Effects of nitrogen fertilization on the fluxes of N_2O, CH_4, and CO_2 from soils in a Florida slash pine plantation

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We measured fluxes of N_2O, CH_4 and CO_2 from control and urea-nitrogen fertilized soils of a mature slash pine (*Pinus elliottii* var. *elliottii* Englem.) plantation in Alachua County, Florida. The fertilization did not affect CO_2 emissions, but significantly increased the emissions of N_2O and lowered the uptake of atmospheric CH_4. Daily average N_2O emissions from the fertilized soils were 8–600 times higher (12–74 $\mu g\ N_2O\text{-}N \cdot m^{-2} \cdot h^{-1}$) than daily average N_2O emissions from control soils (0.02–4.0 $\mu g\ N_2O\text{-}N \cdot m^{-2} \cdot h^{-1}$). Daily average CH_4 uptake by the fertilized soils were 5–20 times lower (0.001–0.007 mg $CH_4\text{-}C \cdot m^{-2} \cdot h^{-1}$) than daily average CH_4 uptake by control soils (0.015–0.035 mg $CH_4\text{-}C \cdot m^{-2} \cdot h^{-1}$). We also measured the relative activities of the bacteria populations that were responsible for CH_4 oxidation in the control and fertilized soils. Results from these measurements suggest that fertilization shifted the relative activities of the CH_4 oxidizing bacteria from those dominated by methanotrophs in the control soils to those dominated by nitrifying bacteria in the surface (0–2 cm) of the fertilized soils. The shift in relative activities of these bacteria may have been responsible for the lower CH_4 uptake by the fertilized soils.

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Les flux de N_2O, CH_4 et CO_2 ont été mesurés dans des sols témoins et des sols fertilisés en azote-urée dans une plantation mature de pin de Floride (*Pinus elliottii* var. *elliottii* Engelm.) du Comté de Alachua, en Floride. La fertilisation n'a pas affecté les émissions de CO_2 mais a significativement augmenté les émissions de N_2O et a diminué le prélèvement du CH_4 atmosphérique. Les émissions moyennes journalières de N_2O des sols fertilisés ont été de 8 à 600 fois plus élevées (12–74 $\mu g\ N\text{-}N_2O \cdot m^{-2} \cdot h^{-1}$) que les émissions moyennes journalières des sols témoins (0,02–4,0 $\mu g\ N\text{-}N_2O \cdot m^{-2} \cdot h^{-1}$). Le prélèvement moyen journalier de CH_4 par les sols fertilisés a été de 5 à 20 fois plus faible (0,001–0,007 mg $C\text{-}CH_4 \cdot m^{-2} \cdot h^{-1}$) que le prélèvement moyen journalier de CH_4 par les sols témoins (0,015–0,035 mg $C\text{-}CH_4 \cdot m^{-2} \cdot h^{-1}$). Les activités relatives des populations de bactéries responsables de l'oxydation de CH_4 ont aussi été mesurées dans les sols témoins et les sols fertilisés. Les résultats suggèrent que la fertilisation a déplacé les activités relatives des bactéries oxydant le CH_4 de celles dominées par les méthanotrophes dans les sols témoins à celles dominées par les bactéries nitrifiantes dans les deux premiers centimètres des sols fertilisés. Le déplacement dans les activités relatives de ces bactéries peut avoir été responsable des plus faibles prélèvements de CH_4 par les sols fertilisés comparés aux sols témoins.

[Traduit par la rédaction]

Introduction

Over the past 40 years, atmospheric concentrations of nitrous oxide (N_2O), methane (CH_4), and carbon dioxide (CO_2) have increased and continue to increase at annual rates of 0.3, 0.6, and 0.5%, respectively (Watson et al. 1992). These increases are of concern because these gases have the potential to affect the earth's climate and atmospheric chemistry.

