

# Mycorrhizal Fungi as Mediators of Soil Organic Matter Dynamics

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## Keywords

arbuscular mycorrhizal fungi, ectomycorrhizal fungi, fungal necromass,  
priming, saprotrophic fungi, soil carbon

## Abstract

Inhabiting the interface between plant roots and soil, mycorrhizal fungi play a unique but underappreciated role in soil organic matter (SOM) dynamics. Their hyphae provide an efficient mechanism for distributing plant carbon throughout the soil, facilitating its deposition into soil pores and onto mineral surfaces, where it can be protected from microbial attack. Mycorrhizal exudates and dead tissues contribute to the microbial necromass pool now known to play a dominant role in SOM formation and stabilization. While mycorrhizal fungi lack the genetic capacity to act as saprotrophs, they use several strategies to access nutrients locked in SOM and thereby promote its decay, including direct enzymatic breakdown, oxidation via Fenton chemistry, and stimulation of heterotrophic microorganisms through carbon provision to the rhizosphere. An additional mechanism, competition with free-living saprotrophs, potentially suppresses SOM decomposition, leading to its accumulation. How these various nutrient acquisition strategies differentially influence SOM formation, stabilization, and loss is an area of critical research need.

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#### Soil organic matter

**(SOM):** complex mixture of plant and microbially derived residues at various stages of decay

#### Stocks, pools, and

**fluxes:** the quantity (stock) of something (e.g., C) in a reservoir (pool) and the transfer of something (e.g., C) in or out (flux) of that reservoir

#### Mycorrhiza:

a mutualistic relationship between a plant and a fungus, where the fungus colonizes host roots, either intra- or extracellularly

#### Rhizosphere:

soil zone influenced by roots, extraradical mycorrhizal hyphae, and associated free-living microorganisms and fauna

#### Extraradical hyphae:

collection of filamentous fungal hyphae that extend outward from mycorrhizal roots into the soil; also referred to as extramatrical mycelium

**Necromass:** organic material composed of or derived from dead microorganisms

## 1. MYCORRHIZAL FUNGI AND SOIL CARBON: AN OVERVIEW

Soil organic matter (SOM) is the primary source of plant-available nutrients in terrestrial ecosystems, and maintenance of SOM levels is critical for ecosystem sustainability. In addition to being an important nutrient reservoir, SOM represents a substantial store of carbon (C), containing twice as much C as the atmosphere and terrestrial vegetation combined. Transfers of C between soils and the atmosphere are one of the largest fluxes in the global terrestrial C budget, with soils releasing 60–75 Pg C to the atmosphere annually through microbial decomposition of organic materials (Schlesinger & Andrews 2000). This makes the study of SOM important not only to manage soils for improved fertility and ecosystem productivity but also to understand its role in climate–soil C feedbacks and its potential to mitigate greenhouse gas emissions (Paustian et al. 2016).

SOM pools and fluxes are driven by dynamic formation, stabilization, and destabilization processes, our understanding of which has fundamentally changed over the past few decades (Schmidt et al. 2011). Historically, stable SOM was thought to form via selective preservation of recalcitrant plant biopolymers coupled with abiotic synthesis of complex, highly aromatic humic substances resistant to decay. This model of SOM formation and stabilization was upended with the observation that plant components predicted to persist in soils (e.g., lignin) turn over rapidly, while more inherently labile compounds (e.g., sugars) can persist for decades (Grandy & Neff 2008, Schmidt et al. 2011). Additionally, compounds making the largest contributions to stable SOM pools are microbially derived, produced during the decomposition and assimilation of plant exudates, litter, and roots (Cotrufo et al. 2013, Simpson et al. 2007). SOM is now understood to be a continuum of organic biopolymers continuously processed by microorganisms and stabilized through interactions with soil minerals and aggregates (Keiluweit et al. 2015, Lehmann & Kleber 2015).

While saprotrophic (i.e., decomposer) microbes have received considerable attention in the emerging conceptual understanding of SOM dynamics, mycorrhizal fungi may play a unique but underappreciated role (**Figure 1**). Inhabiting the interface between plant roots and soil, they control a key entry point for plant C into the rhizosphere. The growth of mycorrhizal extraradical hyphae provides an efficient mechanism for distributing plant-derived C throughout the soil matrix, promoting its deposition onto mineral surfaces and within soil pores, where it can be chemically or physically protected from microbial decomposition. Given that mycorrhizal fungi account for a large proportion of the total soil microbial biomass in some systems (e.g., boreal and temperate forests), the death and turnover of mycorrhizal tissues may also contribute substantially to the pool of dead microbial biomass (necromass) thought to be a dominant factor in SOM formation and stabilization (Cotrufo et al. 2013, Schmidt et al. 2011). New genomic and biogeochemical insights obtained during the past decade suggest that mycorrhizal fungi also likely contribute substantially to SOM destabilization through their nutrient mining activities. In other words, while most mycorrhizal fungi appear to lack the genetic capacity to act as saprotrophs, they use several strategies in their search for nutrients that, directly or indirectly, facilitate SOM decay.

In this review, I discuss the unique position that mycorrhizal fungi hold with respect to the formation, stabilization, and destabilization of SOM. I first discuss how plant C allocation to mycorrhizal fungi in the rhizosphere contributes to SOM formation and stabilization through the production of mycorrhizal biomass, exudates, and necromass. I then explore the mechanisms by which mycorrhizal fungi alter SOM destabilization dynamics. I focus primarily on two mycorrhizal groups, the arbuscular mycorrhizal fungi (AMF) and the ectomycorrhizal fungi (EMF), which have received the most attention with regard to soil C cycling.



### Ectomycorrhizal

**fungi (EMF):** formed by a diverse group of fungi in symbiosis with primarily woody plants; dominant mycorrhiza in boreal and temperate forests, also common in some tropical forests

more than half (50–70%) of the soil C that accumulated in the organic horizon of a boreal forest soil originated from root-derived rather than aboveground plant litter inputs (Clemmensen et al. 2013). Furthermore, much of the accumulated C originated mostly from root-associated fungal hyphae. Although mycorrhizal fungi are critical for plant nutrient acquisition and can receive a large fraction of host net primary production (NPP), estimates of C allocation to mycorrhizal fungi are often not included in ecosystem C budgets (Ouimet et al. 2019), nor is this process well described in current models of ecosystem and global C dynamics, limiting our ability to estimate the relative contribution of mycorrhizal fungi to soil C storage and to predict ecosystem responses to environmental change. Below, I summarize what is known about the proportion of NPP allocated to mycorrhizal fungi, the factors that influence plant C allocation patterns, the fate of photosynthate C allocated to mycorrhizal fungi, and the potential implications for SOM formation and stabilization.

