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Review

Microbial solutions to soil carbon sequestration

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ABSTRACT

Inoculation of soil with living microbes or propagules has grown in interest and in application due to the modification/degradation of soil systems (including native microbial communities), and the need to maintain agricultural yields with fewer synthetic inputs. However, whilst beneficial microorganisms such as plant growth promoting bacteria (PGPB) and mycorrhizal fungi have been employed via inoculation, their utilisation as an agronomic tool remains trivial in the context of large-scale commercial agriculture. The development of inoculation products has thus far largely focused on their capacity to support plant health (and correlating yield/profitability), with little attention paid to the ability of these organisms/products to influence soil carbon. Given the expected growth of the agricultural inoculant industry (estimated to reach US$12.5b in revenue by 2027), the increasing commercialisation of soil carbon sequestration (via carbon credits and other financially linked instruments), and the need to find viable solutions to assist in the drawdown of atmospheric CO_2, a greater understanding of the role of soil microbes in soil carbon cycling is required in order to facilitate the development of products capable of supporting the sequestration and retention of soil carbon.

Here, we review the mechanisms by which microorganisms contribute to soil carbon sequestration and retention and suggest several groups that may be promising candidates for further exploration. Of the many microbial mediated mechanisms identified, we highlight (among others) the capacity of arbuscular mycorrhizal fungi to facilitate the transition of carbon from labile to recalcitrant pools (mineral associated and aggregated), melanising endophytic fungi as a potential source of stabile soil carbon, and PGPB as stimulators of plant growth/reliance and thus carbon entering the soil carbon pool. We put forward the ‘biochar + microbe system’ as a potential avenue to overcome the current limitations to building and retaining soil carbon stocks. This review is timely, given the challenges facing global food production, and the need to find viable solutions to address climate change.

1. Introduction

1.1. *The agricultural ‘green shift’*

Although instrumental to the productivity gains of the 20th century, many modern agricultural practises have resulted in landscape modification and degradation throughout much of the world (Bongaarts, 2019; Sutton et al., 2016; Millennium Ecosystem Assessment, 2005). These modifications contribute to environmental damage and climate change (Johnson et al., 2007; Clay, 2013), in so putting at risk the long-term sustainability of many production systems. For example, excessive use of agrichemicals such as superphosphates, synthetic nitrogen (N), pesticides and herbicides, have contributed to water and air pollution, the re-shaping of natural ecosystems (above- and below-ground), and to the chemical imbalance and general degradation of soils (Guignard et al., 2017; Millennium Ecosystem Assessment, 2005). Large-scale landscape modification through the removal of natural systems with production agriculture has not only been the driving force behind biodiversity loss, but has also triggered further degrading processes such as desertification and soil erosion whilst accelerating greenhouse gas emissions. Taken together, the historic and ongoing practices associated with industrialised agriculture appears a major destabilising force shifting the earth system beyond planetary boundaries (the environmental limits within which humanity can safely operate), with two of the nine boundaries already transgressed beyond ‘safe operating space’ (biosphere integrity and biogeochemical flows) (Campbell et al., 2017).

A growing realisation of agriculture’s ongoing contribution to the earths biophysical destabilisation has bought about an agricultural

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'green shift' (a large-scale transition to more sustainable methods of food and fibre production), with renewed emphasis, and reliance, on natural processes to replace or reduce human produced inputs, whilst also maintaining and/or enhancing productivity (Tittonell, 2014). The development and utilisation of soil microorganisms to reduce or replace synthetic inputs is one such example, along with numerous other practices found in the growing regenerative (and other) agricultural movements, which emphasize not only the abatement of deleterious agricultural practices but the active restoration of natural systems and processes (often termed ecosystem services) to enhance productivity. Such endeavors can be broadly termed 'ecological intensification' (Bommarco et al., 2013) and are of increasing significance given the need to abate further environmental degradation, whilst at the same time increasing agricultural output in-line with future demands (Schmidhuber and Tubiello, 2007). In order for this vision to become a reality further development of the tools required to facilitate a transition from a resource intensive to a resource regenerative food production model is required, along with a greater understanding of how such tools can be utilised to address one of the major biophysical challenges facing life on earth, climate change.

1.2. Agriculture and climate

Widespread recognition of anthropogenic driven climate change has occurred throughout the last decade, driving scientific institutions, governments and global financial markets to develop technological and legislative solutions to address greenhouse gas (GHG) emissions (Eskander and Fankhauser, 2020). Amid the scramble to find solutions, agriculture has emerged an essential figure; both identified as a major contributor to GHG emissions (Johnson et al., 2007), whilst simultaneously possessing the potential to abate and reduce global emissions. Much of this potential centres around the ability to sequester C in agricultural soils (Paustian et al., 1997, 2016; Lal, 2004b). Put simply, soil is the largest reservoir of C in the terrestrial biosphere, estimated between 1100 and 1500 gigatons in the top meter of soil which is roughly double that of the atmospheric C pool (Scharlemann et al., 2014; Jackson et al., 2017; Jobbágy and Jackson, 2000). Given that agriculture accounts for roughly 38% of global land surface (approximately five billion hectares) (FOA, 2020) the management of C across these systems brings the opportunity to influence atmospheric CO_2 concentrations, with flow-on effects to the global climate (Gougoulias et al., 2014; Lal, 2004a, 2004b; Powlson et al., 2011). Such potential has not gone unnoticed, with a myriad of global initiatives and schemes established to promote C sequestration in soil. Launched in 2015 by the French Minister of Agriculture, The '4 per 1000 initiative' aims to increase carbon in agricultural soils by 0.4% annually to help mitigate climate change and increase food security (Soussana et al., 2019). The United Nations Food and Agricultural Organisation recently launched the 'Recarbonization of global agricultural soils' (RECSOIL) initiative with the intention of boosting soil health through the maintenance and enhancement of soil organic C stocks (Dubey, 2022). Similarly, the US 'Farm Bill' incentivises farmers to adopt practices aimed at improving soil health and sequestering C.

