Editorial review

Microbial necromass on the rise: The growing focus on its role in soil organic matter development

Soil organic matter (SOM), as a major sink and source of soil organic carbon (SOC), is the basis for fertile soils, sustained ecosystems, and climate. The immense SOC stock represents the largest pool of terrestrial C, and it is estimated that the magnitude of global soil is twice that of the atmosphere and even greater than atmosphere and vegetation combined (Eswaran et al., 1993). Consequently, relatively small changes in global SOC storage can have a significant impact on atmospheric CO_2 concentrations and climate change (Lal, 2004; Davidson and Janssens, 2006). However, we currently have insufficient capability to forecast and precisely control future changes in SOC pool as well as its response to disturbances. This is mainly due to our still limited understanding of the mechanisms underlying SOC formation and stabilization.

As our thinking on SOM genesis has evolved, SOC transformation and sequestration have been actively discussed (Schmidt et al., 2011; Cotrufo et al., 2015; Lehmann and Kleber, 2015; Liang et al., 2017; Sokol et al., 2019). Empirical studies and conceptual models have both suggested that the incorporation of microbial biomass components into soils via microbial remnants is large (Simpson et al., 2007; Miltner et al., 2012; Cotrufo et al., 2013; Kallenbach et al., 2016; Khan et al., 2016). This means that microbial inputs may play a greater role in C sequestration into soils than traditionally considered, particularly when microbial inputs are more likely to be stabilized than are plant inputs (Kiem and Kögel-Knabner, 2003; Ma et al., 2018). Indeed, recent work has provided the first comprehensive analysis of the contribution of microbial necromass to SOC, which can make up more than 50% of SOC (Liang et al., 2019). However, the microbial controls of biomass formation (Joergensen and Wichern, 2018), how that biomass becomes stabilized SOM (Liang et al., 2017; Kallenbach et al., 2015; Högberg et al., 2020), and their interactions with other factors such as land use, climate change, edaphic properties etc., remain uncertain and elusive.

In order to provide timely knowledge and insightful perspective, quantitatively and mechanically, on microbial necromass, its turnover, and its contribution to SOM storage, we compiled this special issue to focus on studies on soil microbial biomass formation and necromass stabilization. This is necessary not only to enhance our understanding of SOC dynamics and stability, to improve the structure of current C and climate models, but also to create strategies to sequester C, and to support climate policy. This special issue includes **35** papers on soil microbial necromass published in Soil Biology and Biochemistry that conveyed scientific progress from earlier stages to the present day. These papers represent important experiments and field observations, methodological breakthroughs and challenges, as well as innovative concepts for inspiring discussions in the field. We particularly chose articles on soil microbial necromass from different disciplinary domains and the

integrated system-related research. Finally, we provided an integrated framework aimed at initiating next-generation topical studies and spurring new discoveries of the scientific principles relevant to soil microbial necromass.

1. The shifting paradigm

Despite the description of soil microbial biomass by Jenkinson (1977) as "*the eye of the needle through which all the organic materials must pass*", the role of soil microorganisms as agents of SOM formation has been predominantly investigated in terms of its catabolic transformation process, either into mineralized CO_2 or modified compounds in soil. As a result, it had long been believed that remnants of decayed plant matter were the main components of the persistent C in soils. Concerns were vigorously raised by Simpson et al. (2007) who reported that more than half of the alkaline-extracted fraction from a soil might derive from microbial cell residues, a large pool of dead fungi and bacteria that unfortunately have never been quantified in a meaningful way. Our understanding of SOM genesis has made great strides over the past decade, driven by evolving analytical approaches and increasing evidence that has led to the intellectual paradigm shift – dead microbial mass is the dominant component of the long-lasting SOC, rather than decayed plant matter (Miltner et al., 2012; Liang et al., 2019). For example, recent studies showed that fungal and bacterial necromass residues comprise the bulk of the SOM pool (Kindler et al., 2006; Schweigert et al., 2015; Kallenbach et al., 2016; Khan et al., 2016). Accordingly, this evidence is shifting the research from focusing on "humic" matter to the microbial contribution. This shift has led to a growing understanding of microbial anabolism and necromass in soil systems and on the nature of SOM chemistry, production, and turnover.

