Eurasian J. For. Res. 10-1: 79-84 , 2007

N_2O Flux in Alas Ecosystems Formed by Forest Disturbance Near Yakutsk, Eastern Siberia, Russia

MORISHITA Tomoaki[1,2]*, HATANO Ryusuke[1] and DESYATKIN Roman V.[3]

[1] Graduate School of Agriculture, Hokkaido University, Sapporo 060-8589, Japan
[2] Forestry and Forest Products Research Institute, Tsukuba, 305-8687, Japan
[3] Institute of Biological Problems of Cryolithozone, Russian Academy of Science

Abstract

An alas is a round area of grassland with a pond at the center, formed by subsidence associated with permafrost thawing in taiga forests in eastern Siberia. To characterize the relationship between the N_2O dynamics and soil properties of forest–alas ecosystems, we investigated soil N_2O fluxes in four thermokarst ecosystems composed of forest, grassland, and ponds near Yakutsk in July 2000. At all sites, pH, EC, and organic carbon (OC) content in soil were higher in the grasslands (pH 7.3–9.3, EC 22–63 mS m^{-1}, OC 1.4%–15.3%) than in the forests (5.6–6.3, 1.4–6.8 mS m^{-1}, 0.4%–1.7%), and C/N was lower in the grasslands (10–18) than in the forests (18–24). Both emission (positive values) and uptake (negative values) of N_2O occurred in the forests (–2.1 to 1.0 μg N m^{-2} h^{-1}) and grasslands (–1.3 to 31 μg N m^{-2} h^{-1}). N_2O emissions at the edge of ponds varied widely (0 to 140 μg N m^{-2} h^{-1}). N_2O was taken up in the ponds (–2.2 to 0.0 μg N m^{-2} h^{-1}). There were significant differences in N_2O fluxes among land cover types. N_2O flux was positively correlated with soil moisture, but N_2O fluxes were smallest in the ponds because of the biological denitrification there. Therefore, an increase in soil moisture increased N_2O flux.

Key words: alas, eastern Siberia, larch forest, N_2O flux, Yakutsk

Introduction

N_2O is an important greenhouse gas, contributing about 6% of the radiative forcing of the global climate (IPCC 2001). Total N_2O emission is estimated to be 17.7 Tg $year^{-1}$ (IPCC 2001). Major sources of atmospheric N_2O include agricultural soils, natural tropical soils, and the oceans. The major N_2O sink is considered to be the atmosphere, where an estimated 12.3 Tg $year^{-1}$ is consumed by photodissociation and reaction with electronically excited oxygen atoms.

The forest area in the Russian Federation is about 8.5 × 10^6 km^2, the largest in the world, and accounts for 22% of the world total (FAO 2003). The forest area in eastern Siberia is about 3.5 × 10^6 km^2, or 41% of the Russian total (Forest Management Department of Sakha Republic, unpublished data, 2000). This area is larger than the forest areas of Canada (2.4 × 10^6 km^2) and the USA (2.2 × 10^6 km^2) (FAO 2003). Eastern Siberia is characterized by low precipitation (209 mm) and low temperature (–10.4 °C) (Robert 1997), permafrost (Desyatkin 1993), and occasional wildfires (Goldammer and Furyaev 1996). During 1988 to 1994, an average of 3.61 × 10^3 km^2 of forest was burned almost annually (Forest Management Department of Sakha Republic, unpublished data, 2000). Seventy to eighty percent of the fires were caused by human activities, and the rest by natural events such as lightning (Goldammer and Stocks 2000). After a severe forest fire, when the permafrost has thawed considerably, thermokarsts called alases can form (Desyatkin 1993). Water supplied from the thawing permafrost flows laterally into the alas, forming ponds with diameters ranging from several tens to several hundreds of meters. From the center of the pond to the periphery of the basin, there is a succession of belts of excess, normal, and inadequate moisture (Averenskiy and Desyatkin 1996). Microbiological processes of nitrification and denitrification regulate the production and consumption of N_2O (Sahrawat and Keeny 1986). Letey et al. (1980) reported that increasing soil moisture increased N_2O emission from the soil. Aulakh et al. (1992) reported that pH and organic carbon (OC) content in soil were important regulators of denitrification. Therefore, alas formation processes will influence N_2O flux.