1.3. Soil carbon

Farmers, agronomist and scientist have long recognised soil organic carbon (SOC) as a central component in the maintenance of soil health and function, and thus to agricultural productivity. Organic C influences soil structure, water holding capacity (1.5%–1.7% increase in available water holding capacity for every unit increase in soil organic matter) (Libohova et al., 2018), water infiltration, and plant available phosphorus (P), with obvious implications for plant health, resilience and productivity. Despite this understanding, it is estimated that since pre-industrial times human activity has resulted in a loss of up to 78 gigatons of C throughout the worlds degraded and agricultural soils (Lal et al., 1997), with likely implications for the productivity of these systems and for atmospheric CO_2 concentrations. Today, regenerative farming, along with other conservation centric production philosophies, have at their core soil health, key to which is the promotion of practices with the capacity to restore and maintain soil organic C for the long-term sustainability and productivity of farming systems (Jordon et al., 2022; Page et al., 2020).

Other motives (beyond sustainable production) are also at play. Monetization of ecosystem services, or 'nature capital', has grown in recent years out of global climate and environmental concerns, facilitating the birth of environmentally linked financial instruments such as carbon and biodiversity credits (Gómez-Baggethun and Ruiz-Pérez, 2011; Costanza et al., 1997). The development of payment schemes for ecosystem services, such as C sequestration or biodiversity, are intended to provide financial motivation for the protection, and/or restoration of environmental services, directing capital towards otherwise economically valueless services (Balmford et al., 2002). On the demand side are individuals, companies or governments, looking to, or compelled to (often through government regulation), offset their environmental/emissions impacts, creating a marketplace for carbon (termed carbon offsets or credits), and other nascent environmental assets/services, fueling interest in soil C and the development of practices capable of assisting in its sequestration and retention (O'Connor et al., 2019).

A number of standards, protocols and markets exist throughout the world to generate, verify and capitalise on C sequestration. Founded in 2007, the American based VERRA manages one of the largest voluntary carbon market programs, the Verified Carbon Standard (VCS), which provides an avenue for participants to generate carbon credits (VERRA, 2022). Many governments have setup their own voluntary carbon credit schemes. The Australian Emissions Reduction Fund (ERF) aims to incentivise the adoption of new practices/technologies that sequester or reduce CO_2 emissions, bringing about the relatively new land use practice of 'carbon farming' (Nong and Siriwardana, 2017). Participants can earn Australian carbon credit units (ACCUs) for a number of activities eligible under the scheme. Like all carbon credits, one ACCU is one tonne of carbon dioxide equivalent (tCO2 -e) stored or avoided by a participant/project, which is then sold to the government (through a carbon abatement contract), or on the secondary market. The scheme includes two primary methods of reducing emissions; carbon storage (sequestration), and emissions avoidance. Sequestration methods include activities such as revegetation, the protection of native vegetation that is at imminent risk of clearance and soil C sequestration.

1.4. Carbon sequestration

Carbon sequestration can be broadly described as the net transfer of atmospheric CO_2 into long-lived C pools, such as extant biomass (e.g. trees), long-term biomass products (e.g. wood), dead microbial biomass and correlating residues (necromass), or recalcitrant organic and inorganic C in soils and subsurface environments (e.g. deep-sea sediments) (Johnson et al., 2007). Within the soil system, C can be broadly assigned into two pools; labile (high turnover/short-lived), and recalcitrant (stabile, long-lived). Labile C is largely comprised of coarse fraction material ($>$0.4 mm), referred to here as particulate organic matter (POM), which is relatively new decomposed or decomposing soil inputs (detritus), such as plant leaves, animal faeces and other organic material (Kirkby et al., 2013) (Fig. 1). Particulate organic C (POC) is the purely C component of POM (POM includes the mass of the other elements such as N, hydrogen (H) and oxygen (O)), typically making up around 50% of POM (Moody and Worrall, 2017). Recalcitrant soil C pools are made up of fine fraction ($<$0.4 mm) longer-lived stabilised C, such as mineral-association organic matter (MAOM) (consisting of relatively low moleculare weight compounds such as polysaccharides, lipids and other heavily decomposed plant and microbial products), and aggregated carbon (AggC), generated via several direct and in-direct microbial (and plant) mediated mechanisms (Fig. 1).

