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MYCORRHIZAL CONTROLS ON BELOWGROUND LITTER QUALITY

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Abstract. Plant productivity and ecosystem productivity are strongly influenced by nutrient availability, which is largely determined by the decomposition rate of plant litter. Belowground litter inputs (dead roots, mycorrhizae, and exudates) are larger than aboveground litterfall in many systems. Chemical quality and diameter primarily control decomposition for coarse roots, but these patterns do not hold for finer classes of roots, which are frequently colonized by mycorrhizae. Though mycorrhizal status is known to drastically alter root chemistry, morphology, life span, and exudation, it has never been explicitly considered as a factor affecting root decomposition. We hypothesize that mycorrhizal status substantially influences fine root decomposition rates.

Both ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) fungi can change root properties but do so in different ways. Dominant tree species of most cold and temperate forests rely heavily on EM associations. EM fungi form massive structures that envelop fine roots. Roots infected by ectomycorrhizae have higher nitrogen concentrations than nonmycorrhizal roots, which would be expected to increase decomposition rates, but much of this nitrogen is bound in recalcitrant forms, such as chitin, so the net effect on decomposition is difficult to predict. AM fungi lack elaborate, macroscopic structures and may not alter root chemistry as profoundly.

In addition to mycorrhizal roots, external fungal hyphae can contribute significantly to ecosystem carbon budgets and thereby influence rates of soil carbon turnover. Hyphae have commonly been considered a rapidly decomposing carbon pool, though this has never been demonstrated experimentally. If hyphae are produced at the expense of rapidly decomposing root exudates, then the net effect of hyphal litter production might be to reduce soil microbial activity and overall carbon cycling rates. Based on known differences in morphology and chemistry, EM hyphae may be more recalcitrant than AM hyphae. In summary, we submit that mycorrhizal status could substantially influence fine root decomposition and soil carbon processing rates, potentially explaining some of the variation observed within and among individual plant species and ecosystems.

Key words: *arbuscular mycorrhiza; carbon cycling; decomposition; ectomycorrhiza; feedbacks; fine roots; hyphae.*

SPECIAL FEATURE

INTRODUCTION

The first widely appreciated mycorrhizal functions were those that most clearly and directly benefit individual plants, such as enhanced uptake of nutrients and water and inhibition of root pathogens. More recently, ecologists have recognized ecosystem-level influences of mycorrhizal colonization, most notably, the maintenance of soil structure (Miller and Jastrow 1990), the potential for active degradation of organic substrates (Harley 1971, Read 1991) and possible facilitation of plant succession (for review, see Hart et al. 2001). Recent realization of rising atmospheric [CO_2] has underscored the importance of understanding ecosystem carbon (C) cycling, yet much of the research on mycorrhizal response to elevated CO_2 has focused on the mutualistic benefits to plant growth. The direct contributions of mycorrhizal products to ecosystem C and nutrient cycles have yet received only cursory experimental attention (Treseder and Allen 2000). We contend that the mycorrhizal associations, by influencing belowground litter quality, may directly contribute to the C cycling characteristics of host plants and the ecosystems in which they occur. We will demonstrate how mycorrhizal colonization affects the quality of root tissue and extramatrical products and then survey the implications for ecosystem processes.

Belowground products

The majority of energy and nutrients in soils is derived from detritus of plants. The inputs of root and root-associated turnover and exudation can be as great as aboveground litter inputs in magnitude and may have unique feedbacks to plants (Hendricks et al. 1993). Belowground products are deposited near active roots, creating a close coupling between decomposition and plant nutrient uptake (Gordon and Jackson 2000). The technical challenge of quantifying belowground products, and tracking the fates thereof, has hindered ap-

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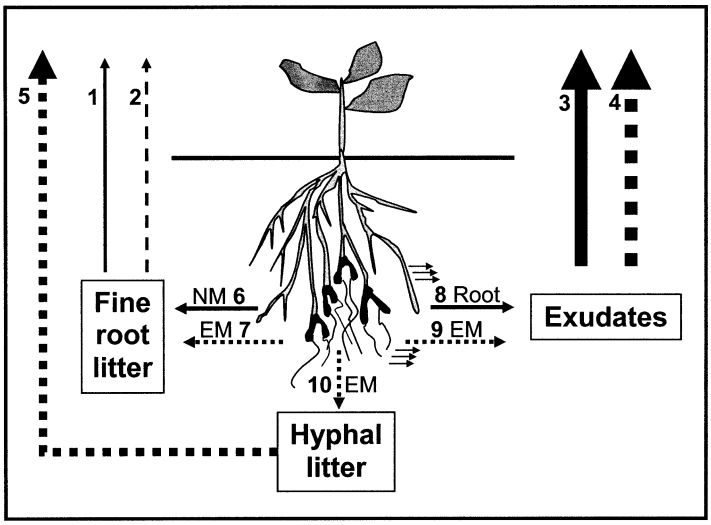

FIG. 1. Representation of carbon (C) fluxes into, and out of, the five primary belowground litters using an ectomycorrhizal example. The relative decomposability of each is represented by the thickness of lines 1–5. Dotted lines indicate mycorrhizal products. Root litter (1) has a mean residence time on the order of one year while exudates (3) reside on the order of days; the influence of mycorrhizal colonization on each of these (2, 4) is unknown. The residence time of hyphal litter (5) also remains unknown but is believed to be from weeks to months. The net effect of mycorrhizal colonization on overall belowground litter quality depends on these unknown decay coefficients and on the distribution of C allocation to each type of litter (6–10).

preciation of the importance and complexity of these inputs. Whereas ecologists typically consider only root turnover, large portions of plant-derived C may enter the soil as root exudates or mycorrhizal tissue (Fig. 1). Though the structure, chemistry and decomposition environment of belowground and aboveground detritus differ greatly, chemical parameters successful for predicting aboveground litter decomposition (primarily N and lignin; Melillo et al. 1982) have been used for root litter, often with less success either within or among ecosystems (King et al. 1997, Robinson et al. 1999, Silver and Miya 2001).