2. The current dilemma

Unfortunately, the slow development of analytical techniques has not been able to catch up with the fast recognition of the importance of the research topic. The prerequisite for assessing the contribution of the microbial necromass in soils is the availability of effective approaches. So far, biomarkers that trace the microbial origin of SOC, such as amino acids and proteins, lipids, DNA, as well as cell envelope compounds like amino sugars including glucosamine and muramic acid, have been applied in soil microbial necromass studies (Amelung, 2001; Drigo et al., 2012; Koyama et al., 2018; Joergensen, 2018; Poeplau et al., 2019). Except for amino sugar analysis, other approaches have been used only sporadically for microbial necromass studies to date. Zhang and

Amelung (1996) published the protocol for extracting and determining soil amino sugars. These components are stabilized in soil after cell death (Glaser et al., 2004), and provide a valuable marker to evaluate soil microbial necromass dynamics; amino sugar analyses can be coupled with isotope technology (He et al., 2006; Liang et al., 2010; Indorf et al., 2015) to trace the kinetics and pathways of necromass transformations (Reay et al., 2019; Wang et al., 2020b). In order to convert amino sugar mass to total necromass mass, conversion factors of 9 and 45 have been suggested for converting glucosamine to fungal necromass C and muramic acid to bacterial necromass C, respectively (Appuhn and Joergensen, 2006; Engelking et al., 2007; Liang et al., 2019). Over the past decades, Soil Biology and Biochemistry has been a central outlet for work using the amino sugar approach to study soil microbial necromass, which indeed assists the development of this research domain. The amino sugar approach has been well employed in a vast range of ecotypes across different climatic zones and varying temporal and spatial scales (e.g., Angst et al., 2018; Ding et al., 2018; Lauer et al., 2011; Luo et al., 2020; Martins et al., 2012; Jia et al., 2017; Shao et al., 2019; van Groenigen et al., 2010; Wang et al., 2020a; West et al., 2020; Ye et al., 2019). The knowledge gained about soil microbial necromass directly benefits to national and global discussions on C budgets, soil vulnerability and sustainability of soils for food production, ecological services, climate health and policy, and hence on soil management.

However, the amino sugar approach has caveats and limitations, some of which serve as a cautionary note regarding common difficulties that are encountered when general biomarkers identified *in vitro* are applied to the environment (Joergensen, 2018; Liang et al., 2019). For example, large variations of microbial necromass exist that are based on calculations using the conversion factors for specific microbial biomarker amino sugars from pure culture, and those conversion factors may also change for microbes under different starvation conditions. In the absence of other reliable alternatives, however, amino sugar analysis may represent the most powerful approach for studying soil microbial necromass. Therefore, we need an array of necromass analysis approaches that go beyond just amino sugars for cross validation. For this purpose, the recent work by Hu et al. (2020) using isotope-labeled amino sugars and muropeptides for direct measurement of the turnover of microbially-derived SOM provided a potential approach for *in situ* microbial necromass studies.

3. The way forward

Microbial communities are both drivers of and contributors to SOM dynamics. Soil organic matter is complex and contains diverse chemical compounds. Thus, linking microbial functions with SOM processes offers opportunities for exciting new studies. Recent progress in -omics technologies on complex communities and cutting-edge chemical analysis of complex mixtures, together with multi-isotope and imaging approaches, enlarge the research opportunities for the topic in focus. The latest modeling approaches (e.g. in systems ecology) and conceptual frameworks open up new vistas to study the topic. Some of these efforts have been recently applied for (e.g. microbial carbon pump, MCP) enriching knowledge in this area, but other more insightful studies are required to elucidate the mechanisms that are responsible for soil microbial necromass dynamics. For example, Buckeridge et al. (2020) recently observed that microbial necromass preferentially adheres with other necromass materials, suggesting that this necromass–necromass interaction should be considered as a new potential stabilization process. Here, we intend to integrate intriguing hypothesis-driving questions and current hot topics into an academic roadmap. We believe such a roadmap will reveal systematic research tasks.

The processes by which microbially-synthesized compounds move into SOM where they are stabilized by intimate physical interaction have been conceptualized as the soil MCP (Liang et al., 2017). This is mechanistically connected with the terrestrial C cycle and global

climate, and serves as a conceptual model for guiding the multidisciplinary perspectives to understand the importance of microbial necromass in the formation and stabilization of SOM. Centering on this model, we extend into four primary foci: **process-based understanding**, **driving mechanisms**, **regulatory mechanisms**, and the **associated microbiome** (Fig. 1).

