Geoderma 327 (2018) 36–44

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Divergent composition and turnover of soil organic nitrogen along a climate gradient in arid and semiarid grasslands

Jiao Feng[a,b], Benjamin L. Turner[c], Kai Wei[a], Jihui Tian[a], Zhenhua Chen[a], Xiaotao Lü[a], Chao Wang[a], Lijun Chen[a,*]

[a] Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China
[b] Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China
[c] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama

ARTICLE INFO

Handling Editor: Jan Willem Van Groenigen

Keywords:
Aridity gradient
Drylands
Global climate change
Organic nitrogen fractions
Nitrogen-hydrolyzing enzymes
Nitrogen cycling

ABSTRACT

Greater aridity predicted with climate change in drylands worldwide will affect soil nitrogen (N) cycling and the associated ecosystem functions. Despite > 90% of soil N occurring in organic forms, the pathways of soil organic N (SON) turnover remain largely unknown in drylands, where biological activity is typically limited by water availability. Here we examined patterns of SON fractions and soil N-hydrolyzing enzyme activities across a 3700 km aridity gradient in arid and semiarid grasslands of northern China. We found that both the concentrations of all SON fractions and the proportion of more stable SON increased with increasing aridity index (AI, defined as mean annual precipitation/potential evapotranspiration). The largest SON fraction was hydrolysable NH_4^+ in arid sites, but amino acid-N in semiarid sites. The activities of enzymes that hydrolyze relatively stable SON polymers (protease, peptidase, and *N*-acetyl-β-glucosaminidase) were negligible in arid sites (AI < 0.2), but increased significantly as AI increased in semiarid sites (AI > 0.2). Structural equation modeling indicated that the direct effect of microbial biomass on soil amidase was insignificant in arid sites, indicating that microbial SON turnover via enzymes is relatively weak. In semiarid sites, however, microbial biomass exerted significant direct positive effects on all soil N-hydrolyzing enzymes, suggesting strong microbial regulation of SON turnover via enzymatic mineralization. Altogether, our findings provide empirical evidence for divergent patterns of storage and turnover of SON between arid and semiarid grasslands.

1. Introduction

Drylands account for 47.2% of the global land area, but are threatened by desertification as a result of increasing aridity (Austin et al., 2004; Feng and Fu, 2013). As a major constraint for plant growth and primary productivity, soil nitrogen (N) availability is considered a key control on soil quality and ecosystem functioning in drylands (Aranibar et al., 2004; Austin et al., 2004; Wang et al., 2014). Given that > 90% of N in surface soil occurs in organic forms (Stevenson, 1982), the release of plant available N from soil organic N (SON) is the primary control on soil N availability and soil N cycling (Nannipieri and Eldor, 2009). However, dryland soils are inherently of low fertility, contain little soil organic matter (SOM), and have slow decomposition rates (Gallardo and Schlesinger, 1992; Zhou and Zhang, 2014), so the microbial regulation of SON turnover in drylands has received relatively little attention (Sinsabaugh et al., 2015). Increasing aridity in drylands depletes SOM and nutrients (Austin et al., 2004; Delgado-Baquerizo et al., 2013), indicating that SON turnover can respond to changes in climatic factors in drylands. This, in turn, could affect the responses of soil N biogeochemical cycles and related ecosystem functions to future changes in global climate.

The release of plant available N from SON is driven by a sequence of different enzymes, among which the commonly measured are those targeting proteins (protease), polypeptides (peptidase), chitins (chitinase) and amides (amidase) (Kandeler et al., 2011; Nannipieri and Eldor, 2009). In drylands, soil N-hydrolyzing enzymes are sensitive to variations in climatic factors (Ladwig et al., 2015; Sinsabaugh et al., 2008). For instance, increasing precipitation can directly increase soil

Abbreviations: N, nitrogen; SON, soil organic nitrogen; SOM, soil organic matter; MAP, mean annual precipitation; MAT, mean annual temperature; PET, mean annual potential evapotranspiration; AI, aridity index; ANPP, above-ground net primary production; SOC, soil organic carbon; TN, total nitrogen; NAG, *N*-acetyl-β-D-glucosaminidase; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; MUB, 4-methylumbelliferone; AMC, 7-amino-4-methylcoumarin; OLS, ordinary least squares; RDA, redundancy analysis; SEM, structural equation modeling; MB, microbial biomass; SONC, first component of soil organic nitrogen fractions