The increasing atmospheric concentrations of N_2O, CH_4, and CO_2 have led to studies of the factors controlling natural sources and sinks of these gases. Results from these studies suggest that N fertilization of soils in many ecosystems increased N_2O emissions into the atmosphere (Duxbury and McConnaughey 1986; Hutchinson and Mosier 1979; Keller et al. 1983, 1988, 1990; McKenney et al. 1980; Mosier et al. 1991). Field studies in temperate grasslands and forests demonstrated that N fertilization lowers CH_4 uptake by the fertilized soils (Mosier et al. 1991; Steudler et al. 1989). Additional ecosystem studies are needed to determine if the N induced suppression of CH_4 uptake is a widespread phenomenon and to better understand the mechanisms responsible for the N induced suppression of CH_4 uptake. The effect of N fertilization on CO_2 emissions from forest soils is not clear; some studies report no changes (Repnevskaya 1967), others report increases and decreases in CO_2 emissions (Brumme and Beese 1992; Silvola et al. 1985). Collectively, results from these studies suggest that the exchange of N_2O, CH_4, and CO_2 between the atmosphere and soils in many ecosystems is affected by N fertilization.

Nitrogen fertilization is common practice in commercial forestry in the southeastern United States. Most of the past research associated with fertilized pine plantations focused

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on stand growth, productivity, and time to harvest (Allen et al. 1990; Colbert et al. 1990; Jokela et al. 1990; Stone 1983). The effects of N fertilization on the fluxes of N_2O, CH_4, and CO_2 from soils of these fertilized pine plantations are not well known. In this paper, we describe the effects of 4 years of urea-N fertilization on the exchange of N_2O, CH_4, and CO_2 between the atmosphere and soils of a mature slash pine (*Pinus elliottii* var. *elliottii* Engelm.) plantation in Florida.

Study site

The study site was a 60-ha block of a slash pine plantation located approximately 20 km northeast of Gainesville in Alachua County, Florida (29°N, 82°W). The overstory was dominated by even-aged slash pines that were 26 years old in 1991. The understory was dominated by saw palmetto (*Serenoa repens*) and a sparse cover of grasses and forbs overlying dead pine needles. The soils (Ultic Haplaquod) are sandy, poorly drained, and have low organic matter and low nutrients (Gholz et al. 1985). The groundwater table fluctuates between the surface and approximately 2 m below the surface throughout the year. Average annual precipitation and temperature (1955–1987) are 1342 mm and 21.7°C, respectively (National Oceanic and Atmospheric Administration 1989).

In 1986, the study site was divided into sixteen 50 × 50 m plots, with at least 100 m separating the plots (Gholz et al. 1991). From February 1987 through December 1991, eight plots were fertilized quarterly with a complete (N–P–K) fertilizer. Micronutrients (Cu, Bo, Fe, Mn, Zn, and Mo) were added to the fertilized plots in 1986. Nitrogen as urea was added at an annual rate of 180 kg N/ha. The other eight plots were not fertilized and were used as controls. We made measurements in two control (plots 2 and 3) and two fertilized plots (plots 1 and 4). We selected these plots because of their close proximity to each other and because we have background data from many previous studies (Curran et al. 1990; Cropper and Gholz 1991; Gohlz et al. 1991).

Gas fluxes

We measured N_2O, CH_4, and CO_2 fluxes at the air–soil interface with static chambers on February 2, May 18, and November 2, 1991. These three samplings dates were intended to be sampling replicates to document differences in gas fluxes between control and fertilized soils. At least 12 h before the start of each gas sampling, we placed four chamber anchors in each of the four plots for a total of 16 chamber locations. The position of each chamber was marked so that samples were collected at the same location on all three samplings dates. During each gas sampling, two paired plots (one control and one fertilized) were sampled simultaneously at 06:00–06:30, 10:00–10:30, 14:00–14:30, and 18:00–18:30. The second pair was sampled immediately after the first. It took 1.5 hours to sample all four plots. Samples were collected, stored in pressurized 20-mL nylon syringes and analyzed within 1 week of collection at The Ecosystems Center in Woods Hole, Mass. Details of our sampling and analytical techniques can be found in Steudler et al. (1989), Bowden et al. (1990, 1991), and Castro et al. (1993).

Soil parameters

During each of the 30-min sampling periods, we measured soil temperatures (0–2.5 cm and 2.5–5.0 cm) at two chambers in each plot with Omega (Stamford, Conn.) dial thermometers.

