Soil organic nitrogen mineralization across a global latitudinal gradient

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[1] Understanding and accurately predicting the fate of carbon and nitrogen in the terrestrial biosphere remains a central goal in ecosystem science. Amino acids represent a key pool of C and N in soil, and their availability to plants and microorganisms has been implicated as a major driver in regulating ecosystem functioning. Because of potential differences in biological diversity and litter quality, it has been thought that soils from different latitudes and plant communities may possess intrinsically different capacities to perform key functions such as the turnover of amino acids. In this study we measured the soil solution concentration and microbial mineralization of amino acids in soils collected from 40 latitudinal points from the Arctic through to Antarctica. Our results showed that soil solution amino acid concentrations were relatively similar between sites and not strongly related to latitude. In addition, when constraints of temperature and moisture were removed, we demonstrate that soils worldwide possess a similar innate capacity to rapidly mineralize amino acids. Similarly, we show that the internal partitioning of amino acid-C into catabolic and anabolic processes is conservative in microbial communities and independent of global position. This supports the view that the conversion of high molecular weight (MW) organic matter to low MW compounds is the rate limiting step in organic matter breakdown in most ecosystems.

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1. Introduction

[2] Understanding the fate of organic carbon (C) and nitrogen (N) in the terrestrial biosphere remains a central goal in ecosystem science particularly with respect to the accurate prediction of ecosystem responses to global climate change [*DeLuca et al.*, 2002; *Betts*, 2000; *van Hees et al.*, 2005]. Soils possess great diversity in terms of their inherent physical, chemical and biological characteristics. In many cases, soils are classified according to the primary factors that regulate their formation (e.g., time, climate, parent material, topography and vegetation), implying that they behave very differently from each other [*Fitzpatrick*, 1980; *Couteaux et al.*, 2001]. Yet global patterns of microbial function remain unstudied. Despite the great variety in global soil characteristics, it is likely that soils retain a set of intrinsic biological functions that operate independently of global location or specific microbial taxa. Our reasoning is that the major input of organic matter into soil is plant residues that are essentially composed of the same primary building blocks (cellulose, hemicellulose, protein, lignin and lipids), leading to the formation of soil organic matter of similar chemical structure [*Mahieu et al.*, 1999]. Whereas the relative amounts and spatial arrangements of these building blocks may differ among plant species and ecosystems, there is little reason to believe that global latitudinal gradients exist for many of these traits, particularly in agricultural ecosystems [*Stevenson*, 1982]. As these primary building blocks do not appear to accumulate preferentially in specific soils from certain regions of the world [*Stevenson*, 1982], despite their potentially intrinsically different sets of organisms, all soil microbial communities might be expected to retain a core set of functions such as protein and cellulose degradation. This is supported by studies showing that despite differences in vertical arrangement, many aerobic horizonated soils at steady state contain similar levels of C on a whole profile basis [*Eswaran et al.*, 1993].

[3] We hypothesize that when constraints imposed by extremes in climate (i.e., temperature and moisture), and the influence of roots and associated mycorrhizal fungi, both of which are capable of assimilating amino acids [*Smith and Read*, 1997], are removed, soils from a wide range of latitudes will behave similarly under the same environmental

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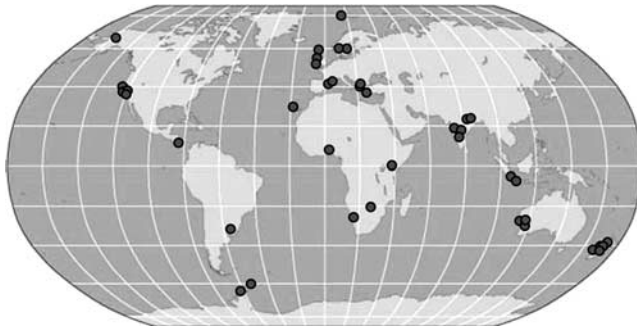
Figure 1. Map showing the locations from which the 40 latitudinal soil samples used in the study were gathered.

conditions. The aim of this study was therefore to directly test this by investigating a key function in soil, namely the biodegradation of amino acids. This function was chosen because amino acids represent the largest input of organic N to soil, they constitute an important source of nutrients to both plants and microorganisms, and they have been implicated as a major factor regulating ecosystem productivity and functioning [*Chapin*, 1995; *Lipson and Näsholm*, 2001; *van Breemen*, 2002; *Vitousek et al.*, 1997].

