and physical properties of the soil (Table 1).

1.2 Laboratory sample preparations and measurements

Incubation experiments were carried out in the laboratory following the method of Zhao et al. (2007). For each forest soil, 20 g of fresh soil was placed inside a flask. The soils in the sealed flasks were then acclimated to four different temperatures (5°C, 15°C, 25°C, and 35°C) in the laboratory for 1 day. Two mL ammonium nitrate solution was applied uniformly over the soil surface, resulting in an

Table 1 Physical and chemical characteristics of the broad-leaved (BF) and coniferous forest (CF) soils studied

	pH (1:2.5 H ₂ O)	Organic C (g/kg)	Organic N (g/kg)	C/N ratio	NH ₄ ⁺ -N (mg/kg)	NO ₃ ⁻ -N (mg/kg)	Clay, < 2 μm (%)
BF	3.59(0.08)a	28.8(6.0)a	1.94(0.29)a	14.8(1.0)a	1.95(1.66)a	10.9(1.9)a	34.8(3.4)a
CF	4.24(0.04)b	17.9(5.3)b	1.02(0.16)b	17.2(2.5)b	5.45(1.47)b	1.70(0.94)b	22.1(3.7)b

Values are means (standard deviation) for oven-dry soils. Different letters within each column denote significant differences at $P < 0.05$.

equivalent addition of 10 mg $\text{NH}_4^+\text{-N}$ and 10 mg $\text{NO}_3^-\text{-N}$ per kg soil, equivalent to a moderate rate of N deposition in the studied region (Cui et al., 2012). The final soil moisture contents were adjusted to 60% water holding capacity using deionized water. All the flasks of the soil samples previously incubated for 1 day at 5°C, 15°C, 25°C, or 35°C were sealed and subsequently incubated at the respective temperature in the dark for an additional 9 days. During incubation, the samples were aerated for 5 min each day to maintain an aerobic condition inside the flasks, and the soil moisture content was maintained by adding deionized water every 3 days when necessary to compensate for the water loss through evaporation. The emission rates of N_2O , NO and CO_2 were measured 1, 2, 5, and 9 days after ammonium nitrate solution application. After the gases were sampled, soils from flasks were destructively sampled and analyzed for $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ concentrations on day 1, 2, 5, and 9 (six replicates per treatment).

At the aforementioned sampling times, 6 flasks of each temperature treatment were taken randomly as replicates. A 20 mL gas sample was collected from each flask using a gas-tight syringe and transferred to an evacuated gas-tight vial (20 mL) for N_2O and CO_2 analysis by gas chromatography after the flasks had been sealed with a butyl rubber stopper for 0 and 4 hr. A 40 mL gas sample was also collected and transferred to a pre-evacuated plastic bag (1000 mL) for the NO analysis.

Prior to NO determination gas samples drawn from flasks were diluted to 1000 mL with highly purified He. The NO concentration was measured using a NOx analyzer (ThermoFisher 42i, Chemiluminescence Detector, USA). Concentrations of CO_2 and N_2O were determined using a Varian CP-3800 gas chromatograph (Varian Canada, Mississauga, Canada) fitted with an electron capture detector. A detailed description of the configuration and working condition of the gas chromatograph was provided in Paterson et al. (2004).

1.3 Soil chemical properties analyses

Soil properties were determined following the Soil Agro-Chemical Analyses procedures (Lu, 2000). The soil pH was measured in a slurry with a soil/water ratio of 1:2.5 (V/V) using a DMP-2 mV-pH detector (Quark Ltd., Nanjing, China). The soil organic carbon was determined by wet digestion with $\text{H}_2\text{SO}_4\text{-K}_2\text{Cr}_2\text{O}_7$ and soil organic nitrogen was determined by semi-micro Kjeldahl digestion with Se, CuSO_4 and K_2SO_4 as catalysts. NO_3^- and NH_4^+ were extracted in a 2 mol/L KCl solution with a soil to water ratio of 1:5. The solution was placed on a 250 r/min mechanical shaker for 60 min at 25°C and NO_3^- -N and NH_4^+ -N concentrations were determined with a continuous-flow analyzer (Skalar Analytical, Breda, the Netherlands). The soil texture was determined with a laser particle characterization analyzer (Beckman Coulter, Los

Angeles, USA).