Once on each of the three samplings dates (at approximately 12:00), we collected soil cores from each plot to measure soil moisture, NH_4-N and NO_3-N concentrations. In February, two soil cores were taken next to two chambers in each plot. In May and November, one core was taken next to all four chambers in each plot. All cores were separated into 0–2 and 2–5 cm increments. Soil moisture was determined gravimetrically; 10-g subsamples were dried at 105°C for 48 h. Separate 10-g subsamples were extracted with 2 M KCl and analyzed for NH_4-N and NO_3-N using an autoanalyzer (Alpkem (Clackamas, Oreg.) Methods No. A303-S020-06 and A303-S170-08).

Microbial activity

Immediately after the February gas sampling, we composited two soil cores collected from each of the four plots (two control and two fertilized), keeping the 0–2 and 2–5 cm increments separate. This resulted in a total of eight samples. All soil was sieved through a nylon window screen. Three 1-g replicate subsamples were run for each of three treatments. The treatments were: (*i*) ^{14}CO addition to saturated soil; (*ii*) ^{14}CO and N-Serve (2-chloro-6-(trichloromethyl)pyridine) addition to saturated soils and (*iii*) $^{14}CH_4$ addition to saturated soil. Saturation was required to distribute the N-Serve. These three treatments were necessary to determine the relative activities of the bacteria populations responsible for CH_4 oxidation using the technique of Jones et al. (1984).

Methane can be oxidized in soils by methanotrophs and nitrifying bacteria. The relative activities of these bacteria in surface soils (0–2 and 2–5 cm) from our control and fertilized plots were determined from the ratio of $^{14}CH_4$ oxidation to N-Serve sensitive ^{14}CO oxidation. The N-Serve sensitive ^{14}CO oxidation is equal to ^{14}CO oxidation by methanotrophs and nitrifying bacteria and is calculated as the difference between the ^{14}CO oxidation rate (treatment 1) and ^{14}CO oxidation rate with N-serve (treatment 2). Since methanotrophs and nitrifying bacteria have about the same ability to oxidize ^{14}CO, dividing the $^{14}CH_4$ oxidation rate by the N-Serve sensitive ^{14}CO oxidation normalizes the $^{14}CH_4$ oxidation rates for the abundance of these bacteria. This is necessary because methanotrophs have a greater (two to four orders of magnitude) ability to oxidize CH_4 than nitrifying bacteria (Jones et al. 1984). If the ratio of $^{14}CH_4$ oxidation to N-Serve sensitive ^{14}CO oxidation was <0.01, then nitrifying bacteria were primarily responsible for CH_4 oxidation in these soils. Higher ratios (>0.01) suggest that methanotrophs were the dominant group of active CH_4 oxidizing bacteria. The 0.01 selection criteria was derived from studies conducted with pure bacteria cultures and environmental samples (R. Jones, personal communcication).

Results

Trace gas fluxes

On each sampling date, the daily average CO_2 emissions from the control and fertilized soils were not significantly different (Table 1; Duncan's multiple range test, $p = 0.05$).

The control and fertilized soils were sources of N_2O (Table 1). On each sampling date, daily averaged N_2O emissions from the fertilized soils were significantly higher (8–600 times) than N_2O emissions from the control soils (Duncan's multiple range test, $p = 0.05$).

The control and fertilized soils were sinks for atmospheric CH_4 (Table 1). On each sampling date, CH_4 uptake by the fertilized soils was significantly lower (5–20 times) than CH_4 uptake by the control soils (Duncan's multiple range test, $p = 0.05$).

Soil parameters

On each sampling date, there were no significant differences in the daily averaged soil temperatures (0–2.5 and 2.5–5.0 cm) in the control and fertilized soils (*t*-test, $p = 0.05$).

In general, the average soil moistures in the fertilized and control soils were not significantly different (*t*-test, $p = 0.05$). However, soil moistures in only the surface soil (0–2 cm) were significantly different in November. At this time, the average soil moisture in the fertilized soil (65%, g H_2O/g dry soil) was ca. two times higher than soil moisture in the control soil.

There were significant (*t*-test, $p = 0.05$) treatment differences in the KCl extractable NH_4^+-N and NO_3^--N concentrations. Ammonium-N concentrations were significantly higher (3–10 times) in the fertilized surface soils (0–2 cm) in May and November and deeper soils (2–5 cm) in February and May (Table 1). In addition, only the fertilized soils had detectable NO_3^--N concentrations (Table 1).