## 2.1. Carbon Allocation to Mycorrhizal Fungi Quantified

Mycorrhizal colonization alters C allocation patterns within the host plant and changes the quantity and quality of C entering SOM pools. However, belowground C allocation to mycorrhizal fungi is challenging to measure because it is difficult to visualize diffuse mycelia in soil and to differentiate mycorrhizal hyphae from those of saprotrophic fungi. As a result, plant C allocation to mycorrhizae is one of the most uncertain parameters of ecosystem-scale C budgets and simulation models of C cycling. Available literature estimates are also sometimes difficult to compare because some refer to fungal biomass production only, whereas others include respiratory costs, a distinction that is not always clearly reported. In culture or pot studies, where mycorrhizal seedlings are grown in the lab or greenhouse, plant C allocation to mycorrhizal fungi ranges from 1% to 20% of NPP for EMF (Hobbie 2006) and from 1% to 30% for AMF (see Drigo et al. 2010, Kaiser et al. 2015, Konvalinková et al. 2017, and references therein). Results from field studies provide mycorrhizal allocation estimates of 8–17% of NPP in arctic tussock tundra (Hobbie & Hobbie 2006), 27–34% in a temperate mixed coniferous–deciduous forest (Allen & Kitajima 2014), and 4–35% across conifer- and deciduous broadleaf–dominated temperate forest stands (Ouimet et al. 2019). Plant C allocation to mycorrhizal fungi is presumably coupled to plant C assimilation as influenced by climate, ecosystem type (Gill & Finzi 2016), successional stage (Wallander et al. 2010), season (e.g., Lekberg et al. 2013), nutrient availability (Brzostek et al. 2015, Lekberg et al. 2013, Vicca et al. 2012), and global change drivers (e.g., Alberton et al. 2005, Drigo et al. 2010, Lilleskov et al. 2019). Although the relative lack of data, particularly under field conditions across a wide range of ecosystems, makes plant C transfer to mycorrhizal fungi difficult to generalize, the above estimates make clear that it is a significant and important conduit of C into the soil.

## 2.2. Fate of Plant Carbon Allocated to Mycorrhizal Fungi and Implications for Soil Organic Matter Storage

Plant photosynthate allocated to mycorrhizal fungi can be partitioned into three primary pools: living fungal biomass and its associated metabolic processes (e.g., respiration), fungal exudates, and dead fungal tissues (necromass). Each of these components likely has different consequences for SOM formation and stabilization, the importance of which is only beginning to be assessed and quantified.

**2.2.1. Living mycorrhizal biomass.** Mycorrhizal extraradical hyphae likely play a critical though understudied role in the formation and stabilization of SOM. Their size, filamentous growth habit, and foraging lifestyle facilitate transport of C and nutrients throughout the mycelial

network. As they forage for nutrient-rich organic matter patches, they also grow and deposit C into nutrient-deficient zones. Living hyphae produce and secrete various extracellular compounds (see Section 2.2.2) that, given their proximity to clay particles, may stabilize C and nutrients onto mineral surfaces (Jilling et al. 2018, Kleber et al. 2015). The formation of mineral–organic associations has been identified as a main control on soil C storage because of the slow turnover of mineral-associated organic matter (Kleber et al. 2015), though the relative contribution of mycorrhizal fungi to this process is largely unknown.

Most research related to mycorrhizal fungi and C storage has focused on aggregate formation. Fungal hyphae adhere to and physically entangle and enmesh soil particles, facilitating the formation of stable aggregates within which SOM is protected from decomposition (Six et al. 1998). Both AMF and EMF enhance soil aggregate formation and stabilization, and a direct link has been established between the amount of water-stable aggregates and the presence of mycorrhizal mycelium, with the extent of aggregation depending on the species involved (Lehmann et al. 2017). Mycorrhizal taxa vary widely in their production of extraradical hyphae (Weigt et al. 2012), and the extent of hyphal proliferation depends on the host plant, soil nutrient availability, pH, and moisture status (Lehmann et al. 2017).

In order to estimate the contribution of mycorrhizal fungal hyphae to soil C dynamics, it is important to quantify the amount of standing biomass, production, and turnover rates, a non-trivial task given the challenges of distinguishing mycorrhizal from saprotrophic fungal hyphae in soil. Mycorrhizal hyphal extension can be up to 8 mm or more per day under lab conditions (see Cairney 2012 and references therein). Field measurements are less common, but estimates of 0.7 mm/day have been documented (Cairney 2012). Fungal hyphal surface areas were estimated to be 16 to 90 times greater than the surface area of fine roots (Hobbie & Hobbie 2008). Annual production of EMF has been estimated to range from 2 to 200 g C/(m<sup>2</sup>·year) (Ekblad et al. 2013, Hagenbo et al. 2017, Ouimette et al. 2019, Wallander et al. 2001), representing up to 30% of NPP (Ouimette et al. 2019). Few comparable estimates are available for AMF or ericoid fungal hyphae. EMF production numbers suggest substantial C investment in extraradical hyphae, but in order to fully assess the role of mycorrhizal fungi in SOM dynamics, accurate estimates of standing biomass are needed, since standing biomass represents the balance between production and turnover. Mycorrhizal hyphal biomass can represent up to a third or more of total microbial biomass in some systems (Högberg & Högberg 2002) and as much as half of the standing mycelial biomass (Bååth et al. 2004), depending on mycorrhizal type, ecosystem, and time of year. However, few actual biomass estimates exist, and those that are available range from 5 to 14 g/m<sup>2</sup> for EMF in the organic horizon of a pine (Högberg & Högberg 2002) or boreal (Hagenbo et al. 2017) forest and from 480 to 580 g/m<sup>2</sup> in the upper 70 cm of the soil profile in EMF-dominated forests (Wallander et al. 2004). Estimates of hyphal turnover are also limited, though it is likely a key mechanism for root-derived C transfer to SOM pools. Available data suggest that the life span of extraradical hyphae can be short, with estimates on the order of days for AMF and up to a few months for EMF, though EMF rhizomorphs may persist for several years (reviewed by Cairney 2012, Hagenbo et al. 2017). Likewise, EMF-colonized root tips turn over on the order of a few months to several years (Cairney 2012). Recent research in EMF-dominated coniferous forests in China suggests that extraradical hyphae account for up to two-thirds of new root C inputs to soil, with estimates of ~79–153 g/m<sup>2</sup> of mycelia-derived C stored in SOM pools annually (Zhang et al. 2019). In summary, C flux through mycorrhizal extraradical hyphae is likely large and important for SOM formation.

**2.2.2. Role of mycorrhizal fungi in exudate production.** The release of low-molecular-weight compounds into the rhizosphere by root or mycorrhizal fungal exudation is hypothesized

to be a dominant route by which photosynthate C enters the soil (Kuzyakov 2002). Plant C allocation to exudation has been estimated at ~2–17% of NPP (Nguyen 2003, Yin et al. 2014), with exudation rates varying with plant species, plant age, soil type, and nutrient availability (Dijkstra et al. 2013). These labile, energy-rich organic inputs include glucose and other sugars, amino acids, organic acids, fatty acids, phenolic compounds, sterols, vitamins, and enzymes (Dakora & Phillips 2002, Pausch & Kuzyakov 2017). Their production promotes plant nutrient acquisition by stimulating rhizosphere microorganisms and their decomposition activities (see Section 3.3). In terms of SOM formation and stabilization, exudates may be secreted into places in the soil that are inaccessible to microbes or sorbed onto mineral surfaces (Keiluweit et al. 2015). As discussed above, mycorrhizal hyphae are instrumental in aggregate formation, and if they exude extracellular products while also physically enmeshing soil particles, then those exudates are likely deposited into aggregates where they are subsequently physically protected from microbial degradation. Deposition of extracellular fungal products onto mineral surfaces also appears to be a common process (Kleber et al. 2015), providing chemical protection of exuded compounds via the formation of mineral–organic complexes.