2. Materials and Methods

2.1. Soil Sampling

[4] Replicate surface soil samples (0–10 cm depth) were collected across a global latitudinal terrestrial gradient from the Arctic to the Antarctic encompassing 40 latitudinal points and covering all the major biomes. Soil sampling followed standard quality control procedures as detailed by *Jones and Willett* [2006]. Briefly, the samples were removed in triplicate using a spade and placed in gas-permeable plastic bags. Samples from regions with a mean annual air temperature <10°C were then immediately shipped by air courier in cool boxes (2–10°C) to the United Kingdom for analysis. The remaining samples were similarly shipped to the United Kingdom but not in cool boxes. At some latitudinal points, replicate sets of soil samples were taken to encompass the dominant land uses (e.g., grassland and forest in the United Kingdom, arable and scrubland in Australia, forest and arable in the United States, etc.). These samples were treated as independent replicates for each latitudinal point. The global location of the individual latitudinal points is shown in Figure 1.

[5] The 40 latitudinal points used in this study represented a diverse range of soil and vegetation types collected from a very broad range of contrasting ecosystems in both the northern and southern hemispheres (Figure 1). Approximately half of the sites were classed as being predominantly agricultural at the time of sampling (e.g., arable, grazed grassland, horticulture, viticulture, n = 19) with the remainder classed as natural ecosystems with minimal human intervention (e.g., arctic tundra, taiga forest, desert, temperate and tropical forest).

[6] Soil solution from field-moist soil was obtained by the centrifugal-drainage method of *Giesler and Lundström* [1993] and the extracted solutions frozen at −20°C to await analysis. Total free amino acids in soil solution was determined fluorometrically by the *o*-phthalaldehyde-β-

mercaptoethanol procedure of *Jones et al.* [2004a] using L-leucine as a standard while NH_4^+ and NO_3^- were determined colorimetrically using a San^{++} autoanalyzer (Skalar Incorporated, Norcross, Georgia, United States).

2.2. Amino Acid Turnover

[7] If the soils were not at field capacity they were moistened to field capacity with artificial rainwater (96 μM NaCl, 10 μM K_2SO_4, 5 μM $CaCl_2$, 6 μM $MgCl_2$, 15 μM NH_4NO_3, 0.1 KH_2PO_4) and left at 10°C for 72 h to equilibrate. The rate of intrinsic amino acid mineralization was determined over a 7 days period at 10°C (unless otherwise stated) with a mixture of ^{14}C-radiolabeled amino acids according to *Jones et al.* [2005]. Briefly, an equimolar mixture of 15 uniformly ^{14}C-labeled amino acids (alanine, arginine, aspartic acid, glutamic acid, glycine, histidine, isoleucine, leucine, lysine, phenylalanine, proline, serine, threonine, tyrosine and valine; total concentration 20 μM, 1.3 MBq L^{-1}, ICN Pharmaceuticals Incorporated, Irvine, California, United States) were added to soil. The soils were then incubated for 0.5, 1, 3, 6, 12, 24, 48, 72 or 168 h in the presence of a 1 M NaOH trap to capture any evolved $^{14}CO_2$ (capture efficiency 98%). At each time point, the $^{14}CO_2$ in the 1 M NaOH traps was determined by liquid scintillation counting. To determine the amount of ^{14}C-amino acid remaining in the soil after 7 days, the soils were subsequently extracted with 0.5 M K_2SO_4 (1:5 w/v), centrifuged (16000 g, 15 min) and the supernatant recovered for ^{14}C analysis as described above. Preliminary trials with sterilized soils showed that the extraction efficiency of amino acids with 0.5 M K_2SO_4 exceeded 95% (data not presented).

