

Section IV: **Mycorrhizal mediation of ecosystem carbon fluxes and soil carbon storage**

Chapter 19: **Introduction: Mycorrhizas and the carbon cycle**

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Abstract

Mycorrhizal fungi channel significant amounts of recently fixed plant carbon (C) through the soil, affecting a number of soil processes including the composition and activity of microbial communities and soil organic matter (SOM) mineralization. Some of the mycorrhizal fungi (particularly those establishing ecto-, ericoid and orchid mycorrhizas) can directly mineralize SOM, although often they do not utilize its C, but only the mineral nutrients such as nitrogen and/or phosphorus locked up in it. Arbuscular mycorrhizal fungi lack efficient exoenzymes to mineralize SOM on their own and thus possibly rely on associated microorganisms to do that job. Often, the mycorrhizal fungi effectively deplete their hyphospheres of mineral nutrients such as nitrogen and phosphorus, inducing localized nutrient deficiency of soil microbial communities and resulting in stabilization of soil organic C on a long run. Involvement of mycorrhizal symbiosis in soil C cycling is briefly outlined in this chapter, introducing following chapters that elaborate on this subject from different perspectives.

Keywords (5-10)

Mycorrhizal types, ecosystem, carbon cycle, food webs, soil organic matter, mineralization, stabilization, redistribution

19.1. The carbon cycle

Carbon (C) is the fourth most abundant element in the current universe, yet much less abundant in Earth's crust (webelements.com). It is the chemical basis of all life as we know it (Bergin *et al.*, 2014). It serves as the main building block of all living organisms on Earth and the main energy carrier for metabolic processes. Its concentration in living organisms fluctuates around 50% on a dry mass basis (Fierer *et al.*, 2009). Because of the importance of C for life as we know it, boundary conditions for habitability of extrasolar planets have been defined based on the potential for C and water cycling (von Bloh *et al.*, 2005; Unterborn *et al.*, 2014). With only few exceptions, photosynthesis is the main mechanism responsible for the entrance of C into the biosphere, with virtually all organic compounds on Earth being dependent on this very process, including fossil fuels (natural gas, crude oil, coal) and materials derived from it such as plastics and tars, timber, all sorts of agricultural products, living biomass of microbes, plants and animals (including humans), organic residues, composts, peats, biochars as well as the soil organic matter (SOM).

The terrestrial C cycle is the biogeochemical cycle in which C is exchanged between its reservoirs in atmosphere, biosphere, hydrosphere, and lithosphere (excluding pedosphere and geosphere from this list because of their overlaps with the previously used terms). It has slow and fast components: The slow C cycle is dominated by fully oxidized C (carbonate or CO₂), moving at geological time scales between oceans, rocks and atmosphere, including processes such as volcanic CO₂ emissions (see also chapter 2, this volume). It moves between 10¹³ and 10¹⁴ grams C annually (earthobservatory.nasa.gov). The fast C cycle is dominated by the SOM pool, which is larger than both biosphere and atmosphere C pools combined, and in terms of size is only surpassed by calcareous rocks and ocean carbonate pools. The fast C cycle moves between 10¹⁶ and 10¹⁷ grams C each year (earthobservatory.nasa.gov), is mostly biologically-dominated, and includes oxidation-reduction reactions such as photosynthesis and respiration. The two components of the C cycle overlap in a number of reservoirs (e.g., hydrosphere and lithosphere), but the position of the atmosphere is somewhat special – it is truly the mixing point, where nearly all the C is present in the same form (CO₂) and the pool is being fed from both the slow and the fast C cycles. Besides, it is largely affected by human-induced CO₂ emissions in a range close to the natural fast C cycle, i.e., 10¹⁵ – 10¹⁶ grams C per year (Kammen & Marino, 1993; Ver *et al.*, 1999).

