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BELOWGROUND RESPONSES TO CLIMATE CHANGE

Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change

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Summary

1. In the conventional view of soil carbon (C) cycling, mycorrhizal fungi are primarily considered vectors for plant C input to soils. However, there is accumulating evidence that mycorrhizal fungi may also contribute to the direct loss of soil C by acting as decomposers, that is by producing extracellular lytic enzymes and metabolizing soil C.

2. Most of the evidence that mycorrhizal fungi can act as decomposers comes from studies of ericoid and ectomycorrhizal fungi, although there is increasing experimental evidence for a role of arbuscular mycorrhizal fungi in soil C decomposition. Decomposition by mycorrhizal fungi implies that soil C balance is subjected to the ecological factors that affect both plant and fungal symbionts; this interaction has important consequences for how soil C stocks respond to global change.

3. In this synthesis, we propose a new model of soil C cycling, including decomposition of soil C by mycorrhizal fungi, and we evaluate how this new integrative model alters our predictions of soil C feedbacks to global change. We present three hypothetical mechanisms by which mycorrhizal fungi may metabolize significant quantities of soil C. The first hypothesis ('Plan B' hypothesis) is that mycorrhizal fungi metabolize soil C as an alternate C source when supplies of photosynthate from the host plant are low. Our second hypothesis ('Coincidental Decomposer' hypothesis) is that mycorrhizal fungi decompose soil C as a consequence of mining soil for organic nutrients. The third hypothesis ('Priming Effects' hypothesis) is that mycorrhizal fungi decompose soil C when allocation of plant photosynthate to mycorrhizal roots is high, such that plant C 'primes' the growth and activity of mycorrhizal fungi.

4. Further empirical tests of these hypotheses will clarify the role of mycorrhizal fungi in soil C balance and improve our understanding of soil C responses to global change.

Key-words: mycorrhizal fungi, decomposition, carbon, soils, global change

Introduction

Mycorrhizal fungi are ubiquitous soil organisms that scavenge nutrients from soils and transfer a portion of these nutrients to their host plant in return for labile plant C (Smith & Read 1997). This exchange has important consequences for soil C balance, in that, mycorrhizal fungi can promote belowground storage of plant C. Indeed, in the conventional view of soil C cycling, mycorrhizal fungi are thought to primarily act as vectors for plant C input to soils.

In contrast to this conventional view, there is accumulating evidence that mycorrhizal fungi may also contribute to the direct loss of soil C from ecosystems by acting as decomposers. Decomposition of soil organic matter involves two sequential processes: (i) the breakdown of polymeric organic substrates into monomers or oligomers by extracellular enzymes, and (ii) the metabolism of these small compounds and the release of CO_2 by soil microbes. Many mycorrhizal fungi can participate in both processes. Ericoid, ectomycorrhizal and arbuscular mycorrhizal fungi can take up simple C compounds from soils while in symbiosis with a host plant (Hawkins, Johansen & George 2000; Taylor, Gebauer & Read 2004), and some species of ericoid and ectomycorrhizal fungi can produce extracellular enzymes that decompose complex organic substrates (Read & Perez-Moreno 2003; Read, Leake & Perez-Moreno 2004). There is some evidence that ericoid

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fungi are better enzyme producers than ectomycorrhizal fungi, which in turn produce more extracellular enzymes than arbuscular mycorrhizal fungi (Read & Perez-Moreno 2003). This observation implies that decomposition of soil C by mycorrhizal fungi should be greatest in ericoid- and ectomycorrhizal-dominated ecosystems such as arctic and boreal systems (Read 1991). However, recent experimental evidence indicates that arbuscular mycorrhizal fungi may play a larger role in organic matter decomposition than was previously assumed (Hodge, Campbell & Fitter 2001; Tu *et al*. 2006). If these three mycorrhizal functional types decompose soil C in ecosystems, this process represents a largely unaccounted C transformation pathway in current models of soil C cycling. Instead of soil C loss being controlled exclusively by the activity of saprotrophic (i.e. free-living) microbes, the fate of soil C could be subject to environmental factors that affect mycorrhizal fungi as well as their host plants.

Decomposition by mycorrhizal fungi has important consequences for how soil C stocks respond to global change. If mycorrhizal fungi decompose significant quantities of soil C, the effects of global change on both plant and microbial communities could control the loss of soil C stocks. Reaching a predictive understanding of soil C feedbacks to atmospheric C pools requires a synthesis of knowledge about the ability of mycorrhizal fungi to act as decomposers as well as an evaluation of how global change regimes could regulate the extent to which this occurs in nature.

