



Ecological stoichiometry controls the transformation and retention of plant-derived organic matter to humus in response to nitrogen fertilisation



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ABSTRACT

Carbon (C) sequestration in soils is a means for increasing soil organic carbon (SOC) stocks and is a potential tool for climate change mitigation. One recommended management practice to increase SOC stocks is nitrogen (N) fertilisation, however examples of positive, negative or null SOC effects in response to N addition exist. We evaluated the relative importance of plant molecular structure, soil physical properties and soil ecological stoichiometry in explaining the retention of SOC with and without N addition. We tracked the transformation of ¹³C pulse-labelled buffel grass (*Cenchrus ciliaris* L.), wheat (*Triticum aestivum* L.) and lucerne (*Medicago sativa* L.) material to the <53 μm silt + clay soil organic C fraction, hereafter named “humus”, over 365-days of incubation in four contrasting agricultural soils, with and without urea-N addition. We hypothesised that: a) humus retention would be soil and litter dependent; b) humus retention would be litter independent once litter C:N ratios were standardised with urea-N addition; and c) humus retention would be improved by urea-N addition. Two and three-way factorial analysis of variance indicated that ¹³C humus was consistently soil and litter dependent, even when litter C:N ratios were standardised, and that the effect of urea-N addition on ¹³C humus was also soil and litter dependent. A boosted regression analysis of the effect of 44 plant and soil explanatory variables demonstrated that soil biological and chemical properties had the greatest relative influence on ¹³C humus. Regression tree analyses demonstrated that the greatest gains in ¹³C humus occurred in soils of relatively low total organic C, dissolved organic C and microbial biomass C (MBC), or with a combination of relatively high MBC and low C:N ratio. The greatest losses in ¹³C humus occurred in soils with a combination of relatively high MBC and low total N or increasing C:N ratio. We conclude that soil variables involved in soil ecological stoichiometry exert a greater relative influence on incorporating organic matter as humus compared to plant molecular structure and soil physical properties. Furthermore, we conclude that the effect of N fertilisation on humus retention is dependent upon soil ecological stoichiometry.

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1. Introduction

Soils under agricultural management have 25–50% lower soil

organic carbon (SOC) stocks compared to soils under native vegetation (Lal, 2008). This is a combined result of the removal of native vegetation, physical disruption of soil macro-aggregates, increased oxidation of humified SOC, soil erosion and decreased OC inputs (Paustian et al., 1997). Sequestration of OC may be an important means toward restoring depleted SOC stocks, and for mitigating rising atmospheric carbon dioxide (CO₂) concentrations (Lal, 2004;

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Hutchinson et al., 2007). Restoring SOC stocks provides numerous benefits including improved soil and water quality, restoration of ecosystem services and increased agricultural production (Lal, 2008). While the capacity for SOC sequestration is ultimately determined by climate and local topography (Mackey et al., 2013) numerous agricultural management practices have been recommended to facilitate SOC sequestration. These include: a) no-till or reduced tillage; b) conversion of cropping soils to permanent pasture or incorporating pasture phases into cropping rotations; c) retention of harvest residues or the addition of organic matter (OM); d) adopting agroforestry; and e) nitrogen (N) fertilisation (Conant et al., 2001; West and Post, 2002; McLaughlan, 2006; Powlson et al., 2011; Lorenz and Lal, 2014).

While N fertilisation can increase the input of fresh OM to soils by improving plant biomass production (Buchanan and Cowan, 1990; Cowan et al., 1995), increasing N availability can have varying effects on SOC stocks by affecting the decomposition of plant material, and the formation and retention of SOM (Carreiro et al., 2000; Al-Kaisi et al., 2008; Frey et al., 2014). Examples exist of N addition increasing SOC stocks (Gregorich et al., 1996; Alvarez, 2005; Dalal et al., 2011; Frey et al., 2014), having site-specific or no effects (Hobbie, 2005; Page et al., 2013; Robertson et al., 2015) or negative effects (Khan et al., 2007; Rabbi et al., 2014). Thus, further complications are involved in using N fertilisation as a management strategy for SOC sequestration.