19.2. The key role of the SOM in soil processes

The SOM is not only by far the largest pool involved in the fast C cycle, but it is also the most heterogeneous pool in terms of chemical variability, spatial heterogeneity and diversity of processes involved in its turnover (Gaillard *et al.*, 1999; Schaumann & Thiele-Bruhn, 2011; Yuan *et al.*, 2013; Angst *et al.*, 2016). By definition, it consists of all C bound in organic molecules in soil, which are not parts of living organisms. This C pool is continuously built up through inputs such as plant (both aboveground and root) litter, exudates, wood and charcoal particles, dung, animal remains and dead microbes. It is recycled through myriads of soil macro- and microorganisms (Fierer *et al.*, 2009) and encompasses particularly labile C compounds like simple organic acids with a half-life counting in minutes to hours (Watt *et al.*, 2006; Fujii *et al.*, 2013) through more recalcitrant compounds such as starch, cellulose, and chitin degrading over weeks to months (German *et al.*, 2011; Zeglin *et al.*, 2013; Tischer *et al.*, 2015), through lignin and black C (metabolically carbonized organic matter or charred

organic materials through exposure to high temperatures upon limited oxygen availability, Waggoner *et al.* (2015)), which could resist decomposition over years to millenia (Valášková *et al.*, 2007; Foereid *et al.*, 2011; Singh *et al.*, 2012). Black C, especially the biochar, which is the intentionally created black C through charring of organic residues, has attracted particular attention in the recent decades as environmentally friendly waste management, efficient soil conditioner and a measure to offset climatic changes, allowing to sequester large amounts of C belowground over long periods of time (Novotny *et al.*, 2015). Current interest in implementing biochar application in agricultural practices, especially in infertile tropical soils, require taking its effects and interactions into account with soil microbes in general and mycorrhizas in particular (Quilliam *et al.*, 2013; Hammer *et al.*, 2014, for more information see also chapter 25).

19.3. Position of mycorrhizal fungi within the soil food webs

Like all fungi, mycorrhizal fungi are heterotrophs and are thus completely dependent on reduced C as their only energy source for all their metabolism and growth. In contrast to many other soil organisms, mycorrhizal fungi derive most or all their energy directly from their living host plants, often becoming literally part of their plant hosts (Fig. 19.1., see also chapters 20 and 21 for more details). Their mycelia either enwrap the roots by dense hyphal mats in case of ectomycorrhizas (EcM) or penetrate deep inside the host plant roots in the other types of mycorrhizal symbioses. Through the intimate physical contact, mycorrhizal fungi obtain exclusive access to simple organic molecules (mainly sugars), in exchange to symbiotic benefits conferred to the plants, mainly in form of improved nutrient acquisition from the soil beyond the reach of roots (van der Heijden *et al.*, 2015). Once in the fungal hyphae, the C obtained from plants is quickly redistributed within the mycorrhizosphere, which is the soil zone colonized by the extraradical (or extramatrical) mycelium (Schrey *et al.*, 2015). The mycelium grows and/or produces extracellular materials – exudates, secretions, exoenzymes, which could potentially be consumed by other soil organisms (Fig. 19.2., see also Chapter 9). The hyphae themselves are either eaten by biotrophic organisms (fungal pathogens such as *Trichoderma*, Rousseau *et al.* (1996)) while they are alive, or processed by soil saprophytes after they have died (e.g., Fernandez *et al.*, 2016). The organisms dependent on the C shuffled through mycorrhizal hyphae, i.e. the mycorrhiza-dependent food chains, recruit from various taxonomic and ecological groups, from bacteria through collembolans and mites (Scheu & Folger, 2004; Schneider *et al.*, 2005), but there is also an intriguing opportunity that some EcM and possibly also other mycorrhizal fungi could actually recycle C from dead mycorrhizal hyphae in the soil (see chapter 23 for more details). Ecologically interesting yet still poorly documented is the possibility of specific association of mycorrhizal hyphae with soil microbes fulfilling complementary functions to the hyphae themselves. For example, microbes capable of degrading complex organic molecules can associate with the surfaces of arbuscular mycorrhizal (AM) hyphae (Jansa *et al.*, 2013), which have in turn very limited capacity to degrade such substrates alone (Joner & Johansen, 2000). In addition, there can be functional dependencies between soil saprotrophs and EcM hyphae in accessing recalcitrant protein-tannin complexes (Wu *et al.*, 2003). Recent developments in molecular techniques such as ¹³C-stable isotope probing allow unprecedented insights into the identity and dynamics of the inter-organismal linkages in complex environments like soils. A number of studies have now used this approach to address the pathways and players active in C channeling through the soil via mycorrhizal fungi (Leake *et al.*, 2006; Drigo *et al.*, 2010; Lekberg *et al.*, 2013, see chapter 22 for further details).

