



# Plant – Microbial and mineral contributions to amino acid and protein organic matter accumulation during 4000 years of pedogenesis



Jinyoung Moon <sup>a</sup>, Li Ma <sup>b, c, d</sup>, Kang Xia <sup>d</sup>, Mark A. Williams <sup>a, \*</sup>

<sup>a</sup> Soil Microbial Ecology and Biogeochemistry Laboratory, Department of Horticulture, Virginia Polytechnic Institute and State University, 312 Latham Hall, 220 Ag Quad Ln., Blacksburg, VA 24061, USA

<sup>b</sup> Department of Environmental Sciences, University of California, Riverside, CA 92521, USA

<sup>c</sup> USDA-ARS, Soil Physics and Pesticides Research Unit, George E. Brown Jr. Salinity Laboratory, Riverside, CA 92507, USA

<sup>d</sup> Department of Crop and Soil Environmental Sciences, Virginia Polytechnic Institute and State University, 1880 Pratt Dr., Blacksburg, VA 24061, USA

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## ABSTRACT

The dynamics and persistence of proteinaceous compounds during pedogenesis are major mechanisms of soil formation and determinants of organic matter (OM) turnover. We investigated the accumulation patterns of proteinogenic amino acids associated with minerals dominated by permanently negative charges (primary silica minerals) and related these to vegetative and belowground microbial succession during soil ecosystem development. Positively-charged amino acids (arginine, lysine, histidine), extracted from whole soil pool using 6 M HCl, showed clear patterns of accumulation, increasing ~65% during 4010 years of development, while negatively charged amino acids (glutamic acid, aspartic acid) decreased ~13%. In the mineral associated sub-pool, positively charged amino acids were approximately ~431% more enriched, while negatively charged amino acids were ~38% depleted as compared to the whole soil pool. The multivariate ordination of soil bacterial community structure based on a 16s ribosomal RNA gene analysis and that of the aboveground plant community structure predicted 71% ( $p < 0.0001$ ) and 66% ( $p < 0.0001$ ) of the amino acid dynamics, respectively, during soil ecosystem development. Ala-rich Actinobacteria abundance declined with the year of development, concomitant with the decrease of Ala content in soil ( $r^2 = 0.82$ ,  $p = 0.0019$ ). His-rich Acidobacteria and His in soil both increased with the year of development ( $r^2 = 0.92$ ,  $p = 0.0022$ ). In support of the main hypothesis, the relative distribution of proteinogenic amino acids changed during pedogenesis with evidence indicating that biological communities and minerals play roles as source and sink of OM in soil, respectively.

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## 1. Introduction

Amino acids (AA), peptides, and proteins are the major form of nitrogen (N) in soil organisms and plants; for example, they comprise approximately 50% and 30% of the cellular weight of bacteria and fungi, respectively (Christias *et al.*, 1975; Neidhardt *et al.*, 1990). These proteinaceous compounds also compose a large fraction of soil organic matter (SOM; ~30%) (Knicker, 2011; Rillig *et al.*, 2007) and are a dominant form of total N (70–90%) in soil (Giagnoni *et al.*, 2010; Knicker and Hatcher, 1997; Miltner *et al.*, 2009; Nannipieri and Eldor, 2009; Schulten and Schnitzer, 1997). The compositions of biotic communities and their proteins, thus,

are important determinants of SOM turnover and global biogeochemical cycles of carbon (C) and N.

Cycling of proteinaceous compounds in soil will determine the relative distribution of bioavailable and long-term stabilized pools of N. The breakdown of soil peptides and proteins to amino acids is a primary rate limiting step for N mineralization (Jones and Kielland, 2002). Amino acids, peptides, and proteins are thus an important determinant of available N for plants and pool sizes of SOM. Soil peptides/proteins, through turnover by microorganisms (Hobara *et al.*, 2014) and mineral associations (Mikutta *et al.*, 2006; Peng *et al.*, 2015), also contribute to SOM formation and preservation.

The role and stabilization of proteinaceous compounds have been described in models such as the molecular aggregates model (Wershaw, 1986), onion layering model (Sollins *et al.*, 2006), and encapsulation model (Knicker and Hatcher, 1997). Amphiphilic and

\* Corresponding author.

E-mail address: [markwill@vt.edu](mailto:markwill@vt.edu) (M.A. Williams).

amphoteric functional groups of proteinaceous compounds are predicted to interact with SOM and minerals so as to be less mobile and more protected from disassociation and decomposition. There remains, however, lack of field-based evidence supportive of protein accrual associated with soil minerals.

The emerging evidence of preferential accumulation and long residence time of proteinaceous compounds in soil (Cotrufo et al., 2013; Schmidt et al., 2011) is counter to the traditional view that peptide bonds are highly labile and readily broken down through heterotrophic-enzymatic activity (Alexander, 1981; Huguet et al., 2008; Kokinos et al., 1998; Schnitzer, 1985; Sollins et al., 1996; Zonneveld et al., 2010) and formerly thought to be an uncommon component of stable SOM. Carbon models have traditionally been dominated by the concept of intrinsic molecular resistance as one of the major controllers of soil C turnover and storage. Accordingly, the molecular structure and lability of organic material has long been thought to determine long-term decomposition rates. However, recent observations have shown that molecular structure is only part of the story. Protein and sugar compounds are more susceptible to chemical attack and biologically labile than aromatic ring structures, but their mean residence times in soil rather tend to be longer (Schmidt et al., 2011). This shift in thinking of the residence time of proteinaceous molecules represents an important change for understanding global biogeochemical C and N cycling.