The ubiquitous, intimate, and often prolific presence of mycorrhizal fungi within and around root systems strongly alters root chemistry, architecture, and rhizoplane biology. Observed inconsistencies in fine root decomposition rates suggest that mycorrhizal status may play an important role in determining root litter quality. Ectomycorrhizal (EM) fungi envelop roots and cortical cells with intensive layering of hyphae. Arbuscular mycorrhizal (AM) fungi form less massive, internal structures. Mycorrhizal fungi divert great portions of plant photosynthate away from the root to support extramatrical hyphae. The decomposition rate and exudant properties of these hyphae remain largely unknown. A number of studies have investigated mycorrhizal influence on rhizosphere activity, and though the precise mechanism is not always clear, mycorrhizae appear play a role in regulating rhizospheric C processing rates (Rygiewicz and Anderson 1994, Olsson et al. 1996*a*, *b*). We hypothesize that the type and intensity of mycorrhizal colonization, by altering quality of roots and rhizosphere products, could substantially influence ecosystem level decomposition rates.

Differences between mycorrhizal types

Different types of mycorrhizae have distinct morphologies and functions that depend on both plant and fungal characteristics. The two most abundant types of mycorrhizal fungi (arbuscular and ectomycorrhizal) come from divergent phyla (Kendrick 2000). While there is considerable phenotypic variation within each type of mycorrhiza, we will focus on the differences between AM and EM associations. Such a comparison is useful for generalizing about mycorrhizal roles in ecosystems, where mycorrhizal species may not be known but the mycorrhizal type of dominant plants frequently is known. The microscopic structure of hyphae differs according to fungal phylogeny (Table 1). EM fungal hyphae have thicker walls, pigmentation, and septa between cells, and are generally believed to live longer than AM hyphae (Harley 1971). The same features that may afford a longer lifespan to EM hyphae also appear to render them more resilient to degradation upon senescence. Because their effects on root and hyphal litter quality are likely to differ, we hypothesize that the two major types of mycorrhiza could substantially differ in their effects on C processing rates.

The first section of our argument addresses mycorrhizal alterations of plant roots and the decomposability of the fungus–root. The second section discusses the fate extramatrical mycorrhizal products. The third describes the importance of these mycorrhizal influences for ecosystem processes. For clarity we will use the term ''mycorrhizal root'' to denote the fungus-root symbiosis, consisting of fungal organs that are inseparable from plant roots (mantle, Hartig net, in ectomycorrhizae; vesicles, arbuscules, intramatrical hyphae in arbuscular mycorrhizae). Any extramatrical structures (e.g., hyphae, rhizomorphs) will be referred to specifically. This distinction is technically appropriate because root decomposition studies often have not differentiated mycorrhizal roots, and likely include the fungus-root organs. Conversely, extramatrical structures are largely left behind when roots are removed

TABLE 1. Life history habits of the two most abundant types of mycorrhizal associations.

Association type	Morphology		Fungal division	Saprotrophic potential	Plant associates	Distribution
	Hyphae	Root				
AM	thin-walled, coenocytic	microscopic internal hyphae, vesicles, arbuscules, coils within root cells	Glomeromycota	entirely dependent on host plant C	most herbaceous species, many angiosperms and primitive gymnosperms	dominant in tropics and grasslands, interspersed in EM-dominated systems
EM	thick-walled, pigmented, septated	macroscopic fungal layering outside roots, hartig net internally between cells	Basidio- and Ascomycota	can live freely, enzymatic capability varies with species	advanced gymnosperm, many angiosperm trees, dipterocarps	dominant in cold coniferous and many temperate forests, spotty in tropics

from the soil, and so are not included in conventional root decomposition studies.

MYCORRHIZAL INFLUENCES ON ROOT LITTER QUALITY

Mycorrhizal roots can make up a large portion of belowground production depending on the mycotropism (dependence and type of mycorrhizae) of dominant plant species. Most temperate conifers and many broadleaf tree species host EM fungi. Though direct estimates are rare, EM roots make up as much as 78% of fine root production in coniferous forests of the northwestern United States (Fogel and Hunt 1983). Studies of other EM systems yielded similar large estimates of mycorrhizal production (e.g., Vogt et al. 1981, Markkola et al. 1995). Most herbaceous plants and many trees form arbuscular mycorrhizal associations, though the extent of colonization varies widely (Smith and Read 1997). AM fungi have a less intensive but more extensive presence than EM fungi. Estimates from young potted plants suggest that AM hyphal biomass constitutes around 3% root weight externally (Jakobsen and Rosendahl 1990) and 5–17% root weight internally (Hepper 1977). In this section, we review the architectural and chemical properties of EM and AM roots compared to nonmycorrhizal roots and present some data on how those traits may affect root decomposition.