The purpose of this study was to characterize the relationship between the N_2O dynamics and soil properties in four forest–alas ecosystems near Yakutsk city, eastern Siberia.

Materials and Methods

Site description

This study was conducted in four alas ecosystems near Yakutsk city (62°05′N, 129°45′E), Russia. Locations of each study site are shown in Figure 1, and the area of each alas is shown in Table 1. The ground level within each alas ranged from 4 to 25 m lower than that in the surrounding forest. Each alas had a pond measuring from several tens to several hundreds of meters in diameter in its center. The water depth of the ponds was 10 cm.

The adjacent forest consists mainly of larch (*Larix*

(Received; Jan. 23, 2007: Accepted; March 19, 2007)

∗ Corresponding author: morisita@affrc.go.jp

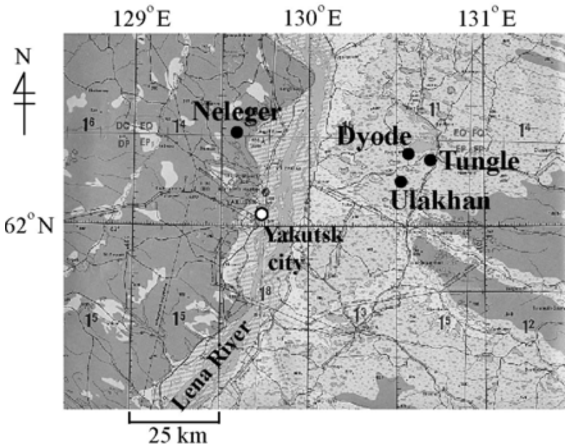

Fig. 1. The four study sites.

Table 1. Properties of forest and grassland soils.

Alas		area km^2	soil texture	pH	EC mS m^{-1}	OC %	TN %	C/N
Dyode	Forest		SL	5.9	2.0	0.68	0.03	23
	Grassland	0.02	SiCL	9.3	24.7	1.42	0.09	18
Neleger	Forest		SiC	6.3	6.8	1.71	0.07	24
	Grassland	0.5	LiC	7.3	34.3	12.17	0.94	13
Ulakhan	Forest		L	5.6	1.4	0.43	0.02	18
	Grassland	1.12	SiL	9.1	63.4	15.30	1.06	15
Tungle	Grassland	83.6	SiCL	9.3	21.9	3.53	0.37	10

SL, sandy loam; SiCL, silty clay loam; SiC, silty clay; LiC, light clay; L, loam; SiL, silty loam; TN, total nitrogen; EC electrical conductivity.

gmelinii) trees more than 200 years old, with *Vaccinium vitisidaea* predominant on the forest floor. The grassland of alases consists predominantly of *Elytrigia repens* and *Calamagrostis langsdorffii*.

Soil sampling and analysis

Soil samples were collected in the forests and grasslands with no replication in July 2000. Disturbed samples (~500 mL in a PVC bag) were collected from 0 to 20 cm below the O horizon. The samples were air-dried for more than 3 weeks in the laboratory, and then sieved through a 2-mm-mesh sieve for chemical analyses.

Soil pH was determined with a glass electrode pH meter in the supernatant suspension of 1:2.5 soil:deionized water. Electrical conductivity (EC) was determined with an EC meter in 1:5 soil:deionized water then multiplied by 5 to approximate that of a water-saturated soil paste. After the air-dried soil samples were ground, total carbon and nitrogen contents were determined by C/N analyzer (Vario-EL, Elementer). Carbonate-C content was analyzed by measuring the amount of CO_2 produced from 0.3 to 0.8 g of soil to which 15 mL of 2 M HCl was added in an Erlenmeyer flask. OC content was calculated by subtracting the carbonate-C content from the total C content (Loeppert and Suarez 1996; Sawamoto *et al.* 2000; Morishita *et al.* 2003).

