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Sticky dead microbes: Rapid abiotic retention of microbial necromass in soil

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1. Main text

Soil organic matter (SOM) is a key indicator for healthy soil and sustainable agriculture (Paustian et al., 2016). Research into SOM stability has traditionally focused on the quality and quantity of plant inputs to soil (Lehmann and Kleber, 2015), however, recent research reveals that SOM is dominated by dead microbial products and residues (hereafter, ‘necromass’) (Kallenbach et al., 2015; Liang et al., 2019, 2021)). The persistence of necromass in soil may be promoted via necromass uptake and immobilization into microbial biomass, but retention ultimately relies on microaggregate formation via adsorption to soil mineral surfaces. In actuality, both biotic (microbial immobilization) and abiotic retention (adsorption and molecular interaction) may co-occur but the relative importance of these short-term processes has not been assessed (Fig. 1).

Necromass has been visualized on mineral surfaces (Kleber et al., 2011), supporting the paradigm that accumulation of stable SOM is dominated by organic-mineral adsorption, and is limited by mineral surface area (McNally et al., 2017). However, necromass is not detected as a smooth coverage on mineral surfaces, but clumpy (Dignac et al., 2017; Vogel et al., 2014), suggesting that SOM stabilization may also involve organic-organic interactions, or necromass adhering to other necromass and organic matter for example by ionic interactions, hydrogen bridges, van der Waals forces, and (partial) entrapment (Schweizer et al., 2018; Vogel et al., 2014) (Fig. 1). Understanding the relative importance of these two abiotic adsorption processes will be critical for predicting upper limits of SOM persistence.

The chemistry of microbial necromass has been assumed unimportant as a regulator of SOM storage, because its chemical composition is more similar than diverse plant inputs (Liang et al., 2017). Previous research on necromass chemistry and persistence has focused on its stability and emphasized chitin retention (Fernandez et al., 2016; Schreiner et al., 2014). However, cell chemistry can alter rates of cell-cell adhesion (Dufrêne, 2015) and organic-mineral adsorption rates (Meissner et al., 2015), particularly for N-rich necromass (Kopittke et al., 2017). Gram-positive bacterial envelopes have a thick cross-linked peptidoglycan layer outside the lipid membrane, whereas a Gram-negative cell envelope has an inner and outer lipid membrane enclosing a thinner peptidoglycan layer in the periplasm. Fungal cell walls are highly heterogeneous; yeast cell walls, for example, are composed of layered mannan, β-glucans and chitin outside a lipid membrane. Therefore, cell-membrane functional groups with a high N-content, such as peptidoglycan-rich Gram-positive bacteria, may be favored for organic-organic interaction, relative to Gram-negative cell membranes.
even seasonality (Buckeridge et al., 2013; Ramirez et al., 2012), necromass cell chemistry may influence SOM stabilization at ecosystem scales. We investigated the importance of biotic and abiotic necromass retention in grassland soil and the influence of necromass chemistry on this retention in short-term laboratory incubations. We hypothesized: H1. both biotic and abiotic necromass retention occur, and that biotic retention is more important; H2. more necromass is retained in soil with higher background concentrations of necromass (implying organic-organic adhesion); and H3. abiotic retention would be higher for Gram-positive bacteria (‘organic-mineral’), but that necromass also adheres to necromass (‘organic-organic’), promoting retention, and that this organic-organic process may be influenced by necromass cell chemistry.

We suspected this was either a side-effect of sterilization, or CO₂ transient abiotic retention in soil. Furthermore, our lab-grown, single-culture additions only approximate the retention of chemically and taxonomically-complex native necromass. Nonetheless, our results illustrate an important short-term effect of abiotic C retention in soil. The lower retention of ¹⁵C in live vs. sterile soils was not predicted and we suspected this was either a side-effect of sterilization, or CO₂ loss from microbial activity. We discounted the sterilization effect, because we did not see a parallel lower retention of necromass-¹⁵N in live compared to dead soils (Fig. 2b). This, combined with no change in C:N ratio of tracer retention in sterile soils and a drop in C:N ratio of retention in live soils (P < 0.001, data not shown) equates with live microbial processing of C, associated with immobilization/loss of 4–10% of the total C added, as extractable biomass or CO₂ (Fig. 3a and b). Losses of N₂O from the labeled necromass were comparable to CO₂ (<2%, Fig. 3c) but we presume that N uptake to microbial biomass (not measured) would be lower than C, reflecting the lower N demand for growth in these N-rich pasture soils. C-starvation during incubation may have resulted in use of necromass-C for maintenance, reflected in a low substrate use efficiency (CUE) (Fig. 3d).

Higher C and N was retained in live and sterile soils with enhanced background necromass compared to controls (~10–40% higher, Fig. 2a and b), supporting the hypothesis (H2) that necromass may be adhering to necromass. Organic-organic adhesion has been suggested previously based on isotopic and visual evidence in laboratory and long-term field studies (Schweizer et al., 2018). We did not observe higher C and N retention in soils with enhanced peptidoglycan (M. luteus) necromass, rejecting H3, that abiotic retention would be higher for Gram-positive bacterial membranes. However, we provide novel evidence that the retention of C and N from the necromass tracer was higher in live and dead soils augmented with S. cerevisiae necromass (C: P < 0.001; N: P = 0.03). This higher microbial C and N retention in S. cerevisiae-amended soils does not appear to be a biotic process, because the CUE of the tracer necromass in live soils did not differ between background necromass types (Fig. 3d) (despite all enhanced background necromass treatments being lower than the no-addition control, which was presumably a response to higher substrate concentration relative to the control (Geyer et al., 2019)). Instead, this enhanced retention of the tracer necromass in the presence of S. cerevisiae necromass may be indicative of faster or stronger interaction between the complex morphogenesis of the Gram-negative outer cell membrane and yeast cell walls, such as occur in live microbial communities (Dufrene, 2015). Further compound-specific research is required to understand if the properties of yeast necromass extend to other fungal necromass generally and to specific bacterial membrane and fungal cell wall compounds. Regardless, this result indicates that cell chemistry contributes to an adhesion mechanism that promotes necromass stability in soil.

We conclude that abiotic processes are important for short-term retention of necromass-C and N in soils and require greater emphasis in studies investigating SOM stability. Our results indicate that organic-organic interactions promote retention of C and N and contribute novel evidence that this mechanism is regulated by cell chemistry. If this short-term abiotic retention occurs in situ and persists, then microbial community structure and possibly the fungal:bacterial ratio, may influence C
and N stabilization through variations in community cell chemistry. Field additions of isotopically-labeled necromass from different taxa, in different soils, would be valuable for investigating the long-term importance of these mechanisms. These findings suggest that abiotic adsorption and interaction of microbial necromass and its functional properties beyond chemical stability (i.e. cell molecular property, aggregations, and morphology), deserve further investigation in the context of soil carbon sequestration.

Data availability

The supporting data and R code for the statistics and figures in this paper can be found at: https://doi.org/10.5281/zenodo.3957441.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2020.107929.

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