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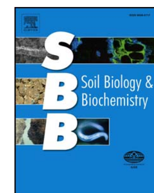

Spatial zoning of microbial functions and plant-soil nitrogen dynamics across a riparian area in an extensively grazed livestock system

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ABSTRACT

Anthropogenic activities have significantly altered global biogeochemical nitrogen (N) cycling leading to major environmental problems such as freshwater eutrophication, biodiversity loss and enhanced greenhouse gas emissions. The soils in the riparian interface between terrestrial and aquatic ecosystems may prevent excess N from entering freshwaters (e.g. via plant uptake, microbial transformations and denitrification). Although these processes are well documented in intensively managed agroecosystems, our understanding of riparian N removal in semi-natural systems remains poor. Our aim was to assess the spatial zoning of soil microbial communities (PLFA), N cycling gene abundance (archaeal and bacterial *amoA*, *nifH*, *nirK*, *nirS*, *nosZ*), N processing rates and plant N uptake across an extensively sheep grazed riparian area. As expected, soil properties differed greatly across the riparian transect, with significant decreases in organic matter, NH_4^+, carbon (C) and N content closest to the river (< 10 m). In addition, different microbial community structures were found along the transect. The abundance of N fixation (*nifH*) increased with distance from the river (> 10 m), while ammonia oxidising archaea (AOA) increased in abundance towards the river. N_2O emissions rates were limited by C and to a lesser extent by N with greater emissions close to the river. Plant uptake of urea-derived ^{15}N was high (ca. 55–70% of that added to the soil) but 30–65% of the N was potentially lost by denitrification or leaching. Percentage recovered also suggests that the spatial patterning of plant and microbial N removal processes are different across the riparian zone. Our study provides novel insights into the underlying mechanisms controlling the spatial variability of N cycling in semi-natural riparian ecosystems.

1. Introduction

The overuse of nitrogen (N) fertilizers, alongside land use change, has caused the N saturation of many terrestrial ecosystems worldwide (Gruber and Galloway, 2008). Further, the resultant N loss from agroecosystems is contributing to many major environmental problems such as marine and freshwater eutrophication, loss of biodiversity, climate change and ecosystem acidification (Canfield et al., 2010; Erisman et al., 2013). Strategies are therefore needed to better retain, or sustainably remove, excess N from land under agricultural production. One potential mechanism is the active management of riparian areas at field margins to intercept and mitigate excess N from migrating towards freshwaters (Mayer et al., 2007). Within these areas, a range of interrelated biotic and abiotic processes may be involved in N attenuation, including nitrification, denitrification, mineralization, plant and microbial uptake, mass flow/diffusion and sorption-desorption (Matheson et al., 2002; Vymazal, 2007). The importance of each process, however, is expected to vary greatly between ecosystems and also from the landscape down to the micrometre scale within the plant-microbial-soil system (Burt et al., 1999; Sanchez-Pérez et al., 2003).

Denitrification has been shown to be of particular importance for riparian wetland biogeochemistry because of the predominance of anoxic conditions, high concentrations of dissolved organic carbon (DOC) and the high rates of N fixation (Groffman and Hanson, 1997). It also represents the ultimate removal mechanism for reactive nitrogen (e.g. NO_3^-, NO_2^-, N_2O) from terrestrial and aquatic ecosystems (Seitzinger et al., 2006; Jacinthe and Vidon, 2017). In some cases, however, complete denitrification to N_2 may not occur due to a lack of N_2O reductase in the microbial community or if certain environmental conditions remain sub-optimal (e.g. soil moisture, O_2 content), leading to

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the potential release of environmentally damaging N_2O (Butterbach-Bahl et al., 2013). Additionally, denitrification is strongly coupled, both spatially and temporally, with other environmental processes such as N fixation, nitrification and anaerobic ammonium oxidation (anammox) (Vymazal, 2007; Groffman et al., 2009).

To optimise N removal by riparian areas and to implement active management, requires a good understanding of the key factors which regulate N cycling across these zones. Fundamental to this, is understanding the spatial abundance and behaviour of the underlying microbial communities which control how and when the different N transformations occur (Herbert, 1999; Chon et al., 2011). In this respect, few studies have tried to combine the analysis of key N cycling genes (abundance and transcription) and quantification of $N_2O:N_2$ production to gain a better insight into the spatio-temporal factors regulating N_2O fluxes (Avrahami and Bohannan, 2009)). However, contradictory studies showing a clear relationship between gene copy number and N_2O emission rates or a total lack of it, are commonly presented, highlighting the need for further research in this area (Bakken et al., 2012; Di et al., 2014). Additionally, research in wetland biogeochemistry has frequently focused on single-ecosystem processes (i.e. denitrification) rather than providing a more holistic view of microbial community functioning (Gutknecht et al., 2006). Therefore, there is a need to improve our understanding of the links (from genes to ecosystems) between physical, biogeochemical and ecological processes that drive the services of freshwater systems.

Alongside the microbial community, wetland vegetation also plays a major role in regulating N losses via denitrification (Schnabel et al., 1996; Veraart et al., 2011). For example, plants can alter the size and composition of the soil microbial community, stimulate microbial activity via C rhizodeposition, and change soil oxidation status (Nijburg and Laanbroek, 1997; Tabuchi et al., 2004; Groffman et al., 2009). In addition, wetland plants employ numerous physiological adaptations to overcome anoxia in waterlogged soils including: shallow rooting, dumping of respiratory by-products into the rhizosphere (e.g. lactic acid) and the formation of aerenchyma (Wheeler, 1999). In light of this, the choice of plant species is likely to be very important for improved riparian management and freshwater protection.