Microbial activity

There were two major differences in the relative activities of the microbial populations that oxidized CH_4 in the control and fertilized soils (Table 2). First, CH_4 oxidation in the control soils was dominated by methanotrophs (i.e., $^{14}CH_4/^{14}CO > 0.01$); their activity was greatest in the deeper soils (2–5 cm). Second, CH_4 oxidation was dominated by nitrifying bacteria in the upper surface (0–2 cm) of the fertilized soil (i.e., $^{14}CH_4/^{14}CO < 0.01$) while methanotrophs dominated CH_4 oxidation in the deeper soils (2–5 cm) of the fertilized plots (Table 2).

Discussion

The effect of N fertilization on the growth of pine plantations in the southeastern United States has been well documented, but there is little information about the effects of this silvicultural practice on trace gas fluxes from soils in this ecosystem. In this study, however, we examined the effects of urea-N fertilization on the exchange of N_2O, CH_4 and CO_2 between the atmosphere and soils of a mature slash pine plantation in Florida.

Results from our study suggest that urea-N fertilization did not affect CO_2 emissions from soils in this plantation during the 4th year of fertilization (Table 1). This result is consistent with results from measurements of CO_2 fluxes made in these same plots with the soda lime static chamber technique (W.P. Cropper and H.L. Gholz, unpublished data) and in situ measurements of fine root respiration (Cropper and Gholz 1991).

On all three samplings dates, the fertilized soils had significantly higher (8–600 times) daily averaged N_2O emissions than control soils (Table 1). This result is consistent with results from other fertilization studies (Duxbury and McConnaughey 1986; Hutchinson and Mosier 1979; Keller et al. 1988; McKenney et al. 1980). At our study site, soil NO_3^- concentrations were detected in only the fertilized soils (Table 1). Nitrate is a precursor for denitrification and during the conversion of urea to NO_3^- nitrification had to occur. Thus, the increased N_2O emissions from the fertilized soils may have been caused by both nitrification and denitrification.

The fertilized soils had significantly lower (5–20 times) CH_4 uptake than the control soils (Table 1). This result is consistent with results from N fertilization field experiments conducted in forests (Massachusetts) and grasslands (Colorado) and laboratory experiments conducted with agricultural (Louisiana) and subarctic soils (Quebec) (Mosier et al. 1991; Steudler et al. 1989; Nesbit and Breitenbeck 1992; Adamsen and King 1993). Collectively, these results suggest that N induced inhibition of CH_4 uptake is a widespread phenomenon and should be considered in global estimates and model forecasts of CH_4 budgets.

The mechanism responsible for the effect of N fertilization

TABLE 1. Gas fluxes and soil nitrogen pools in a Florida slash pine plantation

Sampling date*	Treatment	N_2O flux ($\mu g\ N_2O\text{-}N \cdot m^{-2} \cdot h^{-1}$)	CH_4 flux ($mg\ CH_4\text{-}C \cdot m^{-2} \cdot h^{-1}$)	CO_2 flux ($mg\ CO_2\text{-}C \cdot m^{-2} \cdot h^{-1}$)	NH_4^+ pool ($mg\ NH_4^+\text{-}N/kg$ dry soil)		NO_3^- pool ($mg\ NO_3^-\text{-}N/kg$ dry soil)	
					0–2 cm	2–5 cm	0–2 cm	2–5 cm
2-19-91	Control	0.02±0.74	−0.015±0.002	52.4±6.6	4.2±2.1	0.7±0.2	0	0
	Fertilizer	12.31±3.32	−0.001±0.002	56.2±5.0	5.2±2.6	6.9±3.5	16.0±7.8	5.5±3.9
5-19-91	Control	1.47±1.11	−0.020±0.004	66.8±2.8	4.5±1.6	0.8±0.2	0.03±0.03	0
	Fertilizer	73.66±16.60	−0.001±0.004	68.1±3.9	14.4±5.1	4.6±2.5	2.3±1.1	0.7±0.5
11-2-91	Control	3.93±1.60	−0.035±0.004	78.3±5.8	1.6±0.6	0.7±0.3	0	0
	Fertilized	30.25±4.87	−0.007±0.002	81.5±4.6	6.5±2.3	1.7±0.7	4.5±3.7	0.7±0.5

NOTE: Values are means ± SE.
*Presented as month-day-year.