Historically, exudates were presumed to be produced primarily by roots themselves, with roots passively leaking C from immature root zones close to the tip. However, recent research demonstrates not only that mycorrhizal fungal hyphae release exudates (Toljander et al. 2007) but also that a significant proportion of plant photosynthate is delivered through mycorrhizal hyphae rather than directly released by roots. Both AMF and EMF produce exudates. For example, a large fraction of recently fixed photosynthate was traced through AMF hyphae into soil following in situ  $^{13}\text{C}$  labeling of wheat plants (Kaiser et al. 2015). AMF colonize host roots upstream of the root hair zone such that a significant portion of recent photosynthate appears to be diverted by the hyphae before reaching the root tip, where passive root exudation could occur. In several recent studies, AMF exudate production triggered the growth and activity of phosphate-solubilizing bacteria in the rhizosphere, thereby enhancing organic phosphorus (P) mineralization and increasing P availability (e.g., Zhang et al. 2016). The ectomycorrhizal fungus *Paxillus involutus* secretes substantial amounts (>10% of new biomass C) of aromatic metabolites that subsequently enhance the adsorption of organic matter onto mineral surfaces (Wang et al. 2017). Thus, mycorrhizal fungi act as a major conduit for direct delivery of plant photosynthate to the rhizosphere. However, of the pathways through which plant photosynthate C enters the SOM pool via mycorrhizal fungi, exudation is perhaps the least well understood and quantified, representing a critical research need. The degree to which plant C allocation to exudation is mediated by mycorrhizal fungi has significant consequences for predicting SOM dynamics, particularly in a global change context (Zhang et al. 2019). Specifically, if mycorrhizal fungi are the dominant pathway by which exudation occurs, then data are needed on the types and amounts of mycorrhizal exudates produced, the exudation capacities of different mycorrhizal taxa and types (e.g., AMF versus EMF), and the environmental factors that influence exudate production (e.g., host/ecosystem type, climate, nutrient availability, edaphic properties).

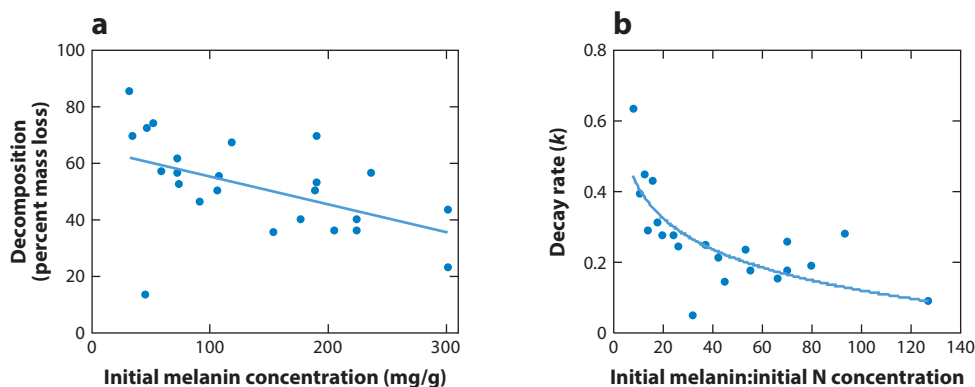
**2.2.3. Mycorrhizal necromass.** The pool of living soil microbial biomass is small relative to the total SOM pool, typically representing 1–3% of total soil C. However, due to rapid turnover, dead microbial biomass (i.e., necromass) can make a disproportionately large contribution to total SOM relative to the amount of standing microbial biomass (Grandy & Neff 2008), and turnover of microbial residues is now considered a dominant factor in SOM formation and stabilization (Cotrufo et al. 2013, Kögel-Knabner 2002, Liang et al. 2011, Schmidt et al. 2011). Microbial necromass can represent more than half of the soluble SOM fraction and account for more than 80% of soil nitrogen (N) (Simpson et al. 2007). Since mycorrhizal biomass is generated directly



from plant C and can represent a large fraction of the total standing soil microbial biomass, it may be a particularly efficient route by which primary production becomes SOM via the turnover and stabilization of mycorrhizal necromass. Indeed, more than half of newly formed SOM has been attributed to extraradical hyphae in EMF-dominated systems (Clemmensen et al. 2013, Godbold et al. 2006), and more than half of EMF biomass added to a forest soil was converted to the nonliving SOM (i.e., necromass) fraction over a few months (Schweigert et al. 2015).

Mycorrhizal necromass can influence SOM storage either by becoming stabilized within the soil matrix itself or by serving as a C and nutrient source for heterotrophic microorganisms whose own tissues subsequently become part of the necromass SOM pool. There is evidence for both mechanisms. Like those of plants, the cell walls of fungi are composed primarily of polysaccharides, with chitin and  $\beta$ -glucans being the dominant materials (Kögel-Knabner 2002). Chitin is labile relative to other fungal necromass constituents (Fernandez & Koide 2012); chitin-enriched fungal cell wall material is readily utilized as a source of both C and N by the soil microbial community (Zeglin & Myrold 2013). Microbial degradation of labile C compounds results in the production of chemically diverse SOM (Kallenbach et al. 2016) that may be physically and/or chemically stabilized through interactions with mineral surfaces and soil aggregates (Kleber et al. 2015).

In addition to chitin, fungal tissues contain smaller quantities of lipids, melanins, proteins, and carbohydrates and various types of phenolic, indolic, and quinone monomers (Kögel-Knabner 2002). Melanin has received particular attention because, like lignin, it is a large, complex, nonhydrolyzable structure designed to protect fungal cell walls against microbial attack (Kögel-Knabner 2002), and its decomposition also requires costly oxidative enzymes. Thus, impaired decomposition of mycorrhizally derived C is hypothesized to be a key driver of necromass accumulation (Clemmensen et al. 2013). Mycorrhizal necromass decomposition is controlled by its biochemical composition, which varies across species (Fernandez & Kennedy 2018, Fernandez et al. 2016), with decay rates negatively correlated with initial melanin concentrations (**Figure 2**) (Fernandez & Koide 2014, Fernandez et al. 2019, Koide & Malcolm 2009). When melanin synthesis was inhibited, EMF tissues decomposed significantly faster (Fernandez & Kennedy 2018), and melanized hyphae were observed to have a higher sorption to soil minerals compared with hyaline (i.e., non-melanized) hyphae (Fomina & Gadd 2003). Additionally, the persistence of stable EMF necromass was greater than that of either plant litter or bacterial biomass (Schweigert et al. 2015). Finally,



**Figure 2**

Decomposition of fungal necromass (percentage of mass loss) as correlated with its (a) initial melanin concentration and (b) ratio of initial melanin to initial nitrogen (N) concentration. Figure adapted from Fernandez & Koide (2014) with permission.