Architecture

Root architecture can affect decomposition, partly by changing the ratio of surface area to mass of root litter (Berg 1984), thereby minimizing the relative mass of root subjected to direct attack by decomposers. EM colonization can profoundly change root architecture. For example, roots colonized by EM fungi tend to slow or halt apical growth (Smith and Read 1997). EM roots lack fine root hairs, have a short, rounded shape, and are usually no thicker than the finest root class. This change in shape, along with the protection of the EM hyphal sheath, greatly diminishes the surface area of plant tissue exposed to free-living heterotrophs. This sheathing in EM roots is believed to protect live roots from root pathogens and herbivores (Harley and Smith 1983) and could potentially decrease decomposability of dead roots as well, depending on the chemical resilience of the surrounding fungal tissue. The thickness of the Hartig net varies greatly among EM types. In EM angiosperms, hyphal infiltration is often restricted to the root epidermal cells; the underlying cortical cells are highly lignified (Brundrett 2002). AM fungi can induce subtle changes in root architecture that do not likely have a strong influence on root decomposability.

Chemistry

Globally, root chemistry appears to have a stronger influence on root decomposition than does climate (Silver and Miya 2001). Because plant and fungal tissues differ in chemical composition, the amount of mycorrhizal fungal tissue on the surface of, and inside, roots could be as important as any single chemical parameter in predicting root decomposition. Fungal tissue often contains higher concentrations of nitrogen (N) and phosphorus (P) than plant root tissue (Table 2). Higher concentrations of these nutrients, especially N, in litter are predicted to accelerate decomposition according to aboveground paradigms (Aber and Melillo 1991). However, fungal cell walls contain up to 60% chitin, which is recalcitrant to decomposition (Swift et al. 1979), but also is 6.9% N, much more than most plant tissues (Table 2). Roots with mycorrhizal colonists could have relatively high [N] and actually be less decomposable than uncolonized roots with lower [N]. Such a suppression of decomposition in N-rich roots would be expected in roots that have higher masses of fungi, and thus, more chitin. More massive fungal structures apparently lead to higher chitin contents in EM roots than AM roots (Table 2). AM colonization may not cause a large, chitin-mediated depression of root decomposition. In fact, in some (typically tropical) systems, litter [Ca] is found to correlate well with root decomposition (e.g., Bloomfield et al. 1993). AM colonization may increase root [Ca] by accumulating calcium phosphates resulting in increased decomposition

TABLE 2. Chemical composition of roots in unknown innate mycorrhizal condition (coarse and fine) and of known mycorrhizal status (arbuscular and ectomycorrhizal), and that of mycorrhizal hyphae.

Chemical component (%)	Roots				Hyphae	
	Coarse (>2 mm)	Fine (<2 mm)	AM	EM	AM	EM
N	0.59[1]	0.94[1]	1.34[5]	1.71[5]	1.58[7]	2.22[10]
P	0.07[1]	0.05[1]	0.28[3]	0.15[10]	0.33[7]	0.08[9]
Ca	0.29[1]	0.23[1]	0.49†	0.12[12]	0.91[8]	0.09[9]
K	0.26[2]	0.26[2]	0.014[3]	0.21[10]	0.90[8]	0.20[9]
Lignin	22.4[1]	23.6[1]	20.3[5]	33.2[5]	~0	~0
Chitin	~0	~0	0.57[4]	2.56[6]	7.73[4]	6[11]

Sources (superscript numbers in table): 1, Silver and Miya (2001), review of 33 root decomposition studies; 2, Gordon and Jackson (2000), review of 56 studies; 3, Giddens and Todd (1984); 4, Frey et al. (1994), means from Greenhouse specimens of *Glomus intraradices* on red clover; 5, J. Langley and B. Hungate, *unpublished data* from *Pinus edulis* (EM) and *Helianthus annuus* (AM); 6, Wallander et al. (1997), means of five EM species throughout one year; 7, Smith and Gianinazzini-Pearson (1987), internal hyphae; 8, Weiersbye et al. (1999), mean values from spores of unidentified AM fungi on grass *Cynodon dactylon*; 9, Wallander et al. (2002), median values from PIXE analysis of 21 field-collected *Rhizopogon* spp. and *Pinus muricata* rhizomorphs; 10, Fogel and Hunt (1983), mean from mixed-species EM roots in Douglas fir stand, hyphae likely to be EM mycelium; 11, Markkola et al. (1995); 12, Kottke et al. (1998), median from 17 EM species in German *Pinus abies* stands.

† Fine roots from graminoid species (Silver and Miya 2001) which are likely to host arbuscular mycorrhizae.

rates where Ca availability limits decomposition (Silver and Miya 2001).

Secondary chemical components, both plant and fungal, could strongly alter the decomposition of roots colonized with fungi. There is some evidence that plants mobilize secondary compounds selectively to mycorrhizal roots, perhaps as a defensive response to initial colonization, or in order to regulate the internal penetration of the fungal hyphae (Brundrett 2002). For example, Marks (1968) reported accumulation of plant-derived tannins in the cortex of dead mycorrhizal roots. Moreover, the fungi forming mycorrhizal associations can produce their own secondary compounds that may affect decomposition. The range of potential compounds produced differs among mycorrhizal types. EM fungi, like many dikaryomycetes, can produce antibiotics (Olsson et al. 1996*b*) and antifungals (Kope et al. 1991) which inhibit saprotrophic soil microbes and could slow root decomposition. Glomeromycetous AM fungi are not known to produce many specialized secondary metabolites, but do store large amounts of lipids in vesicles, dramatically increasing root lipid content (Harley and Smith 1983, Finlay and Söderström 1991), which should increase root carbon quality.