In this synthesis, we explore a new conceptual model of soil C cycling that incorporates the decomposer abilities of mycorrhizal fungi. We also discuss the ecological consequences of soil C decomposition by mycorrhizal fungi and evaluate how this activity would alter our predictions of soil C feedbacks to terrestrial C cycling. First, we evaluate the evidence that mycorrhizal fungi can access soil C directly by decomposing soil organic matter. The conclusions from this analysis lead us to propose a new model for soil C cycling in which mycorrhizal fungi contribute to decomposition of soil C. Second, we outline hypotheses for when mycorrhizal decomposition of soil C could occur in ecosystems. Finally, we describe how each of these hypotheses frame alternative predictions of soil C feedbacks to atmospheric C concentrations under elevated CO_2, alterations in precipitation, N deposition, and fires.

Decomposers in disguise

Mycorrhizal fungi are thought to receive C primarily from their host plants. However, many mycorrhizal fungi also possess the capacity to access C from soils by decomposing soil organic matter. Ericoid and ectomycorrhizal fungi have long been known to metabolize simple organic compounds, such as glucose and amino acids, when grown as isolates in culture (e.g. Melin 1925; Melin & Norkrans 1948; Laiho 1970; Lundeberg 1970; Abuzinadah & Read 1988). Furthermore, ectomycorrhizal (Abuzinadah & Read 1986; Finlay, Frostegard & Sonnerfeldt 1992; Taylor *et al*. 2004), ericoid (Bajwa & Read 1986), and arbuscular mycorrhizal fungi (Hawkins *et al*. 2000) can assimilate intact amino acids while in association with a host plant. Thus, access to photosynthate does not preclude the uptake of exogenous organic compounds by many mycorrhizal fungi. In addition, amino acid transporters that allow uptake of amino acids from soil solution have been identified in several species of ectomycorrhizal fungi (Chalot *et al*. 1996; Nehls *et al*. 1999; Chalot *et al*. 2002). Identification of amino acid transporters in mycorrhizal fungi is significant since amino acids comprise a substantial portion (up to 20%) of the dissolved organic N pool in some soils (Jones & Kielland 2002; Jones *et al*. 2004; Chen & Xu 2006). These observations suggest that simple organic compounds, such as amino acids, could represent a significant C source for mycorrhizal fungi in ecosystems.

In addition to metabolism of low-molecular weight C, certain ericoid and ectomycorrhizal fungi can also decompose large organic compounds that are not otherwise directly available for microbial uptake. These fungi can produce extracellular enzymes that decompose components of each of the major classes of organic compounds commonly found in soils (Table 1, Fig. 1). Thus, species of ericoid and ectomycorrhizal fungi can grow on protein, chitin, pectin, cellulose, hemicellulose, and starch – as well as recalcitrant compounds such as polyphenols – when these compounds are supplied as a C source (reviewed in Read *et al*. 2003; Read *et al*. 2004). The ability to decompose cellulose, hemicellulose, and polyphenols is particularly important, since these are the three most abundant classes of biopolymers on land (Hernes & Hedges 2000; Kogel-Knabner 2002). Production of extracellular lytic enzymes enables ectomycorrhizal fungi to mobilize nutrients from leaf litter (Bending & Read 1995) and pollen (Perez-Moreno & Read 2001) and allows ericoid fungi to decompose macerated fungal mycelia (Kerley & Read 1997; Kerley & Read 1998). The ability of ericoid and ectomycorrhizal fungi to decompose these organic substrates, which are major components of fresh organic matter in soils, implies that they could control the loss of large portions of soil C stocks.

Ericoid and ectomycorrhizal fungi are generally thought to play a larger role in the decomposition of complex organic residues in soils than arbuscular mycorrhizal fungi (Read & Perez-Moreno 2003). However, recent studies suggest that arbuscular mycorrhizal fungi may contribute to decomposition of complex compounds in soils. For example, several species of arbuscular mycorrhizal fungi can accelerate the loss of C and N from patches of decomposing organic matter in microcosms (Hodge *et al*. 2001; Tu *et al*. 2006). If arbuscular mycorrhizal fungi can increase the decomposition of complex organic compounds in soils, they may regulate soil C losses to a greater extent than is conventionally recognized.