1.4 Emission calculation and statistical analyses

The emission rates of N_2O , NO and CO_2 were calculated by the following equation:

$$F = \rho \times \Delta C \times V \times \frac{273}{(273 + T) \times W}$$

where, F is the flux of N_2O , NO (g N/(kg-day)) and CO_2 (mg C/(kg-day)); ρ is the density of N_2O , NO or CO_2 under standard state; ΔC (ppbV/day or ppmV/day) is the change of gas concentration between incubation time of 0 and 4 hr; V (mL) is the gas space volume of conical flasks used in the experiment; T (°C) is the incubation temperature; and W (kg) is the dry weight of soil.

Net mineralization rates were calculated as the difference between final and initial mineral N concentrations ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) divided by 9 days. Net nitrification rates were also calculated in a similar way.

Two-way ANOVAs were used to analyze the effects of temperature, tree species and their interactions on the time weighted average rates of N_2O , NO and CO_2 emissions for the interval between day 0 and 9. All statistical analyses were performed using SPSS 13.0 software (SPSS, Chicago, USA). All results are reported as mean standard deviation for oven-dry soils.

2 Results

2.1 Soil physical and chemical properties

Both soils were found to be strongly acidic, with a much lower pH in the broad-leaved forest soil than in the coniferous forest soil ($P < 0.001$; **Table 1**). The organic C, organic N and clay contents were consistently higher in the soil collected from the broad-leaved forest than in the soil collected from coniferous forest ($P < 0.01$), whereas the trend was reversed for the C/N ratio. The inorganic N pool was dominated by $\text{NO}_3^-\text{-N}$ in the broad-leaved forest soil and by $\text{NH}_4^+\text{-N}$ in the coniferous forest soil as well.

2.2 Net nitrification and N mineralization rates

The net nitrification rates in the coniferous forest soil were no difference from zero, irrespective of incubation temperatures. However, the net nitrification rates gradually increased with an increase in incubation temperatures in the broad-leaved forest soil, although net nitrification rates were negligible at 5°C (**Fig. 1a**). The net N mineralization rates increased with an increase in incubation temperatures in the broad-leaved forest soil, with an increase being much more pronounced when the incubation temperature was raised from 25°C to 35°C (**Fig. 1b**). In the coniferous forest soil, net N mineralization rate was approximately 1.5 mg N/(kg-day) at 35°C, but were negligible at the

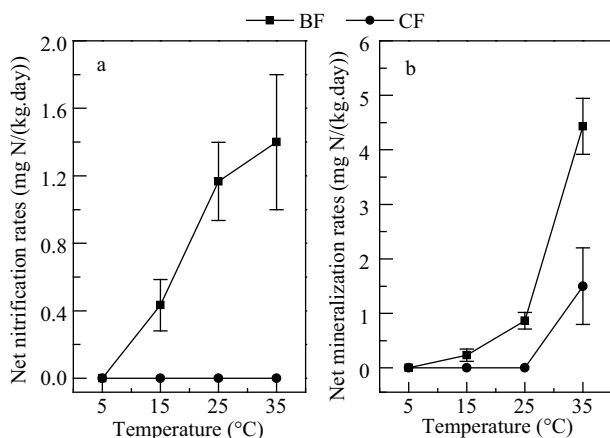


Fig. 1 Effects of incubation temperatures on the net nitrification (a) and N mineralization (b) rates in the broad-leaved (BF) and coniferous forest soils (CF).

three lower temperatures (5°C, 15°C, and 25°C). Similar

to net nitrification rates, net N mineralization rates at the three higher temperatures (15°C, 25°C, and 35°C) were consistently higher in the broad-leaved forest soil as compared with the coniferous forest soil (**Fig. 1b**).