Developing a process-based understanding of the soil MCP is key to elucidating the consequential effects of microbial necromass on quantity and quality of SOM. Carbon incorporation into soils occurs along two different microbial metabolic pathways: *in vivo* turnover within the microbial cells and *ex vivo* mostly extracellular enzymatic modification (Liang et al., 2017). Accordingly, two hypothesis-driving perspectives were proposed that a soil MCP-relevant entombing effect and microbial *in vivo* turnover determine the magnitude and C chemistry of the stable SOC pool, as opposed by a priming effect and microbial *ex vivo* modification (Liang et al., 2017). The strategy of simultaneously taking account of microbial catabolic breakdown and anabolic synthesis for studying SOC dynamics has been encouraged, but limited work has been published combining these two microbial C transformation pathways (*in vivo vs. ex vivo*) or these two effects (entombing *vs.* priming) (Jia et al., 2017; Zhu et al., 2020). Further, the interactive mechanisms between these two pathways remain largely elusive. For example, one recent study found that microbial necromass might be used for nutrient acquisition, i.e. resource mining, but the "primed" C might also be from microbial necromass in some scenarios (Cui et al., 2020). For the latter, the mechanisms of microbial metabolic controls on chemical complexity of SOM are contentious. The distinct microbial C transformation pathways have been empirically substantiated by the convergence or divergence of the fate of position-specific labeled C (Bore et al., 2019), where the convergence of individual C positions supports the importance of recycled microbial products in SOM storage (Dippold and Kuzyakov, 2016). Next, it is critical to evaluate the role of the MCP in shaping belowground C patterns in different soil systems and to link the two microbial C transformation pathways (*in vivo* and *ex vivo*) to the quality of organic inputs and stable SOM.

Homoeostatic growth of microorganisms requires an appropriate ratio of different elements, e.g., C, N and P, which is the basis for the ecological stoichiometry theory and presumably for resource mining to maintain the stoichiometric balance that drives microbial metabolic processes in soils (Mooshammer et al., 2014). In addition to the flow of matter, energy flux is another fundamental driver of metabolic processes (Janzen, 2015). Generations of microbes cycle the energy and matter via the soil MCP and store them in their biomass, which carries over to their necromass, and SOM (Kästner and Miltner, 2018). Because different groups of microorganisms within the microbial biomass have different stoichiometry and energy demands, this leads to different metabolic capabilities, biomass yields, and ultimate necromass production. However, very few studies exist yet that consider microbial necromass production in soils as energy-driven and stoichiometry-controlled.