Despite these striking physical, chemical, and functional differences, no studies have included mycorrhizal parameters (colonization, chitin content, etc.) in initial litter quality assessment nor have any studies examined decomposition in light of mycorrhizal status. Based on chemical and architecture parameters, we predict that EM colonization deters decomposition of dead roots compared to uncolonized roots of the same species, while AM colonization does not have a large effect on root decomposition.

Root decomposition studies

No published studies that explicitly measure root decomposition have considered mycorrhizal roots as a separate class of roots. Sequential coring studies have made inferences about turnover of mycorrhizae (e.g., Vogt et al. 1982, Fogel and Hunt 1983), but these are difficult to translate to estimates of decomposition. With accurate live/dead distinctions, one can estimate the turnover rate of live roots, but independent estimates of root decay constants are necessary for compartment flow models that can predict decomposition (Publicover and Vogt 1993).

Litterbag studies have measured long term decomposition rates in field settings for a number of plant species, typically comparing two or more classes of roots defined by diameter. Several such studies of EM-dependent tree species tend to find anomalous patterns for the finest class of roots, which commonly associate with ectomycorrhizae. McClaugherty et al. (1984) surveyed roots from several hardwood and pine species and consistently found that coarse roots decomposed much more rapidly than finer ones (from 22 to 191% more mass loss) despite lower nutrient concentrations (~50% lower [N] in coarse roots). The authors invoked the modestly higher percentages of nonstructural carbohydrates in the finer roots to explain the pattern. Burke and Raynal (1994) found a similar relationship between mass loss and diameter of roots from a northern hardwood forest, with the finest roots decomposing most slowly. Again, the pattern could not be explained with initial litter chemistry; the finest class of roots had higher concentrations of N and P than intermediate (0.5–1.5 mm) and larger roots (1.5–3.0 mm). Camiré

et al. (1991) found similar depressions of decomposition in the finest root classes in both *Alnus* and *Populus* species, as did Lohmus and Ivask (1995) in *Abies*, all of which frequently form EM associations. Camiré et al. (1991) hypothesized that high N content in these fine roots could stimulate the formation of relatively stable N–lignin complexes and suppress decomposition rates. In loblolly pine, King et al. (1997) found that the 5–10 mm diameter root class decomposed slightly quicker than the 0–5 mm root class (k value = 0.0018 d^{-1} vs. 0.0016 d^{-1}) despite having C:N ratios that were consistently twice as high throughout two years of decomposition. In all of these cases, root decomposition appears to be stunted in the smallest diameter class despite having the highest [N]. We suggest that ectomycorrhizae, which occur in finer classes of roots and increase [N], decelerate decomposition rates in these litterbag studies and contribute to the decoupling of [N] and root decomposition rates.

Robinson et al. (1999) used microcosms to measure decomposition of mixtures of roots from arctic plants. They found decomposition to be unpredictable by any initial chemical parameter measured (C, N, P, soluble carbohydrates, cellulose, lignin). Based on their qualitative mycorrhizal assessment, the most labile roots were nonmycorrhizal, followed by an AM species, with one lightly EM and one heavily EM species being more recalcitrant. However, mycorrhizal status was neither quantified nor invoked to explain decomposability.

In a comprehensive review of root decomposition studies, Silver and Miya (2001) concluded that the indices of litter quality useful for predicting foliar litter decomposition rates (lignin, N) were not accurate predictors of root decomposition. Nor were climatic variables as successful for root litter as for litter deposited on top of the soil. While fine (<2 mm diameter) roots of broadleaves and conifers have mean concentrations of N, P, Ca, lignin (and various ratios thereof) that are not statistically separable, conifer roots decomposed much more slowly. The conifer roots examined (spruce, fir, and pine) are heavily colonized by ectomycorrhizae under most field conditions (Smith and Read 1997). Within conifer studies, root decomposition had a significant *negative* relationship with [N], consistent with a suppression of root decomposition by EM colonization.

We compared the initial decomposability of ectomycorrhizal and nonmycorrhizal roots of *Pinus edulis* in microcosms (Fig. 2; see Plate 1). Regardless of the treatment of the tissue, nonmycorrhizal fine roots decomposed more quickly than mycorrhizal roots despite having less than one-third as much N, 0.63 ± 0.07% and 2.20 ± 0.12%, respectively (df = 6, t = 11.1, P < 0.001). When the tissues were ground, the differences between EM and nonmycorrhizal root decomposition narrowed, suggesting that the mycorrhizal root structure, perhaps the chitinous shell, may contribute to the relative recalcitrance of EM roots. The above