2.3 Emission rates of soil N₂O, NO and CO₂

In the broad-leaved forest soil the temporal pattern of N₂O was characterized by the presence of a high emission rate at the beginning of incubation and then a decreased rate with incubation time at all incubation temperatures except at 35°C, where the N₂O emission rate significantly increased after 5 days of incubation ($P < 0.01$; **Fig. 2**). The temporal pattern of N₂O in the coniferous forest soil incubated at 25°C and 35°C was similar to that observed in the broad-leaved forest soils incubated at the same incubation temperatures, whereas N₂O emission was not detected during the entire incubation period in the coniferous forest soils incubated at 55°C and 15°C (**Fig. 2**).

Similar to N₂O emissions, the NO emission rates gradu-

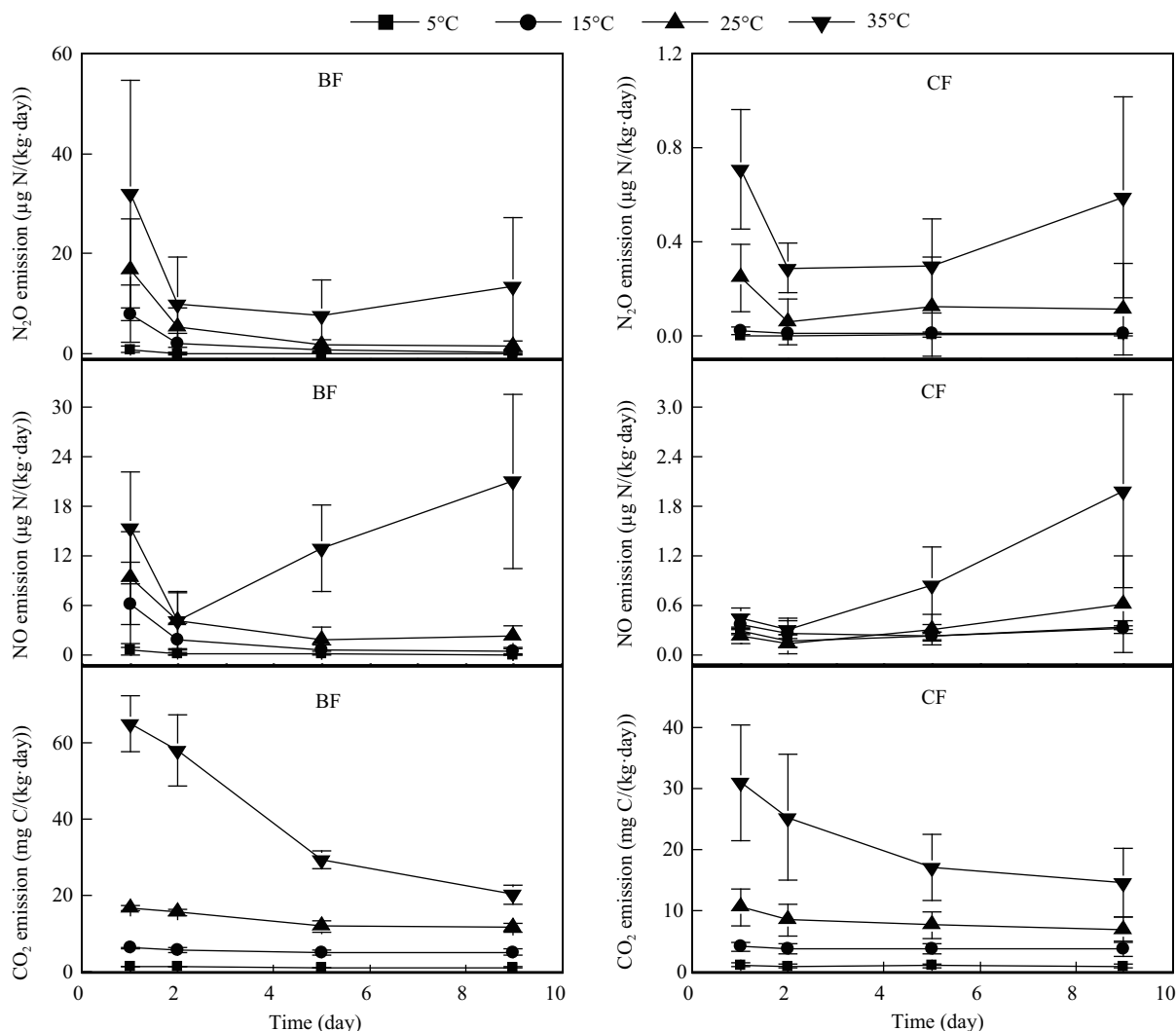


Fig. 2 Change in N₂O, NO, and CO₂ emission rates in the broad-leaved and coniferous forest soil samples under incubation temperatures of 5°C, 15°C, 25°C, and 35°C over a 9-day incubation period.

ally decreased during the whole incubation period for both broad-leaved and coniferous forest soils incubated at all temperatures, except for the broad-leaved forest soil incubated at 35°C and coniferous forest soil incubated at 25 and 35°C, where the NO emission rates decreased during the first 2 days of incubation and thereafter gradually increased during the rest of incubation period ($P < 0.01$; Fig. 2).

The CO₂ emission rates attained their highest values at the first day and subsequently decreased toward the end of the incubation period for both broad-leaved and coniferous forest soils incubated at the two higher temperatures (25°C and 35°C; Fig. 2). This indicated that there was a gradual decrease in available carbon for mineralization through time. However, the CO₂ emission rates for both broad-leaved and coniferous forest soils incubated at the two lower temperatures (5°C and 15°C) remained almost constant during the entire incubation period (Fig. 2).

2.4 Cumulative N₂O, NO and CO₂ emissions