N_2O flux

N_2O flux was measured by using a closed chamber technique in July 2000. Open-bottom stainless steel chambers 25 cm in height and 18.5 to 21.0 cm in diameter were used as described previously (Morishita *et al.* 2003). The day before the measurement, chambers were installed to 3 cm depth in the soil. The flux was measured in the forest (3–8 replications), in the grassland (6–8), at the edge of the ponds (2–4), and in the ponds (2–4). At 0, 10, 20, and 40 min after the chamber was closed, a 20-mL air sample was taken into a 10-mL glass bottle vacuum-sealed with a butyl rubber stopper and a plastic cap.

Back at the laboratory at Hokkaido University, Sapporo, Japan, N_2O concentrations in the gas samples were analyzed with a Shimadzu GC-14B gas chromatograph (GC). Analysis was performed within 3 months after the sampling. The GC was equipped with an electron capture detector and a 1-m Porapak N column. A 1-mL subsample was injected into the GC. The injection, detection, and column oven temperatures were 250, 340, and 60 °C, respectively. Pure Ar incorporated with 4% CH_4 was used as the carrier gas, with a flow pressure of 63 kPa. Standard N_2O of 0.296, 0.592, and 0.888 ppmv were used for calibration.

N_2O fluxes were calculated from the changes in the N_2O concentration in the chamber with time, by using a linear regression relation:

$$N_2O \text{ flux } (\mu g \text{ N m}^{-2} \text{ h}^{-1}) = \rho \times V/A \times \Delta c/\Delta t \times 273/T,$$

where ρ is the density of N_2O-N (1.25×10^9 μg m^{-3}) under standard conditions; V (m^3) and A (m^2) are the volume and bottom area of the chamber; $\Delta c/\Delta t$ (10^{-6} m^3 m^{-3} h^{-1}) is the rate of N_2O concentration change in the chamber during a given period; and T is the absolute temperature (K).

The minimum detectable N_2O concentration was 0.003 μL L^{-1}, which corresponds to a minimum detectable N_2O flux of ± 0.6 μg N m^{-2} h^{-1}. Non-detectable N_2O fluxes were treated as 0 μg N m^{-2} h^{-1}.

Soil temperature and moisture

Soil temperature and moisture were measured when N_2O flux was measured. Soil temperature was measured with a digital thermometer at a depth of 4 cm. Soil moisture was measured as volumetric water content by FDR (ML2 Theta Probe, Delta-T Devices) at a depth of 0 to 7 cm. All measurements were taken with 5 replications.

Statistical analysis

Nonparametric rank-sum tests were conducted for comparisons of N_2O fluxes among different forest–alas ecosystems, and for comparisons of N_2O flux, soil temperature, and soil moisture among land cover types: we used the Wilcoxon test for two-group comparison and the Kruskal–Wallis test for multiple-group comparison. When there was a significant difference, we used the Steel–Dwass test to compare the means by Excel Statistics (Esumi Ltd., Tokyo, Japan).

Result

Soil properties

Soil properties at each site are shown in Table 1. The pH, EC, and OC content were generally much higher in the grasslands, and C/N was lower in the grasslands.

There was a significant difference among the values of both soil temperature and moisture among the land cover types (Table 3). Forest had the lowest soil temperatures, owing to shading by canopy, and the lowest soil moisture, owing to water uptake by trees.

N_2O flux

N_2O flux at each site is shown in Table 2. Both uptake and emission were observed in the forest sites (–2.1 to 1.0 µg N m^{-2} h^{-1}) and in the grassland sites (–1.3 to 31 µg N m^{-2} h^{-1}). At the edge of the ponds, N_2O emission varied widely (0 to 140 µg N m^{-2} h^{-1}). In the ponds, only N_2O uptake was observed (–2.2 to 0 µg N m^{-2} h^{-1}). The median values of N_2O fluxes in each land cover type except grassland were not significantly different among the alases (Table 2). There were significant differences in the mean values of N_2O flux among land cover types (Table 3), in the order of edge of pond ≥ grassland ≥ forest = pond.

Relationship between N_2O flux and soil temperature and moisture

Figure 2 shows the relationship between N_2O flux and soil moisture. N_2O flux increased as soil moisture increased ($P < 0.01$), but the ponds showed N_2O uptake, and some fluxes at the edge of the ponds were small or not detected. The N_2O flux was not significantly correlated with the soil temperature ($P > 0.05$).