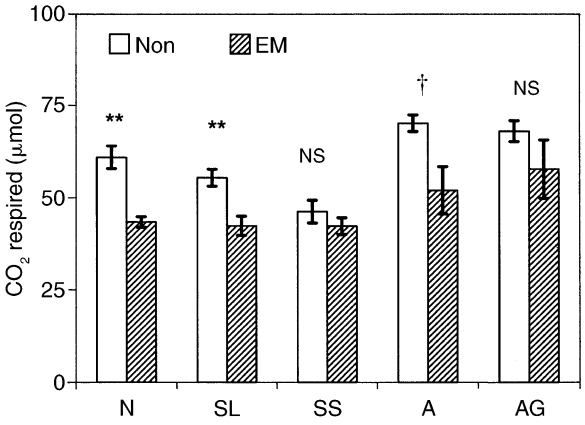

FIG. 2. Cumulative respiration (means ± 1 SE) after two weeks of decomposition of ectomycorrhizal and nonmycorrhizal roots of *Pinus edulis*. Fine roots (<1 mm) were collected near Flagstaff, Arizona, in June 2002, and sorted according to presence of ectomycorrhizal status. A 25-mg sample of each root type (EM and Non) was placed in sterile soil and reinoculated with a slurry of soil from the pine woodland. One group (N) of each root type was allowed to decompose with its native rhizoplane and internal fungi, which could affect decomposition. To control for differing rhizoplane microbial communities, a subset of each type of root was surface sterilized (SL); a sterile inoculum with equivalent organic content was given to half of the surface sterilized samples (SS) in order to compare the relative decomposition potential of internal fungi. To control for differing internal fungi, a subset of ecto- and nonmycorrhizal roots was autoclaved (A). To estimate the importance of architecture on decomposition a set of autoclaved groups was finely ground (AG). Results of t tests (assuming unequal variances) comparing each group of EM and nonmycorrhizal roots (n = 5) are as follows: †P < 0.10; **P < 0.01; NS, no significant difference.

roots were collected in early summer, the very driest part of an extreme drought. Previously, a similar incubation (but without the above sterilization controls) was performed on *P. edulis* roots collected in the winter, a much wetter time. In this case, the EM roots, with native associated community intact, decomposed more quickly than nonmycorrhizal roots, implying that the seasonal viability of the fungus could contribute to the root decomposition rate. In a laboratory culturing study, Kerley and Read (1998) found that more N was mineralized from substrate consisting of ericoid mycorrhizal than nonmycorrhizal root necromass, but only in the presence of viable ericoid mycorrhizae and a host plant. Similarly, the decomposition of EM root litter may in some cases depend on presence of viable fungal hyphae (see *Feedbacks*).

Extramatrical Products

We have discussed the apparent mycorrhizal role in root decomposition, but their greatest influence may be manifested outside the root. Up to one-fifth of anabolized photosynthate may enter the soil in the form of mycorrhizal hyphae (Finlay and Söderström 1991). The direct inputs to the rhizosphere merit particular attention (Table 3). In this section we describe the qual-

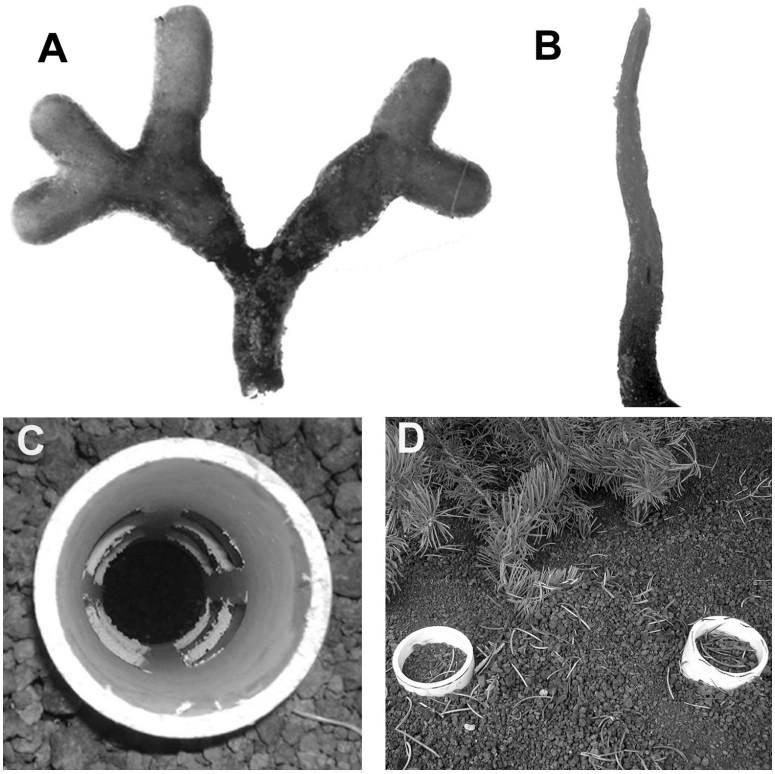

PLATE 1. Comparative architecture of (A) an EM root and (B) an uncolonized fine root of *Pinus edulis*. We placed equivalent masses of each root type in litter bags and buried them under pinyon canopies at Sunset Crater National Monument, near Flagstaff, Arizona. Subsets of litterbags were placed in decomposition cores (C and D). The cores have open windows covered with 45-μm nylon mesh to allow hyphal infiltration and exclude growing roots (C). One core from each pair (D) is periodically rotated to sever and thus exclude ingrowing hyphae as well. This experiment allowed us to examine the interaction between EM status of decomposing roots and the presence of viable, connected EM hyphae on root decomposition. Photo in panel (A) courtesy of K. Haskins; panels (B–D), A. Langley.

TABLE 3. The influence of extramatrical inputs on rhizosphere activity.

