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Carrion decomposition causes large and lasting effects on soil amino acid and peptide flux

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ABSTRACT

Carrion decomposition is a critical component of the biogeochemical cycling of energy and nutrients within the biosphere. Two important and currently overlooked nitrogen (N) pools likely to be affected by carrion are free amino acid (FAA) and peptide pools, which are a newly recognised point of competition between plants and microorganisms for the N resource. A carcass addition experiment was established using recently (<12 h) deceased kangaroo (*Macropus giganteus*) carcasses to quantify soil nutrient changes in a box gum grassy woodland ecosystem. Soil samples were taken every 12 weeks, and analysed for available nutrient content and FAA and peptide turnover rates. Carcasses were a source of N, adding an average of 4.4 kg m^{-2} to the soils directly under the decomposing carcasses in our study, representing a significant redistribution of this resource within the ecosystem. There was also a significant and lasting input of proteins (40 mg/kg) and amino acids (25 mg/kg) into the soil, which increased microbial turnover of these labile N compounds. Dissolved organic N (DON) cycling in rangelands and natural ecosystems is an overlooked part of the N and C cycle despite representing the most important nutrient input into these systems. Based on our results, we argue for a re-think on the removal of carcasses as an ecosystem management tool, as they provide large and lasting resource islands which influence soil N cycling.

1. Introduction

Carrion decomposition is a critical component of the biogeochemical cycling of energy and nutrients in the biosphere, and links all animals to the functioning of ecosystems. Carrion is an important source of nutrients, for example an average of 5000 kg of carcasses within a square kilometre (equating to 180 kg N uniformly distributed km^{-2}) can occur in a *Bison bison* L. (American bison) grazing ecosystem each year (Carter et al., 2007). The nutrients are not uniformly spread across the landscape but mortality and subsequent decomposition creates a fertility patch (Parmenter and MacMahon, 2009), which increases biological activity relative to the surrounding environment (Barton et al., 2013b). Typically, carrion decomposition constitutes <1% of the nutrient budget in ecosystems, but can significantly increase the localised soil nutrient dynamics (Parmenter and MacMahon, 2009), thus driving patchiness in soil fertility and support biodiversity across landscapes (Barton et al., 2013a).

Many forensic and ecosystem studies have examined the development and life span of fertility patches (Barton et al., 2013a; Vass et al., 1992). These studies have focused primarily on soil total and inorganic nitrogen (N), carbon (C) and phosphorus (P) pools and pH and salinity (e.g. Parmenter and MacMahon, 2009), but far less focus has been given to the mechanisms leading to these nutrient changes.

Protein is the main N moiety that carrion deposits in the soil, and these inputs are broken down via proteolysis into proteoses, peptones, polypeptides and amino acids. The process does not occur at a uniform rate and protein degradation products can be released into the soil during early stage decomposition (autolysis) with the majority released during later stages of decomposition (putrefaction, liquefaction and disintegration). A study by Vass et al. (1992) showed that there is an increase in the concentration of volatile fatty acids, a protein decomposition product, in the soil

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solution during later stage decomposition. These proteins are a significant source of nutrients. For example a 100 kg human (*Homo sapiens*) cadaver is composed of approximately 20% crude protein, which contains 3.2 kg of N (Forbes et al., 1956).

Two important and currently overlooked nitrogen pools that are likely to be affected by carrion decomposition are free amino acid (FAA) and peptide pools. These pools have received much attention recently as a newly recognised point of competition between plants and microorganisms for the N resource (Hill et al., 2011a; Farrell et al., 2013). In non-agricultural soils, the degradation of proteins into peptides and amino acids represents a significant N input into the ecosystem which can be used directly and rapidly by plants and microbes through active transport mechanisms (Payne, 1980) before mineralisation (Farrell et al., 2011a,b, 2013; Hill et al., 2011a,b, 2012). This rapid turnover of FAA and peptides by microbes reflects an important evolutionary adaptation to nutrient poor environments by which the bottleneck of nitrogen mineralisation is sidestepped (Chapin et al., 1993; Hill et al., 2011a). Competition between plants and soil microorganisms for FAAs has been demonstrated across many ecosystems, and is particularly important in ecosystems of lower fertility where the N resource is scarce (Schimel and Bennett, 2004). More recently, a growing body of evidence indicates that competition for N occurs at the peptide stage, earlier on in the protein degradation pathway, and that uptake of peptides may be preferred to FAAs on an energetic basis (Payne, 1980; Hill et al., 2011a,b, 2012).