Microbially-mediated C transformation processes mostly coexist in nature with the involvement of soil fauna and viruses, which play a regulatory role in manipulating the soil MCP, and consequently influencing microbial necromass production, recycling, and SOC dynamics (Grandy et al., 2016; Chertov et al., 2017; Williamson et al., 2017). More specifically, soil fauna may influence microbial necromass dynamics by regulating substrate quantity and quality to change activity of soil microbes, governing microbial community composition to change microbial biomass production, and remoulding habitat niche to change physical protection and redox active metals. Soil viruses may influence microbial necromass dynamics directly by speeding microbial cell lysis, or indirectly by changing soil microbial community structure and metabolism. Despite the discussions around these rewarding foci, only few studies have evaluated the importance of soil fauna and virus in generating microbial necromass and SOC stabilization (Crowther et al., 2015; Soong et al., 2016). Therefore, the limited knowledge of regulatory mechanisms on the soil MCP offers opportunities for improving our
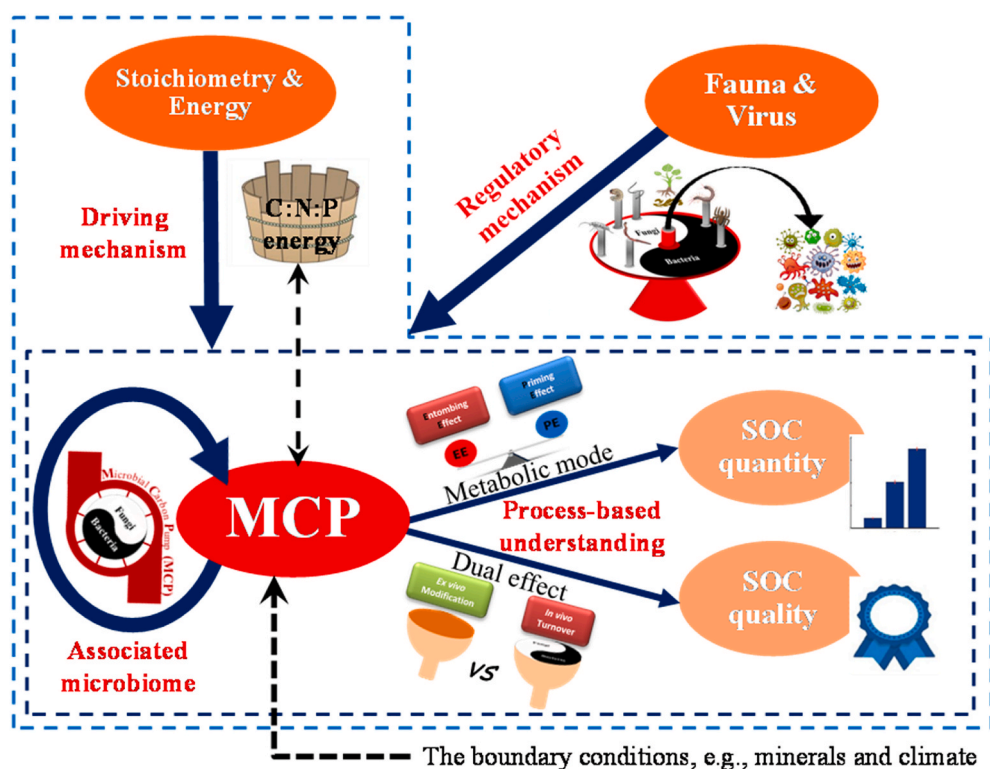
Fig. 1. A conceptual roadmap for future soil microbial necromass studies. Using soil microbial carbon pump (MCP) as a hub, four perspective areas: process-based understanding for controlling soil organic carbon (SOC) quantity and quality, driving mechanisms of stoichiometry and energy, regulatory mechanisms by soil fauna and virus, and the associated microbiome with efficient microbial necromass accumulation, are proposed. The *yin–yang* symbol is used to create a sense of movement of soil MCP and the movement is driven by bacteria and fungi with different trophic lifestyles. The boundary conditions including mineral and climate factors can shape how soil MCP may behavior in soil carbon stabilization.

understanding of how soil fauna and viruses are linked to soil microbial necromass and SOM dynamics.

Finally, we propose the necessity of identifying the microbes associated with the soil MCP. Unlike a specific function by a constrained group of species, microbial anabolic synthesis is a non-specific general physiological process of growth that is carried out by all microorganisms, which however, must behave differently and confer the inputs of C belowground differently. It is insufficiently understood whether certain microbial species associated with certain life strategies will have high microbial C use efficiency and necromass accumulation, and how the interaction of soil microbial guilds and soil necromass influence SOM cycling. Identifying those microbial species responsible for *in situ* necromass formation, and explicitly linking microbial diversity and functional redundancy to microbial anabolic contribution to SOM turnover, storage and sequestration will incorporate microbiology for process understanding and improving SOC models.

4. Concluding remarks

Profound knowledge of soil microbial necromass is largely lacking concerning process understanding, driving and regulatory mechanisms, and the associated microbiomes. Soil microbial necromass research is valuable, and relevant research is timely, given the current state of the SOM paradigm shift. We call for the development of new microbial necromass analysis approaches that go beyond just biomarker amino sugars, and we identify new perspectives to follow up. We are hoping that this collection of soil microbial necromass studies will stimulate discussions that are more relevant and pave the way for future research directions.

Acknowledgments

References

Amelung, W., 2001. Methods using amino sugars as markers for microbial residues in soil. In: Lal, R., Kimble, J.M., Follett, R.F., Stewart, B.A. (Eds.), Assessment Methods for Soil Carbon. CRC/Lewis Publishers, Boca Raton, FL, pp. 233–270.

Angst, G., Messinger, J., Greiner, M., Häusler, W., Hertel, D., Kirfel, K., Kögel-Knabner, I., Leuschner, C., Rethemeyer, J., Mueller, C.W., 2018. Soil organic carbon stocks in topsoil and subsoil controlled by parent material, carbon input in the rhizosphere, and microbial-derived compounds. Soil Biology and Biochemistry 122, 19–30.

Appuhn, A., Joergensen, R., 2006. Microbial colonisation of roots as a function of plant species. Soil Biology and Biochemistry 38, 1040–1051.