Mycorrhizal type	Effect on microbial activity	Reference
Arbuscular	Three times the bacterial CFUs in rhizoplane of AM+ plants.	Meyer and Linderman (1986)
	Proportion of assimilate in belowground respiration twice as high in AM+ as AM−.	Jakobsen and Rosendahl (1990)
	No AM effect after 30 d with live hyphae. Subsequent plant-free soil incubations from AM+ treatment had increased bacterial activity through 17 d.	Olsson et al. (1996*a*)
	Approximately 5% of fixed C was transported through AM fungi and respired within 21 h. Could not distinguish between AM hyphal and heterotrophic CO_2 production.	Johnson et al. (2002)
Ectomycorrhizae	EM+ roots supported bacterial types with more complex nutritional requirements.	Katznelson et al. (1962)
	Bacterial counts of EM+ roots could be higher or lower than EM− roots depending on morphotype.	Neal et al. (1964)
	Increased root/ectomyocrrhizal respiration. Fate of exudates and mycorrhizal products not examined.	Rygiewicz and Anderson (1994)
	EM presence decreased bacterial numbers and reduced rates of bacterial activity.	Olsson et al. (1996*b*)
	No change in nematode abundance with EM addition despite greater root mass. Considered EM structures to be recalcitrant C sink.	Setälä et al. (1999)

ities of EM and AM extramatrical products, and their influence on organic matter decomposition, highlighting studies that have isolated the influence of mycorrhizal inputs on rhizosphere activity.

Hyphae

Both AM and EM hyphae (Finlay and Söderström 1991) can comprise the largest portion of soil microbial biomass depending on the type of system. The quality of hyphae as a microbial substrate is not known, but morphological differences between fungal phyla may indicate patterns of relative decomposability among mycorrhizal fungi. AM-forming fungi, which are glomeromycetes, produce large-diameter, thin-walled hyphae that have no cross-wall barriers to stem the leakage of cytoplasm if a cell wall is breached by soil organisms or disturbance. Ectomycorrhiza-forming fungi, which are dikaryomycetes, typically have thinner hyphae with thicker walls that protect cytoplasm with septa between cells (Kendrick 2000). They commonly form rhizomorphs, aggregates of hyphae with radial specialization, that decrease their surface area to volume ratio. Based on these morphological characteristics, EM hyphae would seem more resistant to microbial degradation.

AM and EM hyphae may differ in chemical quality as well. Extracting hyphae purely from one type of fungus in quantities large enough to perform conventional chemical analyses is extremely difficult. Recent advances in particle-induced x-ray emission (PIXE) in conjunction with microscopic imaging techniques have afforded refined estimations of chemical composition of individual field-grown mycorrhizal hyphae (Weiersbye et al. 1999, Wallander et al. 2002). These few analyses have reported extremely variable values for some elements and are highly dependent on the substrate in which hyphae were grown. The available results suggest that EM hyphae may have lower concentrations of nutrients such as Ca and K than AM hyphae (Table 2), which may indicate a relatively high ratio of recalcitrant structural to labile cytoplasmic components in EM fungi.

Hyphal and root exudates

Along with root and hyphal products, root exudation is an important pathway of organic matter deposition into soil, though they are infrequently considered a component of plant litter. Root systems can exude a large portion of photosynthate in the form of simple compounds like sugars, amino acids, and organic acids (Grayston et al. 1996). Arbuscular mycotropic plants tend to exude more rich sugars than nonmycorrhizal plants under mycorrhizal-sterile conditions, but reduce upon colonization (Schwab et al. 1984), indicating a potential tradeoff between root exudation (flux 8 in Fig. 1) and mycorrhizal C sink activity (mycorrhizal C pathways 7, 9, 10). Mycorrhizal colonization, however, can increase total the amount of exudates (both fluxes 8 and 9, in Fig. 1) by increasing photosynthetic rates and directing higher proportions of photosynthate belowground. It is not known how much exudation originates from the plant and how much is from associated fungi (Grayston et al. 1996). Much less work has been done regarding the effects of EM fungi on exudation from tree roots. Many of the proteinaceous exudates from EM fungi are in the form of proteolytic, cellulytic and lignolytic enzymes (Harley and Smith 1983), compounds that could deter other potential decomposers.

A tremendous advance in the recognition of the influence of external mycorrhizal products on soil C has been the discovery and study of glomalin, a glycoprotein produced by AM hyphae (Wright and Upadhyaya 1996). In addition to the indirect consequences of soil structure for soil C cycling, Rillig et al. (2001) have recently acknowledged the direct inputs of recalcitrant C inputs in the form of glomalin. Using ^{14}C over a Hawaiian chronosequence they estimated the mean turnover time to be roughly on the scale of a decade. This exudate represents a recalcitrant pool that builds up and disappears slowly and has primarily been implicated in maintaining soil structure. Whereas AM hyphae may be readily labile, production of glomalin may retard turnover of soil carbon. The balance of the two apparently opposing influences on total soil C processing is not known.

Mycorrhizal influence on rhizosphere C processing

Photosynthate transported belowground can immediately enter the soil in the form of exudates and fungal tissues, both of which may be subject to rapid heterotrophic degradation. The distinction between this pathway of soil respiration and root/mycorrhizal respiration may be a semantic one, and teasing the two apart presents a daunting technical obstacle, particularly in the field. Using root-free hyphal compartments and controlled inoculations, it is possible to make inferences about the influence of mycorrhizal colonization on the quantity and quality of these ephemeral inputs. Laboratory microcosms employing such techniques have contributed evidence about the direction of mycorrhizal influence on C processing. Because of the short observation period of these experiments, the contribution of root input is negligible. More rapid pathways of photosynthetic input into soil, hyphae and exudation, drive patterns of energy flow into soil.