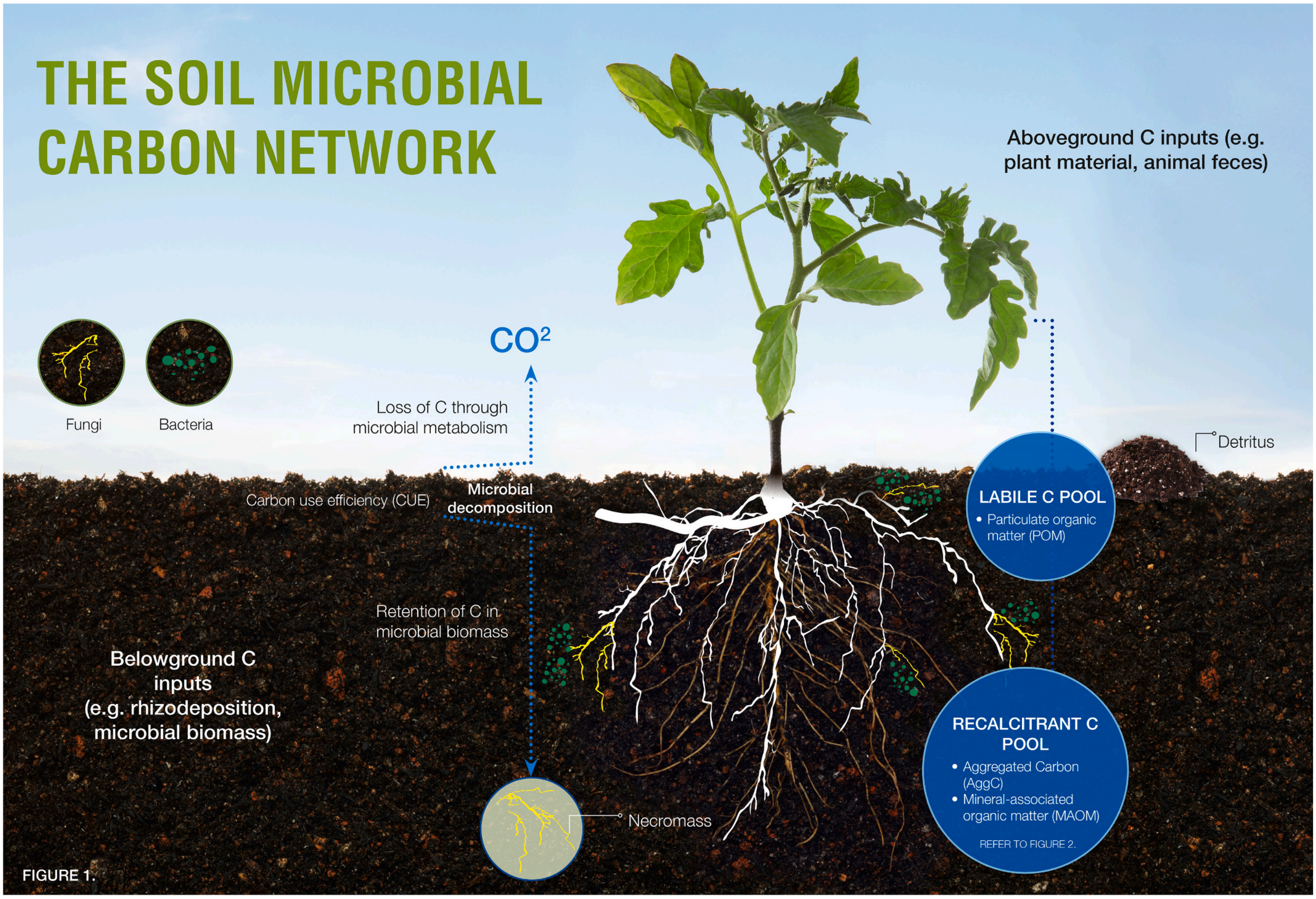


Fig. 1. The Soil Microbial Carbon Network. Displaying the two primary pathways of carbon input into soil systems (aboveground and belowground), the key components that make up recalcitrant and labile C pools, and the cycling of soil C via microbial action.

Sequestration of C in soil requires not only the adoption of management practices with the capacity to build soil C (e.g. conversion from rotation cropping to perennial pasture, reduction of soil tillage, planting of cover crops), but the accumulation of other nutrients. For instance, low nutrient availability (especially N) has been found to hinder soil C accumulation, whilst conversely N fertilisation has been shown to increase C storage (Kirkby et al., 2013). This association is partly driven by higher net primary production (NPP) resulting from N addition (increasing soil C inputs), but also to the stoichiometry (C:N:P:S ratios) of the residual C pool. Kirkby et al. (2013), demonstrated that inorganic nutrient availability is critical to storage of stabile C pools irrespective of soil type and C input, finding that the conversion of organic inputs (wheaten straw) into fine fraction soil C pools doubled when added in concert with additional nutrients (C, N, P, S). Lal et al., 1997, Paustian et al., (1997), and Dignac et al., (2017) have undertaken comprehensive reviews of soil C sequestration as relates to agricultural systems and climate change (Dignac et al., 2017; Paustian et al., 1997; Lal, 2004b).

1.5. *Microbial solutions*

Soil hosts roughly one quarter of the earth's known biodiversity, most of which is comprised of microorganisms, which themselves are among the most diverse and ubiquitous organisms on the planet (Heijden, 2008). Soil microorganisms are vital to plant and soil health (Paul, 2015; Wardle et al., 2004), many having a central role in broader ecosystem function and biogeochemical cycling, including the fluxes of critical greenhouse gasses carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) (Whalen et al., 2022; Singh et al., 2010). Given their significance to soil and plant health, and their role in biogeochemical cycles (particularly the sequestration of C and fixation of N_2), the management and manipulation of soil and plant microbes can contribute to the ecological intensification of production systems, and to the drawdown of atmospheric CO_2 through supporting soil C sequestration and stabilisation (Buragohain et al., 2019; Ahmed et al., 2019; Vishwakarma et al., 2016; King, 2011) and through enhancing plant productivity and resilience.

Microbial products have been used by humans for hundreds of years (Hayes and Nair, 1975), in which time significant progress has been made in the context of soil inoculation, mostly through the lens of improving plant growth/resilience and correlating productivity (Li et al., 2022; Canfora et al., 2021; Santos et al., 2019; Kaminsky et al., 2019). Diazotrophic bacteria, such as rhizobia, are one commonly employed microorganism capable of colonizing roots of several members of the legume family (Fabaceae), stimulating a process of biological nitrification which can often supply the plants full N demand (Santos et al., 2019), theoretically reducing synthetic nutrient inputs. Other plant beneficial microbial groups, such as filamentous fungi (e.g. *Trichoderma* sp.) and arbuscular mycorrhizal fungi (AMF) (e.g. *Rhizophagus* sp.) have likewise been utilised in microbial products, partly fuelling the ongoing growth of the agricultural inoculant industry which is expected to reach US$12.5 billion in revenue by 2027, equating to a compounded annual growth rate of 14.6% from 2022 to 2027 (MarketsandMarkets, 2022). Mukasa Mugerwa and McGee (2017) explored the potential of endophytic fungi to increase soil C in an experimental pot study, finding that over a 14-week period 20 melanised endophytic fungi increased carbon in a carbon-rich Alfisol, with increases of up to 17% observed

(Mukasa Mugerwa and McGee, 2017). Given the potential utilisation of soil microbes in the context of soil C, greater exploration of the role of microbes in soil C sequestration and retention is required to assist in the development of microbial products with the express objective of building and retaining soil C.

2. Pathways to soil carbon sequestration: direct and in-direct mechanisms

There are two primary C sequestration pathways in soils; above-ground plant inputs, plant litter and associated leachates (e.g. dissolved organic carbon), and below-ground plant-inputs (or rhizodeposition), root litter and exudates (Fig. 1). Soil microorganisms play a central role in each, contributing to both the cycling and retention of soil C through a variety of direct and/or in-direct mechanisms (Fig. 2 & Fig. 3).

2.1. *Direct mechanisms*

Here, we define direct mechanisms as microbial mediated mechanisms that make a direct contribution of C to the soil, and/or to the stabilisation of soil C. Among these, the synthesis and accumulation of plant derived C materials in the biomass of microorganisms (microbial biomass) and the resulting residues (necromass) is significant, accounting for between 50 and 80% of stabile SOC (Liang et al., 2019; Kindler et al., 2006) (Fig. 1). Through the process of microbial decomposition, soil microbes assimilate plant C inputs for growth (anabolism), and release C as extracellular products and CO_2 (catabolism), the balance between these metabolic reactions is termed microbial carbon use efficiency (CUE), which in part determines how much C entering the system remains there (Fig. 1) (Buckeridge et al., 2020; Kallenbach et al., 2019). Following microbial death, microbial residues (e.g. necromass) can be either recycled as substrate for new microbial growth, or stabilised into recalcitrant C pools; through either microaggregation, forming aggregated C (AggC), or through absorption to soil mineral surfaces, forming mineral-associated organic matter (MAOM) (Fig. 2).