2.3. Statistical and Data Analysis

[8] To estimate amino acid half-life in soil, a double first-order exponential kinetic decay equation was fitted to the inverse of the amino acid mineralization data using a least squares optimization routine in Sigmaplot v8.0 (SPSS Incorporated, Chicago, Illinois, United States) where

$$y = \left(Y_r \times \exp^{(-k_1 \times t)} \right) + \left(Y_b \times \exp^{(-k_2 \times t)} \right)$$

in which y is the amount of ^{14}C remaining in the soil, t is time, Y_r and Y_b represent the amount of ^{14}C-amino acid partitioned into microbial respiration and biomass production, respectively, and k_1 and k_2 are the exponential coefficients for these two components [*Jones et al.*, 2004a, 2004b; *Boddy et al.*, 2008]. As a 0.5 M K_2SO_4 extraction of the soils at the end of the incubation period recovered <2% of the added ^{14}C-amino acid, a sorption component was not used in the kinetic model [*Boddy et al.*, 2008]. The half-life of the soil solution amino acid pool ($t_{1/2}$) can subsequently be defined as

$$t_{1/2} = \ln(2)/k_1$$

[9] Microbial carbon assimilation efficiency (microbial yield) was defined as $Y_b/(Y_b + Y_r)$.

[10] Where multiple land uses types were sampled at an individual latitudinal location the data was averaged to give a single latitudinal value. Linear regression and ANOVA
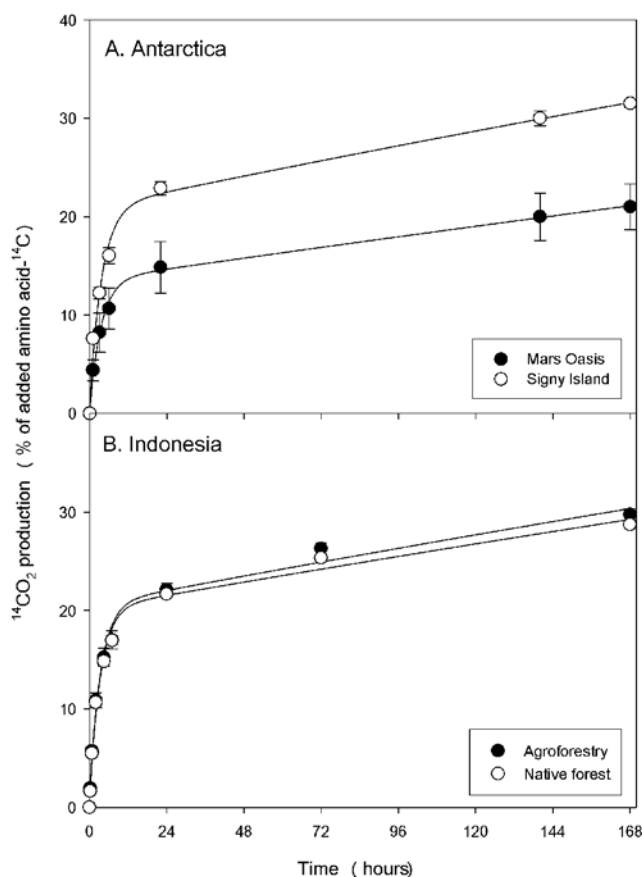
Figure 2. Examples of the ^{14}C-amino acid mineralization profiles from two locations in (a) Antarctica (Mars Oasis, Signy Island) and (b) Indonesia (Agroforestry, Native forest). The symbols represent experimental data points, and the lines represent fits of a double exponential decay model to the experimental data. Data points represent mean ± standard error of mean (SEM) ($n = 3$).

were undertaken with Minitab v14.0 (Minitab Incorporated, State College, Pennsylvania, United States).

3. Results

3.1. Soil Solution Concentrations

[11] Generally, despite the deliberately wide variation in soil type, the free total amino acid concentration in soil solution remained remarkably constant, with a mean global concentration of 23 ± 5 μM ($n = 40$). In contrast, the amount of inorganic N varied dramatically between geographical locations, tending not surprisingly to be higher in agricultural soils (range: 10 to 1000 μM for NH_4^+ and 100 to 3500 μM for NO_3^-) than in natural ecosystems (range: <10 to 70 μM for NH_4^+ and <10 to 2000 μM for NO_3^-). There was no apparent meaningful relationship between latitude and either soil NO_3^- or NH_4^+ concentration (data not presented).