Few studies have directly tested whether mycorrhizal fungi decompose soil organic matter in field settings, yet many have indirectly examined this possibility. Ericoid, arbuscular and ectomycorrhizal plants from boreal forests (Nasholm *et al*. 1998; Nordin, Hogberg & Nasholm 2001), temperate grasslands (Bardgett, Streeter & Bol 2003; Weigelt *et al*. 2003) and wetlands (Henry & Jefferies 2003) accumulate both ^{13}C and ^{15}N from isotopically labelled amino acids applied directly to

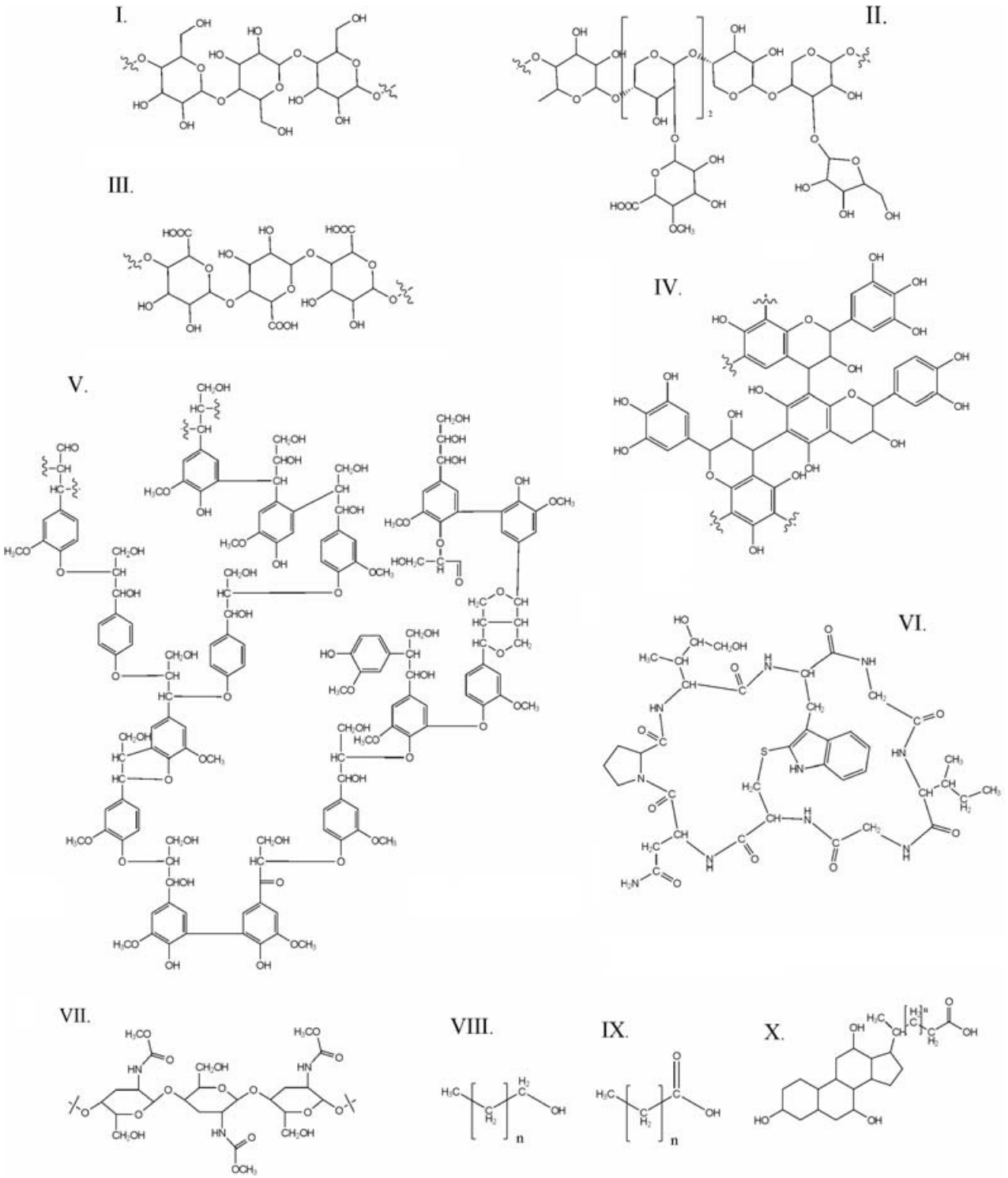

Fig. 1. Structures of carbon compounds that can be decomposed by mycorrhizal fungi; cellulose (I.), hemicellulose (xylanose, II.), pectin (III.), tannins (robinetinidol, a condensed tannin, IV.), lignin (V.), protein (α-Amanitin, VI.), chitin (VII.), and lipids (primary alcohols, VIII.; fatty acids, IX.; sterines, X.). Amended from Kogel-Knabner (2002). [Correction added after online publication 26 September 2008: Fig. 1 replaced by corrected version]

field soil. In addition, field-based studies have indicated that ectomycorrhizal fungi may decompose soil organic matter via the production of extracellular enzymes. For instance, activities of proteases and polyphenol oxidases are often higher in ectomycorrhizal mats than in nearby uncolonized soils (Entry, Donnelly & Cromack 1991; Griffiths & Robinson 1992). Through the production of these extracellular enzymes, ectomycorrhizal fungi should accelerate decomposition of

