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Earthworms reduce soil nitrous oxide emissions during drying and rewetting cycles

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ABSTRACT

Nitrous oxide (N_2O) is a greenhouse gas that is released from both nitrification and denitrification processes. Soil moisture content is a key controller of the biochemical pathways leading to N_2O emission, causing a switch between nitrification and denitrification processes. Earthworms are reported to increase N_2O emissions from soil under aerobic and anaerobic conditions, but how earthworm-induced N_2O emissions are affected by soil drying and rewetting cycles is unknown. The objectives of this study were to (1) evaluate earthworm-induced N_2O emissions from soils with aerobic, anaerobic, and fluctuating soil moisture conditions; and (2) determine the earthworm effects on soil denitrifiers responsible for N_2O fluxes. Soils were kept in mesocosms (polyvinyl chloride plastic tubes, 10 cm diameter, filled with soil to 15 cm depth) at constant 33% water-filled pore space (WFPS), constant 97% WFPS or underwent three wetting-drying cycles (WD). Each soil moisture treatment had 2 earthworm treatments, including (1) a mixture of endogeic *Aporrectodea turgida* and anecic *Lumbricus terrestris* and (2) no earthworm treatment. These gave a total of 6 treatments in this study, with 5 replicates for each treatment. The N_2O fluxes were quantified every one to three days, and the soil denitrifier activities were measured after 69 days, when the experiment ended. Soil moisture significantly affected N_2O emissions and the WD treatment had the highest cumulative N_2O emissions. Earthworms increased N_2O emissions by 50% in the 33% WFPS treatment but decreased N_2O emissions by 34% in the 97% WFPS treatment, probably due to more complete reduction of N_2O to N_2. Earthworms strongly reduced N_2O emission rate in WD treatment, and they significantly reduced cumulative N_2O emissions by 82%. Soil denitrification enzyme activity (DEA) increased significantly when earthworms were present. Abundance of 16S rRNA, *nirS*, and *nosZ* genes was affected significantly by the earthworm × soil moisture interaction, with the highest 16S rRNA and *nosZ* abundance in soil from the WD treatments. We conclude that the decrease in cumulative N_2O emissions from soil at 97% WFPS and the WD treatment by earthworms was due to an alteration of the denitrifying bacterial community composition.

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1. Introduction

Soil moisture changes constantly as a result of rewetting events (e.g., rainfall, snowmelt, irrigation and flooding) and drying, as water drains through the profile or returns to the atmosphere via (evapo)transpiration. Soil moisture regulates redox potential and therefore influences microbially-mediated reactions in the nitrogen (N) cycle. Most nitrogenous compounds in the soil N cycle are produced under a narrow range of soil moisture conditions, but nitrous oxide (N_2O) is released from nitrification and nitrifier-denitrification under aerobic conditions (<70% water-filled pore space (WFPS)), with substantial N_2O fluxes occurring during denitrification in anaerobic soils (≥70% WFPS) (Kool et al., 2011; Linn and Doran, 1984; Wrage et al., 2005, 2001). Rapid rewetting of dry soil can trigger a pulse of N_2O, which is attributed to the following causes: (i) a number of facultative aerobic soil microorganisms can switch to anaerobic metabolism, leading to gaseous N_2 and N_2O emissions (Khahil and Baggs, 2005; Kool et al., 2011; Linn and Doran, 1984); (ii) release of the osmolytes accumulated in the drying phase, cell lysis and breakdown of aggregates supply abundant substrates to denitrifiers (Fierer et al., 2003; Gordon et al., 2008); and (iii) anaerobic microbial activity will be stimulated, especially denitrification enzyme activity (DEA) (Guo et al., 2010). Previous drying-rewetting studies showed that N_2O emissions could be affected by the frequency of the drying and rewetting cycles (Fierer and Schimel, 2002), soil compaction (Beare et al.,

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2009), the type of crop residue present (Zhong et al., 2011) and fertilizer inputs (Ruser et al., 2006). However, most of those studies were conducted in the absence of soil macrofauna, notably earthworms, which contribute to soil N_2O emissions.

There is ample evidence that earthworm interactions with soil microorganisms increase soil N_2O emissions, with 42% more N_2O emitted from earthworm-worked soil, on average, than without earthworms (Lubbers et al., 2013). There are two sources of N_2O from earthworms – the earthworm body, which can release 0–11 nmol N_2O h^{-1} g^{-1} earthworm (Horn et al., 2006) and its biostructures (casts, middens, and burrows) (Drake and Horn, 2006, 2007). Earthworm biostructures modify the soil structure, i.e., fresh casts function like stable macroaggregates while burrows change soil water-flow dynamics and gas diffusivity (Giannopoulos et al., 2010; Lubbers et al., 2011; Shipitalo and Bayon, 2004), and are thus considered to be an indirect effect of earthworms on N_2O emissions. Earthworm-induced N_2O emissions vary depending on earthworm species (Rizhiya et al., 2007; Speratti and Whalen, 2008), food placement (residues incorporated vs. surface applied) (Giannopoulos et al., 2010) and plant N uptake (Lubbers et al., 2011) when soil water content was kept constant (from 40% to 100% WPFS in those studies). Less is known about how earthworm-induced N_2O emissions are affected by soil moisture. Bertora et al. (2007) reported that *Aporrectodea longa* enhanced N_2O production under 25% gravimetric soil water content, but not at 19% or 12.5% gravimetric soil water content, yet Rizhiya et al. (2007) found no difference in earthworm-induced N_2O production at 44% WFPS and 100% WFPS. Earthworm survival and growth are constrained in dry and flooded soils, such that about 57%–69% WFPS is optimal for earthworm activities (Eriksen-Hamel and Whalen, 2006; Moreau-Valancogne et al., 2013), and likely controls the direct and indirect effects of earthworms on soil N_2O emissions. Wetting and drying cycles are expected to cause earthworms to move vertically in the soil profile as they seek zones with favorable soil moisture conditions, although whether this affects the dynamics of earthworm-induced N_2O emissions under fluctuating soil moisture conditions is not known.

