



## Short communication

## Amino acid dynamics across a grassland altitudinal gradient



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## ABSTRACT

Amino acids (AAs) have been the focus of an increasing amount of research in relation to nitrogen fluxes in soils. We use five temperate grassland sites across an altitudinal gradient to establish relationships between soil properties and the size of individual AA pools and their mineralisation rate. Soil and soil solution chemistry, vegetation and microbial community structure, and standing concentrations of free- and peptide-AAAs, were quantified. Mineralisation of AAs was universally rapid ( $t_{1/2} < 5$  h). We found no relationship between standing AA pool chemistry and rate of AA mineralisation. Instead, soil pH and total microbial biomass, and vegetation community structure were most strongly related to AA turnover rate, highlighting the regulatory role of pH on soil microbial function.

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Soil nitrogen (N) is dominated by organic compounds, the majority of which are proteinaceous in nature (Leinweber et al., 2013). When this organic N is solubilised by biotic (e.g. enzymes) or abiotic reactions (e.g. change in pH or release from mineral surfaces) it becomes part of the dissolved organic N (DON) pool. Within this pool, there has been particular focus on the N contained within free amino acids (FAA) N. These products of the degradation of proteins are a source of N that is directly available to both plants and soil microorganisms, thus bypassing extracellular mineralisation (Moe, 2013). Due to their typically low pool concentrations in soil solution (Jämtgard et al., 2010; Warren and Taranto, 2010; Farrell et al., 2011a), FAAs could be considered an insignificant N pool. Their low concentration, however, belies their importance when considered as a flux, due to their universally high turnover rate (Jones et al., 2009). Many studies have

investigated FAA pool sizes and the drivers of FAA distributions (Jämtgard et al., 2010; Warren and Taranto, 2010; Farrell et al., 2011a), but few have also investigated their rate of flux as measured by microbial turnover. Those studies which have either used a cocktail of amino acids to measure bulk turnover (Jones et al., 2009), or a few individual compounds (Vinolas et al., 2001; Ge et al., 2012; Farrell et al., 2013), and consequently, compound-specific differences in turnover rate between FAAs are largely unknown (Moe, 2013).

Based on the contrasting structure, charge and role of individual amino acids in cellular metabolism, alongside their differential interactions with the solid phase, we hypothesise that the behaviour of the amino acids may be radically different. Thus, the aim of this study was to use a grassland altitudinal gradient (see Farrell et al., 2011a for details) with different soil types, and vegetation and microbial communities, to determine the linkages between the microbial mineralisation of 13 common amino acids and amino acid pool composition, plant and microbial community structure, and soil chemistry. Soil samples were collected in December 2008 from five sites along an altitudinal gradient at Abergwyngregyn, Gwynedd, UK (53°14'N; 4°10'W), as detailed by Farrell et al.

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(2011a). Full methodological details are provided in the [Supplementary Information](#).

A general linear model was used to test the significance of site and amino acid type on amino acid mineralisation rate. A significant interaction between site and amino acid was found ( $F_{(48, 195)} = 1.846$ ,  $p = 0.002$ ). We did not detect a linear relationship between mineralisation rates and altitude ( $p > 0.05$ ) for any of the 13 amino acids (Table 1), as might have been expected on the assumption that DON is thought to accumulate and cycle slower in lower productivity systems (Schimel and Bennett, 2004). This univariate analysis is consistent with the permutational multivariate analysis of variance (PERMANOVA) that considers the mineralisation dataset as a whole, which likewise showed no linear relationship between mineralisation rates and altitude.

Principal components analysis (PCA) was used to visualise the variability in soil chemistry, plant and microbial community structure, and AA pool chemistry and mineralisation rate ( $t_{1/2}$ ) across the five sites (Fig. 1). Pair-wise comparisons using PERMANOVA revealed significant differences ( $P \leq 0.05$ ) between all five sites in terms of general chemistry (Fig. 1B) and vegetation community (Fig. 1C). The microbial community structure was less distinct between sites, with only Site one being significantly different from Sites 3–5. No significant differences were observed between the sites for FAA pool structure ( $F = 1.38$ ,  $P = 0.14$ ), though sites one and five differed significantly in their peptide-AA chemistry ( $p = 0.012$ ). For the majority of AAs tested, mineralisation rate was slower at site five, consistent with findings for alanine alone and its peptides (Farrell et al., 2011b). This site was also associated with the highest phenolic-C concentrations in the soil solution. Phenolic compounds retard N cycling, though usually through the precipitation of macromolecular phenol-protein complexes (Majuakim and Kitayama, 2013), rather than direct inhibition of mineralisation processes. The exceptions to the behaviour of the bulk of the AAs are tyrosine, arginine and lysine, with tyrosine turnover rate higher and arginine and lysine turnover rate lower at site 1. Flux rate calculations (Supplementary Information Fig. 1) show lysine to dominate FAA flux at site 5, and aspartate to be a major component of total FAA flux at the four lower sites. Less discrimination between sites was observed in the PCAs of soil

solution FAA and peptide-AA pools (Fig. 1), highlighting the heterogeneity of these standing pools within sites. Across the whole dataset, there is less co-correlation between different FAAs than those bound in peptides, and lysine, aspartate and glycine are present in the highest concentrations as a proportion of the total FAA pool.

