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REVIEW

Earthworm interactions with denitrifying bacteria are scale-dependent: Evidence from physiological to riparian ecosystem scales

Chen Chen, Joann K. Whalen*

Department of Natural Resource Sciences, Macdonald Campus, McGill University, 21,111 Lakeshore Road, Ste-Anne-de-Bellevue, Quebec H9X 3V9, Canada

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Abstract

Earthworms are implicated in denitrification, the microbially mediated reaction that results in gaseous nitrogen (N_2O and N_2) loss from terrestrial ecosystems. At the physiological scale, the anaerobic earthworm gut is a favorable microsite for endemic and transient denitrifiers that produce up to 11 nmol N_2O g^{-1} earthworm h^{-1}. Besides this direct earthworm–denitrifier interaction, the earthworm's ability to consume, fragment and mix organic residues with soil will accelerate N mineralization and create suitable conditions for opportunistic soil denitrifiers. At the drilosphere scale, earthworm biostructures (burrows, casts) and earthworm-worked soil create gradients of redox conditions and are enriched in inorganic N and soluble C substrates used by denitrifiers. Therefore, earthworms indirectly stimulate soil N_2O emissions by soil denitrifiers. Although these small-scale effects may imply that ecosystems with large earthworm populations are more likely to lose N through denitrification, there is scant experimental data to confirm this supposition. Evidence from simulated streams and agroecosystems suggests that earthworms can stimulate N_2O emissions at the ecosystem-scale, but environmental factors (temperature and moisture) may overwhelm earthworm-induced denitrification. A critical review of earthworm–denitrifier interactions in riparian buffers, a hotspot for both groups of organisms, indicated that hydrodynamics controls denitrification during flooding periods by profoundly changing soil moisture and substrate concentrations that favor denitrifier activity. Earthworm effects on denitrifiers may be detected during drier periods. Thus, earthworm–denitrifier interactions cannot be extrapolated from the physiological- and drilosphere-level to explain denitrification in riparian ecotones due to seasonal variation in hydrological processes occurring at this scale.

Zusammenfassung

Regenwürmer sind an der Denitrifikation beteiligt, der mikrobiell vermittelten Reaktion, die die Freisetzung von gasförmigem Stickstoff (N_2O und N_2) aus terrestrischen Ökosystemen bewirkt. Auf der physiologischen Ebene ist der anaerobe Regenwurmdarm ein günstiges Habitat für endemische und vorübergehende Denitrifikanten, die bis zu 11 nmol N_2O g^{-1} Regenwurm h^{-1} produzieren. Neben dieser direkten Regenwurm-Denitrifikanten-Interaktion, beschleunigt die Fähigkeit des Regenwurms, organischen Detritus zu konsumieren, zu zerkleinern und mit Erde zu mischen, die Stickstoffmineralisation und schafft günstige Bedingungen für opportunistische, bodenbewohnende Denitrifikanten. In der Drilosphäre erzeugen vom Regenwurm geschaffene Strukturen (Gänge, Ausscheidungen) und vom Regenwurm verarbeiteter Boden Gradienten von Redox-Bedingungen, und sie sind angereichert mit anorganischem N und löslichen C-Substraten, die von Denitrifikanten genutzt

*Corresponding author. Tel.: +1 514 398 7943; fax: +1 514 398 7990.
E-mail address: joann.whalen@mcgill.ca (J.K. Whalen).

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werden. Deshalb stimulieren Regenwürmer indirekt N_2O-Emissionen durch bodenlebende Denitrifikanten. Obwohl diese kleinräumigen Effekte nahelegen könnten, dass Ökosysteme mit großen Regenwurmpopulationen mit höherer Wahrscheinlichkeit Stickstoffverluste durch Denitrifikation erleiden, gibt es nur wenige experimentelle Daten, um diese Annahme zu stützen. Ergebnisse aus simulierten Fließgewässern und Agrarökosystemen legen nahe, dass Regenwürmer N_2O-Emissionen auf der Ökosystem-Ebene stimulieren können, aber Umweltfaktoren (Temperatur und Feuchte) könnten die regenwurminduzierte Denitrifikation übertönen. Eine kritische Bestandsaufnahme von Regenwurm-Denitrifikanten-Interaktionen in Flussuferzonen, die Hotspots für beide Organismengruppen sind, zeigte, dass die Hydrodynamik die Denitrifikation während der Überflutungsperioden bestimmte, indem Bodenfeuchte und Substratkonzentrationen grundlegend verändert wurden. Einflüsse der Regenwürmer können eher während der trockneren Perioden gefunden werde n. Somit können die Regenwurm-Denitrifikanten-Interaktionen nicht von der physiologischen bzw. Drilosphärenebene extrapoliert werden, um die Denitrifikation in Flussuferzonen zu erklären, was auf die saisonalen Schwankungen der hydrologischen Prozesse zurückzuführen ist, die auf dieser räumlichen Skala auftreten.