* Corresponding author at: Institute of Applied Ecology, Chinese Academy of Sciences, P. O. Box 417, Shenyang 110016, China.
E-mail address: ljchen@iae.ac.cn (L. Chen).

https://doi.org/10.1016/j.geoderma.2018.04.020
Received 4 January 2018; Received in revised form 27 March 2018; Accepted 21 April 2018

N-hydrolyzing enzyme activities by increasing the solubility of organic N substrates (Ladwig et al., 2015; Schjønning et al., 2003). In addition, the productivity and community structure of plant and microbial biomass vary with increasing aridity in drylands (Maestre et al., 2012; Wang et al., 2015), which can also interact to affect soil N-hydrolyzing enzyme activities (Geisseler et al., 2010; Kandeler et al., 2011). In soils containing an array of organic substrates, the degradation of different compounds requires microbial allocation of energy and resources to many distinct enzymes (Allison et al., 2011; Lehmann et al., 2008). However, it is difficult to make direct comparisons of enzyme activities in response to climatic changes among different studies in drylands, due to the measurements of various types of enzymes as well as the spatial variations in edaphic conditions (Evans et al., 2011; Ladwig et al., 2015; Sinsabaugh et al., 2015).

The mineralization of SON via enzymes is tightly related to the concentration and quality of SON compounds (Geisseler et al., 2010; Nannipieri and Eldor, 2009). Numerous studies have reported gradual accumulation of SON as precipitation increases in drylands (Austin and Vitousek, 1998; Wang et al., 2014), but few have examined the chemical nature of the SON. The acid hydrolysis method is effective in fractionating SON into more detailed chemical and functional pools (Bremner, 1965; Stevenson, 1982). Different SON fractions have various characteristics and decomposition potentials (Lü et al., 2013). In arid soils, SON may be less protected through re-adsorption with the soil matrices because of the low contents of both SOM and fine particles such as silt and clay (Evans et al., 2011; Parton et al., 1987; Wang et al., 2014; Wang et al., 2016), leading to lower proportions of complex SON forms (Sowden, 1977; Stevenson, 1982). Given the low concentration of SON in drylands (Post et al., 1985; Wang et al., 2014), even slight changes in chemical characteristics and availabilities of SON forms could transform a site from an N source to a sink or vice versa, exerting influences on soil N mineralization, N storage as well as soil fertility and quality (Nannipieri and Eldor, 2009).

The arid and semiarid grasslands of northern China are fragile regions threatened by global climate change, due to the extreme water limitation as a consequence of the low precipitation coupled with high evapotranspiration (Feng et al., 2016; Wang et al., 2014). Therefore, cross-site investigations covering large-scale aridity gradients in this region can offer insights into the possible implications of future climate change for SON turnover and ecosystem N cycling. Here, we sampled soils from 52 sites along a 3700 km aridity gradient in arid and semiarid grasslands of northern China. We determined the patterns of various N-hydrolyzing enzyme activities and chemical fractions of SON across the aridity gradient. In addition, we analyzed the direct and indirect effects of climatic and edaphic factors on SON fractions and various N-hydrolyzing enzyme activities using structural equation modeling. The objectives of this study were to investigate (1) how N-hydrolyzing enzymes are allocated to affect soil N cycling across the aridity gradient, and (2) how climatic and edaphic factors interact to affect SON stored in different forms and the subsequent SON turnover via enzymes across the aridity gradient.