While much work has been undertaken on N removal in riparian areas adjacent to intensive cropping systems, comparatively little work has been undertaken in extensively grazed livestock systems (Wells et al., 2016). In these systems, urine hotspots represent the major input of reactive N and are expected to greatly modify soil microbial communities involved in N cycling (Di et al., 2010). In this context, the main objectives of the present study were: (1) to gain further insight into the environmental factors controlling riparian soil N cycling and how they contribute to explaining the spatial and temporal variability of N cycling in semi-natural ecosystems; (2) to estimate the role of different vegetation communities in N uptake across the riparian zone; and (3) to link N cycling gene abundance to N removal processes.

2. Materials and methods

2.1. Study site

The experimental site was located in the upper, southern area of the Conwy catchment, North Wales, UK (52° 59′ 8.90″N, 3° 49′ 15.99″W; Fig. 1; Figs. S1 and S2). The study area has been classified as blanket bog according to the New Phase 1 habitat survey (Lucas et al., 2011) and considered a Special Area of Conservation (SAC) under the EC Habitats Directive (94/93/EEC). The climate of the upper reaches of the Conwy catchment is characterized by relatively high rainfall and cool temperatures (mean annual rainfall of 2180 mm and mean annual soil temperature at 30 cm depth is 8 °C; based on 30-year average 1981–2010 data from the UK Met Office). The area was subject to sheep (*Ovis aries* L.) grazing at a low stocking density (0.1 ewe ha^{-1}). A detailed description of the Conwy catchment and land use can be found in Emmett et al. (2016) and Sharps et al. (2017).

2.2. Sampling strategy

Four 25 m long transects, 5–10 m apart, and perpendicular to a headwater stream of the Conwy River, were delineated for sampling during the month of October 2016 (Fig. 2). The maximum length of the transects was decided according to the extent of the riparian zone as defined by the variable buffer delineation method (de Sosa et al., 2017). Intact soil cores (5 cm diameter, 0–15 cm depth) were collected at three different zones (from this point onwards in the manuscript, these are referred to as zones 1, 2 and 3), selected according to their dominant vegetation cover (Fig. 2). Zone 1 was dominated by thick tufts of soft rush (*Juncus effusus* L.) and located $<$ 5 m to the river. Zone 2 corresponded to the transitional area between the grasses and the heathland (5–10 m) and zone 3 ($>$ 10 m) represented the area dominated by typical peat-forming heathland species such as bog-mosses (*Sphagnum* spp.), *Calluna vulgaris* (L.) Hull, *Erica tetralix* L. and *Scirpus cespitosus* L. (Figs. S1–S2). Along each transect, two sample points were located within zone 1 (2 and 5 m from the edge of the river), one sample point was located within zone 2 (5–10 m), and two sampling points were located in zone 3 (i.e. 15 and 25 m; Fig. 2).

Intact soil cores were taken with a Russian auger (5 cm diameter, 15 cm in length; Eijkelkamp Soil & Water, Giesbeek, The Netherlands) to conduct the main denitrification experiment. Additional intact soil cores were taken for analysis of soil physicochemical properties prior to conducting the laboratory study and a further 20 cores for bulk density determination. All soil samples were stored at 4 °C prior to analysis except for subsamples (~25 g) which were used for Phospholipid Fatty Acid analysis (PLFA) and DNA extractions. These samples were stored immediately at −80 °C.

2.3. General soil characterization

Soil samples were passed through a 2 mm sieve to remove any plant material and to ensure sample homogeneity. They were held at field moisture for all subsequent analyses to represent field conditions. Soil water content was determined gravimetrically (24 h, 105 °C) and soil organic matter content was determined by loss-on-ignition (LOI) (450 °C, 16 h). Soil pH and electrical conductivity (EC) were measured using standard electrodes in a 1:2.5 (*w/v*) soil-to-deionised water mixture. Total available ammonium (NH_4-N) and nitrate (NO_3-N) in soil were determined within 0.5 M K_2SO_4 extracts (1:5 *w/v*) via the colorimetric salicylate procedure of Mulvaney (1996) and the vanadate method of Miranda et al. (2001), respectively. Available phosphate (P) was quantified with 0.5 M acetic acid extracts (1:5 *w/v*) following the ascorbic acid-molybdate blue method of Murphy and Riley (1962) and total C (TC) and N (TN) were determined with a TruSpec® elemental analyzer (Leco Corp., St Joseph, MI). Dissolved organic C (DOC) and total dissolved N (TDN) were quantified in 1:5 (*w/v*) soil-to-0.5 M K_2SO_4 extracts (Jones and Willett, 2006) using a Multi N/C 2100 TOC analyzer (AnalytikJena, Jena, Germany). Total soil porosity was determined using the equation of 1-(bulk density/particle density for organic soils) and percent water-filled pore space (WFPS) was obtained from the relationship between the volumetric water content and total soil porosity. Anaerobic mineralizable N (AMN) was determined by the anaerobic incubation of soil samples for 14 days at 25–30 °C in the dark, followed by extraction with 1 M KCl and measurement of NH_4-N produced as described above (Bundy and Meisinger, 1994). Anaerobically mineralizable organic C (AMOC) was calculated as described in Ullah and Faulkner (2006). Briefly, moist soil samples were placed in gas-tight containers and NO_3^- was added to remove any soil limitation. Containers were purged with N_2 gas to induce anoxic conditions and stored in the dark at room temperature (25 °C). The headspace of the containers was sampled after 1, 24, 48 and 72 h of incubation and analysed for CO_2 concentration on a Clarus 500 gas chromatograph

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