19.4. Mycorrhizal symbiosis and the soil C cycling

Mycorrhizal fungi contribute to the C cycle through redistribution of recently fixed C through the soil (Jakobsen & Rosendahl, 1990; Drigo *et al.*, 2010; Nottingham *et al.*, 2013; Fernandez *et al.*, 2016), feeding (and potentially also priming) organic matter mineralization pathways (Staddon *et al.*, 2003; Balasooriya *et al.*, 2013; Lindahl & Tunlid, 2015; Fernandez *et al.*, 2016), as well as immobilizing/stabilizing the C in highly recalcitrant organic compounds (Sousa *et al.*, 2012). These pathways are further discussed in chapters 21, 23, and 24. Yet, there is another key mechanism by which mycorrhizal fungi are involved in soil C cycling, and this is related to their important contribution to the mineral nutrition of their plants hosts (see section II of this book). Soil colonized by mycorrhizal hyphae could quickly be depleted of easily available phosphorus and/or nitrogen (N), and the mineralization of the SOM may be slowed as a consequence of starvation for mineral nutrients of the (saprotrophic) microbes involved in the SOM mineralization. This so called 'Gadgil effect' has been described for ectomycorrhizal pines in New Zealand (Gadgil & Gadgil, 1971), but similar results have also been reported recently for AM systems (Verbruggen *et al.*, 2016). Although the outlined mechanism of the 'Gadgil effect' could further be confounded by other factors such as water availability (Koide & Wu, 2003) and/or mycorrhiza-mediated increase of primary productivity (Orwin *et al.*, 2011), it seems that the differential exploitation (high and low, respectively) of nutrients and the C/energy locked up in the SOM (Lindahl & Tunlid, 2015) is the most important mechanism behind the observed stabilization of SOM due to mycorrhizal activity (see also chapters 20 and 24 for more details). On the other hand, there is at least one case where mycorrhizal fungi do indeed mineralize SOM in order to obtain C/energy. This C is then used by the fungi and also transferred to the host plant. Such a lifestyle is the rule in the orchids and other plants with dust seeds (Eriksson & Kainulainen, 2011) during seed germination and sometimes during the entire life span of achlorophyllous species (Zettler *et al.*, 2005; Keel *et al.*, 2011; Rasmussen & Rasmussen, 2014; Stockel *et al.*, 2014, see also chapter 21 for more details). Yet in some orchid and also other types of mycorrhizas, where the plant gains (or at least is thought to gain) the C from the fungal partner, in the so called mycoheterotrophic plant species, it is more likely that the mycorrhizal fungus obtains C from a neighboring green plant rather than from the SOM (Taylor *et al.*, 2004; Barrett *et al.*, 2010; Courty *et al.*, 2011). In some of these cases, particularly those involving achlorophyllous plants associating with the AM fungi (e.g., Bidartondo *et al.*, 2002), mechanism of C transfer from the fungus to the plant is remaining completely unknown and actually contradicts earlier experimental evidence of absence of C transfer from AM fungal hyphae to the plant tissues (Fitter *et al.*, 1998; Pfeffer *et al.*, 2004).

19.5. Functional diversity in mycorrhizal symbioses with respect to C cycling

Different types of mycorrhizal fungi (e.g., EcM, ericoid, orchid and AM fungi) have been traditionally viewed as fulfilling different ecosystem roles in terms of utilization of soil nutrients, supporting plant nutritional demands, and access to the different C sources, apart from colonizing phylogenetically (mostly) disjunctive groups of plant taxa (Table 1.1, Read & Perez-Moreno, 2003; Gartner *et al.*, 2012; van der Heijden *et al.*, 2015). However, recent research blurs some of the previously established wisdoms and tends to include a broader range of fungal taxa among the mycorrhizal (or mycorrhiza-like) fungi such as Mucoromycotina, *Sebacina*, *Colletotrichum* and the elusive group of dark septate endophytes (Jumpponen, 2001; Weiss *et al.*, 2011; Field *et al.*, 2015; Hiruma *et al.*, 2016). In addition,

recent findings have demonstrated unusual partner associations such as *Russula* with some mixotrophic or mycotrophic orchids (Girlanda *et al.*, 2006; Ogura-Tsujita *et al.*, 2012; Kong *et al.*, 2015). Moreover, we now have evidence for complex interactions and their functional consequences between various soil microorganisms (saprotrophs, chemolithotrophs) and mycorrhizal fungi (Lindahl *et al.*, 1999; Herman *et al.*, 2012; Bukovská *et al.*, 2016). Besides, recent studies have detected some typical mycorrhizal fungi (e.g., *Tuber* sp.) in roots of many non-host neighboring plants (Gryndler *et al.*, 2014), which suggests either much broader specificity of (some) mycorrhizal associations or a possible shortcut in C cycling from a non-host plant to mycorrhizal fungi, effectively bypassing SOM formation. Below we specifically elaborate on the traditional and novel aspects of functioning and mutual interactions between the different mycorrhizal types, with a particular attention to C/energy fluxes, some of which are addressed in more detail in subsequent chapters.