Microorganism with higher CUE and growth rate may be advantageous to the sequestration and stabilisation of soil C, given these organisms theoretically convert more C from labile to recalcitrant pools, through more efficient biomass production (Tao et al., 2023). Indeed, the promotion and preservation of microbial biomass and necromass has been identified as a strategy to build stabile pools of soil C (Liang et al., 2019), through the promotion of practices that lead to higher fungal activity and fungal-to-bacterial ratios (F:B), such as no-till farming (Bailey et al., 2002). The identification and utilisation of specific taxa with relevant traits is far more difficult, as these traits (high microbial growth rate and CUE) are likely more closely linked to environmental variables (e.g. soil type, temperature, nutrient concentrations and stoichiometry) than to any one microbial group. Environmental factors are critical in the cycling of C within soil systems. For instance, soil texture, nutrient concentration and climate are well recognised significant determinants of a soils ability to store and stabilise C (Ogle et al., 2019; Abdalla et al., 2016; Nichols, 1984). Likewise, climate, land use, and nutrient management can be the driving force behind microbial growth and the correlating soil C decomposition and stabilisation rates (Maharjan et al., 2017; Liang et al., 2019; Buckeridge et al., 2020). Nevertheless, some groups can be highlighted regarding biomass and necromass production.

Bacteria and fungi form the dominate portion of soil microbial biomass (>90%), for this reason these groups, and the ratio between them (F:B ratio) can play a significant role in the flux of soil C. A fungal dominated soil system is suggested to imply a higher C ratio, as fungal groups are thought to apportion more C to biomass per unit of substrate used than other key decomposers (bacteria) (Soares and Rousk, 2019;

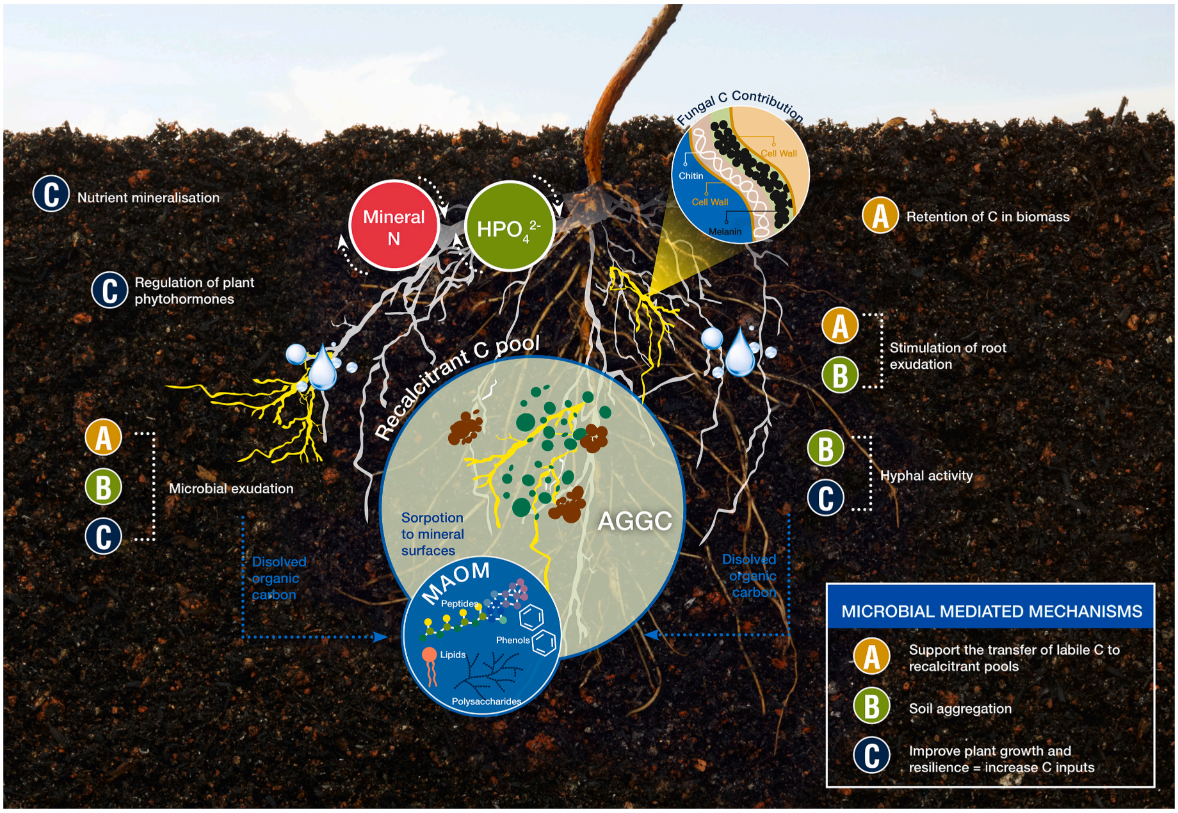
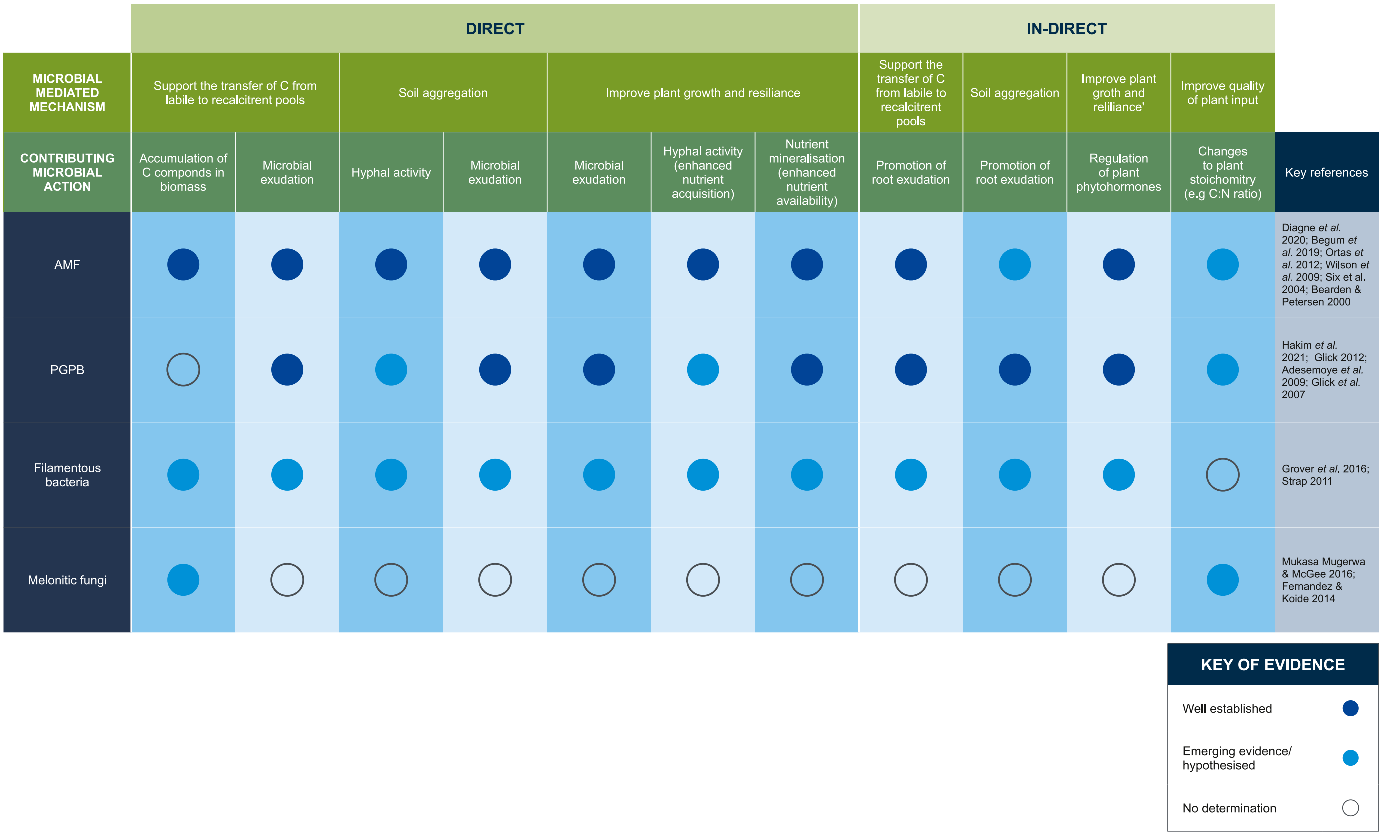


