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Effect of added nitrogen on plant litter decomposition depends on initial soil carbon and nitrogen stoichiometry

Damien Finn [a, *], Kathryn Page [b], Kerrilyn Catton [b], Ekaterina Strounina [c], Marco Kienzle [a, d], Fiona Robertson [e], Roger Armstrong [f], Ram Dalal [a, b]

[a] School of Agriculture and Food Science, University of Queensland, 4072, Australia
[b] Department of Science, Information Technology and Innovation, Queensland Government, 4001, Australia
[c] Centre for Advanced Imaging, University of Queensland, 4072, Australia
[d] Department of Agriculture and Fisheries, Queensland Government, 4001, Australia
[e] Department of Economic Development, Jobs, Transport and Resources, Hamilton, Victoria, 3300, Australia
[f] Department of Economic Development, Jobs, Transport and Resources, Horsham, Victoria, 3400, Australia

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ABSTRACT

Increasing organic carbon inputs to agricultural soils through the use of pastures or crop residues has been suggested as a means of restoring soil organic carbon lost via anthropogenic activities, such as land use change. However, the decomposition and retention of different plant residues in soil, and how these processes are affected by soil properties and nitrogen fertiliser application, is not fully understood. We evaluated the rate and extent of decomposition of ^{13}C-pulse labelled plant material in response to nitrogen addition in four pasture soils of varying physico-chemical characteristics. Microbial respiration of buffel grass (*Cenchrus ciliaris* L.), wheat (*Triticum aestivum* L.) and lucerne (*Medicago sativa* L.) residues was monitored over 365-days. A double exponential model fitted to the data suggested that microbial respiration occurred as an early rapid and a late slow stage. A weighted three-compartment mixing model estimated the decomposition of both soluble and insoluble plant ^{13}C (mg C kg^{-1} soil). Total plant material decomposition followed the alkyl C: O-alkyl C ratio of plant material, as determined by solid-state ^{13}C nuclear magnetic resonance spectroscopy. Urea-N addition increased the decomposition of insoluble plant ^{13}C in some soils ($\leq$0.1% total nitrogen) but not others (0.3% total nitrogen). Principal components regression analysis indicated that 26% of the variability of plant material decomposition was explained by soil physico-chemical characteristics ($P = 0.001$), which was primarily described by the C:N ratio. We conclude that plant species with increasing alkyl C: O-alkyl C ratio are better retained as soil organic matter, and that the C:N stoichiometry of soils determines whether N addition leads to increases in soil organic carbon stocks.

1. Introduction

Organic carbon (OC) sequestration has been suggested as a means of restoring soil OC (SOC) lost via anthropogenic activity, such as land use change and intensive agriculture (Lal, 2004; Hutchinson et al., 2007; Mackey et al., 2013). One strategy for the sequestration of OC in agricultural soils is to use management practices that result in greater OC inputs (Conant et al., 2001; West and Post, 2002; Lal, 2004; Ogle et al., 2005; Hutchinson et al., 2007). For example, increasing the amount of pasture in cropping rotations, or converting a site completely from cropping to pasture may significantly increase SOC stocks (Paustian et al., 1997; Weston et al., 2002; Ammann et al., 2007; Young et al., 2009; Chan et al., 2011). Likewise in cropping systems, retention of crop harvest residues may, in some circumstances, significantly increase SOC stocks (Chan et al., 2011; Dalal et al., 2011; Robertson et al., 2015).

However, there remain significant gaps in our understanding as to how soil nitrogen (N) availability influences OC sequestration. While increases in soil N content may increase plant biomass production (Buchanan and Cowan, 1990; Cowan et al., 1995; Dubeux et al., 2007; De Deyn et al., 2009), and therefore SOC input, it may either increase or decrease the extent and rate of decomposition of organic matter (Fog, 1988; Carreiro et al., 2000;

* Corresponding author.
E-mail address: damien.finn@uqconnect.edu.au (D. Finn).

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Waldrop et al., 2004; Cusack et al., 2010; Frey et al., 2014). This can have varying effects on net OC sequestration in soil. Studies have found that the turnover of more labile OC pools tends to increase with N addition, while turnover rates of more slowly cycling pools decrease, often leading to an overall increase in SOC (Hagedorn et al., 2003; Cusack et al., 2010, 2011). However, overall decreases in SOC have also been observed with N fertilisation in cropping environments, despite overall increases in organic matter input from biomass production (Khan et al., 2007).

While the direct evidence to explain the mechanism(s) responsible for the different effects of N on decomposition is often absent, several hypotheses have been suggested. These include: a) the inhibition of lignin degrading microorganisms and/or the enzymes responsible for the breakdown of more resistant material (Berg and Matzner, 1997; Carreiro et al., 2000; Sinsabaugh et al., 2002; Cusack et al., 2010); b) shifts in the relative abundance of specific soil microbial phyla in response to N amendment, with N addition favouring copiotrophic microorganisms that preferentially metabolise labile OC at the expense of oligotrophic microorganisms involved in recalcitrant OC metabolism (Fierer et al., 2012; Ramirez et al., 2012); c) nitrogen or general nutrient limitation may drive the catabolism of C substrates, resulting in overflow metabolism or reduced carbon use efficiency (Moorhead and Sinsabaugh, 2006; Craine et al., 2007); and d) carbon and N co-metabolism is essential for decomposition due to cellular stoichiometric requirements, with decomposition controlled by a critical C:N threshold (Manzoni and Porporato, 2009; Zechmeister-Boltenstern et al., 2015). These hypotheses have been termed the enzyme inhibition (Fog, 1988), copiotrophic (Fierer et al., 2007), N-mining (Craine et al., 2007) and ecological stoichiometry (Zechmeister-Boltenstern et al., 2015) hypotheses, respectively.