For the broad-leaved forest soils, the cumulative N₂O and NO emissions over the 9 days of the incubation period gradually increased with an increase in incubation temperature. The relationships between the cumulative N₂O and NO emissions and the incubation temperature can be well fitted by exponential models (Fig. 3a and b). In contrast, the cumulative N₂O and NO emissions in the coniferous forest soil at the three lower temperatures (5°C, 15°C and 25°C) were similar and significantly lower than those at the 35°C (Fig. 3a and b). For both forest soils, the cumulative CO₂ emission increased exponentially with increasing incubation temperature (Fig. 3c). Generally, the cumulative

N₂O, NO and CO₂ emissions were significantly higher in the broad-leaved forest soil than in the coniferous forest soil at all incubation temperatures except at 5°C ($P < 0.01$).

3 Discussion

3.1 Soil temperature effects

Numerous studies have shown that soil N availability, net N mineralization and nitrification rates increase with an increase in soil temperatures (Rustad et al., 2001; Melillo et al., 2002; Zaman and Chang, 2004; Xu et al., 2010; Yin et al., 2012). But our results have clearly demonstrated that the effects of temperature on soil net N transformation rates varied with tree species. Both net N mineralization and nitrification rates gradually increased with an increase in incubation temperature in the broad-leaved forest soil, but temperature had a negligible effect on net N transformations in the coniferous forest soil, except at 35°C, in which net N mineralization rates were measured at significant level. A lack of nitrification in similar temperatures (5–25°C) has also been reported in other studies and attributed to limited readily available C (Stottlemeyer et al., 1995; Stottlemeyer and Toczydowski, 1999; Cookson et al., 2002). In contrast, the no responses of nitrification to temperature change in the coniferous forest soil were due to the negligible nitrification rates. It was found that the negligible nitrification rates in the forest soil were probably due to pH-related factors (Nugroho