Comparison with previous studies

Owing to the lack of N_2O flux data from Siberia, we compared our data with values measured in northern Europe and in temperate and tropical regions. Our study forests acted as both sinks and sources of N_2O (–2.1 to 1.0 µg N m^{-2} h^{-1}) (Table 2). These values were similar to those previously reported in forests on mineral soil, but were smaller than those in forests on peat soil in northern Europe (Table 4). All of those values were smaller than those previously reported in tropical and temperate forests (Table 4). The N_2O fluxes in grasslands, at the edge of ponds, and in the ponds were similar to those previously reported in grasslands in the temperate region, in marsh in the temperate region, and in wetland in Finland (Table 4).

Table 2. N_2O flux at each site.

Cover	Alas	N_2O flux µg N m^{-2} h^{-1} median		min	max	Soil temperature °C	Soil moisture m^3 m^{-3}
Forest	Dyode	0.0	a	-1.0	0.9	20.3	0.03
	Neleger	0.0	a	-1.5	0.0	15.2	0.01
	Ulakhan	0.0	a	-2.1	1.0	17.7	0.05
Grassland	Neleger	3.5	a	2.1	31.0	18.7	0.24
	Ulakhan	0.0	b	-1.3	0.0	28.4	0.02
	Tungle	2.6	ab	0.0	12.4	27.2	0.17
Edge of pond	Dyode	35.6	a	0.0	113.3	25.5	0.43
	Neleger	120.8	a	54.2	139.7	18.1	0.60
	Ulakhan	2.8	a	0.0	4.1	23.2	0.46
	Tungle	90.5	a	53.2	127.7	31.3	0.42
Pond	Neleger	-0.3	a	-0.8	0.0	19.4	-
	Ulakhan	-1.6	a	-2.2	-1.6	27.5	-

Values followed by different letters are significantly different by Steel–Dwass test ($P < 0.05$) among alases within each land type.

Table 3. Summary of N_2O flux, soil temperature, and soil moisture by cover type.

Cover	N_2O flux µg N m^{-2} h^{-1}	Soil temp. at 4 cm °C	Soil moisture m^3 m^{-3}
Forest	0.0 bc	17 b	0.02 b
Grassland	2.1 ab	23 a	0.20 b
Edge of pond	53.7 a	24 ab	0.46 a
Pond	-0.8 c	21 ab	-

Values followed by different letters are significantly different by Steel–Dwass test ($P < 0.05$).

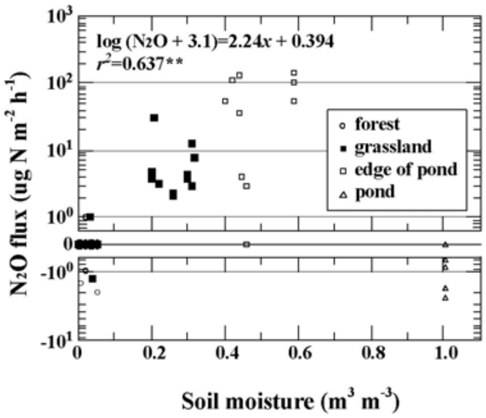

Fig. 2. Relationship between N_2O flux and soil moisture content (m^3 m^{-3}). The regression equation excludes plots of ponds.

Table 4. N_2O flux from natural ecosystems.