Bore, E., Kuzyakov, Y., Dippold, M., 2019. Glucose and ribose stabilization in soil: convergence and divergence of carbon pathways assessed by position-specific labeling. Soil Biology and Biochemistry 131, 54–61.

Buckeridge, K.M., La Rosa, A.F., Mason, K.E., Jeanette, W., McNamara, N.P., Grant, H.K., Nick, O., 2020. Sticky dead microbes: rapid abiotic retention of microbial necromass in soil. Soil Biology and Biochemistry 149, 107929.

Chertov, O., Komarov, A., Shaw, C., Bykhovets, S., Frolov, P., Shanin, V., Grabarnik, P., Priputina, I., Zubkova, E., Shashkov, M., 2017. Romul_Hum—a model of soil organic matter formation coupling with soil biota activity. II. Parameterisation of the soil food web biota activity. Ecological Modelling 345, 125–139.

Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K., Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Global Change Biology 19, 988–995.

Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.L., Wall, D.H., Parton, W.J., 2015. Formation of soil organic matter via biochemical and physical pathways of litter mass loss. Nature Geoscience 8, 776–779.

Crowther, T.W., Thomas, S.M., Maynard, D.S., Baldrian, P., Covey, K., Frey, S.D., van Diepen, L.T., Bradford, M.A., 2015. Biotic interactions mediate soil microbial feedbacks to climate change. Proceedings of the National Academy of Sciences of the United States of America 112, 7033–7038.

Cui, J., Zhu, Z., Xu, X., Liu, S., Jone, D., Kuzyakov, Y., Shibistova, O., Wu, J., Ge, T., 2020. Carbon and nitrogen recycling from microbial necromass to cope with C:N stoichiometric imbalance by priming. Soil Biology and Biochemistry 142, 107720.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

Ding, X., Chen, S., Zhang, B., Liang, C., He, H., Horwath, W.R., 2018. Warming increases microbial residue contribution to soil organic carbon in an alpine meadow. Soil Biology and Biochemistry 135, 13–19.

Dippold, M.A., Kuzyakov, Y., 2016. Direct incorporation of fatty acids into microbial phospholipids in soils: position-specific labeling tells the story. Geochimica et Cosmochimica Acta 174, 211–221.

Drigo, B., Anderson, I.C., Kannangara, G.S.K., Cairney, J.W.G., Johnson, D., 2012. Rapid incorporation of carbon from ectomycorrhizal mycelial necromass into soil fungal communities. Soil Biology and Biochemistry 49, 4–10.

Engelking, B., Flessa, H., Joergensen, R.G., 2007. Shifts in amino sugar and ergosterol contents after addition of sucrose and cellulose to soil. Soil Biology and Biochemistry 39, 2111–2118.

Eswaran, H., Van Den Berg, E., Reich, P., 1993. Organic carbon in soils of the world. Soil Science Society of America Journal 57, 192–194.

Glaser, B., Turrion, M.B., Alef, K., 2004. Amino sugars and muramic acid – biomarkers for soil microbial community structure analysis. Soil Biology and Biochemistry 36, 399–407.

Grandy, A.S., William, R.W., Wicking, K., Kyker-Snowman, E., 2016. Beyond microbes: are fauna the next frontier in soil biogeochemical models? Soil Biology and Biochemistry 102, 40–44.

He, H., Xie, H., Zhang, X., 2006. A novel GC/MS technique to assess N-15 and C-13 incorporation into soil amino sugars. Soil Biology and Biochemistry 38, 1083–1091.

Högberg, M.N., Skyllberg, U., Högberg, P., Knicker, H., 2020. Does ectomycorrhiza have a universal key role in the formation of soil organic matter in boreal forests? Soil Biology and Biochemistry 140, 107635.

Hu, Y., Zheng, Q., Noll, L., Zhang, S., Wanek, W., 2020. Direct measurement of the in situ decomposition of microbial-derived soil organic matter. Soil Biology and Biochemistry 141, 107660.

Indorf, C., Dyckmans, J., Joergensen, R.G., 2015. Short-term changes in amino sugar-specific δ13C values after application of C4 and C3 sucrose. Soil Biology and Biochemistry 91, 92–98.

Janzen, H.H., 2015. Beyond carbon sequestration: soil as conduit of solar energy. European Journal of Soil Science 66, 19–32.