The presence of earthworms should enhance N_2O production from nitrification and nitrifier-denitrification because earthworm activity stimulates N mineralization and nitrification (Costello and Lamberti, 2009; Lubbers et al., 2011). Nitrification was the source of 12%–85% of the N_2O production in soil containing *Aporrectodea turgida* alone or in a mixed population with *Lumbricus terrestris*, and there was about 30 times more N_2O production from earthworm-worked soil than the control without earthworms (Speratti and Whalen, 2008). Considering that denitrification is a major source of soil N_2O emissions (Kool et al., 2011), how earthworms affect the activity and composition of microbial denitrifier communities needs to be considered. For instance, denitrifying activity is affected by access to labile carbon, so earthworm activities that increase soil labile carbon could change the N_2O/N_2 ratio (Miller et al., 2008; Nebert et al., 2011). Soils with low mineral N (especially NO_3^-) and high moisture often favor N_2O consumption, since NO_3^- is preferred as an electron acceptor over N_2O (Chapuis-Lardy et al., 2007; Rosenkranz et al., 2006; Ruser et al., 2006), so earthworm activities that result in nitrification and therefore high NO_3^- concentration are expected to produce N_2O and increase N_2O emissions from soil. If earthworm intestinal tract or biostructures are favorable micro-habitats for denitrifying bacteria that lack nitrous oxide reductase (N_2OR, synthesized by the *nosZ* gene), the terminal reaction product would be N_2O (Chapuis-Lardy et al., 2010; Depkat-Jakob et al., 2013; Nebert et al., 2011; Zumft and Körner, 2007). Still, there have been relatively few studies to investigate denitrifiers in earthworm-worked soil, and none that have studied earthworm–denitrifier interactions under fluctuating soil moisture conditions.

The objective of this study was to measure the earthworm-induced N_2O emissions under constant soil moisture, both aerobic and anaerobic conditions, and in soils with repeated wetting and drying cycles. A secondary objective was to determine how earthworms influenced the activity of soil denitrifiers, and whether this was related to the N_2O emissions. This laboratory mesocosm experiment was conducted with a mixed population of endogeic (*A. turgida*) and anecic (*L. terrestris*) earthworms, since these species typically co-habit soils in our region.

2. Materials and methods

2.1. Soil and earthworm collection

Individuals of *A. turgida* and *L. terrestris* were extracted with dilute (0.5%) formaldehyde solution from a red clover (*Trifolium pretense* L.) field at the Macdonald Campus Research Farm, Ste-Anne-de-Bellevue, Quebec, Canada (45°28′ N, 73°45′ W). Earthworms were washed several times with tap water to remove formaldehyde on the body surface and then transferred into 37 L culture boxes for at least one month. Earthworms were fed with grass-based plant compost from the Macdonald Campus Research Farm. Soil for earthworm culture and the incubation study was Chateauguay clay loam soil (fine, mixed, nonacid, frigid, Hapludalf), with 36.8 g organic C kg^{-1} and a pH of 6.5.

2.2. Experimental design

This experiment used a completely randomized factorial design with 2 earthworm treatments (with and without earthworms, referred as EW and nEW, respectively) and 3 soil moisture conditions (constant 97% WFPS, constant 33% WFPS, and wetting–drying cycles (WD) from 97% WFPS to 33% WFPS) (Table 1). The experiment was conducted in mesocosms, 1.57 L polyvinyl chloride plastic tubes with 10 cm diameter and a height of 20 cm. Soil (sieved < 6 mm mesh) was packed to 15 cm height at a bulk density of 1.20 ± 0.003 g cm^{-3}, leaving 5 cm of headspace. Although the redistribution of water may occur in a 15 cm tall soil core (Guo et al., 2013), the cores needed to be sufficiently large to accommodate earthworm movement, including possible vertical displacement in response to the WD treatment. Although the natural burrowing habits of *L. terrestris* would be better simulated in cores tall enough to hold 1 m of soil (Shipitalo and Bayon, 2004), a taller soil core was not selected because soil moisture at the surface and at soil depths lower than 20 cm would be significantly differently (Paul et al., 2012), which would affect the estimation of earthworm effects on N_2O emissions under different soil moisture conditions. Each soil moisture treatment was repeated in 15 mesocosms, which included undisturbed EW ($n = 5$) and nEW ($n = 5$) treatments for gas sampling as well as a disturbed EW treatment ($n = 5$), where earthworms were removed periodically to assess their survival and biomass, giving 45 mesocosms in total.

After soil was added, the moisture content was adjusted to 33% WFPS in 30 mesocosms (for the 33% WFPS and WD treatments) and 97% WFPS in 15 mesocosms that were then pre-incubated for 4 d at constant temperature (20 °C) in the dark to achieve a stable N_2O flux rate. Then, the earthworm treatment was added to mesocosms in the undisturbed and disturbed EW treatments. Each earthworm treatment included 3 adult *A. turgida*, 1 juvenile *L. terrestris* and 1 adult *L. terrestris*, giving 382 individuals m^{-2} of endogeic and 255 individuals m^{-2} of anecic earthworms. This earthworm density is greater than field populations in this region, which range from 46 to 422 individuals m^{-2} (Eriksen-Hamel et al., 2009; Whalen, 2004; Whalen et al., 2012). Two days before adding the earthworm treatment, we removed all earthworms from culture boxes, washed

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