Lat.	Location	Soil	Vegetation	Study period	N_2O flux range $\mu g\ N\ m^{-2}\ h^{-1}$	Reference
			Forest			
	tropical forest				10 - 30	Bowman, 1990
	temperate forest				1.0 - 75	Bowman, 1990
N 53	Saskatchewan, Canada	sandy, clay loam	Aspen	annual	0.22	Corre et al., 1999
N 58	Gardsjon, Sweden	orthic podzol	Norway spruce	annual	0.81 - 1.3	Klemedtsson et al., 1997
N 61	Hameenlinna, Finland	carvic podzol	Scot pine	May - Oct.	0 - 7.5	Paavolainen et al., 1998
N 61	Ruotsinkyla, Finland	peat	*Picea abies*	Jun. - Oct.	3.6	Huttunen et al., 2003
N 61	Vesijako, Finland	peat	*Picea abies*	Jun. - Oct.	12	Huttunen et al., 2003
N 62	Finland	organic	Birch	Jun. - Dec.	28 ± 8.2	Maljanen et al., 2003
N 62	Yakutia, Russia		Larch	Jul.	-2.1 - 1.0	this study
			Grassland			
	temperate grassland				0.50 - 104	Bowman, 1990
N 53	Saskatchewan, Canada	sandy, clay loam		annual	0.44	Corre et al., 1999
N 62	Yakutia, Russia		grassland	Jul.	-1.3 - 31	this study
			Wetland			
	temperate wetland				1.0 - 149	Bowman, 1990
N 62	Finland (wetland)			Apr. - Dec.	-1.2 - 0	Regina et al., 1996
N 62	Yakutia, Russia		edge of pond	Jul.	0 - 140	this study
N 62	Yakutia, Russia		pond surface	Jul.	-2.2 - 0	this study

Discussion

N_2O flux increased as soil moisture increased, but ponds took up N_2O (Table 2). Letey *et al.* (1980) reported that when soil is wetted, N_2O is produced more rapidly than it is consumed. Bowman (1990) reported that N_2O production increased owing to the dominance of denitrification at very high soil moisture content. Terry et al. (1981) reported that the major gaseous product before flooding was N_2O, and that after flooding was N_2. Aulakh *et al.* (1992) observed the largest N_2O flux at 60% of water-filled pore space. These findings support our result that N_2O emission increased as soil moisture increased, and show that N_2O flux is largest when the water table is near the soil surface, but the soil is not completely saturated, and is due to biological processes of denitrification.

There was no significant difference among the mean N_2O fluxes at the edge of the ponds of different alases (Table 2), but flux varied widely. Although the reason was not clear, both pH and OC content might have an influence. pH is an important factor affecting denitrification (Bandibas *et al.* 1994; Dalal 2003), with an optimum value (Valera and Alexander 1961; Stevens *et al.* 1998; Simek and Hopkins 1999; Simek *et al.* 2002), and a change in pH produces a change in the N_2O/N_2 ratio during denitrification (Cady and Bartholomew 1960; Firestone *et al.* 1980; Letey *et al.* 1980; Koskinen and Keeny 1982; Scholefield 1997; Simek *et al.* 2002; Rochester 2003). Carbon content is another important factor in denitrification (Beauchamp *et al.* 1989). An increase of soil carbon content will increase denitrification to N_2 (Stanford *et al.* 1975; Weiter *et al.* 1993; Pu *et al.* 1999; Davidsson and Stahl 2000; Simek *et al.* 2000; Cosandey *et al.* 2003; Freibauer and Kaltschmitt 2003). Therefore, the wide range of N_2O flux at the edge of the ponds might be due to the wide ranges of soil pH and soil carbon contents.

Conclusion

The mean values of N_2O flux were significantly different among the land cover type, and highest at the edge of the ponds. N_2O fluxes increased as soil moisture increased, but fluxes were smallest in the ponds due to biological process of denitrification.

Acknowledgement

We thank Prof. M. Fukuda, Hokkaido University, leader of the CREST program of the Japan Science and Technology Corporation (JST), for supporting this study and for his valuable comments. We also thank Prof. K. Takahashi and Drs. M. Shibuya, H. Saito, K. Kushida, Y. Kobayashi, and G. Iwahana, Hokkaido University; Drs. T. C. Maximov and A.P. Isaev and the staff of the Institute of Biological Problems of the Cryolithozone, Russian Academy of Sciences; and Dr. A. N. Fedrov and the staff of the Permafrost Institute, Siberian Branch, Russian Academy of Science, for their assistance in the fieldwork in Yakutsk. This study was supported by the CREST program of the Japan Science Technology Corporation (JST).