In many wilderness and rangeland areas the cycling of nutrients via carcass decomposition has been altered through human intervention, including the removal of top predators, hunting, and increased populations of grazing vertebrates (Wilson and Wolkovich, 2011; Bump et al., 2009). In Australia, kangaroos (*Macropus* spp.) are a diverse group of large herbivores, and the Red (*Macropus rufus*) and Eastern Grey (*Macropus giganteus*) kangaroos are the largest native herbivores. Prior to European settlement they were primarily hunted by the indigenous people and the dingo, the Australian native dog (*Canis lupus dingo*). It could be assumed that the nutrients from kangaroo carcasses were incorporated into the soil at or near the kill site and also at different but nearby locations after defecation. After natural mortality the carcass may have been torn apart by native carnivores, and raptors, corvids and insects would also feed on the soft tissues. Nutrients would be incorporated at the site of death but similar to the kangaroo killed by hunting some of the nutrients would be smeared across the landscape. It has been shown where kangaroo culling and harvesting occurs, that decomposition of kangaroo (*Macropus* sp.) harvesting off-cuts are an important supply of mineral nitrogen in nutrient poor rangelands (Wilson and Read, 2003). Kangaroo muscle and fat has a high crude protein content (22.5%; Tribe and Peel, 1963) and would be an important ecosystem energy and nutrient source. In nutrient-poor natural and rangeland soil ecosystems prior to European settlement, kangaroo carcass decomposition was an important localised fertilisation event, where a significant input of peptide and FAA and other degradation products were added to the soil ecosystem. It is expected that the soil microorganisms should respond to this input and metabolise the peptide and FAA.

Since European settlement the nutrient cycle through kangaroo carrion has been significantly altered. Hunting and predation have been greatly reduced in Eastern Australian allowing kangaroo populations to increase, further facilitated by land clearing and the provision of year round water points through agricultural expansion. Kangaroo populations are now controlled by culling in many places in Australia, with carcasses removed from the landscape for consumption or off-site burial. The effects of this loss of nutrients from already nutrient-poor ecosystems is poorly understood, and quantifying the effect of carrion on soil proteinaceous N cycling we hope to contribute to improved management and rehabilitation of non-agricultural and rangeland ecosystems.

The aim of this study was to determine the impact of *M. giganteus* carcasses on the dynamics of L-alanine (amino acid) and L-trialanine (peptide) in a nutrient poor box gum grassy woodland. The change in the temporal protein and nutrient fluxes over a 24 week period were investigated. We also examined the effect of carrion decomposition on the organic and inorganic carbon and nitrogen pools, pH and salinity and plant available phosphorus. We anticipated that the addition of carrion would cause significant and long lasting effect on the FAA and peptide flux compared to control sites. This would indicate the importance of these protein-derived N compounds as a nutrient source in natural ecosystems.

2. Materials and methods

2.1. Study area and experimental design

In November 2010, carcasses of kangaroos were added to 18 sites in temperate woodland reserve near Canberra (Australia). Each carcass was paired with a control site 10 m away to allow spatial comparisons of the magnitude of the effect of carrion on soil through time (Fig. 1). The reserve consisted of box gum grassy woodland, and is characterised by two dominant eucalypt species (*Eucalyptus melliodora*, and Blakely's Red Gum *Eucalyptus blakelyi*), interspersed by grassland comprising mostly native grass species, with some exotics (McIntyre et al., 2010). The reserve (35.191°S 149.1817°E) is characterised by undulating low hills, which have shallow rudosols and tenosols, and the deeper soils of valleys and plains are chromosols and sodosols or regosols, leptosols and luvisols and solonetz respectively (McIntyre et al., 2010). Mean organic litter depth is 11 mm and surface soil textures are predominantly sandy clay loam (McIntyre et al., 2010). The A horizon was generally shallow (<10 cm) and was under laid by a textured B horizon. This study was part of the broader Mulligans Flat – Goorooyarroo Woodland Experiment (www.mfgowoodlandexperiment.org.au), a long-term project examining ways to improve critically endangered box gum grassy woodlands for biodiversity (Manning et al., 2011; Shorthouse et al., 2012).

The dominant vertebrate herbivore in much of south-eastern Australia is *M. giganteus*, which can reach densities of more than two animals per hectare in the reserve (Barton et al., 2011). These kangaroos are therefore an important source of carrion in the study ecosystem. Eighteen *M. giganteus* carcasses were sourced from recent road kill in the region, and placed unsecured at the study site

Fig. 1. Example of a carcass within the experiment site. Note the carcass was placed directly on the ground and was not enclosed or protected by any mesh. Soil samples were taken near the centre of each carcass.