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Denitrification and associated N_2O emissions are limited by phosphorus availability in a grassland soil

Kazi Rehnuma Mehnaz *, Feike A. Dijkstra

Centre for Carbon, Water and Food, Faculty of Agriculture and Environment, The University of Sydney, 1 Central Avenue, Eveleigh, NSW 2015, Australia

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ABSTRACT

Effects of phosphorus (P) availability on nitrogen (N) loss through microbial nitrification and denitrification processes remain poorly understood. We conducted an incubation experiment to study the responses of N_2O production after P (0 and 3 mg P kg^{-1} soil) addition with and without NH_4^+ or NO_3^- (0 and 15 mg N kg^{-1} soil) in a high P-fixing grassland soil. The N addition included a ^{15}N tracer (1 mg ^{15}N kg^{-1}). In a separate experiment, we also investigated the effect of P availability on potential nitrification and denitrification. We hypothesised that the addition of P in the soil would increase N_2O emission from microbial nitrification and denitrification and thereby less soil ^{15}N-NH_4^+ and ^{15}N-NO_3^- would be recovered. We found that P addition only significantly increased cumulative N_2O emission and respiration in the NO_3^- treatment, suggesting stimulated activities of denitrifying microorganisms due to their relief from P limitation. However, a decrease in soil ^{15}N recovery after P addition in the NO_3^- treatment was not detected because of the very small loss of N as N_2O (<0.3% of the applied ^{15}N tracer). Potential denitrification marginally increased with P addition, while potential nitrification was not affected by P addition. We conclude that P addition may increase gaseous loss of N as N_2O in P-poor soils through microbial denitrification rather than nitrification when inorganic N is abundant.

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1. Introduction

Nitrous oxide (N_2O) is an important greenhouse gas with a global warming potential 298 times greater than carbon dioxide (CO_2) over a 100-year period (Forster et al., 2007). It is also identified as the dominant stratospheric ozone-depleting substance, emitted in the present century (Ravishankara et al., 2009). Atmospheric N_2O concentration is increasing at approximately 0.26% $year^{-1}$ and reached a concentration of 319 ppb in 2005 (Forster et al., 2007). Soils are the major sources of N_2O production, globally emitting an estimated 9.5 Tg N_2O-N $year^{-1}$ to the atmosphere (65% of global annual N_2O emission), of which fertilized agricultural fields contribute 2.8 Tg N_2O-N $year^{-1}$ (Bouwman et al., 2002; Flechard et al., 2007).

N_2O is primarily produced in soil by microbial nitrification and denitrification processes (Braker and Conrad, 2011; Kool et al., 2011; Maag and Vinther, 1996; Skiba et al., 1993; Wrage et al., 2001). Nitrification is the aerobic oxidation of ammonium (NH_4^+) to nitrate (NO_3^-), primarily carried out by chemoautotrophic bacteria, where N_2O is produced through chemical decomposition of hydroxylamine (NH_2OH) and/or nitrite (NO_2^-) (intermediates of nitrification), or through reduction of NO_2^- under limited oxygen (O_2) conditions (Firestone and Davidson, 1989; Skiba and Smith, 2000; Williams et al., 1992; Wrage et al., 2001). Denitrification is the anaerobic reduction of NO_3^- to molecular nitrogen (N_2), predominantly conducted by heterotrophic facultative anaerobes, where a variable fraction of nitrogen (N) can be released as nitric oxide (NO) and N_2O (intermediates of denitrification) when the process is incomplete (Braker and Conrad, 2011; Signor and Cerri, 2013; Wrage et al., 2001). The rate of N_2O production from these two processes is strongly influenced by availability of mineral N (substrates for nitrification and denitrification), availability of labile organic carbon (for denitrification), soil moisture and aeration, soil temperature, pH and availability of phosphate (Bremner, 1997; Firestone and Davidson, 1989; Flechard et al., 2007; Signor and Cerri, 2013; Skiba and Smith, 2000; Wang et al., 2014).