Table 1. Complex carbon compounds that can be decomposed by ericoid and ectomycorrhizal fungi. Adapted and extended from Chalot and Brun (1998) and Read *et al.* (2004)

Compound	Structure*	Enzyme	Fungal Type
Cellulose	I.	Cellulase	ERM, ECM
		Cellobiohydrolase	ERM, ECM
Hemicellulose	II.	Xylanase	ERM, ECM
		Mannosidase	ERM
		Galactosidase	ERM
		Arabinosidase	ERM
		Glucanase	ERM
Pectin	III.	Polygalacturonase	ERM, ECM
Tannins	IV.	Polyphenol oxidase	ERM, ECM
		Peroxidase	ERM, ECM
		Catechol oxidase	ERM, ECM
		Tyrosinase	ERM, ECM
		Laccase	ERM, ECM
Lignin	V.	Manganese peroxidase	ECM
		Lignase	ERM
Proteins	VI.	Acid protease	ERM, ECM
Chitin	VII.	Chitinase	ERM, ECM
Lipids	VIII.–X.	Fatty acid esterase	ECM

ERM, ericoid mycorrhizal fungi; ECM, ectomycorrhizal fungi.
*See Fig. 1.

both labile (via proteases) and recalcitrant (via polyphenol oxidases) soil organic matter. Two studies using natural ^{14}C signatures in ectomycorrhizal sporocarps have also provided indirect evidence that ectomycorrhizal fungi may metabolize soil-derived C (Chapela *et al*. 2001; Hobbie *et al*. 2002). In each study, the $\Delta^{14}C$ of sporocarps matched the atmospheric $\Delta^{14}C$ of the previous year, suggesting that at least a portion of sporocarp biomass was derived from litter or soil C.

In contrast to these studies, Treseder, Torn & Masiello (2006) found that ectomycorrhizal root tips did not accumulate C from ^{14}C-labelled leaf litter in a temperate deciduous forest of the eastern US. These results suggested that mycorrhizal fungi do not use litter C as a significant C source. However, it is possible that any ^{14}C acquired from the litter was respired in the mycorrhizal mycelium soon after uptake. Alternatively, mycorrhizal fungi might acquire C from soil organic matter rather than leaf litter. In a recent boreal forest study in central Sweden, Lindahl *et al*. (2007) observed that ericoid and ectomycorrhizal taxa colonized primarily the fragmented litter and lower soil layers. Mycorrhizal fungi were spatially separated from saprotrophs, which almost exclusively occupied the upper fresh and partially decomposed litter layers (Lindahl *et al*. 2007). Moreover, mycorrhizal abundance was positively correlated with increasing soil C : N with organic matter depth and age (Lindahl *et al*. 2007), indicating that mycorrhizal fungi may mobilize N-rich compounds from organic matter in these soils (Hobbie & Horton 2007).

Consequences for soil C balance

If mycorrhizal fungi decompose C compounds in soils, this pathway represents a largely unaccounted fate of soil C in current models of soil C balance. Under the traditional paradigm of soil C cycling, mycorrhizal fungi act solely as vectors for plant C input to soils while soil C losses are controlled entirely by the activity of saprotrophic soil microbes (Fig. 2a). However, mycorrhizal fungi have the potential to decompose a range of C compounds directly from soils, including simple to complex, and labile to recalcitrant substrates. Mycorrhizal decomposition of soil C is an alternative mechanism of soil C loss (Fig. 2b) in which soil C balance depends on the ecological factors that affect mycorrhizal fungi and their plant partners in addition to traditional saprotrophs.

The most notable factor affecting the activity of mycorrhizal fungi rather than saprotrophic microbes is the physiology and functioning of mycorrhizal plants. Given that C usually flows from plants to mycorrhizal roots (e.g. Grimoldi *et al*. 2006) and nutrients from mycorrhizal fungi to their host plants (Smith & Read 1997), it is likely that the resource requirements of both plants and fungi determine when mycorrhizal fungi decompose soil organic matter. We present hypotheses for three mechanisms by which mycorrhizal fungi may contribute to soil C decomposition.