#### Fenton chemistry:

nonenzymatic mechanism by which lignocellulosic materials are depolymerized via the production of destructive hydroxyl radicals

#### Lignocellulose:

a complex aromatic biopolymer composed of cellulose, hemicellulose, and lignin; the main constituent of most plants

estimated soil melanin content was positively correlated with total soil C and soil peroxidase activity in pine forests across North America (Siletti et al. 2017). All of these results indicate that mycorrhizal necromass plays a significant, yet largely unquantified, role in SOM formation and stabilization.

### 3. MYCORRHIZALLY INDUCED LOSSES OF SOIL ORGANIC MATTER

While mycorrhizal fungi likely play a substantial role in influencing the C input side of the SOM storage equation, their presence and activities can also lead to its destabilization, facilitating SOM loss. There is consensus that AMF and EMF are unlikely to act as saprotrophs by metabolizing SOM to acquire C or energy (Lindahl & Tunlid 2015, Treseder et al. 2006, Zak et al. 2019). Thus, it is presumed that the primary driver of mycorrhizally induced SOM destabilization and loss is the mining of organic matter for nutrients, particularly N and P (i.e., the nutrient-mining hypothesis). A large fraction of soil N is immobilized in polyphenolic complexes—N- and P-containing compounds (i.e., proteins, inositol phosphates, phospholipids, nucleic acids) associated with polyphenols and other degradation products of plant and microbial biopolymers—that are resistant to enzymatic degradation. There is also a potentially large organic N pool stabilized on mineral surfaces (Jilling et al. 2018). For this reason, mycorrhizal fungi would benefit from having some ability to facilitate SOM decay (see the sidebar titled Decay and Decomposition Defined) to release nutrients directly or indirectly, and indeed, this capacity has been speculated for more than a century (Read 1991).

There are at least three mechanisms by which mycorrhizal fungi are thought to access nutrients locked in SOM and thereby promote its decay (**Figure 3**): direct enzymatic breakdown (Section 3.1), oxidation via Fenton chemistry (Section 3.2), and stimulation of microbial activity and enzyme production by providing C subsidies to the rhizosphere (Section 3.3). A fourth mechanism, competition with free-living saprotrophs (Section 3.4), is hypothesized to suppress SOM decomposition, leading to its accumulation. There is differential support for each of these mechanisms, and the degree to which they operate under field conditions is far from clear. Below, I describe each of these mechanisms in turn and discuss what is currently known about their role in soil C loss (or accumulation).

#### 3.1. Direct Enzymatic Breakdown

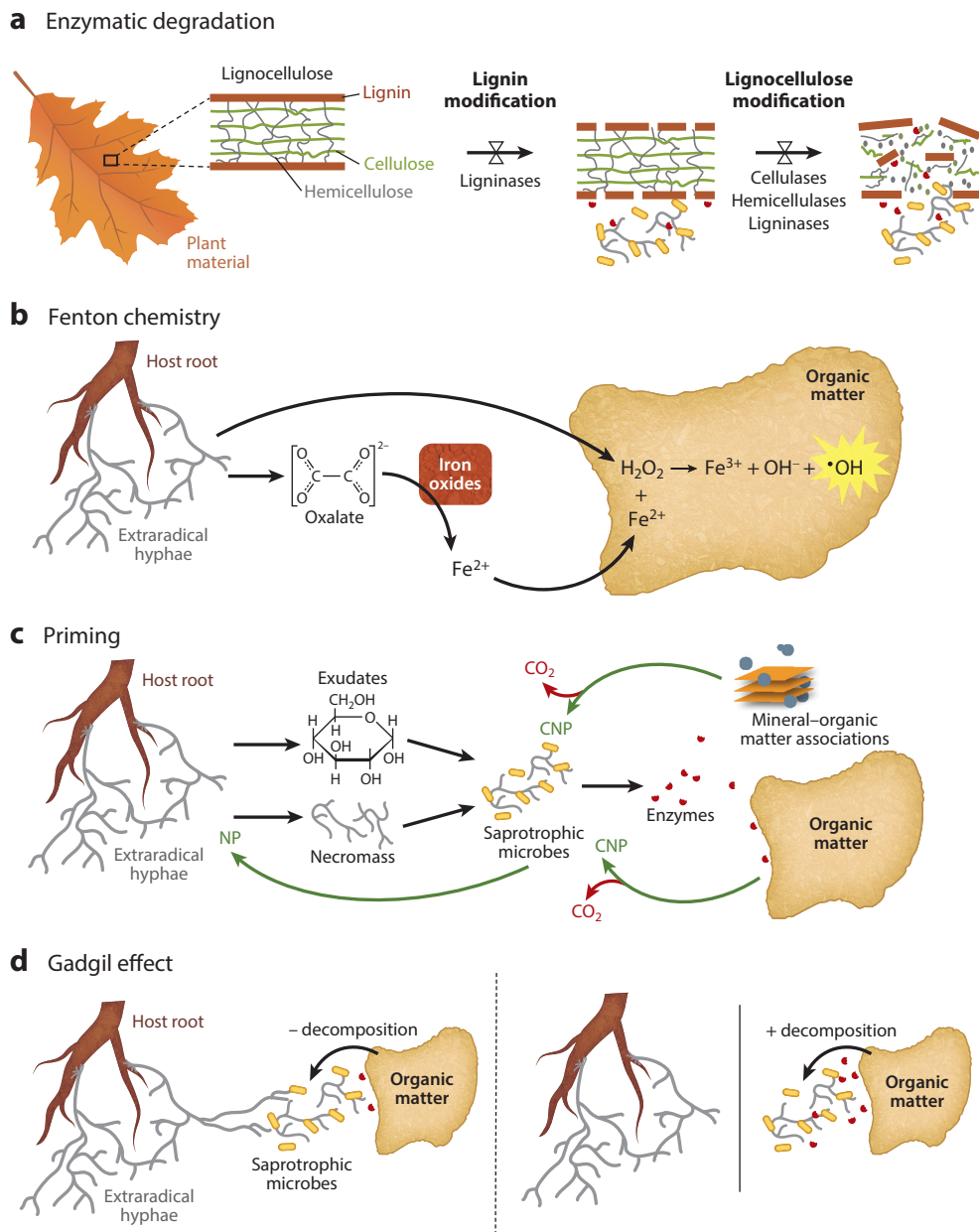
Cellulose and lignin are two of the most abundant compounds in plant material and, together with hemicellulose, form the complex structure referred to as lignocellulose (Dix & Webster 1995).

### DECAY AND DECOMPOSITION DEFINED

Note that the terms decay and decomposition, used throughout this review, are as defined by Zak et al. (2019). SOM decay refers to the modification of chemical bonds present in organic matter which may transform organic matter into small molecules, alter molecular functional groups, or change the physical structure of SOM. Decomposition describes the process by which organic materials of plant or microbial origin are metabolized by saprotrophs to obtain metabolic energy, C, and nutrients via extracellular hydrolytic and oxidative processes.