2. Materials and methods

2.1. Site, climate and soil sampling

The study was performed along a 3700 km west-east grassland transect across the Xinjiang, Gansu Province and Inner Mongolia (Fig. 1). The climate along the transect is temperate continental, characterized by high precipitation and temperature during the growing season (between May and August). The transect mainly follows a climate gradient, with distinct variations in the mean annual precipitation (MAP) and mean annual temperature (MAT). Climate data i.e., MAT, MAP and mean annual potential evapotranspiration (PET) for each sampling site were obtained from the WorldClim database (Hijmans et al., 2005) using ArcGIS version 9.3 (Esri, Redlands, CA). Along the transect, MAP ranges from 34 mm to 436 mm, and is strongly negatively ($R^2 = 0.889$, $P < 0.001$) correlated with MAT (between −3 °C and 10 °C) (Feng et al., 2016). The aridity index (AI, calculated as the ratio of MAP to PET) includes the effect of both MAP and MAT (United Nations Environment Programme, 1992) and is a more accurate metric of water availability. The AI increases from 0.03 to 0.57 along the transect from west to east, indicating increasing humidity. The ecosystem type changes gradually from arid grassland to semiarid grassland as AI increases, with an AI boundary of 0.20 (United Nations Environment Programme, 1992). The dominant grassland types are desert shrub, desert steppe, typical steppe and meadow steppe, sequentially as the AI increases. The main soil types are Haplic Calcisols, Calcic Cambisols and Calcic Kastanozems, sequentially as the AI increases (Food and Agriculture Organization, 1993).

Fifty-two sites were selected along the aridity gradient from July to August in 2012, with an interval of approximately 50–100 km. The longitudes range from 91°15′E to 120°21′E, and the latitudes range from 39°51′N to 50°30′N (Fig. 1). At each site, five sub-plots (1 m × 1 m) were selected within one 50 m × 50 m plot (one in the center and one in each corner). The above-ground net primary production (ANPP) was obtained from Wang et al. (2014). Twenty soil cores (0–10 cm depth, 2.5-cm diameter) were collected randomly within each sub-plot and homogenized. Visible roots and stones were removed and fresh soil samples were sieved (< 2 mm) in-situ. A subsample was stored in a plastic bag at 4 °C in the field and immediately frozen at −20 °C after it was returned to the laboratory for biological analysis; a second subsample was air dried and stored in a cloth bag for the measurement of abiotic properties. More detailed descriptions of the test region, climate data, soil type, vegetation type and sampling protocol can be found in Wang et al. (2014) and Feng et al. (2016).

2.2. Soil physicochemical properties and measurement of soil organic N fractions

Values of soil pH, soil organic C (SOC), total N (TN), microbial biomass C (MBC) and microbial biomass N (MBN) were obtained from Wang et al. (2014). Values of soil particle sizes were derived from Wang et al. (2016), and values of soil exchangeable ammonium (NH_4^+) and nitrate (NO_3^-) were obtained from Liu et al. (2017).

Soil organic N fractions were analyzed using an acid-hydrolysis method as described by Stevenson (1996). Briefly, soil samples were heated with 20 mL 6 M HCl in an autoclave at 1 kg cm^{-2} for 6 h. The mixture was cooled, filtered through 30–50 μm sintered discs, and aliquots were taken for the determination of hydrolysable NH_4^+, amino acid-N, amino sugar-N and hydrolysable total-N (Stevenson, 1996). Hydrolysable unknown-N was obtained by subtracting the hydrolysable NH_4^+, amino acid-N and amino sugar-N from the hydrolysable total-N. Soil acid insoluble-N was determined by subtracting the total hydrolysable N from the TN (Stevenson, 1996). For an accurate calculation of the SON fractions, soil inorganic N (exchangeable NH_4^+ and NO_3^-) was subtracted from hydrolysable SON fractions (Bremner, 1965).

2.3. Analyses of soil N-hydrolyzing enzyme activities

Protease activity (EC 3.4.2.21-24) was determined following the method described by Ladd and Butler (1972). Briefly, 1.00 g soil sample was incubated with 5 mL of Tris buffer (0.05 M, pH 8.1) and 5 mL of 2% Na-caseinate solution (W/V) at 50 °C for 2 h. Then, the reaction was terminated by adding 5 mL trichloroacetic acid (0.92 M). The tyrosine concentration was measured using the colorimetrical method at 700 nm after 5 min (Ladd and Butler, 1972). The same procedure was followed for the control, except that the Na-caseinate was added after the incubation. Protease activity was calculated by subtracting control absorbance from sample absorbance, and expressed as μg tyrosine g^{-1} soil h^{-1}.

Soil amidase activity (EC 3.5.1.4) was assayed using method