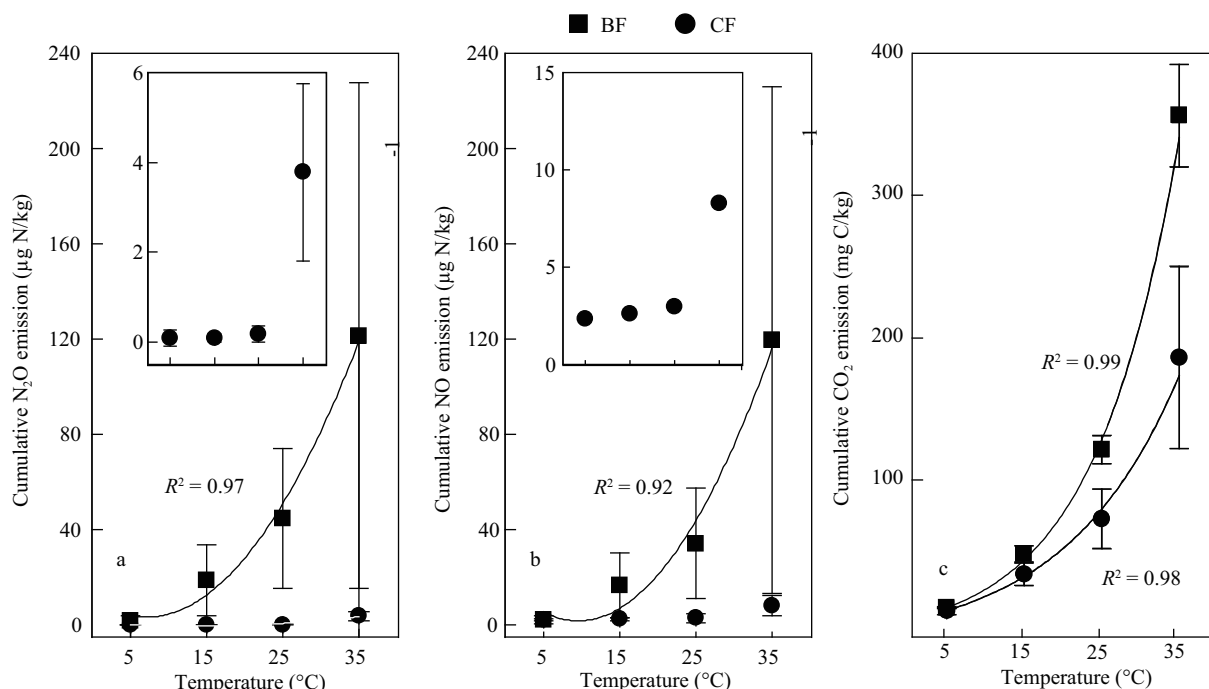


Fig. 3 Effects of incubation temperatures on the cumulative emissions of N₂O (a), NO (b) and CO₂ (c) over a 9-day incubation period in the broad-leaved (BF) and coniferous forest soils (CF).

et al., 2007). The net N mineralization proceeded only at 35°C in the coniferous forest soil, which suggests that the temperature change (5–25°C) did not reach the threshold needed to change the mineralization process in the coniferous forest soil during the study period.

In this study, both N₂O and NO emissions increased exponentially with an increase in temperature in the broad-leaved forest soil, which was consistent with the previous reports on European forest soils (Schindlbacher et al., 2004; Pilegaard et al., 2006; Schauffler et al., 2010). This could be attributed to the fact that rates of enzymatic processes generally increase exponentially with temperature when other factors (substrate or moisture availability) are not limiting (Meixner and Yang, 2006). In contrast, both N₂O and NO emissions in the coniferous forest soil were not sensitive to temperature change (5–25°C). Other studies have also reported that soil temperature (5–20°C) had no significant effect on both N₂O and NO emissions in pine dominated coniferous forests (Schindlbacher et al., 2004; Schauffler et al., 2010). These results suggest that pine forest soils may be more prone to experience temperature constraints (5–25°C) on microbial activity.

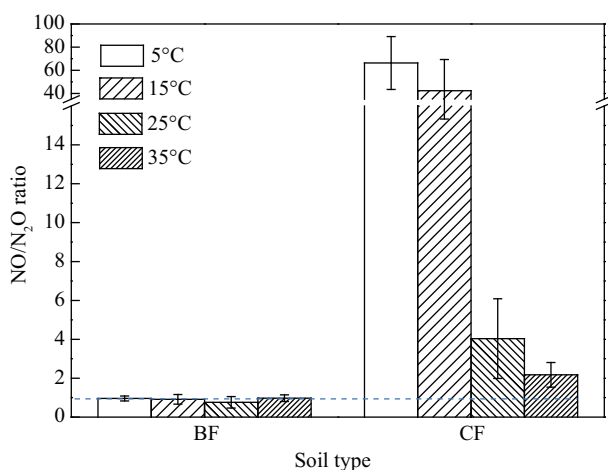


Fig. 4 Effects of incubation temperatures on the NO/N₂O ratio in the broad-leaved (BF) and coniferous forest soils (CF).