Mycorrhizal fungi do not obtain C or energy from organic matter (i.e., they are not saprotrophs); however, they may be involved in SOM decay via hydrolytic and oxidative activities, or they may facilitate SOM decomposition by stimulating the activities of free-living saprotrophic organisms. The term decomposer often connotes saprotrophy and is misleading when applied to mycorrhizally mediated SOM decay. Its use in this context is discouraged for the sake of clarity.





**Figure 3**

Mechanisms of organic matter decay. (a) Breakdown of lignocellulose via extracellular enzymes produced by microorganisms. (b) Mycorrhizally mediated soil organic matter oxidation via Fenton chemistry. (c) Mycorrhizal stimulation of microbial decomposition through carbon (C) subsidies to the rhizosphere (i.e., priming). (d) Depiction of microbially mediated decomposition before (*left*) and after (*right*) mycorrhizal fungi are removed (i.e., the Gadgil effect). Abbreviations: CNP, carbon, nitrogen, and phosphorus; NP, nitrogen and phosphorus.

#### Brown-rot fungi:

saprotrophic fungi capable of modifying lignin using primarily nonenzymatic modes of attack (e.g., hydroxyl radicals); efficiently decompose hemicellulose and cellulose once lignin depolymerization begins

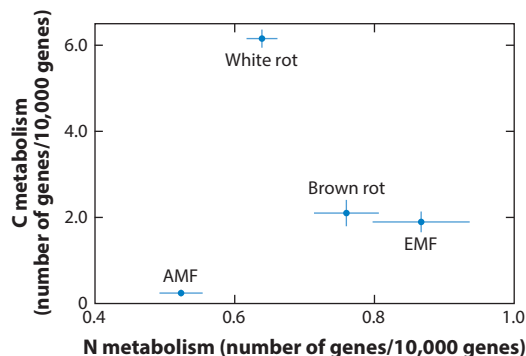
#### White-rot fungi:

the most efficient decomposers of lignin, completely converting it to CO<sub>2</sub> by using direct enzymatic mechanisms (e.g., class II peroxidases); some species selectively decompose lignin, while others simultaneously decompose lignin, cellulose, and hemicellulose

Microbial necromass, now thought to constitute a large fraction of SOM (see Section 2.2.3), contains compounds that are structurally similar to cellulose and lignin (i.e., chitin and melanin, respectively). The complete decay of plant and microbial residues involves a suite of extracellular enzymes. Saprotrophic fungi are generally considered the primary producers of these enzymes (Schneider et al. 2012), and the presence of enzyme-coding genes determines whether a particular fungal species has the genetic machinery to enzymatically break down plant lignocellulose or microbial necromass. In the case of plant materials, cellulose and hemicellulose are degraded by the synergistic activities of various cellulases (**Figure 3a**). Lignin decay involves two main groups of lignolytic enzymes: peroxidases and phenol oxidases (Dashtban et al. 2010). Peroxidases initiate the depolymerization of lignin, while phenol oxidases catalyze the oxidation of phenolic monomers once the larger lignin structure has been broken apart. Individual fungal taxa vary considerably in their decay capacity. Some saprotrophic species possess complete lignocellulolytic enzyme capabilities (e.g., produce cellulases, hemicellulases, peroxidases, and phenol oxidases) and can completely decompose lignocellulose, while others only partially degrade lignocellulose (e.g., produce only cellulases, hemicellulases, and/or phenol oxidases).

Mycorrhizal fungi are likewise highly variable in their capacity to produce extracellular SOM-degrading enzymes, although, as noted above, these enzymes are used for nutrient acquisition, not for securing C and energy (i.e., SOM decay, not decomposition; see the sidebar titled Decay and Decomposition Defined). New genomic insights over the past decade have provided clear evidence regarding which mycorrhizal taxa have the genetic capacity to facilitate SOM decay enzymatically. AMF are a monophyletic clade (Glomeromycotina) of early-diverging fungi and represent one of the oldest fungal lineages. The inability of AMF to grow in vitro was taken as early evidence that AMF are entirely dependent on their plant host for C. The recent genomic sequencing and analysis of several AMF species (e.g., *Rhizophagus irregularis*, *Rhizophagus clarus*, *Gigaspora rosea*, and *Gigaspora margarita*) have confirmed their status as obligate biotrophs (Kamel et al. 2017, Tang et al. 2016, Tisserant et al. 2013). Of greatest relevance to soil C cycling is the finding that AMF have a decreased repertoire of genes encoding for plant cell wall-degrading enzymes, with no genes encoding cellobiohydrolases or  $\beta$ -1,4-glucosidase. Most gene families acting on hemicellulose and pectin are also missing (Tang et al. 2016), and no genes involved in lignin degradation, such as class II peroxidases, have been found (Tisserant et al. 2013). While AMF species other than those sequenced to date might have a greater genetic capacity for SOM decay, at present only limited genomic information is available, since AMF cannot be cultured without a host plant (Kamel et al. 2017). While AMF apparently do not have the capacity for direct enzymatic decay of SOM, there is increasing evidence that they play a significant role in the indirect mobilization of nutrients from SOM by stimulating the activities of heterotrophic microorganisms (see Section 3.3).

Unlike AMF, EMF have evolved multiple times from a diverse group of saprotrophic ancestors, including brown-rot, white-rot, and other saprotrophic fungi (Hibbett et al. 2000, Martin et al. 2016). Thus, many EMF have the genetic potential to decay SOM to some degree (Zak et al. 2019). However, their ability to enzymatically modify SOM is considerably lower than that of saprotrophic fungi (Martin et al. 2016), and the degree to which individual taxa have retained or lost genes with SOM decay function is dependent on the ancestral precursor from which they evolved. All EMF species sequenced have a much-reduced complement of genes encoding plant cell wall-degrading enzymes (cellulases, hemicellulases, pectinases) and lignin-oxidizing class II peroxidases compared with saprotrophic fungi (Martin et al. 2008, Strullu-Derrien et al. 2018, Treseder & Lennon 2015). However, because they evolved from functionally diverse saprotrophic ancestors, they have retained distinct suites of lignocellulolytic genes, indicating a diverse ability to decay SOM enzymatically. Moreover, they are similar to saprotrophs in the frequency of N metabolism genes (**Figure 4**), including those of amino acid permeases involved in the transport of



**Figure 4**

Frequency of carbon (C) versus nitrogen (N) metabolism genes for arbuscular mycorrhizal fungi (AMF;  $n = 9$  genomes) and ectomycorrhizal fungi (EMF;  $n = 63$  genomes) in comparison to saprotrophic white-rot (97 genomes) and brown-rot (29 genomes) fungi. Error bars represent  $\pm 1$  standard error. Data and figure adapted with permission from A. Romero-Olivares.

amino acids across the cell membrane (Treseder & Lennon 2015). This finding supports previous observational research that EMF can utilize organic N (Hobbie et al. 2013, Lindahl et al. 2007, Nasholm et al. 2013).