Jenkinson, D.S., 1977. The soil biomass. New Zealand Soil News 25, 213–218.

Jia, J., Feng, X., He, J., He, H., Lin, L., Liu, Z., 2017. Comparing microbial carbon sequestration and priming in the subsoil versus topsoil of a Qinghai-Tibetan alpine grassland. Soil Biology and Biochemistry 104, 141–151.

Joergensen, R.G., 2018. Amino sugars as specific indices for fungal and bacterial residues in soil. Biology and Fertility of Soils 54, 559–568.

Joergensen, R.G., Wichern, F., 2018. Alive and kicking: why dormant soil microorganisms matter. Soil Biology and Biochemistry 116, 419–430.

Kallenbach, C.M., Frey, S.D., Grandy, A.S., 2016. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. Nature Communications 7, 13630.

Kallenbach, C.M., Grandy, A.S., Frey, S.D., Diefendorf, A.F., 2015. Microbial physiology and necromass regulate agricultural soil carbon accumulation. Soil Biology and Biochemistry 91, 279–290.

Kästner, M., Miltner, A., 2018. Chapter 5 - SOM and microbes—what is left from microbial life. In: Garcia, C., Nannipieri, P., Hernandez, T. (Eds.), The Future of Soil Carbon. Academic Press, pp. 125–163.

Khan, K.S., Mack, R., Castillo, X., Kaiser, M., Joergensen, R.G., 2016. Microbial biomass, fungal and bacterial residues, and their relationships to the soil organic matter C/N/P/S ratios. Geoderma 271, 115–123.

Kiem, R., Kögel-Knabner, I., 2003. Contribution of lignin and polysaccharides to the refractory carbon pool in C-depleted arable soils. Soil Biology and Biochemistry 35, 101–118.

Kindler, R., Miltner, A., Richnow, H.H., Kästner, M., 2006. Fate of gram-negative bacterial biomass in soil mineralization and contribution to SOM. Soil Biology and Biochemistry 38, 2860–2870.

Koyama, A., Harlow, B., Kuske, C.R., Belnap, J., Evans, R.D., 2018. Plant and microbial biomarkers suggest mechanisms of soil organic carbon accumulation in a Mojave Desert ecosystem under elevated CO2. Soil Biology and Biochemistry 120, 48–57.

Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. Science 304, 1623–1627.

Lauer, F., Kösters, R., du Preez, C.C., Amelung, W., 2011. Microbial residues as indicators of soil restoration in South African secondary pastures. Soil Biology and Biochemistry 43, 787–794.

Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature 528, 60–68.

Liang, C., Amelung, W., Lehmann, J., Kästner, M., 2019. Quantitative assessment of microbial necromass contribution to soil organic matter. Global Change Biology 25, 3578–3590.

Liang, C., Balser, T.C., 2010. Mass spectrometric characterization of amino sugar aldononitrile acetate derivatives used for isotope enrichment assessment of microbial residues. Soil Biology and Biochemistry 42, 904–909.

Liang, C., Schimel, J.D., Jastrow, J.D., 2017. The importance of anabolism in microbial control over soil carbon storage. Nature Microbiology 2, 17105.

Luo, R., Kuzyakov, Y., Liu, D., Fan, J., Luo, J., Lindsey, S., He, J., Ding, W., 2020. Nutrient addition reduces carbon sequestration in a Tibetan grassland soil: disentangling microbial and physical controls. Soil Biology and Biochemistry 144, 107764.

Ma, T., Zhu, S., Wang, Z., Chen, D., Dai, G., Feng, B., Su, X., Hu, H., Li, K., Han, W., Liang, C., Bai, Y., Feng, X., 2018. Divergent accumulation of microbial necromass and plant lignin components in grassland soils. Nature Communications 9, 3480.

Martins, M.R., Angers, D.A., Corá, J.E., 2012. Co-accumulation of microbial residues and particulate organic matter in the surface layer of a no-till Oxisol under different crops. Soil Biology and Biochemistry 50, 208–213.

Miltner, A., Bombach, P., Schmidt-Brücken, B., Kästner, M., 2012. SOM genesis: microbial biomass as a significant source. Biogeochemistry 111, 41–55.

Mooshammer, M., Wanek, W., Zechmeister-Boltenstern, S., Richter, A., 2014. Stoichiometric imbalances between terrestrial decomposer communities and their resources: mechanisms and implications of microbial adaptations to their resources. Frontiers in Microbiology 5, 22.