The first hypothesis, which we call the 'Plan B' hypothesis, is that mycorrhizal fungi decompose soil organic C as an alternate C source when supplies of photosynthate from the host plant are low or unavailable. This mechanism may be employed by mycorrhizal fungi when the host plant experiences a decline in rates of photosynthesis, such as during increased cloud cover or shadiness, or during plant dormancy. Several recent studies in temperate forests have supported this hypothesis, demonstrating that ectomycorrhizal fungi produce high extracellular enzyme activity during the winter months when photosynthetic rates decline (Buee, Vairelles & Garbaye 2005; Buée *et al*. 2007; Mosca *et al*. 2007). Courty, Bréda & Garbaye (2007) also found that ectomycorrhizal root tips in an old-growth oak forest produce a suite of extracellular enzymes in the early spring that show peak activity immediately before and following bud break. Given that bud burst is a strong C sink, these

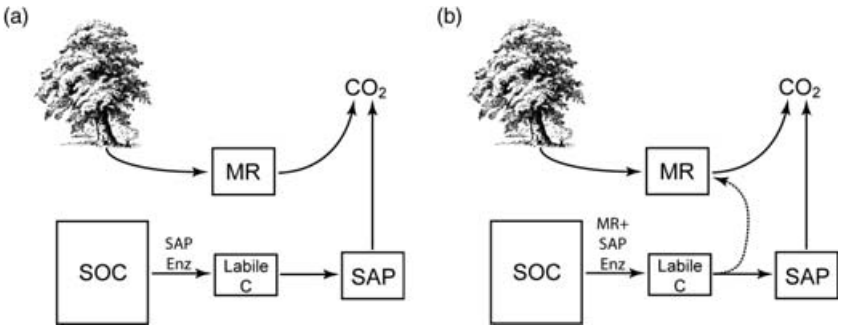

Fig. 2. The classic model (a) of soil organic carbon (SOC) cycling and the new (b) model incorporating the use of soil C by mycorrhizal fungi (MR) and saprotrophic microbes (SAP). In the new model (b), extracellular enzymes (Enz) from both SAP and MR convert complex SOC into labile C (such as amino acids). This labile C can then be taken up and respired by both SAP and MR (dotted arrow). Clipart courtesy Florida Center for Instructional Technology.

observations are consistent with the hypothesis that mycorrhizal fungi facilitate the formation of new tissues during this time by supplying C to their host plants (Courty *et al*. 2007). Furthermore, Mosca *et al*. (2007) showed that tree thinning led to significantly higher laccase, chitinase and glucosidase production by ectomycorrhizal root tips in a declining European oak forest (Mosca *et al*. 2007). Plant allocation of photosynthate to mycorrhizal fungi could also decline if soil nutrient availability is high enough to preclude the need for mycorrhizal fungi to facilitate nutrient acquisition by the plant. In many cases, soils with high N availability have low colonization of roots by mycorrhizal fungi (Treseder 2004), suggesting that plant allocation to mycorrhizal fungi is potentially at risk in fertile soils such as in agricultural systems. It is possible that in either of these two situations, mycorrhizal fungi that have decomposer abilities could acquire C from other sources, such as soil organic compounds. These compounds could be metabolized directly from labile pools present in soil solution, or acquired by enzymatic decomposition of complex organic matter (Fig. 2b).

Our second hypothesis, the 'Coincidental Decomposer' hypothesis, is that mycorrhizal fungi decompose soil C as a consequence of mining soil for nutrients. If mycorrhizal fungi take up organic forms of nutrients, such as amino acids, then they would facilitate the loss of nutrient-rich soil organic matter. Similarly, if mycorrhizal fungi use extracellular enzymes to release nutrients from complex organic matter, then they would accelerate the rate-limiting step of soil organic matter decomposition (Schimel & Bennett 2004) and the loss of large portions of soil C stocks. Through this mechanism, the nutrient demands of mycorrhizal plants and fungi could influence soil C balance. This situation is likely to occur in sites where inorganic nutrient availability does not meet plant or mycorrhizal nutrient demands, such as in high latitude and altitude ecosystems (Bunnell *et al*. 1977; Nadelhoffer, Aber & Melillo 1984). Indeed, a number of mycorrhizal plant species in boreal and arctic regions can take up intact amino acids directly from field soils (Schimel & Chapin 1996; Nasholm *et al*. 1998) and ericoid and ectomycorrhizal fungi are thought to be largely responsible for the mobilization of N-rich organic matter in some boreal forest soils (Hobbie & Horton 2007; Lindahl *et al*. 2007).