Those EMF taxa most closely related to brown-rot fungi have lost all copies of two gene families critical for cellulose breakdown (i.e., *GH6*, *GH7*) and lack class II peroxidase genes necessary for efficient lignin degradation. These species have lost the capacity to depolymerize SOM and grow saprotrophically on complex cellulosic substrates (Wolfe et al. 2012). However, there is evidence that they can oxidize organic matter via a nonenzymatic pathway (see Section 3.2). Although many EMF have lost much of their capacity for efficient SOM decay in comparison with saprotrophs, genes mediating SOM decay have been observed in some lineages (Bödeker et al. 2009, Kohler et al. 2015). In particular, those species more closely related to white-rot fungi have multiple class II peroxidase genes (Kohler et al. 2015) and thus have the genetic potential to modify lignocellulose. Several widespread and abundant EMF genera (e.g., *Cortinarius*, *Russula*, *Lactarius*) possess peroxidase genes, potentially allowing them to access N sequestered in complex polyphenolic substrates (Bödeker et al. 2009, Lindahl & Tunlid 2015). It is also well documented that EMF with enzymatic genetic capacity can produce hydrolytic and oxidative enzymes and use those enzymes to decay SOM and mobilize and assimilate organic N in culture (Bending & Read 1996, Nicolás et al. 2018, Shah et al. 2016, Talbot et al. 2015). What is less clear is whether these fungi elicit significant SOM modification under field conditions while in symbiosis, providing significant organic N resources to their host.

Pellitier & Zak (2018) presented the minimum set of conditions necessary for EMF to enzymatically access a significant amount of organic N from SOM while in symbiosis: (a) Genes for lignocellulose decay must have been retained in the genome, (b) those genes must be expressed in root tips and extraradical hyphae, (c) transcribed genes must operate to liberate N from SOM, and (d) organic N assimilation must be sufficient to significantly influence the nutrient budget of the fungus and/or host. There is evidence that at least some EMF meet most of these conditions. For example, the genomes of *Cortinarius* species (e.g., *C. glaucopus*) encode a comparable number of peroxidases as many white-rot fungi, and transcription of *Cortinarius* peroxidase genes under field conditions has been observed to correspond to high peroxidase enzyme activity (Bödeker et al. 2014). Additionally, oxidative enzyme activity in this system was significantly reduced when soil was amended with inorganic N. Thus, it appears that *Cortinarius* may play an important role in

**Priming:** stimulation of microbial decomposition of SOM due to inputs of labile C

SOM decay and organic N mobilization while in symbiosis. However, for other taxa, there appears to be a strong energetic trade-off between being a high-quality host partner (e.g., a strong root colonizer) and producing costly extracellular enzymes (Moeller & Peay 2016).

In summary, the genetic capacity for direct enzymatic SOM decay is not uniform, and there is a continuum of capacities across mycorrhizal taxa. Moreover, the extent to which this variable genetic capacity is realized under field conditions is still unclear. Host and environmental factors likely interact with taxon-specific genetic capacity to influence the degree to which direct (enzymatically catalyzed) lignocellulose and/or microbial necromass decay is significantly facilitated by mycorrhizal fungi.

### 3.2. Soil Organic Matter Oxidation via Fenton Chemistry

It has been hypothesized that EMF that evolved from brown-rot ancestors have adapted the brown-rot degradation system involving Fenton chemistry to degrade organic matter–protein complexes and mobilize N (Beeck et al. 2018). In brown-rot fungi, lignocellulose depolymerization is initiated extracellularly by destructive hydroxyl radicals, produced when hydrogen peroxide reacts with ferrous iron ( $\text{Fe}^{2+}$ ) (Arantes & Goodell 2014). After this initial hydroxyl radical attack, hydrolytic enzymes further degrade cellulose (**Figure 3b**). Recent research has documented that the EMF taxon *P. involutus* is able to use this mechanism to liberate and assimilate organic N from proteins (Beeck et al. 2018; Nicolás et al. 2018; Rineau et al. 2012, 2013; Wang et al. 2017). Organic matter decay by *P. involutus* is a two-step process of oxidation and hydrolysis controlled by C and N availability, with at least four conditions required to elicit organic matter oxidation and organic N assimilation—inorganic N limitation and the presence of a labile C source (e.g., glucose), a protein source, and iron in its reduced form ( $\text{Fe}^{2+}$ ) (Beeck et al. 2018, Nicolás et al. 2018). Thus, it appears that the Fenton oxidation mechanism as employed by this fungus works in concert with proteolysis, enhancing N liberation from proteins. Unlike saprotrophic fungi, *P. involutus* does not exhibit expression of genes encoding extracellular enzymes needed to metabolize released C (Rineau et al. 2013), supporting the hypothesis that this mechanism is used to mobilize organic N rather than C. Thus, *P. involutus* acts as a “coincidental decomposer” (sensu Talbot et al. 2008), releasing C as a by-product of organic N acquisition. In the process, *P. involutus* secretes substantial amounts (>10% of new biomass C) of aromatic metabolites that enhance organic matter adsorption onto mineral surfaces (Wang et al. 2017), contributing not only to SOM degradation but also to its formation and potential stabilization (see Section 2.2.2). Note that this research has been done primarily in pure culture in the lab with one EMF taxon (i.e., *P. involutus*) and not while in symbiosis with a host plant. However, if this mechanism is employed by EMF during symbiosis, it could have important ecosystem-scale implications for C and N cycling.

### 3.3. Mycorrhizal Stimulation of Microbial Decomposition Through Carbon Subsidies to the Rhizosphere

As discussed in Section 2.2.1, mycorrhizal extraradical hyphae are a primary sink for plant photosynthate transferred belowground. Since AMF and many EMF taxa lack the genetic capacity to efficiently enzymatically mine organic materials for nutrients (see Section 3.1), an alternate strategy is to stimulate free-living saprotrophic microbes in the rhizosphere to carry out this function (Kuzakov 2002, 2010; Phillips et al. 2012). This mechanism accelerates the mineralization of native SOM by priming the growth and extracellular enzyme production of rhizosphere microbes with plant C subsidies (i.e., mycorrhizal exudates and necromass). Release of plant C via mycorrhizal hyphae, rather than passive root exudation, may allow for greater precision in targeting photosynthate toward the saprotrophic microbial community (Dickie et al. 2015). Thus, free-living

microbial decomposers (saprotrophic bacteria and fungi) and their grazers (e.g., protozoa, collembolans, nematodes) represent the third leg of the mycorrhizal symbiosis stool, significantly influencing soil C dynamics and plant nutrient availability. Priming as a mechanism for mycorrhizal acquisition of nutrients is likely particularly important in soils where N or P availability is low or in systems where these nutrients are bound primarily in complex organic compounds (Dijkstra et al. 2013, Orwin et al. 2011).