The factors involved in the stabilisation and turnover of SOC have been expertly reviewed elsewhere (Sollins et al., 1996; Baldock and Skjemstad, 2000; von Lützow et al., 2007; Schmidt et al., 2011; Dungait et al., 2012). Briefly, SOC stabilisation and turnover involves complex interactions between: a) the relative recalcitrance of organic molecular structures; b) molecular interactions between OM and inorganic substances, such as sorption to form organo-mineral complexes, or with other organic molecules to form complexes via abiotic condensation; c) soil physical properties such as soil aggregation which may limit the physical accessibility of SOC by microbes; and d) the size, composition and metabolic activity of the soil microbial community. Soil OC is considered the organic fraction of biologically derived OC located within and on the surface of soil (Baldock and Skjemstad, 2000). The OC associated with the <53 µm particle size fraction of soil, or silt + clay fraction, represents a relatively slow-cycling C pool (Skjemstad et al., 2004; von Lützow et al., 2007). Here we name this fraction “humus” OC (HOC). The HOC often represents the quantitative majority of the SOC, and observable changes in HOC can be informative in predicting total SOC changes over time (Six et al., 2002; Skjemstad et al., 2004). Pyrolysis-gas chromatography/mass spectrometry and ¹³C nuclear magnetic resonance (¹³C-NMR) spectroscopy have demonstrated that this C pool primarily consists of microbially-associated C, either directly as microbial biomass and its products or as products of decomposition (Grandy and Neff, 2008; Baldock et al., 2013). The molecular nature of the HOC fraction is consistently microbially-derived, however, processes that affect soil microbial communities, such as those affected by N fertilisation, can alter the relative abundance of specific molecular structures in this fraction (Grandy and Neff, 2008). The quantity of HOC is dependent on the above-mentioned processes affecting SOC turnover (Gleixner, 2013).

Nitrogen addition directly affects the microbial community composition and metabolic activity, which can have long-term effects on SOC cycling (Fog, 1988; Carreiro et al., 2000; Fierer et al., 2012). A high C use efficiency (CUE) of the microbial community favours microbial biosynthesis as opposed to greater mineralisation of SOC to CO₂ with low CUE (Manzoni et al., 2012). Carbon use efficiency, in turn, is a consequence of cellular C:N stoichiometric requirements and the soil ecological stoichiometry of the system

(Manzoni and Porporato, 2009; Manzoni et al., 2012; Zechmeister-Boltenstern et al., 2015). This reflects the interconnectedness of soil N and C cycling (Knicker, 2011). The link between CUE, plant litter quality (including molecular structure and C:N ratio of plant biomass) and SOM formation and stabilisation has been well illustrated as the microbial efficiency-matrix stabilisation (MEMS) framework (Cotrufo et al., 2013). Presumably N fertilisation improves SOM formation and retention by improving microbial CUE, dependent on plant litter quality.

In a previous study, we concluded that N addition had varying effects on plant material decomposition, dependent upon the initial C:N stoichiometry of the system (Finn et al., 2015). The objective of this study was to investigate and compare the importance of soil edaphic and plant variables on: A) the transformation and retention of plant-derived OM as HOC in four varying soils and plant litter from three species of varying C:N ratios; B) whether standardising the C:N ratio of plant litter with urea-N addition would equilibrate the retention of HOC between plant species; and C) whether urea-N addition would improve the retention of HOC in plant species of relatively high C:N ratio (Fig. 1). We hypothesised that: A) HOC retention would be dependent upon soil type and plant species, with greater HOC in litter with decreasing C:N ratio and in soils capable of limiting microbial physical accessibility to HOC; B) HOC retention would be independent of plant species once the C:N ratio was standardised; and C) HOC retention would be improved by urea-N addition due to increased CUE during decomposition. To do this, fresh OM of varying molecular recalcitrance was supplied as ¹³C pulse-labelled wheat (*Triticum aestivum* L.), buffel grass (*Cenchrus ciliaris* L.) or lucerne (*Medicago sativa* L.), which are species common to three contrasting agricultural systems – a cereal, pasture and a legume component of mixed pastures, respectively. Residues were added to four agricultural soils of contrasting physico-chemical properties involved in SOC accessibility by microbes (variable values of sand, silt, clay, bulk density, C, N, phosphorus and metal contents). Finally, variable amount of N was added to wheat or buffel grass in the form of urea-N to achieve similar C:N ratios in all of the plant materials and simulate N fertilisation. Changes in HOC were monitored in a temperature and moisture-controlled laboratory incubation over 365-days.

2. Materials and methods

2.1. Soil and ¹³C-labelled plant materials

The soils and plant materials used in this study have been described previously (Finn et al., 2015). Briefly, soil (0–10 cm depth) was sampled from four pasture sites in Australia: Rockies (Queensland): –26.89726 N, 148.88844 E; Akaringa (Queensland):

Interaction A		Buffel	Wheat	Lucerne
Soil	←→ Litter	C:N 33.8	23.2	11.2
Interaction B		Buffel	Wheat	Lucerne
Soil	←→ Litter + urea-N	C:N 11.2	11.2	11.2
Interaction C		Buffel	Wheat	
+ or – urea-N	C:N – urea-N	33.8	23.2	
Soil	←→ Litter	C:N + urea-N	11.2	11.2

Fig. 1. Graphical visualisation of the three interactions compared in this study, and the litter C:N ratios of the treatments: Interaction A) Soil × Litter; Interaction B) Soil × Litter with standardised C:N ratio; and Interaction C) Soil × Litter × urea-N addition.

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