19.5.1. Arbuscular mycorrhiza

In the AM symbiosis, few hundred fungal species establish the symbiosis with tens of thousands of unrelated plant species (van der Heijden *et al.*, 2008; Krüger *et al.*, 2012, see also Table 1.1). This means that a single AM fungus can possibly colonize several to many plant species (individuals) at once, forming so called common mycorrhizal networks (Egerton-Warburton *et al.*, 2007; Bever *et al.*, 2010; Lekberg *et al.*, 2010). It has been shown that under such situations one plant partner could feed the AM hyphal network with the C, whereas another plant preferentially derives the symbiotic benefits (mainly in terms of improved mineral nutrition) without giving much C in return (Walder *et al.*, 2012; Walder & van der Heijden, 2015). How common this is in nature and how consistent is it with biological market theory (Fellbaum *et al.*, 2014; Werner & Kiers, 2015) is currently a subject to much controversy. Previous experimental evidence also showed that the C flow is always unidirectional, i.e. from plant to the AM fungus, ascribed to a very effective trehalose/lipid 'valve' effectively preventing a reverse flow of C from the fungus to the plant (Pfeffer *et al.*, 2004). Yet how would the presumed mycoheterotrophic AM hosts (Bidartondo *et al.*, 2002) acquire their C then if not from its mycorrhizal partner? With the experimental proof still missing of the C transfer from a neighboring green plant to the achlorophyllous host via AM hyphae, this remains one of the major and long-standing research challenges. It is also one of the great hopes of mycorrhizal physiology with respect to elucidating the molecular mechanisms and their regulation of C transfer from plant host to the AM fungus, by using the exceptional case where it is possibly not working the ordinary way.

19.5.2. Ectomycorrhiza

Similarly as in the AM symbiosis, the fungal partner in EcM symbiosis is fed mainly by plant sugars, although many of the EcM fungi (unlike the AM fungi) are capable of degrading complex organic molecules (Lindahl & Tunlid, 2015). In contrast to AM fungi that have not yet been grown in absence of host roots, many EcM fungi can easily be grown on axenic nutrient media in absence of a host plant (Langdale & Read, 1990; Nehls *et al.*, 2007; Larsen *et al.*, 2011). Compared to the AM fungi, there is also much greater progress with respect to identification of missing key genes/pathways of C transfer from the plant to the EcM fungi, due to available genome sequences of several of the EcM fungi and their plant hosts (Larsen *et al.*, 2011; Ceccaroli *et al.*, 2015; Kohler *et al.*, 2015). By using combinations of isotopic and molecular approaches, previous assertions on the partially saprotrophic

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lifestyle of some truffles and other EcM fungi under field conditions (e.g., Hobbie *et al.*, 2013) seem to have been largely refuted now (Le Tacon *et al.*, 2015; Lindahl & Tunlid, 2015). Yet, there are some cases where ECM fungi obviously feed mycoheterotrophic (achlorophyllous) plants with the C obtained from a neighboring green plant host. These mycoheterotrophic plants recruit from a variety of plant groups, often not typically EcM ones, such as a liverwort *Cryptothallus* sp. (Wickett & Goffinet, 2008), all monotropes (Cullings *et al.*, 1996) and some orchids (Selosse *et al.*, 2004; Girlanda *et al.*, 2006; Barrett & Freudenstein, 2008), parasitizing hyphal networks formed by truffles (*Tuber* sp.), *Tulasnella*, *Russula* and other typically EcM fungi. The molecular mechanisms and their regulation of this atypical C transfer from the EcM fungus to the plant remain unknown thus far.