The priming process seems to be especially important for AMF, since these obligate biotrophs lack the genetic capacity to directly liberate N and P from organic sources (Tisserant et al. 2013). AMF hyphae preferentially grow toward organic matter patches where, once in a patch, AMF hyphal growth significantly increases, as does plant nutrient acquisition (Hodge et al. 2001). Plant C is rapidly transferred to AMF hyphae (Kaiser et al. 2015), followed by slower release to rhizosphere bacterial and fungal populations (Drigo et al. 2010). This process suggests that AMF hyphae growing in organic matter patches may control C release similarly to a slow-release fertilizer, making labile C available to associated microbes in the rhizosphere as nutrients are needed by the AMF fungus or plant. AMF colonization induces changes in rhizosphere bacterial populations, promotes bacterial growth, and stimulates the activities of microbial extracellular enzymes targeting N and P acquisition (Bukovská et al. 2018, Toljander et al. 2007, Vázquez et al. 2000). In particular, AMF-mediated C release stimulates the growth and activity of phosphate-solubilizing bacteria in the rhizosphere, enhancing the mineralization of organic P and increasing its availability to the fungus (Zhang et al. 2016, 2018).

The evidence that EMF hyphae prime SOM decomposition is more circumstantial. In an arctic tussock tundra ecosystem, *Cortinarius*, a C-demanding, rhizomorph-forming EMF taxon that develops an extensive mycelial network in the rhizosphere of colonized plants, can transfer plant photosynthate among host plants, and some of this C is accessed by rhizosphere microbes (Deslippe et al. 2016). In several recent studies, nearly half of chitinolytic and lignolytic enzyme activity in the rhizosphere (Brzostek et al. 2015) and 80% of the stimulated N mineralization (Zhang et al. 2019) were driven by the presence of EMF. However, the degree to which these observations are due to priming versus direct enzymatic decay of SOM by EMF is unclear.

Rhizosphere priming is often assumed to be due primarily to the release of labile exudates; however, priming may also result from the turnover of mycorrhizal necromass, stimulating saprotrophic microbes in a similar way (Fernandez & Kennedy 2016). A large proportion of C assimilated by the bacterial rhizosphere community can be derived from AMF hyphal turnover rather than exudates (Drigo et al. 2010), suggesting an important role for fungal necromass in the priming process. Microbes are generally N-rich, and accelerated turnover of microbial necromass may increase N availability to a greater extent than decomposition of other SOM pools (Phillips et al. 2012). Some mycorrhizal fungi also produce organic acids with strong metal-complexing ability. For example, oxalic acid, an abundant rhizosphere compound, can stimulate SOM mineralization by liberating organic compounds from protective associations with soil minerals (Keiluweit et al. 2015). Mineral-associated organic matter includes a range of N-rich molecules, and mycorrhizal exudation may influence the mobilization of mineral-associated organic matter by stimulating microbial activity on or near mineral surfaces, stimulating the destabilization and degradation of mineral-associated SOM while at the same time releasing N and other nutrients (Jilling et al. 2018).

### 3.4. Mycorrhizal Competition with Saprotrophic Fungi

The above-described mechanisms focus on how mycorrhizal fungi stimulate SOM decay, presumably leading to soil C loss, although partial SOM decay may also facilitate SOM stabilization.

#### Gadgil effect:

hypothesis that mycorrhizal fungi suppress SOM decomposition through antagonistic interactions with free-living saprotrophs

However, field observations indicate that litter or SOM decomposition by free-living saprotrophs is sometimes enhanced when mycorrhizal fungi are absent from soil (Gadgil & Gadgil 1971, 1975). This phenomenon, often referred to as the Gadgil effect, has been observed principally in soil trenching or tree girdling experiments where living roots and their extraradical hyphae are either severed (trenching) or cut off from host C supply (girdling). In both cases, declines in living mycorrhizal hyphae in the soil have been associated with increased litter decay (Sterkenburg et al. 2018), decreased plant litter accumulation (Gadgil & Gadgil 1975), enhanced C and N mineralization (Averill & Hawkes 2016, Moore et al. 2015), and increased activities of SOM-degrading enzymes (Kaiser et al. 2010; but see Brzostek et al. 2015). Negative correlations between mycorrhizal densities and rates of litter decay have also been observed in litter decomposition studies (Koide & Wu 2003). Although the Gadgil effect is most often discussed in the context of EMF colonization, the presence of AMF also suppresses microbial decomposition (Leifheit et al. 2015). The primary explanation for these observations is that mycorrhizal fungi compete through antagonistic interactions (e.g., production of antimicrobial compounds) with free-living saprotrophs for shared limiting resources, namely nutrients and/or water (Averill 2016, Koide & Wu 2003, Leifheit et al. 2015, Peay 2016), suppressing the activities of free-living saprotrophs. However, other mechanisms are possible. For example, mycorrhizal fungi may parasitize nutrient-rich saprotrophic fungi as an alternate resource-acquisition strategy (Fernandez & Kennedy 2016).

Although the Gadgil effect is invoked frequently in the literature, there is little direct empirical support for it due to methodological limitations. Manipulating root and mycorrhizal abundance through soil trenching or tree girdling produces confounding effects, including altered soil moisture dynamics and the introduction of a fresh pool of severed roots and fungal hyphae for heterotrophic microbes to utilize. There is also limited consensus on the magnitude or direction of the Gadgil effect across ecosystem types (Fernandez & Kennedy 2016). For example, results from several recent girdling experiments suggest that (*a*) the Gadgil effect is limited to the plant litter layer (Sterkenburg et al. 2018); (*b*) saprotrophic fungi do not exploit the empty niche left by mycorrhizal fungi after trenching (Sterkenburg et al. 2018); and (*c*) the presence of roots and mycorrhizal fungi actually accelerates rather than suppresses SOM decomposition via the priming mechanism (see Section 3.3), particularly at EMF-dominated sites (Brzostek et al. 2015).

## 4. IMPLICATIONS FOR SOIL CARBON DYNAMICS AT THE ECOSYSTEM SCALE

The different evolutionary histories of EMF versus AMF have resulted in a suite of nutrient acquisition traits and strategies that have implications for soil C cycling at the ecosystem scale, with nutrient cycling rates and SOM storage differing significantly between EMF- and AMF-dominated ecosystems. For example, EMF-colonized trees are associated with leaf litters having higher ratios of C to N (Jo et al. 2019, Lin et al. 2017, Read 1991, Zhu et al. 2018) and slower rates of decomposition (Cornelissen et al. 2001, Hobbie et al. 2006, Keller & Phillips 2018) compared with AMF-associated trees. Plant roots, which are significant contributors to SOM formation, also decompose more slowly for EMF- than AMF-colonized trees (Jacobs et al. 2018). Total fungal and mycorrhizal extraradical hyphal biomass is higher in EMF-dominated forests (Cheeke et al. 2017), as is the total amount of C stored in mycorrhizal-associated pools (Soudzilovskaia et al. 2015).

Nutrient cycles also vary by mycorrhizal type, with EMF-dominated sites typically having higher dissolved organic C concentrations (Phillips et al. 2013) and organic P availability (Rosling et al. 2016), and lower inorganic N concentrations (Corrales et al. 2016, Lin et al. 2017) and rates of nitrate leaching (Midgley et al. 2015). These observations have been synthesized into the



mycorrhizal-associated nutrient economy (MANE) framework (Phillips et al. 2013), providing an integrated synopsis of how EMF- versus AMF-colonized trees differentially influence C and nutrient cycles. The overarching MANE hypothesis is that these two mycorrhizal types elicit fundamentally different nutrient economies: the EMF organic nutrient economy, with slow C and nutrient cycling, resulting in a limited loss of inorganic nutrients compared with the AMF inorganic nutrient economy, characterized by fast decomposition of high-quality plant litter and rapid C and nutrient cycling. While the above observations have been documented mostly for temperate forests, emerging evidence suggests that similar dynamics occur in other systems, including a subarctic alpine plant community (Soudzilovskaia et al. 2015) and tropical forests (Corrales et al. 2016, Waring et al. 2016).