Fig. 2. Microbial contributions to soil C sequestration and retention. Displaying the key microbial mediated mechanisms that have potetial to influence soil C stocks (A, B, C bubbles), and the microbial actions associated with these mechanisms.



	DIRECT							IN-DIRECT				
MICROBIAL MEDIATED MECHANISM	Support the transfer of C from labile to recalcitrent pools		Soil aggregation		Improve plant growth and resiliance			Support the transfer of C from labile to recalcitrent pools	Soil aggregation	Improve plant groth and reliliance'	Improve quality of plant input	
CONTRIBUTING MICROBIAL ACTION	Accumulation of C componds in biomass	Microbial exudation	Hyphal activity	Microbial exudation	Microbial exudation	Hyphal activity (enhanced nutrient acquisition)	Nutrient mineralisation (enhanced nutrient availability)	Promotion of root exudation	Promotion of root exudation	Regulation of plant phytohormones	Changes to plant stoichomitry (e.g C:N ratio)	Key references
AMF	●	●	●	●	●	●	●	●	🔵	●	🔵	Diagne *et al.* 2020; Begum *et al.* 2019; Ortas *et al.* 2012; Wilson *et al.* 2009; Six et al. 2004; Bearden & Petersen 2000
PGPB	○	●	🔵	●	●	🔵	●	●	●	●	🔵	Hakim *et al.* 2021; Glick 2012; Adesemoye *et al.* 2009; Glick *et al.* 2007
Filamentous bacteria	🔵	🔵	🔵	🔵	🔵	🔵	🔵	🔵	🔵	🔵	○	Grover *et al.* 2016; Strap 2011
Melonitic fungi	🔵	○	○	○	○	○	○	○	○	○	🔵	Mukasa Mugerwa & McGee 2016; Fernandez & Koide 2014

KEY OF EVIDENCE

Well established	●
Emerging evidence/ hypothesised	🔵
No determination	○

Fig. 3. Contributions of key microbial groups to soil C storage. Dots represent the level of evidence suggesting that the microbial group contributes to the corresponding mechanism. Dark shading indicates that it is well established that the microbial group contributes to the mechanism/action, light shading indicates there is emerging evidence and/or it is hypothesised that the microbial group contributes to the mechanisms/action. We do not consider there to be enough evidence to make a determination for unshaded dots. Arbuscular mycorrhizal fungi (AMF), plant growth promoting bacteria (PGPB).

Waring et al., 2013; Six et al., 2006). Many groups of fungi produce extensive vegetive mycelium networks, consisting of interwoven thread like hypha. These structures contain C compounds, which after death can be transformed into recalcitrant C pools, through aggregation or sorption to mineral surfaces (as outlined above). Of particular significance to the agricultural industry are a group of fungi that form symbiotic relationships with agricultural production plants.

Mycorrhizal fungi account for roughly 10% of identified fungal species forming several distinct associations, including arbuscular, ectomycorrhiza, ericoid and orchid (Lewis, 2016). Mycorrhizal fungi have received much research attention largely due to their ability to support plant health and resilience, and thus productivity/yield (Smith and Read, 2010). Of the recognised mycorrhizal associations, arbuscular mycorrhizal fungi (AMF) are of most significance to regenerative agriculture and to the cycling of soil C in production systems (Hawkins et al., 2023). Arbuscular mycorrhizal fungi are obligate biotrophs forming mutually beneficial relationships with a wide range of symbiotic partners (estimated 80% of vascular plants including many production plants) (Lewis, 2016), making the exploration of traits relating to soil C sequestration within the group promising. Plants allocate C (through root exudation and detritus) to fungal partners (up to 20%) (Bago et al., 2000), in effect, transforming labile C compounds to potentially recalcitrant soil C through a variety of mechanisms. In their 2011 study, Cavagnaro & Martin found that the proportion of AMF associated crops in rotation had a positive influence on soil C (ca. 50% higher where more AMF crops were in rotation) (Cavagnaro and Martin, 2010). Although the direct fungal contribution to this positive correlation was not determined, and there are likely several unrelated factors at play (e.g. greater general biomass of mycorrhiza crops, more legumes in rotation). There is some suggestion that AMF may contribute to subsoil C cycling and stabilisation through the transfer of plant inputs (e.g. exudates) to deeper soil horizons where there is less exposure to microbial action and degradation (Sosa-Hernandez et al., 2019). These, and other findings (Rillig et al., 2001), provide grounds for further exploration of AMF and soil C cycling in production systems.