We used BEST (Clarke, 1993) analysis to examine relationships between the six multivariate datasets (Fig. 1), revealing that both the plant community ( $\rho = 0.60$ ,  $p \leq 0.01$ ) and soil chemistry ( $\rho = 0.62$ ,  $p \leq 0.01$ ) were significantly related to FAA mineralisation rate, though these two datasets were also strongly co-correlated ( $\rho = 0.88$ ,  $p \leq 0.01$ ). This reflects the plant species present and the anthropogenic (grazing and fertiliser application), climatic and edaphic constraints on their distribution along the altitudinal gradient (Rodwell, 1992). Microbial community structure, and the FAA and PAA pool structures were unrelated to AA mineralisation ( $p > 0.05$ ).

Overall, soil pH and microbial biomass (estimated by total PLFA concentration on a per gram dwt soil basis) were identified as the most useful variables in explaining the relationship between soil biogeochemistry and FAA mineralisation ( $\rho = 0.62$ ,  $p \leq 0.01$ ), with a positive relationship observed between pH and FAA mineralisation, and the inverse relationship observed between microbial biomass and FAA mineralisation. This second relationship may appear counter-intuitive, but as there is a large decrease in bulk density across the sites from  $1.09 \text{ g cm}^{-3}$  at site one to  $0.08 \text{ g cm}^{-3}$  at site five (Farrell et al. 2011a), microbial biomass is much lower at site five on a per-area basis, and such confounding factors are unavoidable when conducting incubation studies on soils of such differing qualities. Soil pH is recognised as a major driver of microbial biomass, community structure (Wakelin et al., 2008; Griffiths et al., 2011), and growth rate and activity (Rousk et al., 2010). Across the whole dataset, AA mineralisation was rapid ( $t_{1/2} < 5 \text{ h}$ ) which is in agreement with earlier studies using a mixed cocktail of amino acids (Jones et al. 2009), and whilst it is apparent that there are differences in the behaviour of some amino acids, notably tyrosine, arginine and lysine, our data demonstrate that vegetation community, pH and microbial biomass are the main drivers of amino acid turnover in grassland soils.

**Table 1**

Half-life ( $t_{1/2}$ ; h) of amino acids in the soil solution calculated from the mineralisation of  $^{14}\text{C}$ -labelled amino acids. Values represent means  $\pm$  SEM ( $n = 4$ ).

	Site 1 – lowland eutric cambisol	Site 2 – lowland dystric gleysol	Site 3 – semi-improved haplic podzol	Site 4 – unimproved organic podzol	Site 5 – unimproved oligotrophic peat
Alanine	2.38 $\pm$ 0.18	2.29 $\pm$ 0.07	2.13 $\pm$ 0.05	2.45 $\pm$ 0.11	2.97 $\pm$ 0.35
Arginine	2.60 $\pm$ 0.39	2.15 $\pm$ 0.09	1.80 $\pm$ 0.05	1.92 $\pm$ 0.06	2.33 $\pm$ 0.26
Aspartate	1.83 $\pm$ 0.08	1.61 $\pm$ 0.11	1.35 $\pm$ 0.05	2.00 $\pm$ 0.08	2.13 $\pm$ 0.34
Glutamate	3.37 $\pm$ 0.83	1.91 $\pm$ 0.08	2.19 $\pm$ 0.19	2.40 $\pm$ 0.21	3.43 $\pm$ 0.67
Glutamine	3.17 $\pm$ 0.65	2.38 $\pm$ 0.15	3.43 $\pm$ 0.56	4.18 $\pm$ 0.08	4.66 $\pm$ 0.19
Glycine	2.34 $\pm$ 0.33	1.63 $\pm$ 0.10	1.72 $\pm$ 0.05	1.98 $\pm$ 0.16	2.80 $\pm$ 0.57
Isoleucine	2.91 $\pm$ 0.40	2.90 $\pm$ 0.39	2.60 $\pm$ 0.05	2.62 $\pm$ 0.07	3.22 $\pm$ 0.31
Leucine	3.01 $\pm$ 0.46	2.38 $\pm$ 0.07	2.77 $\pm$ 0.37	3.87 $\pm$ 0.27	3.26 $\pm$ 0.30
Lysine	2.80 $\pm$ 0.14	2.53 $\pm$ 0.12	2.28 $\pm$ 0.11	2.43 $\pm$ 0.07	2.31 $\pm$ 0.09
Phenylalanine	2.86 $\pm$ 0.37	2.27 $\pm$ 0.19	2.35 $\pm$ 0.07	2.38 $\pm$ 0.08	3.30 $\pm$ 0.52
Proline	2.64 $\pm$ 0.09	2.47 $\pm$ 0.10	2.48 $\pm$ 0.05	3.58 $\pm$ 0.75	3.42 $\pm$ 0.53
Serine	1.85 $\pm$ 0.15	1.66 $\pm$ 0.09	1.87 $\pm$ 0.09	1.99 $\pm$ 0.12	3.16 $\pm$ 0.64
Tyrosine	2.50 $\pm$ 0.13	3.45 $\pm$ 0.42	3.18 $\pm$ 0.31	4.36 $\pm$ 0.46	3.59 $\pm$ 0.08

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