Reference

Aulakh, M. S., Doran, J. W. and Mosier, A. R. (1992) Soil denitrification: significance, measurement, and effects on management. *In* Advances in Soil Science volume 18. Eds. Stewart BA, pp. 1–58, Springer-Verlag, New York

Averenskiy, A. I. and Desyatkin, R. V. (1996) Mesofauna of soils of alas–taiga ecosystems of the Lena–Amga interfluve, Eurasian Soil Sci., 28 (10), 208–216

Bandibas, J., Vermoesen, A., De Groot, C. J. and Van Cleemput, O. (1994) The effect of different moisture regimes and soil characteristics on nitrous oxide emission and consumption by different soils. Soil Sci., 158(2), 106–114

Beauchamp, E., Trevous, J. T. and Paul, J. W. (1989) Carbon sources for bacterial denitrification. *In* Advances in Soil Science volume 10, Eds. Stewart BA, pp. 57–112, Springer-Verlag, New York

Bowman, A. F. (1990) Exchange of greenhouse gases between terrestrial ecosystems and the atmosphere. *In* Soils and the Greenhouse Effect. Eds. Bowman AF. pp. 100–119, John Wiley and Sons, New York

Cady, F. B. and Bartholomew, W. V. (1960) Sequential products of anaerobic denitrification in Norfolk soil material. Soil Sci. Soc. Am. Proc., 477–482

Corre, M. D., Pennock, D. J., Van Kessel, C. and Elliott, D. K. (1999) Estimation of annual nitrous oxide emissions from a transitional grassland–forest region in Saskatchewan, Canada. Biogeochemistry, 44, 29–49

Cosandey, A. C., Maitre, V. and Guenat, C. (2003) Temporal denitrification patterns in different horizons of two riparian soils. Eur. J. Soil Sci., 54, 25–37

Dalal, R. C., Wang, W., Robertson, G. P. and Parton, W. J. (2003) Nitrous oxide emission from Australian agricultural lands and mitigation options: a review. Aust. J. Soil Res., 41, 165–195

Davidsson, T. E. and Stahl, M. (2000) The influence of organic carbon on nitrogen transformations in five wetland soils. Soil Sci. Soc. Am. J., 64, 1129–1136

Desyatkin, R. V. (1993) Syngenetic soil salinization during thermokarst Alas formation. Eurasian Soil Sci., 25(4), 38–46

FAO (2003) http://www.fao.org/forestry/fo/fra/main/index.jsp

Firestone, M. K., Firestone, R. B. and Tiedje, J. M. (1980) Nitrous oxide from soil denitrification: factors controlling its biological production. Science, 208(16), 749–751

Freibauer, A. and Kaltschmitt, M. (2003) Controls and models for estimating direct nitrous oxide emissions from temperate and sub-boreal agricultural mineral soils in Europe. Biogeochemistry, 63, 93–115

Goldammer, J. G. and Furyaev, V. V. (1996) Fire in ecosystems of boreal Eurasia. Ecological impacts and links to the global system. *In* Fire in Ecosystems of Boreal Eurasia, Ed. JG Goldammer and VV Furyaev, pp. 1–20, Kluwer Academic Publishers, The Netherlands

Goldammer, J. G. and Stocks, B. J. (2000) Eurasian perspective of fire: dimension, management and policies, and scientific requirements. *In* Fire, Climate Change, and Carbon Cycling in the Boreal Forest, Ecological Studies 138, Eds. Kasischke ES and Stocks BJ, pp. 49–65, Springer-Verlag, New York

Huttunen, J. T., Nykänen, H., Martikainen, P. J. and Nieminen M. (2003) Fluxes of nitrous oxide and methane from drained peatlands following forest clear-felling in southern Finland. Plant Soil, 255, 457–462

IPCC (2001) Climate change 2000: the scientific basis. http://www.ipcc.ch

Klemedtsson, L., Klemedtsson, Å. K. and Moldan, F. (1997) Nitrous oxide emission from Swedish forest soils in relation to liming and simulated increased N-deposition. Biol. Fertil. Soils, 25, 290–295

Koskinen, W. C. and Keeney, D. R. (1982) Effect of pH on the rate of gaseous products of denitrification in a silt loam soil. Soil Sci. Soc. Am. J., 46, 1165–1167