Grasslands cover approximately 25% of the earth's land area, and are important sources of N_2O emission (Saggar et al., 2009). Application of inorganic and organic N fertilizers is a common practice for grassland soils, especially in developed countries, for achieving increased grass yield to support the production of grassland-based livestock (Bouwman et al., 2002). It is estimated that 8% of the world's grasslands are fertilized with mineral N fertilizers and manures, which is estimated to contribute 0.14 Tg N_2O-N $year^{-1}$ to the atmosphere, or about 5% of the global annual N_2O emission from fertilized agricultural fields (Bouwman et al., 2002). Addition of P fertilizers is a common practice to overcome P limitation in grassland systems (Bennett and Adams, 2001). The addition of P may affect N_2O fluxes by influencing the activities of nitrifying and denitrifying microorganisms (Fig. 1) (Minami and

* Corresponding author at: Centre for Carbon, Water and Food, Faculty of Agriculture and Environment, The University of Sydney, Biomedical Building, 1 Central Avenue, Australian Technology Park, Eveleigh, NSW 2015, Australia.
E-mail address: kazi.mehnaz@sydney.edu.au (K.R. Mehnaz).

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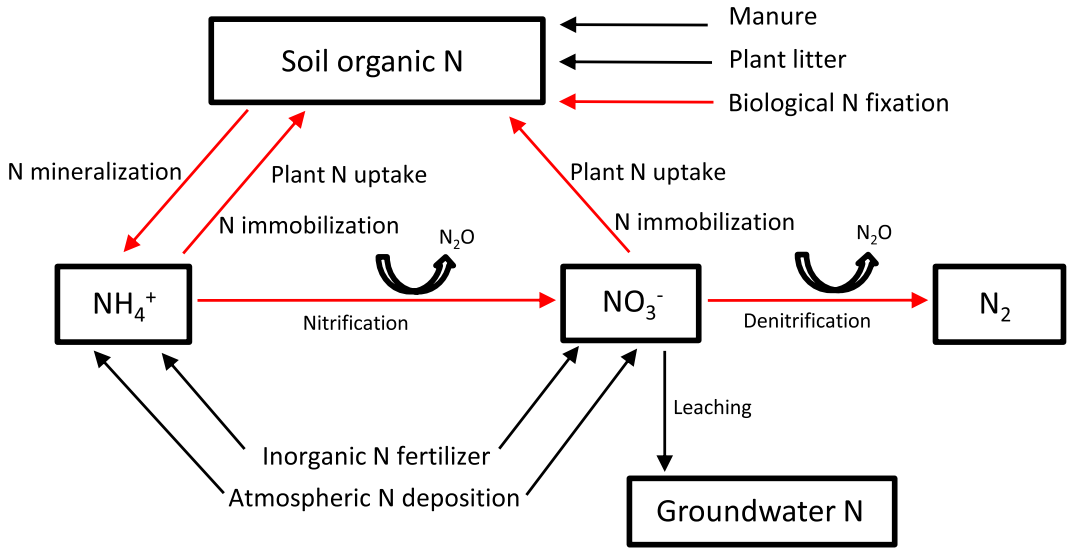

Fig. 1. Major elements of N transformation in soil. Those processes influenced by P application are indicated with red arrows.

Fukushi, 1983; Mori et al., 2010, 2013b; Sundareshwar et al., 2003; Wang et al., 2014; White and Reddy, 1999; White and Reddy, 2003; Zhang et al., 2014). P availability can also affect microbial N_2O production by influencing organic N mineralization, plant and microbial N immobilization and biological nitrogen fixation (Falkiner et al., 1993; Hall and Matson, 1999; Houlton et al., 2008; White and Reddy, 2000).