This mechanism of organic matter decomposition by mycorrhizas is consistent with the hypothesized mechanism underlying global patterns of the abundance and distribution of mycorrhizal functional types. On a global scale, the increasing percentage of nutrients bound in organic matter with increasing latitude and altitude is thought to select for mycorrhizal fungi that exploit the most abundant forms of nutrients along these gradients (Read 1991). In particular, ericoid and ectomycorrhizal fungi are dominant in temperate, boreal, and arctic regions, where organic matter contents of soils are high. These fungi are thought to be superior decomposers compared to arbuscular mycorrhizal fungi, which are abundant in temperate grasslands and the tropics (Read 1991).

The third hypothesis, the 'Priming Effect' hypothesis, is that mycorrhizal fungi decompose soil C when allocation of plant photosynthate to mycorrhizal roots is high. In this case, plant C 'primes' the growth and activity of mycorrhizal fungi. Priming effects occur when inputs of fresh organic C accelerate the decomposition of native soil organic C by providing an easily-metabolizable energy source for microbes. Priming effects on microbial activity and co-metabolism of recalcitrant substrates by saprotrophic microorganisms are well documented in the literature (Kuzyakov, Friedel & Stahr 2000; Fontaine, Mariotti & Abbadie 2003; Fontaine *et al*. 2004). For example, the addition of cellulose to soils can increase the activity of microbes that specialize on decomposing soil organic matter, thus accelerating the respiration of soil organic C (Kuzyakov *et al*. 2000; Fontaine *et al*. 2003; Fontaine *et al*. 2004). Furthermore, deposition of C in the rhizosphere of crop plants can increase rates of soil organic C decomposition by up to 353% (Cheng, Johnson & Fu 2003).

Likewise, priming effects could occur in mycorrhizal fungi receiving labile C subsidies from plant hosts. If transfer of plant C to mycorrhizal fungi is substantial, this could have major impacts on the ability of mycorrhizal fungi to control soil C loss. Elevated supplies of plant C could enable mycorrhizal fungi to access soil C that would be spatially or energetically unavailable to traditional saprotrophs. For example, mycorrhizae can invest plant C in hyphal structures to traverse resource-poor environments, such as pockets of C-depleted mineral soil. Mycorrhizal fungi are well known to use plant C to construct extraradical hyphae (Smith *et al*. 1997), which can rapidly colonize patches of mineral soil and soil organic matter (Bending *et al*. 1995; Read *et al*. 2004) and significantly enhance plant nutrient uptake (Bending & Read 1995; Bucking & Shachar-Hill 2005; Hu *et al*. 2005). Plant C also represents a resource that mycorrhizae could use to construct enzymes for degrading more recalcitrant C forms (Zhu,

Table 2. Hypothesized mycorrhizal responses to global change

Global change	Mycorrhizal abundance	Mycorrhizal decomposition of soil C		
		'Alternate C source' hypothesis	'Organic nutrient uptake' hypothesis	'Priming' hypothesis
Elevated CO_2	↑	↓	↑	↑
Drier soil	↑	↓	↑	↑
Wetter soil	↓	↑	↓	↓
Nitrogen fertilization and deposition	↓	↑	↓	↓
Fires	↓ ECM ↓ no change in AM	↓	↓	↓

AM, arbuscular mycorrhizal fungi; ECM, ectomycorrhizal fungi.

Dancik & Higginbotham 1994; Eaton & Ayres 2002; Allison & Vitousek 2005). In contrast, saprotrophic microbes must scavenge labile, energy-rich C substrates from soils to use for metabolism and growth, which requires that saprotrophs expend large amounts of C-energy on growth and mechanisms of C uptake. Thus, any priming effects of plant C on soil C uptake by mycorrhizal fungi could allow mycorrhizas to outcompete saprotrophic microbes for soil C in areas where exogenous supplies of labile C are low.

If mycorrhizal fungi decompose soil C by any of these three hypothetical mechanisms, the consequences for soil C cycling are likely to be dramatic. Given the dominance of mycorrhizal taxa in many fungal communities (O'Brien *et al*. 2005; Lindahl *et al*. 2007; Allison, Hanson & Treseder 2007), even a relatively small contribution to soil C metabolism by individual mycorrhizal fungi could translate into a large ecosystem-scale impact. Furthermore, mycorrhizal fungi need not necessarily take up all the products of enzymatic decomposition to alter soil C balance. For example, mycorrhizal fungi might preferentially take up N-rich products of decomposition, while other soil heterotrophs may take up and mineralize the 'leftover' labile compounds (Fig. 2b).