Letey, J., Valoras, N., Hadas, A. and Focht, D. D. (1980) Effect of air-filled porosity, nitrate concentration, and time on the ratio of N_2O/N_2 evolution during denitrification. J. Environ. Qual., 9(2), 227–231

Loeppert, R. H. and Suarez, D. L. (1996) Carbonate and gypsum, In Method of Soil Analysis Part 3—Chemical Methods, Ed. D.L. Sparks, SSSA Book Series: 5, pp. 437–474

Maljanen, M., Liikanen, A., Silvola, J. and Martikainen P.J. (2003) Nitrous oxide emissions from boreal organic soil under different land-use. Soil Biol. Biochem., 35, 689–700

Morishita, T., Hatano, R. and Desyatkin, R. V. (2003) CH_4 flux in an Alas ecosystem formed by forest disturbance near Yakutsk, eastern Siberia, Russia. Soil Sci. Plant Nut., 49(3), 369–377

Paavolainen, L. and Smolander, A. (1998) Nitrification and denitrification in soil from a clear-cut Norway spruce (*Picea abies*) stand. Soil Biol. Biochem., 30, 775–781

Pu, G., Saffigna, P. G. and Strong, W. M. (1999) Potential for denitrification in cereal soils of northern Australia after legume or grass–legume pastures. Soil Biol. Biochem., 31, 667–675

Regina, K., Nykanen, H., Silvola, J. and Martikainen, P. J. (1996) Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. Biogeochemistry, 35, 401–418

Robert, H. (1997) Climate com. http://www.worldclimate.com/climate/

Rochester, I. J. (2003) Estimating nitrous oxide emissions from flood-irrigated alkaline grey clays. Aust. J. Soil Res., 41, 197–206

Sahrawat, K. L. and Keeny, D. R. (1986) Nitrous oxide emission from soils. *In* Advances in Soil Science volume 4, Eds. Stewart BA, pp. 103–148, Springer-Verlag, New York

Sawamoto, T., Hatano, R., Yajima, T., Takahashi, K., and Isaev, A. P. (2000) Soil respiration in Siberian taiga ecosystems with different histories of forest fire. Soil Sci. Plant Nutr., 46 (1), 31–42

Scholefield, D., Hawkins, J. M. B. and Jackson, S. M. (1997) Use of a flowing helium atmosphere incubation technique to measure the effects of denitrification controls applied to intact cores of a clay soil. Soil Biol. Biochem., 22(9/10), 1337–1344

Simek, M. and Hopkins, D. W. (1999) Regulation of potential denitrification by soil pH in long-term fertilized arable soils. Biol. Fert. soils, 30, 41–47

Simek, M., Cooper, J. E., Picek, T. and Santruckova, H.

(2000) Denitrification in arable soils in relation to their physico-chemical properties and fertilization practice. Soil Biol. Biochem., 32, 101–110

Simek, M., Jisova, L. and Hopkins, D. W. (2002) What is the so-called optimum pH for denitrification in soil? Soil Biol. Biochem., 34, 1227–1234

Stanford, G., Vander, Pol, R. A. and Dzienia, S. (1975) Denitrification rates in relation to total and extractable soil carbon. Soil Sci. Soc. Am. J., 39, 284–289

Stevens, R. J., Laughlin, R. J. and Malone, J. P. (1998) Soil pH affects the processes reducing nitrate to nitrous oxide and di-nitrogen. Soil Biol. Biochem., 30(8/9), 1119–1126

Terry, R. E., Tate III, R. L. and Duxbury, J. M. (1981) The effect of flooding on nitrous oxide emissions from an organic soil. Soil Sci., 132(3), 228–232

Valera, C. L. and Alexander, M. (1961) Nutrition and physiology of denitrifying bacteria. Plant Soil, 15(3), 268–280

Weiter, K. L., Doran, J. W., Power, J. F. and Walters, D. T. (1993) Denitrification and the dinitrogen/nitrous oxide ratio as affected by soil water, available carbon, and nitrate. Soil Sci. Soc. Am. J., 57, 66–72