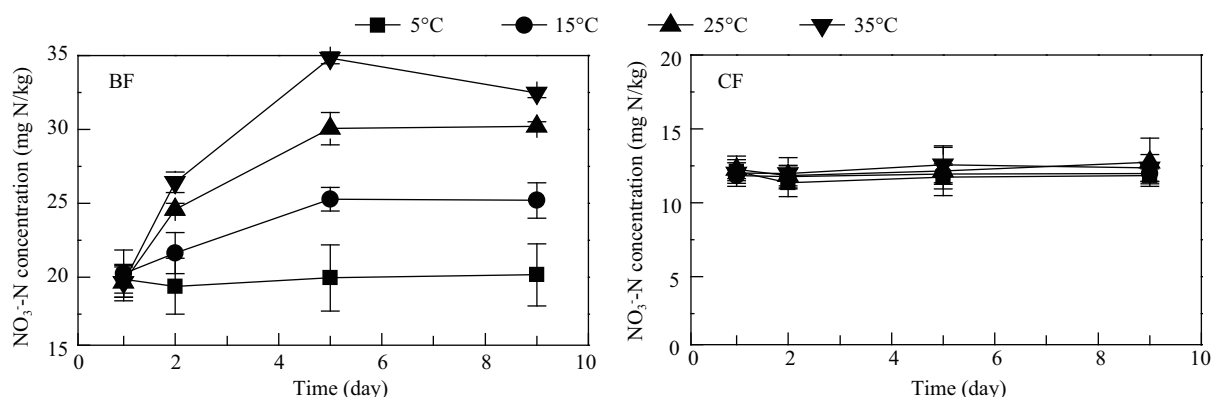


Fig. 5 Change in NO₃⁻-N concentrations in the broad-leaved and coniferous forest soils samples under incubation temperatures of 5°C, 15°C, 25°C, and 35°C over a 9-day period.

The production of N₂O and NO in soils is primarily driven by simultaneous nitrification and denitrification events (Firestone and Davidson, 1989). However, the NO/N₂O ratio is greater than 1 during nitrification and less than 1 during denitrification (FAO and IFA, 2001). In this study, the NO/N₂O ratio was close to 1 in the broad-leaved forest soil at all incubation temperatures, but was much greater than in the coniferous forest soil and gradually decreased to 1 with an increase in incubation temperature (Fig. 4). These results may suggest that approximate equal contribution of nitrification and denitrification to N₂O and NO emissions in the broad-leaved forest soil was independent of incubation temperatures, while the importance of denitrification to N₂O and NO emissions increased with an increase in incubation temperature in the coniferous forest soil. Previous studies have found that increasing temperature could cause a significant increase in soil denitrification rates and consequently N₂O and NO emissions from soils (Abdalla et al., 2009; Yin et al., 2012). The higher denitrification rate in the broad-leaved forest soil incubated at 35°C resulted in a significant decline in NO₃⁻-N concentrations after day 5 ($P < 0.05$; Fig. 5).

3.2 Tree species effects

Previous studies have documented that N₂O and NO emissions in forest soils varied among European forests with different dominant tree species (Butterbach-Bahl et al., 2001; Schindlbacher et al., 2004; Pilegaard et al., 2006). It was generally found that N₂O emissions were significantly higher in deciduous forest as compared to coniferous forest soils, while NO emissions were significantly lower in deciduous forest as compared to coniferous forest soils of temperate regions (Butterbach-Bahl et al., 1997, 2001, 2002; Gasche and Papen, 1999; Ambus et al., 2006; Pilegaard et al., 2006). In contrast, our study showed that both N₂O and NO emission rates were significantly higher in the broad-leaved forest soil as compared to the coniferous forest soil at all incubation temperatures except at 5°C. The no difference in N₂O and NO emissions between the broad-leaved and coniferous forest soils incubated at 5°C was

most likely due to low temperatures restricting microbial activities.

