



Importance of heterotrophic nitrification and dissimilatory nitrate reduction to ammonium in a cropland soil: Evidences from a ^{15}N tracing study to literature synthesis

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ABSTRACT

Future climate change is predicted to influence soil moisture regime, a key factor regulating soil nitrogen (N) cycling. To elucidate how soil moisture affects gross N transformation in a cultivated black soil, a ^{15}N tracing study was conducted at 30%, 50% and 70% water-filled pore space (WFPS). While gross mineralization rate of recalcitrant organic N (N_{rec}) increased from 0.56 to 2.47 mg N kg⁻¹ d⁻¹, the rate of labile organic N mineralization declined from 4.23 to 2.41 mg N kg⁻¹ d⁻¹ with a WFPS increase from 30% to 70%. Similar to total mineralization, no distinct moisture effect was found on total immobilization of ammonium, which primarily entered the N_{rec} pool. Nitrate (NO_3^-) was mainly produced via autotrophic nitrification, which was significantly stimulated by increasing WFPS. Unexpectedly, heterotrophic nitrification was observed, with the highest rate of 1.06 mg N kg⁻¹ d⁻¹ at 30% WFPS, contributing 31.8% to total NO_3^- production, and decreased with WFPS. Dissimilatory nitrate reduction to ammonium (DNRA) increased from near zero (30% WFPS) to 0.26 mg N kg⁻¹ d⁻¹ (70% WFPS), amounting to 16.7–92.9% of NO_3^- consumption. A literature synthetic analysis from global multiple ecosystems showed that the rates of heterotrophic nitrification and DNRA in test soil were comparative to the forest and grassland ecosystems, and that heterotrophic nitrification was positively correlated with precipitation, soil organic carbon (SOC) and C/N, but negatively with pH and bulk density, while DNRA showed positive relationships with precipitation, clay, SOC, C/ NO_3^- and WFPS. We suggested that low pH and bulk density and high SOC and C/N in test soil might favor heterotrophic nitrification, and that C and NO_3^- availability together with anaerobic condition were crucial for DNRA. Overall, our study highlights the role of moisture in regulating gross N turnover and the importance of heterotrophic nitrification for NO_3^- production under low moisture and DNRA for NO_3^- retention under high moisture in cropland.

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1. Introduction

As a fundamental element in terrestrial ecosystems and a limiting factor for food production, nitrogen (N) has gained increasing interest because it is associated with anthropogenic

activities that intensively accelerate the N cycle (Gruber and Galloway, 2008). In agricultural ecosystem, a large amount of fertilizer N inputs has induced manifold negative consequences, such as surface and ground waters pollution, ammonia volatilization, and emission of the potent greenhouse gas nitrous oxide (N_2O) (Chen et al., 2014a). Better understanding of N transformations is of vital importance to improve N fertilizer management and reduce the adverse environmental costs (Schlesinger, 2009; Chen et al., 2014a).

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Soil N cycle is driven by the community and activity of soil microorganisms, and regulated by a number of environmental and soil factors (Booth et al., 2005). Among these factors, soil moisture is a key determinant (Galloway et al., 2004; Wang et al., 2014). This is because not only the water and oxygen (O_2) supply but also the diffusion of substrates and enzymes and microbial biomass and activity are largely influenced by soil moisture regime (Tiedje et al., 1984). For example, in a conceptual model proposed by Curtin et al. (2012), soil N mineralization was largely mediated by moisture content via its indirect influence on soluble substrates supply as well as direct impact on microbial biomass. Furthermore, varying moisture status may cause shifts in the microbial community as well as affecting the activity of soil organisms, e.g. fungi and actinomycetes are more dry-tolerant than bacteria, while gram positive bacteria are more dominant than gram negative bacteria in dry soil (Manzoni et al., 2012). All these changes may have strong impacts on soil N transformations rates (e.g. Hartmann et al., 2013; Harrison-Kirk et al., 2014; Hu et al., 2014). However, most of these studies focused on net N turnover, which does not provide an unambiguous representation of the complex soil N cycles with its simultaneously occurring gross transformations (Davidson et al., 1990; Hart et al., 1994). The responses of gross N transformation rates to changing soil moisture condition remain equivocal or contradictory. Zaman and Chang (2004) reported increased gross mineralization rates with increasing soil moisture within a range of 50–100% water holding capacity (WHC), which was in line with the studies by Bengtson et al. (2005) and Chen et al. (2011). In contrast, a weak and negative correlation between soil moisture and gross mineralization rate was observed in a temperate forest ecosystem (Rosenkranz et al., 2010). Meanwhile, other studies did not detect distinct variations of gross mineralization under different soil moisture regimes (Burger and Jackson, 2003; Dannenmann et al., 2006). Based on the literature data, Booth et al. (2005) found a strong relationship between ammonium (NH_4^+) immobilization and mineralization. As a consequence, their responses to moisture are commonly alike (Corre et al., 2002; Bengtson et al., 2005; Cheng et al., 2014). In general, nitrification shows higher sensitivity to moisture than mineralization because nitrification is considered to be carried out by autotrophic nitrifying bacteria, which are sensitive to changed moisture and aeration status, while organic N mineralization is driven by a large variety of bacteria and stress-tolerant fungi (Gleeson et al., 2008; Manzoni et al., 2012). Accordingly, gross nitrification rates generally enhance up to optimum moisture content and decrease if the soil moisture is above optimum (Zaman et al., 1999; Dannenmann et al., 2006; Kiese et al., 2008). However, Cheng et al. (2014) detected that gross nitrification rate increased as soil moisture rising up to 90% WHC. In contrast, no significant effects of moisture on gross nitrification rate have also been reported (Arnold et al., 2009; Chen et al., 2011). Hence, quantification of the gross N transformation rates in response to soil moisture condition is necessary for in-depth insights into the mechanisms of N dynamics, especially in the cropland ecosystem where studies are remarkably scarce.