Keywords: Denitrification; Denitrifier activity; Earthworm nitrogen gains; Earthworm nitrogen losses; Earthworm biostructure; Drilosphere; Nitrous oxide; Riparian ecosystem; Redox gradient; Hydrodynamics

Denitrification, denitrifiers, and earthworms

Denitrification is the most important biological source of gaseous nitrogen (N) emission from soil, accounting for global N losses of about 7.1×10^{12} mol y^{-1} (Canfield et al., 2010). The term ‘denitrifier’ refers to any organism that catalyzes at least one step in this complex, multi-step reaction, including species from more than 60 genera of Bacteria as well as Archaea and Eukaryotes (Zumft and Körner 2007; Demanèche et al., 2009). Nitrous oxide (N_2O), an intermediate byproduct of denitrification, is a potent greenhouse gas and the most important ozone-depleting substance in the atmosphere (IPCC 2007; Ravishankara et al., 2009). Soils are the dominant source of N_2O emissions and produce 6–7 Tg N_2O-N y^{-1} (Syakila and Kroeze 2011).

Earthworms could contribute to soil N_2O emissions, according to meta-analysis that reported greater net N_2O emission from soil with than without earthworms (Lubbers, López González, Hummelink, & Van Groenigen, 2013). This meta-analysis was based on 13 studies about earthworm-induced N_2O emissions, mostly performed under laboratory conditions. These small-scale studies provide strong evidence of a stimulatory effect of earthworms on denitrifying bacteria in the earthworm gut and in earthworm drilosphere (Drake and Horn 2006; Paul et al., 2012), but it is not known if such earthworm–denitrifier interactions can be extrapolated to the ecosystem-level, given the limited experimental data from field-scale studies. In this review, we examined earthworm–denitrifier interactions at the physiological scale (within individual earthworms), drilosphere scale (earthworm-worked soils) and ecosystem scale, with the goal of determining whether or not earthworm–denitrifier interactions could be expected to increase soil N_2O emissions in riparian buffers, a natural biofilter that reduces runoff and attenuates excess nutrients. Riparian buffers are a special ecotone that support larger earthworm populations and greater denitrification than the adjacent terrestrial or riverine ecosystems, although a dynamic relationship exists between earthworms and denitrifiers because of fluctuating water levels in the riparian buffer.

Earthworm–denitrifier interactions at the physiological scale: direct effects

At the physiological scale, earthworm–denitrifier interactions are regarded as direct effects because earthworm gut provides a “heaven” for transient denitrifiers (Horn, Schramm, & Drake, 2003; Drake & Horn, 2006). Populations of transient microorganisms increase when earthworms mix organic residues and soil in their middens prior to consuming them. Upon ingestion of this pre-digested material, facultative denitrifiers are activated within the anoxic earthworm gut which possesses neutral pH, high mineral N and labile C concentrations (“sleeping beauty paradox”) (Brown, Barois, & Lavelle, 2000; Horn et al., 2003). Although the “sleeping beauty paradox” is not perfect, as it is hard to explain how transient microorganisms could significantly improve earthworm N nutrition during their short gut transit time (<24 h), it does illustrate a mutualistic relationship between earthworms and ingested microorganisms (Brown et al., 2000). Denitrifying bacteria are up to 300-fold more numerous in the earthworm gut than in the bulk soil (Karsten and Drake 1995; Ihssen et al., 2003) and biologically active. The earthworm gut can emit 0–11 nmol N_2O g^{-1} earthworm h^{-1} with the N_2O accounting for around 50% of the total $N_2O + N_2$ due to incomplete denitrification (Karsten and Drake 1997; Matthies et al., 1999; Horn et al., 2006). In situ microsensor reveals most N_2O production occurred in the foregut (2.7 μM N_2O) and midgut (5.6 μM N_2O) and declines in the hindgut (0.2 μM) (Horn et al., 2003). The N_2O-emitting bacteria in the earthworm gut are widely found across earthworm species and aquatic macrofauna, suggesting the