How MANE dynamics influence SOM storage is less clear, with studies reporting higher soil C concentrations or stocks in EMF-dominated (Averill et al. 2014, Lin et al. 2017, Taylor et al. 2016) or AMF-dominated (Craig et al. 2018, Jo et al. 2019) sites. Other studies have shown no correlation between relative EMF or AMF dominance and soil C (Jo et al. 2019, Zhu et al. 2018). These conflicting results may be due to differences in soil depth analyzed. Surface soils (~0–20 cm) in EMF-dominated sites tend to exhibit enhanced soil C relative to AMF-dominated sites (Jo et al. 2019, Lin et al. 2017, Taylor et al. 2016; but see Zhu et al. 2018), whereas a recent analysis of deeper soils showed that AMF-dominated sites store more C to a depth of 1 m (Craig et al. 2018; but see Averill et al. 2014). Cross-biome analyses also yield different results compared with more localized studies that control for climate and edaphic factors. For example, in a global analysis of soil C content to a depth of 1 m, Averill et al. (2014) reported greater C storage in EMF systems, whereas Craig et al. (2018) found a negative correlation between relative EMF dominance and soil C in an analysis of soil C stocks (also to a depth of 1 m) at three midlatitude broadleaf forests with similar climate. An analysis of three million mycorrhizal trees showed that the consequences of differential mycorrhizal association on soil C stocks varies by ecoregion; the relationship between AMF tree dominance and soil C stock is positive in mesic temperate regions but negative in dry regions (Jo et al. 2019).

As discussed above, AMF and EMF deploy different nutrient acquisition strategies as a result of their evolutionary history and resultant genetic capacity. A general supposition is that AMF, because of their inability to produce extracellular SOM-degrading enzymes, scavenge mineral nutrients, as they are dependent on and even enhance SOM decomposition by free-living rhizosphere saprotrophs (i.e., rhizosphere priming; see Section 3.3). EMF, in contrast, mine nutrients from SOM either directly (i.e., through enzymatic breakdown; see Section 3.1) or indirectly (i.e., oxidation via Fenton chemistry), potentially leaving C-rich, nutrient-poor substrates behind (Lambers et al. 2008, Orwin et al. 2011). The effect of these two different nutrient-acquiring strategies (i.e., scavenging versus mining) on SOM storage depends on how they differentially affect SOM stabilization versus destabilization. On the surface, the AMF scavenging strategy might be expected to drive soil C loss as the activities of heterotrophic microbes are stimulated. This hypothesis is supported by the observation that AMF-associated C inputs stimulated higher rates of decomposer activity and soil C loss (Wurzburger & Brookshire 2017). However, labile plant C inputs and microbial by-products are now known to be important precursors of stable SOM that become protected within soil aggregates and through association with mineral surfaces (Cotrufo et al. 2013). Thus, an alternative prediction is that a scavenging strategy promotes the formation of stable SOM, consistent with the observation that concentrations of amino sugars (an index of microbially derived SOM) and N in mineral-associated organic matter were positively correlated with AMF tree dominance (Craig et al. 2018). Additionally, some studies suggest that priming is more important in EMF- versus AMF-dominated systems (Brzostek et al. 2015, Sulman et al. 2017) and that the activities of N- and P-acquiring enzymes are greater at EMF- compared with

AMF-dominated sites (Phillips et al. 2013), as a result of either priming or direct EMF production of extracellular enzymes. However, reduced extracellular enzyme activities have also been observed when EMF are reduced or removed from the soil (Kaiser et al. 2010, Kyaschenko et al. 2017). Thus, the nutrient acquisition activities of EMF, like those of AMF, could either stimulate decomposition and soil C loss (e.g., Baskaran et al. 2017) or facilitate the stabilization of more C on mineral surfaces and within soil aggregates.

Mycorrhizal fungi are perhaps the best-studied group of soil organisms, yet our understanding is limited as to how their presence and activities ultimately affect soil C cycling. There is observational evidence that mycorrhizal nutrient acquisition strategies have implications for soil C dynamics at the ecosystem scale; however, direct experimental evidence is lacking for how these strategies differentially influence soil C storage. The various ways in which mycorrhizal fungi influence SOM formation, stabilization, and destabilization (discussed in Sections 2 and 3) all potentially operate to some degree and are not mutually exclusive, with synergies likely among them. The overall impact of mycorrhizal fungi on SOM storage will be the net effect of these contrasting processes, which are context dependent, varying by mycorrhizal type (e.g., AMF versus EMF), species (e.g., EMF evolved from brown-rot versus white-rot ancestors), host plant, season, edaphic properties, and other factors. Obtaining direct empirical evidence of the mechanisms by which mycorrhizal fungi influence SOM dynamics, the degree to which they occur in the field, and the conditions under which they operate is an area of critical research need.

### SUMMARY POINTS

1. Mycorrhizal fungi are a major conduit of plant photosynthate to the rhizosphere.
2. Mycorrhizal extraradical hyphae secrete significant quantities of rhizosphere exudates.
3. Mycorrhizal necromass likely plays a significant, yet largely unquantified, role in SOM formation and stabilization.
4. Mycorrhizal fungi do not have the genetic capacity to act as saprotrophs but rather employ several nutrient acquisition strategies that facilitate SOM decay.
5. Enzymatic degradation (white-rot relatives) and oxidation via Fenton chemistry (brown-rot relatives) are potentially important mechanisms by which EMF enhance SOM decay and nutrient release.
6. Rhizosphere priming is a potentially important nutrient acquisition strategy for AMF due to their inability to produce extracellular SOM-degrading enzymes.
7. Mycorrhizal type (e.g., AMF versus EMF) differentially influences SOM dynamics at the ecosystem scale.

### FUTURE ISSUES

1. What are the contributions of mycorrhizal exudation and necromass production to SOM formation and stabilization?
2. What is the relative importance of mycorrhizally mediated SOM decay mechanisms for nutrient acquisition (i.e., enzymatic degradation, oxidation via Fenton chemistry, rhizosphere priming), and under what conditions do they operate?

3. Do EMF enzymatically access a significant amount of organic N from SOM while in symbiosis?
4. Do mycorrhizal fungi suppress SOM decomposition through antagonistic interactions with free-living saprotrophs (i.e., the Gadgil effect)? If so, what host and environmental factors modulate this effect, and what are the overall consequences for soil C storage?
5. How universal are MANE dynamics, and what are the underlying mechanisms explaining these ecosystem-scale observations?
6. Will explicit representation of plant–mycorrhiza–SOM dynamics in ecosystem and Earth system models improve their predictive capacity?

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