In addition to autotrophic bacteria, a wide phylogenetic range of heterotrophic bacteria and fungi can carry out nitrification, particularly in acid soils where autotrophs are inhibited by low pH (De Boer and Kowalchuk, 2001). Heterotrophic nitrification is regarded to play an important role in soil N cycling, because this pathway provides, next to mineralization, another direct way of producing mineral N from organic N (Müller et al., 2011; Staelens et al., 2012; Zhu et al., 2014). It has been shown that heterotrophic nitrification might even become a predominant pathway for nitrate (NO_3^-) production in soils at low pH and high recalcitrant organic carbon (C) primarily in the grassland and forest ecosystems (Müller et al., 2004, 2011; Zhang et al., 2014). In a previous study,

we showed that heterotrophic nitrification was also an important source of N_2O in the cultivated black soil in northeast China (Chen et al., 2014b). Consequently, understanding heterotrophic nitrification and its controlling factors in cropland is pivotal.

Dissimilatory nitrate reduction to ammonium (DNRA) has recently attracted more attention because it can convert NO_3^- to NH_4^+ , which can be reused for the primary producers but is less prone to losses via leaching or gaseous emission through denitrification (Silver et al., 2001; Kraft et al., 2014). Compared with denitrification, more electrons can be transferred per unit of NO_3^- through DNRA (8 vs. 5 electrons), so a higher ratio of electron donor to acceptor (C/ NO_3^-) is considered to favor DNRA (Tiedje, 1988; Silver et al., 2005; Kraft et al., 2014). As an anaerobic microbial process, DNRA is traditionally well documented under reducing settings, such as sludge, sediments and rumen (Tiedje, 1988). Recent studies, however, have shown that it might be of more importance in terrestrial ecosystems than previous thought (Rütting et al., 2011; Thamdrup, 2012). For example, in a temperate rainforest soil in Chile, almost all NO_3^- was detected to be consumed by DNRA (Huygens et al., 2007; Rütting et al., 2008), and DNRA was also observed in natural wetland, grassland and paddy soils (Yin et al., 2002; Müller et al., 2009; Sgouridis et al., 2011). However, in cropland DNRA is usually ignored and its regulating factors are still largely unclear (Schmidt et al., 2011; Sgouridis et al., 2011).

Black soil (Mollisols) in Northeast China is inherently fertile and occupies an important place in China's crop production. However, its organic C content has generally declined, which in association with the high input of chemical fertilizers for maintaining crop yield (Fan et al., 2012) will probably affect soil microbial N dynamics. Most black soils are at present cultivated as rainfed uplands, thus, soil moisture is mainly regulated by precipitation and evaporation, with large seasonal variation (Ni et al., 2012). Moreover, future global climate change is predicted to cause changes of precipitation in the Northern Hemisphere mid-latitudes, likely resulting in alterations of soil moisture regimes and in turn the soil N cycling (Manzoni et al., 2012; Wang et al., 2014). Therefore, the objectives of this study were to: (1) investigate the effect of soil moisture on the simultaneous gross N transformation rates using ^{15}N tracing technique; and (2) assess the functional role of heterotrophic nitrification and DNRA in cropland and their controlling factors based on the experiment results and synthetic analysis of literature data.

2. Material and methods

2.1. Field site and soil sampling

Soil was sampled from a rainfed upland field with a single crop per year under a maize-soybean rotation for about three decades in the Hailun National Agro-ecological Experimental Station, Heilongjiang Province, China (47°26'N, 126°38'E). The region is characterized by a temperate continental monsoon climate with a short hot summer and long cold winter. The 30-year mean annual air temperature (MAT) is 1.5 °C, and the mean annual precipitation (MAP) is 550 mm, with more than 80% falling during the crop growing season of May to September. The prior crop was maize with a fertilizer N application rate of 150 kg N ha⁻¹ as urea. The soil is derived from loamy loess, and classified as black soil according to the genetic classification and Typic Hapludolls in the US soil taxonomy.

Surface (0–20 cm) soil samples were collected at ten randomly arranged positions on 15 May 2012. The soil was composited and sieved (<2 mm) to reduce the heterogeneity and better assess the moisture effects on N cycling (Burger and Jackson, 2003; Dannenmann et al., 2006). Roots were removed and part of the

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