New predictions for soil C balance under global changes

Our hypotheses for when mycorrhizal fungi could decompose soil C highlight the dynamic relationship between plants and fungi in mycorrhizal symbiosis. How does this relationship alter our predictions for soil C balance under global change? One notable difference is that instead of being subject to changes in the activity of saprotrophs, soil C balance could be influenced by changes that affect the physiology and functioning of host plants as well as their mycorrhizal fungi.

SENSITIVITY OF MYCORRHIZAL FUNGI TO GLOBAL CHANGES

As a consequence of their direct association with plants, the abundance of mycorrhizal fungi is frequently sensitive to elevated CO_2, changes in precipitation, anthropogenic N deposition, and fires (Table 2) (Rillig, Treseder & Allen 2002). For example, in field studies the enrichment of atmospheric CO_2 to 550–700 p.p.m. increases the abundance of arbuscular mycorrhizal fungi by 84% and ectomycorrhizal fungi by 19%, on average (Treseder 2004). The degree of CO_2 enrichment can also influence the extent of response; in Southern Californian chaparral exposed to CO_2 concentrations that ranged from 250 to 750 p.p.m., arbuscular mycorrhizal hyphal lengths peaked at 650 p.p.m. (Treseder *et al*. 2003). Likewise, drier conditions, which are predicted for middle latitudes under climate change (Hennessy, Gregory & Mitchell 1997), tend to promote arbuscular mycorrhizal growth (Auge 2001), although the response is more variable for ectomycorrhizal fungi (Swaty *et al*. 2004; Valdes *et al*. 2006; Di Pietro, Churin & Garbaye 2007). In contrast, N fertilization results in a 24% decline in arbuscular mycorrhizal biomass and a 5% decrease in ectomycorrhizal biomass, on average (Treseder 2004). Fertilization rates ranged from 56 to 1000 kg N ha^{-1} $year^{-1}$ in the meta-analysis, but no significant relationship between degree of fertilization and degree of mycorrhizal response was observed.

For CO_2 enrichment and N fertilization, mycorrhizal responses are consistent with predictions based on plant allocation theory. In particular, soil resources should be more limiting to plant growth when C supplies are augmented and when water supplies are low. Under these circumstances, plants should invest more C in their mycorrhizal symbionts to alleviate these nutrient limitations and to improve water use efficiency (Mosse & Phillips 1971; Read 1991). The reverse should occur where soil resources are abundant, such as under anthropogenic N deposition and under wetter precipitation regimes that are predicted in higher latitudes (Hennessy *et al*. 1997).

PREDICTIONS FOR SOIL C BALANCE

The sensitivity of mycorrhizal fungi to global changes such as elevated CO_2 and N fertilization implies that their role in soil processes should shift under future environmental conditions. If mycorrhizal fungi decompose soil C, any shift in mycorrhizal activity could influence losses of soil C in ways that differ from those predicted by conventional models of soil C dynamics. We might expect soil C loss under global change to

scale proportionately with shifts in mycorrhizal abundance. For instance, changes that lead to declines in the abundance of mycorrhizal fungi, such as N deposition, may result in parallel declines in soil C decomposition by mycorrhizal fungi. Conversely, elevated CO_2 levels may increase loss of soil C simply by increasing the abundance of mycorrhizal fungi. However, it is likely that global change regimes will alter soil C decomposition by mycorrhizal fungi in more complex ways, such as by changing the physiology or community composition of mycorrhizal fungi in soils (Lilleskov *et al*. 2002). Depending on the mechanism and magnitude of soil C processing by mycorrhizal fungi, these changes could have dramatically different effects on the amount of C lost from soils.

Under the 'Plan B' hypothesis, mycorrhizal fungi decompose soil organic matter to access soil C as an alternative C source when supplies of photosynthate are low. Thus, when plant allocation of carbon to mycorrhizal fungi increases, the carbon status of the fungi should likewise increase (Treseder 2005) and preclude the need for mycorrhizal fungi to metabolize soil C as an energy source. This would occur under elevated CO_2 and drought, which could augment mycorrhizal carbon stocks and lead to increased concentrations of labile soil C (Table 2). By contrast, if the availability of soil resources is high, such as under anthropogenic N deposition and heavier rains, plants may be deterred from allocating extra C belowground. This response may cause a decline in mycorrhizal abundance over time (Lilleskov *et al*. 2002), or it may force mycorrhizal fungi to scavenge C from soils (Table 2). In fact, Tu *et al*. (2006) observed that additions of mineral N increased arbuscular mycorrhizal-mediated decomposition of plant litter.