The chemistry of the plant material being decomposed also affects decomposition in response to N addition (Carreiro et al., 2000; Cusack et al., 2010). For example, plant material with high lignin content (di-O-alkyl, aryl and/or O-aryl functional C groups) are likely to show declining rates of plant material decomposition following the addition of N (Dijkstra et al., 2004; Waldrop et al., 2004; Wang et al., 2004). Furthermore, soil physico-chemical properties, such as texture and pH, are also involved in decomposition via the structure and activity of the microbial community, and individual sites can respond quite differently to N addition (Hobbie, 2005; Wakelin et al., 2008; Geisseler and Scow, 2014).

Therefore, the objective of this study was to examine the process of plant C decomposition as affected by changes in N availability in four agricultural soils of contrasting physico-chemical properties (sand, silt, clay, C, N and phosphorous content, and pH and electrical conductivity) and three plant species varying in relative abundance of functional C groups. We utilized a temperature and moisture-controlled laboratory incubation to determine how the addition of N as urea to plant material of differing C:N ratios affected the decomposition of ^{13}C pulse-labelled wheat (*Triticum aestivum* L.), buffel grass (*Cenchrus ciliaris* L.) and lucerne (*Medicago sativa* L.) in two Vertisols and Alfisols of varying soil characteristics.

2. Materials and methods

2.1. Soil and ^{13}C-labelled plant materials

Four soils were collected from four pasture sites in Australia: Rockies (Queensland): −26.89726 N, 148.88844 E; Akaringa (Queensland): −28.30264 N, 150.21728 E; Wimmera (Victoria): −36.672547 N, 142.288467 E; and Hamilton (Victoria): −37.839358 N, 142.086697 E. A bulk sample of soil from each site was collected from the top 0–10 cm soil layer. Soil was thoroughly mixed and dried at 40 °C before sieving to <2 mm. Sub-samples were ground to <100 μm and total organic carbon (TOC) and total nitrogen (TN) were determined by direct combustion with an Isoprime Isotope Ratio Mass Spectrometer (GV Instruments, Manchester, UK). Carbon measured via the Heanes method (Rayment and Lyons, 2010) indicated that inorganic C was not present in significant quantities (<0.1%). Bicarbonate-extractable (Colwell) phosphorous analysis, particle size analysis, pH and electrical conductivity (EC) were measured as described by Rayment and Lyons (2010). Bulk density was measured from the oven-dry weight of soil (105 °C) extracted with a sampling core in relation to the core volume. Physical and chemical properties of the four soils are provided in Table 1.

All plant materials were pulse-labelled with enriched $^{13}CO_2$ to increase the resolution with which decomposition could be tracked. The ^{13}C-labelled material was prepared using a procedure similar to that used by Butterly et al. (2015) except that plants were not grown in a labelling cabinet but under glasshouse conditions in large (20 L) buckets filled with a nutrient deficient Vertisol. ^{13}C pulse-labelling was performed seven times for wheat and lucerne, and eight times for buffel grass between 18th March and 7th May 2013 in Victoria, Australia. For pulse-labelling, the buckets were removed from the glasshouse and arranged on a plastic sheet, and a labelling chamber was placed over the top and sealed around the base using PVC tape. The chamber (140 cm long × 140 cm wide × 150 cm high) was gas-tight, consisting of an aluminium frame (2.54 cm^2 tube) fitted on all sides except the base with polycarbonate sheet (1.5 mm thick, Tufglaze Clear, Plastral, Australia). A PVC duct (50 cm ID × 195 cm long) fitted with 12-V computer fans (12 cm diameter) at both ends and an air pump (O_2 PLUS 4000, PondOne, England) were used to invert and circulate air within the chamber. Prior to pulse-labelling, the ambient CO_2 concentration was reduced by diverting air from the chamber, through an alkali trap (1 M NaOH). A black plastic sheet was used to cover the chamber while atmospheric CO_2 was removed to limit plant photosynthesis. $^{13}CO_2$ was generated by injecting 12 mL of 9.2 M H_2SO_4 into a reaction vessel containing 90 mL of 1.23 M $Na_2^{13}CO_3$ (98% ^{13}C atom abundance, Sigma–Aldrich, USA) (Baumann et al., 2011). Labelling was performed between 8 am and 2 pm, varying with external air temperature (average air temperature was 23.1 °C) in natural daylight. Air within the chamber was allowed to mix for 10 min and the black plastic sheet was removed from the chamber. After periods ranging from 90 to 150 min (depending on temperatures within the chamber) the labelling was terminated and the buckets returned to the glasshouse. The buckets were watered to field capacity weekly with reverse osmosis water to ensure dehydration did not limit plant growth. All three species were harvested soon after reproductive components had fully emerged from the shoot. Labelled plant material was dried and ground to <2 mm. Soluble and insoluble plant components were separated as described by Richter et al. (2009) for isotope ratio mass spectrometry (IRMS) analysis. The soluble fraction was filtered through 0.2 μm nylon filter membranes and ethanol washed insoluble material was dried at 80 °C overnight. Plant material was analysed via dry combustion with a Flash 2000 Organic Elemental Analyser (Thermo-Fisher Scientific, Scoresby, VIC, Australia). Isotope ratios were measured with a Delta V Advantage Isotope Ratio MS (Thermo-Fisher Scientific, Scoresby, VIC, Australia).

2.2. Solid-state NMR spectroscopy

Solid-state nuclear magnetic resonance spectroscopy (NMR) was performed on the Avance III spectrometer (Bruker), operating at 300.13 MHz for ^1H and 75.468 MHz for ^{13}C. The samples were

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