Olsson et al. (1996*a*, *b*) measured microbial thymidine and leucine incorporation to assess microbial activity. Inoculation with each of six EM fungi suppressed bacterial numbers and activity in *Pinus contorta* pots. The pattern was attributed to a diversion of C from rich exudates into recalcitrant EM structures. In a similar experiment, they found that live AM associations had no effect. However, rhizospheric soil around colonized roots did support greater activity when removed from the plant, than uncolonized roots. These results suggest that dead AM hyphae and as-

sociated products decompose easily compared to other belowground sinks such as EM hyphae and root exudates. Setälä et al. (1999) inoculated *Pinus sylvestris* microcosms with fungi and different guilds of nematodes. The presence of EM fungi greatly increased the flow of C below ground, but the energetic increase did not cascade up to fungivores and predators. This study, too, concluded that EM fungi tied up C in relatively inaccessible pools.

Ecologists have contrastingly regarded dead hyphae as labile (e.g., Fitter et al. 2000, Lindahl et al. 2002) and recalcitrant (e.g., Setälä et al. 1999, Treseder and Allen 2000) despite the lack of published reports of hyphal decomposition rates. Taken together, the studies above demonstrate that mycorrhizae can redistribute soil C within the rhizosphere, and the ultimate fate of that C may depend on mycorrhizal type. Based on their chemistry, architecture, and influence on microbial activity, we propose that EM products are less labile than AM ones. Equally as important and elusive as hyphal decomposition are the effects of mycorrhizal status on C allocation to, and fate of, alternative C pools. For instance, if EM inoculation depresses rhizospheric microbial activity in a short-term incubation (in which root turnover is negligible) as in Setälä et al. 1999, then either EM hyphae or EM exudates must be recalcitrant compared to the C exuded from roots of nonmycorrhizal plants (in Fig. 1, the sum of fluxes 4 and 5 must be $<$ flux 3).

Translating the effect of hyphal inputs from microcosms to intact ecosystems is further complicated by the other influences imposed by mycorrhizal hyphae, which can alter soil factors and host physiology, indirectly affecting soil C processing (Olsson et al. 1996*b*). The production, functions and fates of mycorrhizal hyphae and mycospheric exudates remain difficult to investigate, particularly in intact ecosystems. Controlled inoculum and substrate laboratory studies like those above have outlined the parameters of mycorrhizal potential to influence C quality and processing in the rhizosphere. The use of isotope tracers and gas exchange techniques in tandem with soil meshes that allow ingrowth of hyphae but exclude roots has recently provided promise for investigating the effects of mycorrhizal status on belowground C processing rates even in the field (Johnson et al. 2002).

Feedbacks

Ecologists have recently recognized the relationship of plant mycorrhizal status and plant C cycling traits (Cornelissen et al. 2001), as well as the importance of senescent mycorrhizal hyphae in ecosystem N cycling (Lindahl et al. 2002). It is commonly hypothesized that plant species can influence C and nutrient cycling via inputs of aboveground litters (Hobbie 1992) which can feed back to influence plant competition (Berendse 1994). We contend that mycorrhizal influence on belowground litter quality may contribute to such plant–litter–soil feedbacks.

Belowground litter production often exceeds that aboveground (Fogel and Hunt 1983, Hendricks et al. 1993) and may have an inordinate importance because it is deposited below the soil surface where microenvironments are often more favorable for rapid nutrient release and uptake (Berg 1984). Unlike most aboveground tissues, different portions of root systems can grow and die simultaneously in close proximity and so, plant root litter decomposition dynamics could have important feedbacks directly to the nutrient availability for an individual plant. We hypothesize that inputs of mycorrhizal litter can directly influence nutrient availability in the soil environment where they occur and these influences feed back to the nutrition and productivity of the host plants and possibly to the composition of plant communities.

Nitrogen cycling

Based on laboratory and field decomposition studies, EM fungi, through their alteration of roots and rhizosphere products, appear to render belowground litters less accessible to N mineralizing microorganisms. In actual ecosystems, intact hyphal networks may partially compensate for the ''poor'' litter quality apparent in litterbag studies, which disturb the soil, by rapidly mobilizing hyphae with specialized enzymes to the site of degradation (Leake et al. 2001). It has long been recognized that mycorrhizal fungi may directly mineralize organic N and transfer it to host plants (Went and Stark 1968). Direct mineral cycling by mycorrhizal fungi will be significant in systems where litter quality is poor and nutrients are not readily available to free-living heterotrophs (Read 1991). For instance, Northrup et al. (1994) proposed that pines produce litter with high phenolic content that may be relatively more accessible to the ectomycorrhizae that are associated with the pine than to other microbes and plants. We believe this direct mycorrhizal mineralization could be much tighter and quite common in litters deposited underground.

EM fungi appear to produce recalcitrant litters and are well positioned to first access the nutrients therein. They have close proximity to senescing root tissues as well as an enzymatic specialization in degrading plant cell walls (Cairney and Burke 1994), and some ability to digest fungal ones like chitin (Leake and Read 1990). Accordingly, intramatrical EM hyphae, unlike other types of mycorrhizal hyphae, appear to remain viable throughout root senescence (Harley and Smith 1983). If EM hyphae remain connected to viable roots, a host plant could subsidize the fungus with C and energy that free-living organisms must obtain from soil substrates (Harley 1971). Indeed, hyphal connections from live to dead roots are commonly observed (Went and Stark 1968). Live EM hyphae are also well positioned to first colonize and efficiently exploit other mycorrhizal hy-

phae as a nutrient source (Lindahl et al. 2002). The sum of this evidence indicates that ectomycorrhizae may largely contribute to their own mineralization in soil. This internalized mycorrhizal recycling could have implications for N competition among plants and soil heterotrophs (Kaye and Hart 1997).