Actinomycetes (also known as filamentous bacteria or Actinobacteria) are aerobic, spore forming gram-positive bacteria, belonging to the order Actinomycetales (Strap, 2011). The group are recognised for their filamentous structures, wide distribution, and ability to survive under extreme conditions. Several taxa exhibit plant-growth promoting properties, including the production of indole acetic acid (IAA), phosphate solubilization, biocontrol of phytopathogens, siderophore production and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity (Grover et al., 2016). Beyond their plant growth promoting attributes, Actinobacteria may have some application in the retention and stabilisation of soil C, due to their contribution to soil biomass/necromass via the production of filamentous structures, an attribute not yet explored in the group. The group also contains the largest proportion of acetogenic bacterial species, capable of converted CO_2 to acetate using hydrogen (H_2) as electron donor, a process known as the Wood–Lungdahl pathway (WLP) (Jiao et al., 2021). Chemoautotrophic microbes (such as acetogenic bacteria) have been employed to convert CO_2 to other organic molecules, representing one of the oldest carbon fixation pathways. Over 100 species of acetogenic bacterial species have been classified, some of which have been isolated from soil (Drake et al., 2008). Oxalotrophic bacteria are a microbial group possessing the ability to transform organic C molecules to recalcitrate pools (Syed et al., 2020). Oxalotrophic bacteria use oxalate as their sole source of carbon and energy, in the process producing carbonates following the oxidation and degradation of oxalate (oxalate-carbonate pathway). Oxalic acid and its salts are produced by many species of plants and fungi, including several production crops (e.g. Amaranth, Taro, Spinach), providing (together with oxalotrophic bacteria) an organic to inorganic C pathway, resulting in the accumulation of stabile mineralized C in the form of calcium carbonate ($CaCO_3$). This potential, although recognised, remains little explored.

Other microbial processes contribute to soil C storage and stabilisation. Sclerotia are resting structures produced by many unrelated fungi with diverse trophic modes (Smith et al., 2015). These hardened, primarily lipid and glycogen containing masses of hyphae serve as survival structures for ascomycetes and basidiomycetes, ranging in size from the 0.1 mm diameter to 30 cm (Money, 2016). Sclerotia are extremely resistant to desiccation, capable of surviving in soil systems for many years (Williams and Western, 1965). Sclerotia forming soil taxa may hold promise for the long-term retention of soil C. Melanised fungi likewise possess promising traits relating to soil C stabilisation. Melanin is a complex biopolymer, produced by a wide range of fungi, most notably dark septate fungi (DSE) (Butler and Day, 1998). Dark septate fungi are a taxonomically diverse group of fungal endophytes characterised by the presence of melanin in their hyphae and by the production of microsclerotia (Jumpponen and Trappe, 1998). Melanin protects fungal cell walls from environmental oxidative stress, potentially influencing the accumulation and long-term retention of soil C (Mukasa Mugerwa and McGee, 2017). Research has found that melanin content is negatively correlated to the decomposition rate of ectomycorrhizal fungi, suggesting that fungal groups with higher melanin content could be utilised to slow the decomposition of fungal (and potentially plant) material (Fernandez and Koide, 2014; Lenaers et al., 2018). Melanised endophytic fungi have also been found to increase polyaromatic C associated with microaggregates, representing a potential avenue to increase the recalcitrant soil C pool (Mukasa Mugerwa and McGee, 2017). Given their diversity of host plants and habitats, and propensity to contain melanin, further exploration of melanotic endophytic and mycorrhizal fungi may yield promising candidates in the search for microbes that contribute to the long-term retention of soil C. Endophytic fungi differ from mycorrhizal fungi due to their capacity to not only colonise intra-and-inter cellular space but also plant vascular tissue and seeds. This ability provides an avenue for endophytic microbes to be transmitted vertically (from parent to offspring), eliminating the need for physical application of inoculums via the delivery of microbes within the seed (Shahzad et al., 2018).

Soil aggregation is another important direct microbial mediated mechanism of soil C sequestration (Fig. 2). Soil microaggregates are increasingly recognised as a characteristic of healthy soil, improving soil structure, gas exchange, water infiltration and water holding capacity (Six et al., 2004). Soil aggregates protect SOC from degradation, increasing residence time by facilitating the transition of C compounds form labile to recalcitrant pools. Microorganisms, specifically fungi and bacteria, play a central role in the formation of micro (20–250 μm in diameter) and macro (>250 μm in diameter) aggregates, binding soil particles via their secretions and biomass (e.g. hyphal activity) (Wilson et al., 2009). Bhattacharyya et al. (2022) investigated the interplay between soil microbial communities (SMC) and soil organic matter, highlighting several mechanisms by which SMC influence soil C storage, including the contribution of SMC to soil aggregation (Bhattacharyya et al., 2022). The study identified several key taxa involved, including fungi (*Fusarium* sp.*; Mucor* sp.*; Gibberella* sp.), AMF (*Rhizophagus* sp.), bacteria (*Rhizobium* sp.), and Actinobacteria. Lehmann et al. (2019) investigate a broad suite of fungal traits (including morphological, chemical and biological) and their relation to soil aggregation (Lehmann et al., 2019). Results revealed a positive relationship between fungi and soil aggregation, adding further support for the general assumption that filamentous fungi improve soil aggregation (Miller and Jastrow, 1990; Cavagnaro et al., 2006). Biomass/hyphal density (the density with which a mycelium grows) was identified as an important contributor to soil aggregation, whilst leucine aminopeptidase activity was found to be a negative indicator. Fungal strains belonging to Ascomycota with low leucine aminopeptidase activity and high biomass density were found to be the most efficient soil aggregators (Lehmann et al., 2019). Interestingly, hyphal production (total amount of hyphae produced) was not a significant explanatory variable, suggesting that hyphal density rather than total quantity may be the more significant trait in relation to soil aggregation. Microbial (and plant) exudation can also support the binding of soil particles and the flow of soil C to recalcitrant pools (MOAM) deeper in the soil complex.