19.5.3. Ericoid mycorrhiza

The typical ericoid mycorrhizal (ErM) fungi belong to the most efficient degraders of the complex organic materials in soil (Bending & Read, 1996; Bending & Read, 1997; Kohler *et al.*, 2015). These fungi are also capable of axenic cultivation on both simple and complex sugars (Varma & Bonfante, 1994; Hughes & Mitchell, 1995; Midgley *et al.*, 2004). Nevertheless, as with the EcM symbiosis, it remains unclear to what extent they utilize SOM to cover for their energy demand under natural conditions or just to derive mineral nutrients (above all the N) from it. Very little work has been done so far on the molecular basis of C exchanges between the ErM fungi and their plant hosts, as well as on deciphering the stoichiometry of trades of mineral nutrients for C between the symbiotic partners as depends on environmental conditions such as nutrient and/or light availability (Michelsen *et al.*, 1996; Hofland-Zijlstra & Berendse, 2009). One notable exception is the work by Grelet *et al.* (2009), directly demonstrating reciprocal exchange of C and N between symbiotic partners in ErM symbiosis – although the fungus used in that experiment has originally been isolated from EcM root tips of a pine. These and other (e.g., Vrålstad, 2004) results thus suggest a possible fungal partner overlap between EcM and ErM symbioses. The arbutoid and monotropoid mycorrhizas established between phylogenetically close relative plant taxa to typical ErM plants and typical EcM fungi could then be regarded rather as one extremity of a gradient than as a true exception.

19.5.4. Orchid mycorrhiza

Orchid mycorrhizas represent one of the evolutionarily youngest types of mycorrhizal symbiosis, involving a great number of extant orchid species (Brundrett, 2002, see also Table 1.1 for more details). From the C cycling perspective, it is clearly distinct from the other types of mycorrhizal symbiosis because the C flow is typically bidirectional – the fungi often supply significant amounts of C to the germinating dust seeds of orchids (Selosse *et al.*, 2011) whereas at later stages of plant ontogeny the net C flux is typically reversed, dominated by the C flow from the green plant to the fungus (Cameron *et al.*, 2006; Cameron *et al.*, 2008). Among the orchids, there is also a high number of mixotrophic and mycoheterotrophic species, supposedly feeding on their fungal partner (Selosse & Roy, 2009), yet the direct experimental evidence for the C exchange and C sources (another plant or the SOM) in such relationship remains mostly unclear. See chapter 21 for more details.

19.6. Open questions, experimental challenges

Carbon fluxes between the plant and fungal partners in mycorrhizal symbiosis still remain largely enigmatic with respect to their mechanistic basis (genes and proteins), their magnitude, temporal

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variation, and their interactions with environmental conditions such as light intensity. For example, mycorrhizal C costs may well be, on average, significantly lower than the 20% net photosynthetic production previously measured in young cucumber plants (Jakobsen & Rosendahl, 1990); indeed, the measured figures rarely exceed 10% of the plant's C budget (Paul & Kucey, 1981; Grimoldi *et al.*, 2006; Lendenmann *et al.*, 2011). With the technical issues of high-throughput screening of whole (meta)transcriptomes and use of ^{13}C for tracing the C fluxes in plant-mycorrhiza-soil systems being solved or nearly so (Slavíková *et al.* 2016), we just need carefully designed experiments to answer many of the remaining open questions. Among those, particular attention should be paid to mycoheterotrophic plants, and especially those associating with AM fungi. Our future experiments should also pay due attention to the shared mycorrhizal networks interconnecting several different plant individuals belonging to the same or to different species. Ecological significance of recycling C from the SOM by mycorrhizal fungi (Hobbie *et al.*, 2013) and transfer of this "dead C" from the fungus to associated plants should be quantified and compared to the "recent C" fixed by a living mycorrhizal host plant. Interactions between plant hosts, mycorrhizal fungi and other soil microbes should be studied mainly from the perspective of metabolic/trophic dependencies and competition for resources. In this regard, direct interactions between mycorrhizal fungi belonging to different functional types (e.g. AM and EcM) should be studied in relevant ecosystem settings where their hyphospheres intermingle, such as in some mixed deciduous forests or tropical rainforests (see also Table 1.1.). And the consequences of these interactions for ecosystem processes (Fig. 19.3.) should finally be established and fed into the global C cycling models (see chapter 26 for more details). Mycorrhizas are mostly missing from C cycling models in spite of large amounts of C being fluxed through their hyphal networks globally (Talbot *et al.*, 2008). Yet with experimental evidence mounting on the role of mycorrhizas in both soil C loss and soil C stabilization as well as plant nutrition and performance in nearly all terrestrial ecosystems, they emerge as important ecosystem engineers, strongly modulating ecosystem productivity, functioning and resilience as well as SOM turnover (Jastrow *et al.*, 2007; Bever, 2015; Fernandez & Kennedy, 2015; Sochorová *et al.*, 2016; Verbruggen *et al.*, 2016).