3.2. Amino Acid Mineralization

[12] Amino acid mineralization in all of our soils was very rapid and followed similar mineralization profiles to those

reported in previous studies with an initial rapid phase of mineralization followed by a secondary slower phase of $^{14}CO_2$ evolution (Figure 2). Overall, a double first-order kinetic model conformed very well to the experimental amino acid mineralization data ($r^2 = 0.996 \pm 0.001$; $n = 40$; Figure 2). In all soils, the mean amino acid half-life was <6 h, which is similar to previous studies on European and polar soils (range 0.8 to 5.9 h; Figure 3). The average half-life of the soil amino acid pool across the global soil transect was 1.8 ± 0.1 h and showed no significant latitudinal trend ($P = 0.65$, $n = 40$; Figure 3). Similarly, the amount of amino acid-C immobilized in the microbial biomass (Y_b) relative to that respired (Y_r) was similar for all soils with the global average Y_b value being $71 \pm 1\%$ of the total amino acid-C added to the soil (Figure 4). Similarly to the rate of amino acid turnover, the global pattern of microbial partitioning of amino acid-C into catabolic and anabolic processes showed no significant latitudinal trend ($r^2 = 0.001$, $P = 0.97$). No significant correlations were observed between the parameters $t_{1/2}$, Y_b or Y_r and major soil chemical characteristics (e.g., pH (range 3.7 to 8.4), free amino acid concentration (soil solution range 4 to 53 μM), soil organic matter (range 2 to 441 g C kg^{-1}), $CaCO_3$ (<0.1 to 143 g kg^{-1}), NH_4^+ (soil solution range 0.01 to 43 mg N l^{-1}), NO_3^- (soil solution range < 0.01 to 479 mg N l^{-1}); all $P > 0.05$; data not presented).

4. Discussion

4.1. Global Patterns of Amino Acid Turnover

[13] Our study presents clear evidence to suggest that despite the remarkable diversity of soils in the terrestrial biosphere, the flow of low molecular weight organic N compounds through these systems may be fundamentally similar for key compounds such as amino acids. This might be expected, given the central role of many of these com-
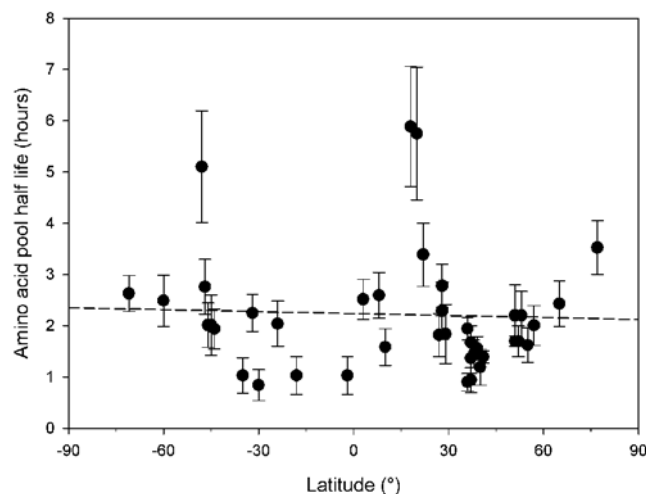