TABLE 2. Results from laboratory oxidation experiments

Site	N-Serve sensitive ^{14}CO oxidation (nmol·g^{-1}·h^{-1})	$^{14}CH_4$ oxidation (nmol·g^{-1}·h^{-1})	Ratio $^{14}CH_4$ oxidation To N-Serve sensitive ^{14}CO oxidation	Dominant bacteria
Control 2				
0–2 cm	0.199±0.047	0.0057±0.0001	0.0333±0.0100	CH_4 oxidizers
2–5 cm	0.209±0.013	0.0419±0.0010	0.2025±0.0166	CH_4 oxidizers
Control 3				
0–2 cm	0.090±0.097	0.0060±0.0008	0.0664±0.0102	CH_4 oxidizers
2–5 cm	0.175±0.028	0.0631±0.0004	0.3786±0.0594	CH_4 oxidizers
Fertilized 1				
0–2 cm	0.198±0.021	0.0015±0.0001	0.0077±0.0005	NH_4 oxidizers
2–5 cm	0.193±0.029	0.0104±0.0004	0.0578±0.0122	CH_4 oxidizers
Fertilized 4				
0–2 cm	0.303±0.032	0.0012±0.0001	0.0038±0.0003	NH_4 oxidizers
2–5 cm	0.182±0.036	0.0057±0.0002	0.0346±0.0087	CH_4 oxidizers

NOTE: Values are means ± SE.

on CH_4 uptake by soils is not well known. Currently, there are two hypotheses to explain this effect. First, high inorganic N concentrations in the fertilized soil may lower microbial oxidation of CH_4 (Steudler et al. 1989; Melillo et al. 1989). This is supported by laboratory experiments that show that high concentrations of both NO_3^- and NH_4^+ inhibit CH_4 oxidation by pure cultures of methanotrophs and nitrifying bacteria (Ferenci et al. 1975; Hyman and Wood 1983; Jones and Morita 1983). Results from a laboratory study conducted with fresh soil samples suggest that NH_4^+, and not NO_3^-, appears to be an irreversible inhibitor of CH_4 oxidation and the inhibitory effect persists after oxidation of NH_4^+ (Nesbit and Breitenbeck 1992). Although our data suggest that CH_4 uptake was lowest in the soils with the highest NH_4^+ and NO_3^- concentrations, our data set was not large enough to establish a strong statistical relationship. Second, results from field studies in grasslands suggest that soil N cycling, rather than inorganic soil N concentrations, influences CH_4 uptake by grassland soils (Mosier et al. 1991). Since we did not measure soil N turnover at our study sites, we do not have the appropriate data to examine the effect of N turnover on CH_4 uptake.

Results from our measurements of the relative activities of the bacteria responsible for CH_4 oxidation suggests that nitrifying bacteria dominated CH_4 oxidation in the surface (0–2 cm) of the fertilized soils and methanotrophs dominated CH_4 oxidation in the control soils (Table 2). The fertilized soils also had significantly lower CH_4 uptake than the control soils (Table 1). This pattern is consistent with laboratory measurements of CH_4 oxidation by these bacteria. Pure cultures of nitrifying bacteria had between two to four orders of magnitude lower CH_4 oxidation rates than pure cultures of methanotrophs (Jones et al. 1984). Thus, the shift in the relative activities of the microbial populations that oxidize atmospheric CH_4 towards bacteria less effective at oxidizing CH_4 in response to the N fertilization may have been responsible for the lower CH_4 uptake by the fertilized soil.

In summary, 4 years of N fertilization of soils in this slash pine plantation did not affect the CO_2 emissions, but increased N_2O emissions into the atmosphere and lowered the uptake of atmospheric CH_4. Alterations in the CH_4 fluxes may have resulted from N induced changes in the relative activities of the soil bacteria responsible for CH_4 oxidation. These results imply that the soil N status of this ecosystem affects the atmospheric fluxes of N_2O and CH_4 and that alterations in the soil N status resulting from N fertilization is likely to affect the exchange of N_2O and CH_4 between the atmosphere and soils in this ecosystem.

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