2.2. *In-direct mechanisms*

We define in-direct mechanisms of soil C sequestration as those that contribute to soil C through enhancing plant growth/resilience and exudation, which in-turn increases biomass entering the soil, a fraction of which is then cycled into recalcitrant C pools, as outlined above. The ability of particular groups of microorganisms to enhance plant growth has been widely investigated (Malgioglio et al., 2022; Hakim et al., 2021; Malusa et al., 2012), largely due to the associated benefits to plant yield/agricultural productivity. Of these, two overarching groups can be identified; plant growth promoting bacteria (PGPB), and mycorrhizal fungi.

Along with playing a significant role in the accumulation of necromass, and the aggregation of soil C, mycorrhizal fungi also play an in-direct role in soil C cycling via enhancing plant nutrient uptake and availability (Fig. 2). Mycorrhizal fungi can explore bulk soil more efficiently than plant roots, extending plant nutrient uptake beyond the nutrient depletion zone that develops around roots, via often extensive hyphal networks (Johnson and Gehring, 2007). Fungal hyphae are also capable of exploring and extracting nutrient from soil pore spaces too small for plant roots to exploit, further improving plant nutrient acquisition (van Breemen et al., 2000). Mycorrhizal fungi are often critical for plant uptake of poorly-labile inorganic nutrients, such as phosphate ion and other (relatively) insoluble ions (Smith and Read, 2008).

Bacteria are also important players in plant/soil systems, many directly supporting plant growth and resilience. Bacteria can act as biofertilizers, assisting in plant nutrient uptake by providing plant available nutrients (Adesemoye et al., 2009, Kennedy and Islam, 2001) (Fig. 2). For instance, N-fixers (diazotrophic bacteria) that convert molecular N^2 to plant available forms (ammonia) (Riggs et al., 2001), and mineral-solubilizers that assist in plant uptake of inorganic phosphates (Abd-Alla, 1994). Bacteria can act as phytostimulators, producing phytohormone that directly promote plant growth and resilience (Glick et al., 2007; Spaepen et al., 2007) and biological control agents, that protect plants against phytopathogens (Dawar et al., 2010), in so supporting plant health. Several PGPB have been identified and commercialised, most prominent among which are members of *Bacillus, Rhizobia, Bradyrhizobium* and *Pseudomonas*. However, numerous taxa have been identified and utilised, including *Azospirillum* sp., *Streptomyces* sp., *Agrobacterium radiobacter, Azotobacter chroococcum, Burkholderia cepacia, Delfitia acidovorans, Paenobacillus macerans, Pantoea agglomerans,* and *Serratia entomophilia* (Glick, 2012).

Of the symbiotic associations listed above, all have the potential to support plant growth (through increasing plant nutrient acquisitions and availability) and resilience (through supporting plant pathogenic defence, and resilience to other environmental stressors) increasing plant biomass (above and belowground), and thus C entering soil systems. Beyond their direct influence on plant growth/resilience, we also note the potential of various soil microbes to influence direct mechanisms of soil C sequestration. Through promotion of root exudation (which contributes to soil binding) fungi and bacteria in-directly contribute to soil aggregation, and plant growth, and thus C sequestration, highlighting the complex network of interactions that contribute to belowground C cycling. Whilst stimulation of plant exudation may assist in the accumulation of soil C, it is recognised that these inputs can also stimulate soil C decomposition through priming, potentially leading to a net loss of soil C (Huang et al., 2021). Microbial and plant induced priming via exudation is increasingly recognised as a significant factor in soil C cycling and should be further explored in the context of microbial inoculation and agricultural soil systems.

2.3. Plant stoichiometry and microbial community composition

The ability of microbial symbionts to alter plant stoichiometry and thus the 'quality' of C entering the soil can influence the flux of soil C. Several microbial groups, most notably AMF, can mediate plant uptake of key nutrients such as N and P, thus altering plant and soil stoichiometry (Begum et al., 2019; Ortas, 2012). The chemical composition (specifically N:P and C:N ratios) of plant material entering soil systems influences the decomposition rate and correlating CUE of microbes acting upon this material. For example, organic material with a high C:N ratio (>30:1) will be slow to break down, as microbes require sufficient N relative to C to decompose this material and release nutrients for plants. This situation can result in N immobilisation where N is unavailable to plants until microbial biomass is turned over. Conversely higher quality organic material (C:N, 20–25:1) can be broken down more quickly with sufficient N leftover for plants.

Microbial tissue inside and/or on the surface of roots may be an important parameter determining root decomposition, due to the addition of recalcitrant compounds such as chitin and melanin found in the cell walls of associated microbe (specifically fungi) (Langley and Hungate, 2003). There is some suggestion that fungal endophytes influence plant photosynthesis. Fungal endophytes within the plant leaf may improve the CO_2:O_2 ratios of internal ground tissue, altering the CO_2 concentration gradient between the subepidermal layer and chloroplast carboxylation sites, potentially leading to greater diffusion of CO_2 to the chloroplasts, and thus greater C assimilation (Suryanarayanan et al., 2022). It is important to note that the response of particular microbial groups to both plant and soil nutrient composition may be varied, and dependent on other environmental variables, and on the life history of the organisms involved. As with all life on earth, individual soil microorganism have evolved to thrive or decline under certain environmental conditions. Accordingly, soil nutrient concentration/availability may be a strong determinant of the correlating microbial community composition, and of the functioning of individual taxa, which in turn may influence the cycling of soil C.

Whilst this review has focused on the role of specific taxa or groups of microbes, it is recognised that microbial community composition is a significant factor in soil C cycling. The impact of inoculation on the existing microbial community and how these potential changes in community composition effects soil ecological processes cannot be easily determined (or generalised) given the complexity of soil systems and the variation often found within soil microbiomes. The impacts of inoculation on indigenous microorganisms and on aboveground systems should be assessed (e.g. shifts in functional groups/diversity, impacts on plant growth/health) via inoculation of small scale sites prior to broader application. Consideration should also be given to how inoculation may affect the broader environment, specifically adjacent production systems and native vegetation.