Figure 3. Half-life of amino acids across a global latitudinal transect of soils. Half-life values were calculated from a double exponential decay kinetic model fitted to experimental amino acid mineralization profiles. Values represent means ± SEM. The dotted line is a linear regression fit to the data.
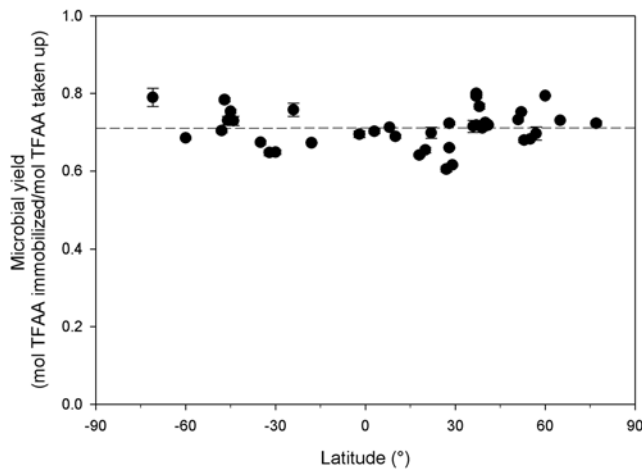
Figure 4. Soil microbial partitioning of amino acid-C across a global latitudinal transect of soils. The microbial yield coefficient describes the relative amount of ^{14}C-amino acids allocated to anabolic versus catabolic metabolic processes in soil microbial communities. Values represent means ± SEM. The dotted line represents a linear regression fit to the data. TFAA indicates total free amino acids.

pounds in microbial metabolism, the substantial functional redundancy apparently present in the soil microbial community and the widespread distribution of many microbial taxa in the natural environment [*Bardgett*, 2002; *Finlay*, 2002; *Horner-Devine et al.*, 2004]. Our findings lend further credence to the approach taken by current global-scale climate change models, which assume that common soil C and N cycling pathways at different latitudes are primarily regulated by climate variables (i.e., moisture and temperature [*Alpert et al.*, 2006; *Li et al.*, 2007]).

4.2. Amino Acid Dynamics in Soil

[14] Our finding that amino acids cycle very rapidly in soil demonstrates the highly dynamic nature of C and N flow through the terrestrial biosphere. The data demonstrate that parts of the dissolved organic nitrogen (DON) pool, which is the dominant soluble N pool in many soils, are very dynamic and that the pool size does not represent the flux of N cycled through the pool. Further, our findings suggest that the intrinsic amino acid pool in soil will turnover several times each day in most ecosystems. Assuming a temperature-dependent Q_{10} of 2 to 3 [*Fang and Moncrieff*, 2001; *Jones et al.*, 2004b], even amino acids in soils of polar ecosystems will exhibit this rate of turnover during summer. Indeed, measurements of amino acid turnover in our three polar soils at 1°C yielded relatively short half-lives of 21 ± 2 h [*Jones et al.*, 2004b]. The rapid rate of amino acid turnover, alongside the low soil solution concentrations in all of our soils, probably reflects the C, rather than N, limitation of the microbial communities [*Lipson et al.*, 2005]. This is supported by the lack of relationship between amino acid half-life and inorganic N concentrations in soil. Given that C fixed by plants may be partitioned belowground and subsequently respired or exuded from roots within hours [*Dilkes et*

al., 2004; *Rangel-Castro et al.*, 2005], our results also suggest that a large proportion of this fixed C which is exuded will return as CO_2 to the atmosphere daily [*van Hees et al.*, 2005].

[15] Amino acids have recently emerged as an important nutrient driver in many terrestrial ecosystems [*van Breemen*, 2002]. This study indicates that the microbial community in all soils possess a similar innate capacity to mineralize and assimilate amino acids rapidly. This implies that the preferential uptake of amino acids by plants in some ecosystems [*Lipson and Näsholm*, 2001] is probably due to increased root competition, or the presence of mycorrhizal symbionts, rather than a reduction in the microbial sink. The underlying mechanisms responsible for these differences, however, remain to be identified.

5. Conclusions

[16] Here we demonstrate that irrespective of global latitude, soil microbial communities possess a similar intrinsic capacity to process key elements of the soil organic C and N cycle. In addition, we show that the internal partitioning of this resource into catabolic and anabolic processes is conservative between communities and independent of global position. This study gives hope that there may be commonalities within C and N cycling in the terrestrial biosphere at a time when there are increasing reports of the inherent complexities of ecosystems [*Montoya et al.*, 2006; *Rooney et al.*, 2006]. It suggests that functional redundancy in the soil biota results in processes being rather insensitive to local characteristics. We anticipate that future elucidation of the rate of organic matter transformation at the global scale will deepen our understanding of the factors regulating C and N cycling and ecosystem responses to environmental perturbation.

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