Poeplau, C., Helfrich, M., Dechow, R., Szoboszlay, M., Tebbe, C.C., Don, A., Greiner, B., Zopf, D., Thumm, U., Korevaar, H., Geerts, R., 2019. Increased microbial anabolism contributes to soil carbon sequestration by mineral fertilization in temperate grasslands. Soil Biology and Biochemistry 130, 167–176.

Reay, M.K., Charteris, A.F., Jones, D.L., Evershed, R.P., 2019. 15N-amino sugar stable isotope probing (15N-SIP) to trace the assimilation of fertiliser-N by soil bacterial and fungal communities. Soil Biology and Biochemistry 138, 107599.

Schmidt, M., Torn, M., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D., Nannipieri, P., Rasse, D., Weiner, S., Trumbore, S., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56.

Schweigert, M., Herrmann, S., Miltner, A., Fester, T., Kästner, M., 2015. Fate of ectomycorrhizal fungal biomass in a soil bioreactor system and its contribution to soil organic matter formation. Soil Biology and Biochemistry 88, 120–127.

Shao, P., Liang, C., Lynch, L., Xie, H., Bao, X., 2019. Reforestation accelerates soil organic carbon accumulation: evidence from microbial biomarkers. Soil Biology and Biochemistry 131, 182–190.

Simpson, A.J., Simpson, M.J., Smith, E., Kelleher, B.P., 2007. Microbially derived inputs to soil organic matter: are current estimates too low? Environmental Science and Technology 41, 8070–8076.

Sokol, N.W., Sanderman, J., Bradford, M.A., 2019. Pathways of mineral - associated soil organic matter formation: integrating the role of plant carbon source, chemistry, and point of entry. Global Change Biology 25, 12–24.

Soong, J.L., Vandegehuchte, M.L., Horton, A.J., Nielsen, U.N., Denef, K., Shaw, E.A., Tomasel, C.M., Parton, W., Wall, D.H., Cotrufo, M.F., 2016. Soil microarthropods support ecosystem productivity and soil C accrual: evidence from a litter decomposition study in the tallgrass prairie. Soil Biology and Biochemistry 92, 230–238.

van Groenigen, K.J., Bloem, J., Bååth, E., Boeckx, P., Rousk, J., Bodé, S., Forristal, D., Jones, M., 2010. Abundance, production and stabilization of microbial biomass under conventional and reduced tillage. Soil Biology and Biochemistry 42, 48–55.

Wang, C., Wang, X., Pei, G., Xia, Z., Peng, B., Sun, L., Wang, J., Gao, D., Chen, S., Liu, D., Dai, W., Jiang, P., Fang, Y., Liang, C., Wu, N., Bai, E., 2020a. Stabilization of microbial residues in soil organic matter after two years of decomposition. Soil Biology and Biochemistry 141, 107687.

Wang, X., Zhang, W., Zhou, F., Liu, Y., He, H., Zhang, X., 2020b. Distinct regulation of microbial processes in the immobilization of labile carbon in different soils. Soil Biology and Biochemistry 142, 107723.

West, J.R., Cates, A.M., Ruark, M.D., Deiss, L., Whitman, T., Rui, Y., 2020. Winter rye does not increase microbial necromass contributions to soil organic carbon in continuous corn silage in North Central US. Soil Biology and Biochemistry 48, 107899.

Williamson, K.E., Fuhrmann, J.J., Wommack, K.E., Radosevich, M., 2017. Viruses in soil ecosystems: an unknown quantity within an unexplored territory. Annual Review of Virology 4, 201–219.

Ye, G., Lin, Y., Kuzyakov, Y., Liu, D., Luo, J., Lindsey, S., Wang, W., Fan, J., Ding, W., 2019. Manure over crop residues increases soil organic matter but decreases microbial necromass relative contribution in upland Ultisols: results of a 27-year field experiment. Soil Biology and Biochemistry 134, 15–24.

Zhang, X., Amelung, W., 1996. Gas chromatographic determination of muramic acid, glucosamine, mannosamine, and galactosamine in soils. Soil Biology and Biochemistry 28, 1201–1206.

Zhu, X., Xie, H., Masters, M.D., Luo, Y., Zhang, X., Liang, C., 2020. Microbial trade-off in soil organic carbon storage in a no-till continuous corn agroecosystem. European Journal of Soil Biology 96, 103146.

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