The differences in both N₂O and NO emissions between broad-leaved and coniferous forest soils could be related to the differences in soil characteristics and microbial community structure due to the differences in litterfall input, root turnover and root exudates (Priha et al., 2001; Brant et al., 2006). In this study, the higher N₂O and NO emissions in the broad-leaved forest soil could have been due to relatively higher organic C concentration and clay content, and lower pH value.

A higher organic C concentration in the broad-leaved forest soil could provide more C availability for microbial growth and activity, and hence create anaerobic microsites favoring denitrification and associated N₂O production (Goek and Ottow, 1988; Pilegaard et al., 2006). On the other hand, the higher clay content in the broad-leaved forest soil may also allow for the formation of anaerobic microsites, which may increase the proportion of N₂O emissions from denitrification events (Freney et al., 1979; Smith, 1980; Barton et al., 1999). The higher temperatures could enhance both aerobic respiration and denitrification, and aerobic respiration further enhanced denitrification by the consumption of oxygen (Maag and Vinther, 1999; Yin et al., 2012).

In addition, lower pH and higher organic C contents in the broad-leaved forest soil would be conducive to the presence of heterotrophic nitrification, an important and possibly dominant pathway for NO₃⁻ production (Pedersen et al., 1999; Li et al., 2000; Venterea et al., 2003; Corre et al., 2007; Islam et al., 2007). This would have resulted in the large N₂O and NO emissions in the broad-leaved forest soil. A recent study on N₂O production pathways in subtropical acid forest soils in China has demonstrated that denitrification and heterotrophic nitrification were responsible for 53.5%–56.1% and 27.3%–41.8% of N₂O production, respectively, whereas the contribution of autotrophic nitrification to N₂O production was minimal (Zhang et al., 2011).

Soil pH is also an important factor that influences biotic and abiotic processes of NO formation (Nägele and Conrad, 1990; Mørkved et al., 2007). Numerous studies of European forest sites have shown that the highest NO emission was often found for predominantly coniferous forests with relatively lower soil pH values (< 4.0) (Butterbach-Bahl et al., 1997, 2001, 2002; Gasche and Papen, 1999; Ambus et al., 2006; Pilegaard et al., 2006). In contrast, our study showed that NO emissions were much higher in the acidic broad-leaved forest soil (pH 3.6) as compared to relatively less acidic coniferous forest soil (pH 4.2). Therefore, the level of NO production in the forest soils probably depends on the development of different soil pH levels due to the dominant vegetation present, but not by the dominant vegetation itself. The lower soil pH that increased NO emissions in the broad-leaved forest soil may be related to

increased NO production via a chemodenitrification event, which is a non-biological reaction that takes place in low pH soils (Li et al., 2000; Wrage et al., 2001).

3.3 Significance of the present findings and limitations

This study showed that the effects of temperature on soil net N transformation rates and N₂O and NO emissions varied with tree species in subtropical regions. Both N₂O and NO emissions increased exponentially with an increase in temperature in the broad-leaved forest soil, whereas they were not sensitive to temperature change between 5°C and 25°C in the coniferous forest soil. Both N₂O and NO emission rates were significantly higher in the broad-leaved forest soil as compared to the coniferous forest at all incubation temperatures except at 5°C. At this temperature the N₂O and NO emission rates for both forest soils were not significantly different from each other, most likely, due to the restriction on microbial activity at low temperatures. Our results suggest that the broad-leaved forest could contribute more N₂O and NO emissions than the coniferous forest for most of the year in the subtropical region. However, it should be noted that the direct extrapolation of this laboratory result to field situations may be troublesome as an increase in temperature can result in the decrease in soil moisture, which will counteract the temperature effect *in situ*. In addition, long term field studies need to be conducted to examine how soil temperature, soil moisture and their interaction influence forest soil N₂O and NO emissions in the subtropical region.

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