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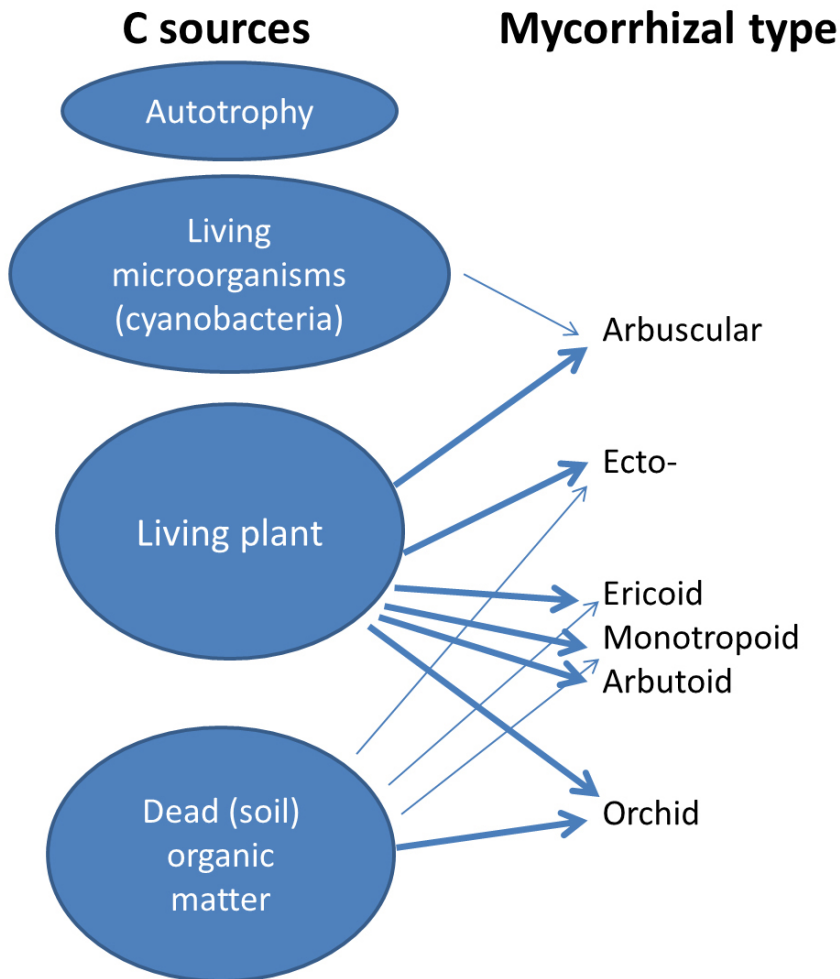


Figure 19.1. Direct dependency of the different mycorrhizal types (recruiting from different taxonomic group of fungi, see Table 1.1. for details) on different carbon (C) sources, illustrating the central role of a living plant for all mycorrhizal fungi and the quantitatively less important role of the soil organic matter, with a complete absence of autotrophy and a very special case of symbiosis of *Geosiphon* (Glomeromycota) with phototrophic prokaryotes (Schüßler, 2002).

