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Environmental stress response limits microbial necromass contributions to soil organic carbon

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ABSTRACT

The majority of dead organic material enters the soil carbon pool following initial incorporation into microbial biomass. The decomposition of microbial necromass carbon (C) is, therefore, an important process governing the balance between terrestrial and atmospheric C pools. We tested how abiotic stress (drought), biotic interactions (invertebrate grazing) and physical disturbance influence the biochemistry (C:N ratio and calcium oxalate production) of living fungal cells, and the subsequent stabilization of fungal-derived C after senescence. We traced the fate of ^{13}C-labeled necromass from 'stressed' and 'unstressed' fungi into living soil microbes, dissolved organic carbon (DOC), total soil carbon and respired CO_2. All stressors stimulated the production of calcium oxalate crystals and enhanced the C:N ratios of living fungal mycelia, leading to the formation of 'recalcitrant' necromass. Although we were unable to detect consistent effects of stress on the mineralization rates of fungal necromass, a greater proportion of the non-stressed (labile) fungal necromass C was stabilised in soil. Our finding is consistent with the emerging understanding that recalcitrant material is entirely decomposed within soil, but incorporated less efficiently into living microbial biomass and, ultimately, into stable SOC.

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1. Introduction

Soil organic carbon (SOC) is the largest active carbon (C) pool in the terrestrial environment. The decomposition and formation of SOC are essential processes in determining SOC stocks, and interest in these processes has increased substantially in recent years due to their importance in global C cycling and associated feedbacks to climate change (Bellamy et al., 2005). It has historically been assumed that most of the C in stable SOC is directly plant-derived, but it is now accepted that a large proportion of organic material enters the soil C pool indirectly, following incorporation into microbial biomass (Kögel-Knabner, 2002; Liang and Balser, 2011; Liang et al., 2011; Miltner et al., 2012; Schimel and Schaeffer, 2012; Cotrufo et al., 2013). Although the potential for microbial cells to contribute to SOC formation has been recognised for several decades (McGill et al., 1975), the extent of these contributions is only recently becoming apparent. Living microbial biomass only represents up to 1–2% of SOC, but the turnover of this biomass is a rapid, iterative process and so microbial necromass in mineral soils can ultimately contribute up to 50–80% of the C in stable SOC fractions (Simpson et al., 2007; Liang and Balser, 2011). Despite being widely acknowledged as a dominant pathway in the formation of stable SOC (Grandy and Neff, 2008; Kögel-Knabner et al., 2008; Cotrufo et al., 2013), the mechanisms governing microbial necromass decomposition, and subsequent incorporation into stable SOC, have received relatively little attention.

As with the traditional thinking in plant litter decomposition, the majority of microbially-derived SOC is assumed to originate from chemically or structurally 'recalcitrant' (complex or difficult to decompose) microbial components that are selectively avoided during decomposition (e.g. fungi with chitinous cell walls: Nakas and Klein 1979, Moore et al., 2005; Six et al., 2006). Litter chemistry (e.g. lignin concentrations or C:N ratios), and structural properties (e.g. leaf toughness or thickness) consistently emerge as the primary controls on plant decomposition rates (Melillo et al., 2002; Santiago, 2007; Dray et al., 2014), and it is not surprising that equivalent processes are expected to govern the breakdown of microbial necromass. An emerging paradigm, however, asserts that recalcitrant macromolecules are fully degraded, but less efficiently

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than labile material, and a greater proportion of recalcitrant C is thus lost through respiration, without being incorporated into decomposer biomass and ultimately into SOC (Lutzow et al., 2006; Cotrufo et al., 2013). Exploring the relative importance of these opposing mechanisms (selective preservation vs. reduced assimilation efficiency) for necromass mineralization and soil C stabilization has been highlighted as a high priority for ecosystem ecologists (Cotrufo et al., 2013).

As with plant litter, the biochemical structure (recalcitrance) of microbial necromass is a product of both constitutive and induced characteristics; taxonomic groups differ in their inherent biochemical composition (Six et al., 2006; Throckmorton et al., 2012), but can be altered drastically by both biotic and abiotic processes (Dijksterhuis and de Vries, 2006; Schimel et al., 2007). Although '*inherent recalcitrance*' of microbial necromass is a strong determinant of initial mass loss (Sollins et al., 1996; Koide and Malcolm, 2009), a recent study suggests that microbial taxa cultured under similar conditions do not vary in their contributions to SOC formation (Throckmorton et al., 2012). However, all microbes *in situ* are subject to a variety of stressors (environmental stress, biotic antagonism and/or mechanical disturbance), which can alter the biochemical composition of cells, yet the effects of '*induced recalcitrance*' on necromass stabilization remain unexplored.