The distribution of proteinaceous compounds were investigated in a Hawaiian rainforest chronosequence soil (~4.1 million years of development), showing the important role of noncrystalline or short-range ordered minerals in the retention of negatively charged amino acids (aspartic- and glutamic-acid) (Mikutta et al., 2010). The research revealed, furthermore, that at least a portion of mineral associated OM is microbial-derived (Dümig et al., 2012; Mikutta et al., 2010). These results further highlight the connection between mineralogy and some of the molecular details of OM accumulation over tens of thousands of years and more (Torn et al., 1997). It is expected that different dynamics would occur in soils associated with different parent materials over hundreds of years of pedogenesis, which could provide more information relevant to time scales related to anthropogenic induced global change.

In this study, we investigated the variation in the distribution of proteinaceous compounds over hundreds and thousands of years of pedogenesis by analyzing soil amino acids — the structural unit of peptides/proteins — along an eolian sand dune chronosequence adjacent to northern Lake Michigan. We hypothesized that patterns of proteinogenic amino acids in soil will change with pedogenesis; and the changes would be associated with both biotic and abiotic shifts across the chronosequence. The primary objective of this study was to determine pedogenesis-related amino acid change in the whole soil pool and the mineral-associated sub-pool. To relate with biotic and abiotic factors, we investigated amino acid change with successional shifts of vegetative and microbial communities (Williams et al., 2013) associated with pedogenesis.

## 2. Materials and methods

### 2.1. Site descriptions and sampling

Soil chronosequences are a key tool for studying chemical, biological, and physical changes that occur in soil ecosystems as a consequence of pedogenesis. The study site consisted of a series of beach-dune ridges bordering Lake Michigan (N 45.72729, W84.94076), which was located in the Wilderness State Park. The chronosequence of eolian sediments were derived from intermittent deposition of Lake Michigan over the past ~5000 years. The site was located at the interface of a temperate and boreal climate region. Temperature and precipitation averaged 6.28 °C and 77.2 cm

per year, respectively, between 1951 and 1980 at Mackinaw City, 15 km to the east.

The dune ridges had parent material originating from glacial deposits and Paleozoic bedrock underlying the lake basin. The parent material was thought to be similar across the dune sequence. Fine sands deposited on the lake shore are dominated by quartz and contain other minerals in minor quantities (Lichter, 1995). The youngest soils (<100y) were mapped as dunes which then developed into Deer Park sands (soil series) and described taxonomically as mixed, frigid, Spodic Udipsamments. The oldest soils (>1475y) tended to be mapped to the Roscommon series, and were mixed, frigid, Mollic Psammaquents.

The change in aboveground vegetative community structure was greater during early compared to later ecosystem development (Williams et al., 2013). Dune-building grass species were replaced by evergreen shrubs, and these were then replaced by mixed pine forests. This shift in early-to later-succession plant species occurred at 450y when the early-succession species began to disappear and the mixed pine forest began to develop. The compositions of the plant community at 105–155y were completely different from those at 210y, which were again taxonomically different from those at >450y of ecosystem development. Once the forest matured, the plant species composition stabilized and there was no major change in the plant community structure during later ecosystem development.

Belowground bacterial communities changed during early ecosystem development (<450y) but changed little during later ecosystem development (>450y) (Williams et al., 2013). The chronosequence gradients showed a number of changes in phylum composition but were generally dominated by the abundance and dynamics of Acidobacteria, Actinobacteria, and Alphaproteobacteria, comprising 71% of all the sampled sequences. Between early (<450y) and later (>450y) ecosystem development, Acidobacteria increased approximately 6-fold from ~4% to ~30%. Actinobacterial abundance declined, in contrast, from ~60% to ~35% during this same period.

Five replicates of top soil samples were collected from the incipient A-E horizon (0–15 cm, 5-cm dia.) in nine dunes of age 105, 155, 210, 450, 845, 1475, 2385, 3210, and 4010y, using the same method in previous published literature (Williams et al., 2013). Each replicate was separated by 10-m intervals across transects along each dune's crest. The soil samples were stored in sterile Whirlpak bags and frozen immediately in coolers with dry ice. Five replicates of sand samples were also collected along the beach to simulate source materials that formed the eolian deposits of the dunes. Samples were collected in August 2008. The vegetation and soil properties were characterized (Lichter, 2000; Williams et al., 2013).

### 2.2. Whole soil hydrolysable amino acid analysis

The hydrolysable amino acids in the whole soil were acid digested, purified, and then analyzed by high performance liquid chromatography (HPLC) after derivatization. Two to 5 g (dry weight basis) of moist soil was hydrolyzed in 10 ml of 6 M HCl with an internal standard (L-norvaline) at 110 °C for 24 h (Amelung and Zhang, 2001). After hydrolysis, the soil hydrolysates were centrifuged at 10,000g for 10 min. An aliquot of the supernatant (400 µl) was diluted in 55 ml ultra-pure water and cleaned on a preconditioned Dowex 50W X8 resin (hydrogen form, 50–100 mesh; Alfa Aesar, Cat# B22109) (Küry and Keller, 1991; Norman and BOAS, 1953). The interfering metals were removed by rinsing with 0.1 M oxalic acid (pH 1.6–1.7). Amino acids retained on the resin were eluted with 30 ml of 3 M NH<sub>4</sub>OH, filtered through a 0.22 µm polyvinylidene fluoride (PVDF; Thermo Scientific™ Target2™

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