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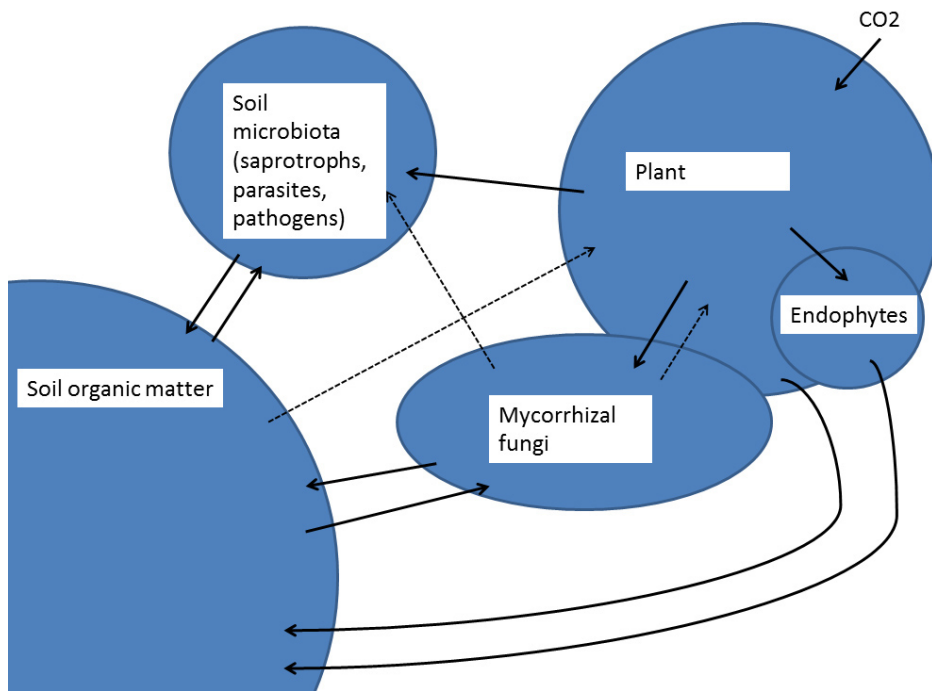


Figure 19.2. Schematic representation of carbon fluxes between plant, soil microbes and the soil organic matter. Thick lines represent common and quantitatively important pathways, dashed lines represent less common/less important pathways. Overlaps between circles representing different pools stand for tissues composed of two entities (e.g., root and rhizobia in the nodules or mycorrhizal hyphae inside roots). Pools are not exactly to scale.

MYCORRHIZAL MEDIATION OF SOIL: FERTILITY, STRUCTURE, AND CARBON STORAGE

Johnson, Gehring, Jansa (eds.)

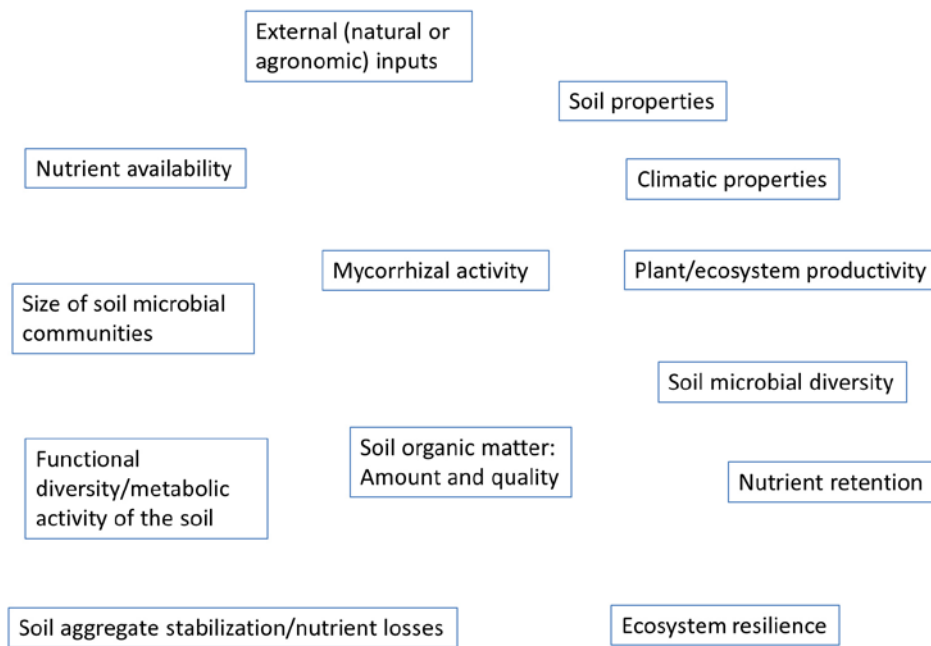


Figure 19.3. Various ecosystem features impacting and feeding back on the soil organic matter, causing changes in its pool size, turnover rates and/or quality. Although multiple pieces of evidence documented several direct and indirect interactions between the different ecosystem features displayed here under specific environmental situations, the arrows representing direct and indirect linkages are intentionally left out of this picture. This is to illustrate as yet unmet challenge to assign broadly valid, mutually comparable, quantitative, and dynamically changing values to such arrows in this heavily interlinked multidimensional space in order to allow for realistic predictions of interactions between mycorrhizal communities and soil carbon pools and their dynamics.