A growing body of evidence highlights the importance of long-lasting effects in soil, where factors influencing the activity of living organisms can affect ecosystem functioning after cell death (e.g. Kostenko et al., 2012). Analogous to plant (Findlay et al., 1996) and animal (Hawlena et al., 2012) physiology, stress generally increases microbial C:N ratios as C demands rise to facilitate the synthesis of osmolytes, heat-shock proteins and structural defences (Schimel et al., 2007; Crowther et al., 2014). Many fungi, for example, increase the uptake of C, relative to N, to facilitate the synthesis of polyols (C-rich osmolytes), which allow fungal cells to maintain osmotic pressure during drought stress (Dijksterhuis and de Vries, 2006). Fungal investment in structural compounds has also been widely documented during biotic interactions and abiotic stress. For example, the stress-induced increases in the formation of calcium oxalate crystals, by-products of lignin decomposition, on the surface of fungal hyphae can serve as a physical barrier between living cells and the harsh local environment (Dutton et al., 1993). Such stress-induced changes in physiology and biochemistry have been proposed to limit the decomposition rates of plant and animal biomass (Findlay et al., 1996; Hawlena et al., 2012). Given the dominant role of microbial necromass decomposition in the formation of stabilized SOM, it is possible that similar changes might represent an important control on the balance between terrestrial and atmospheric carbon pools under current and future climate scenarios.

We explored the potential effects of stress on the C:N ratio and calcium oxalate crystal formation in saprotrophic fungi, and the consequent effects on microbial necromass decomposition and initial stabilization in soil. We grew two widespread fungal species, labeled with 13C, in soil microcosms, and exposed them to a dominant abiotic stress (drought), biotic stress (isopod grazing) and mechanical disturbance (simulated by cutting). Following fungal death, we used a second set of soil microcosms to trace the fate of labeled C into living soil microbial biomass, dissolved organic carbon (DOC), mineralized (respired) C and total SOC. We tested the initial hypothesis that interactive biotic and abiotic stressors influence the C:N ratio and calcium oxalate production by fungal hyphae. We then tested the competing hypotheses that: (i) 'stressed' fungi contribute more C to SOC because of the selective preservation of recalcitrant macromolecules (Moore et al., 2005; Six et al., 2006); or (ii) 'unstressed' fungi will contribute more C to SOC because of the reduced efficiency of microbes degrading 'stresses' (recalcitrant) necromass (Lutzow et al., 2006; Cotrufo et al., 2013).

2. Materials and methods

2.1. Overview of study design

Two cord-forming basidiomycete fungi, *Phanerochaete velutina* (DC.: Pers.) and *Resinicium bicolor* (Abertini and Schwein.: Fr.) (Cardiff University Fungal Genetic Source Collection), were selected due to their global distribution and contrasting responses to biotic and abiotic stress: *R. bicolor* is highly combative and shows reduced growth and enzyme production following temperature or grazing stress, whilst *P. velutina* is less combative but displays increased growth and enzyme production following stress (Crowther et al., 2012). These fungi were grown on ^{13}C-labeled soil with water potentials of either −0.006 or −0.06 MPa to replicate optimal and drought conditions, respectively. Isopod grazing (*grazing*), a dominant biotic control on fungal communities in temperate woodland ecosystems (Crowther et al., 2013), was also used as a stress, as was physical cutting (*cutting*), to simulate physical soil disturbance. These stressors and un-disturbed control treatments were each replicated five times per taxon across both moisture conditions (2 fungi x 2 moisture conditions x 3 disturbance treatments x 5 replicates = 60 microcosms). Mycelia from stressed and unstressed environments were then harvested from the soil surface, added to soil within a second set of microcosms (60 centrifuge tubes containing fresh soil) so that fungal-derived C could be traced into (i) living microbial C, (ii) dissolved organic C, (iii) total soil C and (iv) respired C.

2.2. Fungal culturing and microcosm preparation

Both fungi were subcultured onto beech wood blocks (2 × 2 × 1 cm) within non-vented 9-cm dia. Petri dishes on 2% malt extract agar (MEA; 15 g L^{-1} Lab M agar no. 2, 20 g L^{-1} Munton and Fiston malt). Petri dishes were incubated in the dark at a constant temperature of 20 °C for 3 months prior to experimental use.

Soil microcosms were prepared following Crowther et al. (2011b). Briefly, loamy soil (pH: 5.52, % C: 11.57, % N: 0.63, % sand: 89.2, % silt: 4.1, % clay: 6.7%) was collected from temperate deciduous woodland (Yale-Myers Forest; 41° 57′ 7.8″ N, −72° 7′ 29.1 W″) to a depth of 10 cm and sieved on site through a 10 mm mesh. Sieved soil was air-dried in plastic trays and sieved again through 2-mm mesh before being frozen overnight at −20 °C to kill any remaining fauna. Prior to use, soil was re-wetted with 400 or 200 mL DH_2O kg soil^{-1}, giving final water potentials of −0.006 and −0.06 MPa for optimal and drought treatments, respectively. Moistened soil (200 g) was then compacted to a depth of 5 mm within 34 × 34 cm bioassay dishes and smoothed to provide a flat surface for fungi to grow into. Fungal-colonised wood blocks were then inoculated centrally onto the surface of the soil microcosms so that mycelial cords would emerge and grow across the soil surface.

All fungi were labeled by adding 0.269 mL of a 0.1 M solution (to avoid toxic effects of high glucose concentrations) of ^{13}C-labeled (99 atom %) glucose to soil, 5 mm ahead of the growing mycelial front. The solution was added immediately following mycelial emergence from wood blocks and repeated daily for a week to promote gradual incorporation throughout the mycelial system. Mycelia were then allowed to grow for 2 weeks to allow uniform labeling throughout each fungal system (Tordoff et al., 2011), before mycelia reached the edges of the dishes (which might have induced unintentional stress).

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