Hall and Matson (1999) suggested that shortage of available P can cause high N_2O emissions by reducing microbial N immobilization in P-limited tropical ecosystems at high anthropogenic N inputs. Sundareshwar et al. (2003) demonstrated that increased P availability in a coastal wetland soil decreased the rate of N_2O production through denitrification by alleviating P limitation of heterotrophic microorganisms. In contrast, some other researchers concluded from their soil incubation studies that P addition may increase N_2O emission from nitrification and/or denitrification by stimulating the activities of nitrifying and/or denitrifying microorganisms (Minami and Fukushi, 1983; Mori et al., 2010, 2013b). Furthermore, several studies identified increased microbial respiration after P addition suggesting increased microbial activity (Cleveland et al., 2002; Cleveland and Townsend, 2006; Gnankambary et al., 2008; Ilstedt and Singh, 2005; Mori et al., 2013a, 2013c), which could also influence N_2O emissions affecting N transformations and/or immobilization. Plants may also control N_2O emission. Alleviation of plant P limitation can enhance plant N uptake and reduce N_2O emission through a reduction in soil mineral N concentrations (Baral et al., 2014; Mori et al., 2013d, 2014). Conversely, He and Dijkstra (2015) observed reduced ^{15}N recovered in plants, microbes and soil after P addition, suggesting larger gaseous loss of N through microbial nitrification and denitrification based on zero leaching occurrences. However, it is important to understand the relative responses of nitrification and denitrification, and their associated N_2O emissions to P enrichment.

In this study, we examined the effects of P addition with and without NH_4^+ or NO_3^- (substrate for nitrification or denitrification) on N_2O emissions from a high P-fixing grassland soil in New South Wales, Australia. A laboratory incubation experiment was conducted involving a ^{15}N tracer (to measure the ^{15}N recovery in soil), and excluding plant effects through N uptake. We also investigated the effect of P availability on potential nitrification and denitrification while removing all the factors potentially limiting nitrification and denitrification, respectively. We hypothesised that the addition of P in the soil would increase N_2O emission from microbial nitrification and denitrification and thereby show less ^{15}N recovery in soil.

2. Materials and methods

2.1. Study area and soil used

In August 2014, soil samples were collected for this study from a grassland located at Westwood farm (latitude 33°59′46″S, longitude 150°39′16″E) near Camden in New South Wales, Australia. The area is characterised by an annual precipitation of 790 mm, and mean air temperature of 10.4 °C in July and 23.0 °C in January (Dijkstra et al., 2015). *Paspalum dilatatum* Poir. (C_4) was the dominating grass of Westwood farm which was moderately grazed by cattle and not fertilized. The soil of this grassland is a sandy loam red Kurosol with a high P-fixing capacity reported in Dijkstra et al. (2015). We collected soil samples at 0–20 cm depth after removing the grass layer. The soils were air-dried, crushed and sieved through a 2 mm sieve, and visible roots were removed. The properties of the soil are shown in Table 1.

2.2. Incubation experiment

200 g air-dried, sieved soil was placed in 1.89 L glass jars. The following six treatment combinations were evaluated: ammonium sulphate ($(NH_4)_2SO_4$), with and without mono-potassium phosphate (KH_2PO_4); potassium nitrate (KNO_3), with and without KH_2PO_4; and no N addition (none), with and without KH_2PO_4. N and P were added as 15 mg N kg^{-1} soil and 3 mg P kg^{-1} soil, respectively, to the jars. When N was added, 1 mg kg^{-1} soil was added as ^{15}N (99 atom %) and the other 14 mg kg^{-1} soil was added as non-labelled N (i.e., the final ^{15}N atom% of the added N was 6.6 atom %). Each treatment was performed with four replicates. The soil water content was adjusted to 60% field capacity. The samples were incubated for 20 days at 20 °C in the dark. Jars were closed during the incubation to reduce water loss. Small amounts of water loss that did occur during gas sampling were replenished each day at the end of gas sample collection.

N_2O and CO_2 fluxes were measured at 0, 1, 3, 6, 10 and 20 days after the beginning of the incubation. On each day of sampling, the jars were flushed with ambient air and kept open for half an hour before starting gas sample collection. After half an hour, the jars were closed with jar lids equipped with sampling ports and first gas samples (at time zero) were taken. A second gas sample was taken after 45, 60, 120, and 240 min on day 0, 1, 3, and 6 respectively. For days 10 and 20, the second gas samples were taken after 300 min. The period between the collection of first and second gas samples was increased with time because

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