In systems where N is limiting, conservative plants can retranslocate up to half of foliar N upon leaf senescence, but are not believed to retranslocate significant amounts of N or P from senescing roots (Nambiar and Fife 1991, Gordon and Jackson 2000). Fine roots of perennial plants grow and die simultaneously. EM associations, by directly accessing nutrients in dead roots, may allow an individual plant to ''reallocate'' crucial nutrients from inefficient or dying roots/mycorrhizae to support new tissues incurring only an energetic cost. Likewise, EM hyphal networks could transfer nutrients from dead roots of one plant, to other live plants of the same or different species (Harley and Smith 1983). As well as preserving N for individual plants, the accumulation of N-rich recalcitrant EM structures could represent a mechanism for N retention in forest ecosystems. Temperate coniferous forests, where EM fungi occur in great abundance, tend to retain higher proportions of N inputs than temperate broadleaf forests (broadleaf systems have 7.8 times higher leaching rates than coniferous forests but only 2.7 times the inputs; summarized from Johnson 1992 and references therein). Though other mechanisms are certainly active, we believe that EM immobilization can contribute to the retentive properties of EM dominated systems.

Plant community dynamics

A plant species, by altering abiotic resources and soil communities, can render the affected soil more or less suitable for its own propagation, thereby potentially affecting plant succession and maintenance of plant diversity within a system (Bever et al. 1997). For example, it has been suggested that the changes in the quality of aboveground litter inputs, from herbaceous to woody litters, during succession may lead to the shift from AM to EM plants, the latter of which can access more recalcitrant organic compounds, in temperate forest systems (Pankow et al. 1991). Belowground plant products enter the soil in close spatial and temporal proximity to nutrient uptake and could drive such feedbacks. The differences between belowground litters produced by AM and EM plants could also contribute to such patterns observed throughout ecosystem development. EM roots can account for up to 5% of organic mass in soil, but the turnover of EM roots can account for 50% of organic matter throughput in coniferous forests; hyphae (mostly EM) may contribute another 31% of total throughput (Fogel and Hunt 1983). The accumulation of EM detritus could sequester large portions of ecosystem N in recalcitrant organic forms. Plants that rely on readily available mineral N for growth may give way to those that can access the nutrients bound in EM structures. Mycorrhizal influence on belowground litter quality, coupled with mycorrhizal control of plant ability to access that litter, could represent an important feedback pathway influencing plant community diversity and dynamics.

Consequences for ecosystems

EM root and fungal structures, owing to chemical and structural qualities, appear to be more recalcitrant than AM structures. These differences could have important consequences for explaining ecosystem-level C cycling among system types. Forests with dominant trees reliant on EM fungi, tend to have higher proportions of litter from belowground sources (Vogt et al. 1986) and lower rates of total soil respiration than other forest types when controlling for covarying soil and climatic factors (Raich and Tufekcioglu 2000). Large amounts of mycorrhizal litter could contribute to slower heterotrophic respiration rates in EM dominated ecosystems. Such systems also have higher proportions of soil respiration from autotrophic sources, namely roots and mycorrhizae (reviewed in Raich and Tufekcioglu 2000), also suggestive of mycorrhizal domination of soil activity. Mycorrhizal processing of belowground litter that is relatively inaccessible to free-living heterotrophs could contribute to these global patterns in soil processes.

Effects of mycorrhizae on decomposition could also be important in light of ongoing global environmental change. For both AM and EM species, the degree of mycorrhizal infection is sensitive to a number of anthropogenic perturbations, including N deposition, elevated CO_2, ozone, and land-use change, to name a few (reviewed in Cairney and Meharg 1999). The implications of such changes in mycorrhizal infection for plant nutrient acquisition, water relations, and pest resistance has been studied extensively (Harley 1971, Smith and Read 1997). Additionally, however, through the mechanisms outlined here, such changes in mycorrhizal status could also modulate the effects of these environmental changes on decomposition and soil C processing. Shifting allocation to AM structures under elevated CO_2, for example, has been predicted to increase soil C sequestration in fungal products (Treseder and Allen 2000). Though glomalin appears to sequester C because of its recalcitrant nature (Rillig et al. 2001), enhanced AM hyphal production could stimulate soil microbial activity causing a net acceleration of CO_2 return to the atmosphere (as seen in Jakobsen and Rosendahl 1990, Olsson et al. 1996*a*). Similarly, we have argued above that morphological and chemical characteristics of EM structures and associated hyphae may retard their decomposition compared to uncolonized roots or root exudates. If this is the case, increased allocation to EM structures in response to elevated CO_2 could slow soil carbon turnover. Other factors that influence mycorrhizal status, such as herbivory (Gehring

and Whitham 1991) and natural disturbance (Harley 1971), could also elicit indirect effects on decomposition and soil carbon processing.

To our knowledge, the hypotheses outlined here have neither been tested nor articulated previously, yet anomalous patterns of fine root decomposition, suggest that mycorrhizae could be important for fine root decomposition in many terrestrial ecosystems. Likewise, the fate of extramatrical mycorrhizal products (hyphae, exudates) in soils remains unknown but warrants further experimental attention. Each belowground product must be examined a context that allows for identification of complex feedbacks to communities and ecosystems.

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