Changes in resource availability could also influence mycorrhizal decomposition of soil C under the 'Coincidental Decomposer' hypothesis, in which mycorrhizal fungi decompose soil C as a consequence of mining soil for organic nutrients. Higher rates of plant C fixation under elevated CO_2 exacerbate plant demand for nutrients (Oren *et al*. 2001), which often leads to plant allocation of C belowground. Thus, under increased CO_2 concentrations, mycorrhizal fungi may use extra plant-derived C to scavenge for organic nitrogen and phosphorus compounds (Table 2). Soil chemistry may shift toward a reduction in organic N and P concentrations, and a proportional increase in more C-rich compounds like lignocellulose and microbially-derived C compounds as fungal biomass increases. This change could be further exacerbated by increases in mycorrhizal abundance. By contrast, anthropogenic N deposition may preclude the need for mycorrhizal fungi to facilitate capture of limiting resources by the plant root and result in lower losses of nutrient-rich organic matter from soils.

Under the 'Priming Effect' hypothesis, global changes that augment C allocation to mycorrhizal roots could drive increased decomposition of soil carbon by mycorrhizal fungi and higher soil C losses. Elevated CO_2 and drought could produce these effects, whereby mycorrhizal fungi could use lant C to produce enzymes that degrade both labile and recalcitrant compounds in soils (Table 2). Drier soils may inhibit the effectiveness of extracellular enzymes. However, this mechanism should operate on mycorrhizal- and saprotrophic-derived enzymes to the same extent. Thus, the main effect of drought might be an increase in the relative abundance of mycorrhizal enzymes simply because mycorrhizal fungi proliferate more than saprotrophic fungi might This would potentially lead to the loss of older soil organic matter, such as humic and fulvic acids, that are energetically unavailable to C-limited saprotrophic microbes. In contrast, N deposition and heavy rains would decrease soil C losses via this mechanism (Table 2).

Mycorrhizal effects on C dynamics and storage may depend on the fungal taxa involved. It is widely believed that ericoid and ectomycorrhizal fungi have more extensive enzymatic capabilities than arbuscular mycorrhizal fungi (Read *et al*. 2003) and slower rates of biomass turnover. Thus, the potential for saprotrophic tendencies among mycorrhizae to affect the soil C cycle should be greatest among ericoid and ectomycorrhizal fungi. Global changes that influence these specific functional groups of fungi may result in proportionately larger effects on soil C balance compared to global changes that influence arbuscular mycorrhizal fungi. Fire and conversion from forests to croplands tend to reduce the abundance of ectomycorrhizal fungi, which may result in declines in soil C loss. These disturbances also directly remove organic material from the soil via combustion, erosion, and other processes (Wilson 1978; Kasischke *et al*. 1995; Houghton 1999). Thus, smaller stocks of organic substrates should be available for ericoid and ectomycorrhizal fungi to exploit. Together, these two shifts should result in a slower rate of soil carbon use by mycorrhizal fungi on a landscape scale (Table 2).

Conclusion

Observations that mycorrhizal fungi have the potential to decompose soil C lead to a new model of soil C cycling in which mycorrhizal fungi influence both the inputs and losses of soil C from ecosystems (Fig. 2b). This new model enhances our conceptual understanding of the processes that regulate soil C balance in ecosystems. Furthermore, it allows us to make clear predictions about the response of soil C stocks to global change. The effects of global change on mycorrhizal decomposition of soil C should be mediated by the response of both mycorrhizal plants and fungi to future global change regimes; from this concept we have developed three hypotheses for mechanisms by which mycorrhizal fungi act as decomposers. Empirical tests of these hypotheses will improve our understanding of the dynamic relationship between plant and fungal symbionts and clarify the role of mycorrhizal fungi in soil C balance under global change.

The recognition that mycorrhizal fungi may participate in the mobilization and loss of soil C raises new questions about the role of mycorrhizas in ecosystem processes. Given the sensitivity of mycorrhizal fungi to plant productivity and environmental conditions, how does soil C decomposition by mycorrhizal fungi vary across geographic and ecological gradients? In what ways is soil C balance influenced by aboveground and belowground diversity of mycorrhizal plants and

fungi? The use of molecular techniques is a promising tool to answer questions about the composition and activity of mycorrhizal communities (Treseder 2005), yet few studies have employed these techniques to look directly at patterns of soil C metabolism by mycorrhizal fungi. Examining resource use by mycorrhizal fungi in field settings is an avenue for future research that will clarify the role of mycorrhizal fungi in the microbial community and the effects of environmental conditions on the functional diversity of mycorrhizal fungi.

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