3. Future work and recommendations

Soil amendments applied in tandem with specific microbial groups may be one way to 'supercharge' the sequestration potential of microbial products, and to improve a soils C ceiling. In the context of large-scale commercial agriculture, the recognition must be made that any attempt to increase soil C must be reconciled with the maintenance of productivity and the natural limits of a given soil to store C (storage potential). The transformation and utilisation of internal organic 'waste' streams is one way to lift a soils C storage potential, however the consequences for cycling and availability of other nutrients (e.g. N) needs to be taken into account, as this may have negative impacts on productivity. Kirkby et al. (2011) suggests that for each new tonne of stabile C stored in the soil, 80 kg nitrogen, 20 kg phosphorus and 14 kg sulphur will also be locked up (Kirkby et al., 2011). Carbon neutral/negative amendments generated through pyrolysis of agricultural organic waste such as crop residues and other materials generated during the production process (e.g. plant pruning, nut husks, grape marc) should be explored as a stabile C input (biochar) to both deliver additional nutrient to production plants and as a way of protecting soil C from decomposition, in so increase the C storage potential of soils.

Biochar possesses several characteristics favourable to C protection. Weng et al. (2022) investigated the mechanisms by which biochar lifts the SOC ceiling, putting forward direct visual evidence and three-dimensional analyses highlighting the ability of biochar to protect new soil C inputs (including microbial products). Evidence also suggests that biochar may act to improve microbial CUE through reducing enzyme activity, resulting in a negative priming affect (decrease in SOC mineralization, i.e. soil respiration) (Weng et al., 2022). We put forward the biochar + microbial (specifically AMF) system for further exploration with the objective of increasing the stabile MAOM C pool. Utilising the mycorrhizal network to facilitate the transfer of primary metabolite C sources to mineral surfaces could improve the stabilisation of low moleculare weight organic molecules via sorption and protection within the mineral complex. Mycorrhizal networks could be exploited through the identification/development and inoculation of specific AMF isolates that contribute to and/or enhance C transport and protection. Several less researched microbial groups and mechanisms mention here should also be further explored, specifically those with capacity to support the long-term stabilisation of soil C. The ability of melanotic fungi to generate stabile C material (melanin) requires quantification in order to verify the potential of this mechanisms to have a meaningful impact on soil C. Likewise, the impacts of PGPB on soil C accumulation requires greater attention, specifically the degree in which any initial C increases are retained over extended timeframes. The plant-microbial oxalate--carbonate pathway should be further explored in the context of fixing atmospheric CO_2 in the form of carbonates in agricultural soils. Utilising oxalogenic plants (e.g *Amaranthus* sp.) as cover/rest crops together with the inoculation of oxalotrophic bacteria could provide a novel way to address soil acidification, improve soil aggregation, and increase the accumulation of relatively stabile (10^4–10^6 years) inorganic C, specifically $CaCO_3$. Addressing material deficiencies in soil, such as acidification and poor structure, will not only improve productivity but is a well-recognised strategy to build soil C stocks.

4. Other considerations

Several significant challenges can be identified in the attempt to proliferate specific groups of soil microorganisms through inoculation. The success of foreign/introduced taxa to persist and function as expected will be strongly influenced by not only interactions with the native microbiome, but also by local environmental conditions. Microbial trait plasticity is common, and often determined by local environmental factors, such as nutrient availability, soil type and environment. For instance, morphologically complex filamentous fungi exhibit different structural forms depending on the growth substrate and other external edaphic factors (Papagianni, 2004). Predicting the response (trait expression) of inoculated taxa to specific environments requires an understanding of these interactions, and of the specific conditions that elicit traits of interest. In this regard, a so called 'scatter gun' approach, in which a consortium of desired microbial groups are included in inoculation products may be most effective in achieving a desired outcome.

Whilst promising laboratory and greenhouse experimental results lead to high hopes for the role of microbial inoculants in soil C dynamics and regenerative agriculture more broadly, realising this potential will require delivery of these results under real-world field conditions. The longevity of sequestered soil C also requires greater considered as C inputs, or gains, may be short lived, in some cases even resulting in a net loss of soil C via priming of the initial C stock. Global warming impact models should explore C cycling over 80 plus year time horizons in order to ensure management changes and/or implementation of technological solutions achieve desired impacts over a relevant timeframe. Delivery of viable propagules or living microbes to soil systems represents a major bottleneck, and a barrier to greater adoption of microbial inoculants. In a recent evaluation of commercial arbuscular mycorrhizal inoculants Salomon et al. (2022) found that of 28 commercial AMF inoculants tested 84% did not lead to mycorrhizal root colonization, highlighting the challenge of successful microbial delivery (Salomon et al., 2022). Assuming products do contain viable microbes, the introduction of foreign organisms to new environments presents other risks. Commercial microbial products containing filamentous fungi *Trichoderma harzianum* and *T. afroharzianum* have been developed due to the groups' general status as a plant symbiont or antagonist of fungal phytopathogens. However, recently several strains of the species have been identified as a pathogen causing ear rot disease in maize with the potential to cause significant yield losses (Pfordt et al., 2020). Such an example serves to highlight the unpredictable nature of many microorganisms and the unintentional consequences that could stem from their introduction to foreign environments.

5. Conclusion

It is clear that some soil microbes possess the ability to influence soil C sequestration and retention, and that this ability may be utilised and promoted via inoculation of soil systems. We have outlined several microbial groups that possess traits advantageous to this endeavour (e.g. Melanotic fungi, Ascomycota with high biomass density, AMF, filamentous PGPB). However, the ability to harness these traits, and their capacity to influence soil C cycling under real-world conditions is yet to be confirmed. Further research is required to assess potential candidates for inoculation development in the context of soil C, along with a more complete understanding of the underlying mechanisms by which soil microbes influence the stabilisation of soil C under field conditions. We call for the systematic testing of potential microbial candidates via plant-microbe interaction studies with specific emphasis on the ability of soil microorganisms to influence/support the accumulation of recalcitrant mineral associated C. The ability of abovementioned fungal groups to facilitate delivery of C molecules to mineral surfaces, or to deeper soil horizons, should be explored through inoculation of these groups together with targeted soil amendments.

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.

Data availability

No data was used for the research described in the article.

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