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The Role of Arbuscular Mycorrhiza Fungi in the Decomposition of Fresh Residue and Soil Organic Carbon: A Mini-Review

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Abstract

Arbuscular mycorrhizal fungi (AMF) are widespread in terrestrial ecosystems. In addition to their contributions to plant nutrient uptake, AMF also provide many ecological functions including regulation of soil C dynamics. However, both stimulating and retarding soil organic decomposition by AMF have been observed. Here we discuss the possible reasons for such a contradiction. Arbuscular mycorrhizal fungi contribute to soil aggregation mainly through hyphal enmeshment, saprotrophic suppression, and production of glomalin-related soil proteins, while AMF can also stimulate organic decomposition through promoting degradative enzymes, modifying root production and activity, and/or through regulating the microbial community in the mycorrhizosphere and hyphosphere. The role of AMF in C decomposition is strongly dependent on the quality and quantity of different soil C pools. Arbuscular mycorrhizal fungi can stimulate fresh residue decomposition initially through stimulating the decomposition of fresh residues (particularly those having high C/N ratio), whereas for older or decomposed soil organic C, AMF tend to suppress decomposition by promoting soil aggregation. Under elevated CO₂ (eCO₂), AMF show additive effects on residue decomposition, priming effects, and changes in soil aggregation. Despite organic decomposition rates differing in the short term and long term following litter experiments, our discussion highlights the role of AMF in organic C dynamics. We hypothesize that AMF would benefit soil C gain in the long term and thereby predict that disturbances that impacts negatively on AMF, such as tillage, residue burning, fertilization, and fungicide application, would lead to soil C decline particularly under eCO₂.

Abbreviations: AMF, arbuscular mycorrhizal fungi.

Soil is the major long-term C pool in terrestrial ecosystems (60). A shift in the decomposition rate of soil C could lead to profound changes in ecosystem C storage (29). Arbuscular mycorrhizal fungi are associated with greater than 200,000 plant species, including most herbs and grasses, and many trees and hornworts, representing more than 80% of terrestrial plant species (66). Notably, under elevated atmospheric CO₂ (eCO₂), the growth of AMF and their colonization rate generally increase (17; 11). Given their ubiquitous distribution and their capacity in controlling soil C dynamics (50; 72; 11; 10), understanding how AMF influence soil C balance is crucial to predict future global C dynamics. However, studies have observed both stimulating and retarding effects on organic C decomposition by AMF presentation. To untangle the contradiction, we focused our discussion on different C pools—fresh residues and old soil organic C. We also included litter quality (C/N ratio) and climate change effects in our discussion given their intimate involvement in the regulation of organic C pools.

THE ROLE OF ARBUSCULAR MYCORRHIZAL FUNGI IN ORGANIC DECOMPOSITION

Contribution to Soil Aggregation

Arbuscular mycorrhizal fungi can facilitate soil aggregation and contribute to soil stability through their extensive hyphae system (50; 51; 37). A hypothetical framework based on the aggregate hierarchy hypothesis (63; 46) in coupled with a “life cycle” conceptual model (58) describes the involvement of AMF hyphae in the soil aggregation process. Namely, macro-aggregates (250–2500 µm in diameter) are formed first and hyphal enmeshment helps to stabilize the macro-aggregates (50; 51; 37; Fig. 1). This is followed by the formation of micro-aggregates (<250 µm) within macro-aggregates with the aid of biological binding agents, including glomalin-related soil proteins which is produced by the hyphal of AMF (58; 57; 15; Fig. 1). Using a stable isotope-tracing technique, an

incubation study provided direct evidence to confirm the process of residue retention within macro-aggregates (48). The study shows that macro-aggregates are formed initially and enriched in ^{13}C and ^{15}N when ^{13}C - ^{15}N -labeled corn residues applied, and then the accumulation of ^{13}C and ^{15}N continued throughout the incubation. The results show micro-aggregates are enmeshed within macro-aggregates and become highly persistent due to the protection created by spatial effects of occlusion (58, 57; 48).

Figure 1. The role of hyphal enmeshment and glomalin-related soil protein (GRSP) in soil aggregation.

The role of AMF in soil aggregation described in this conceptual framework has been also confirmed indirectly by empirical studies. For example, soils with less AMF (i.e., treated with a fungicide) have a significant delay in macro-aggregate formation compared with the untreated soils (30). A long-term (17 and 6 yr) ecosystem-scale study shows that soil aggregation and C sequestration

are tightly correlated with the abundance of AMF in multispecies prairie communities (72). By using a root experiment, a direct positive effect of AMF hyphae on soil aggregate formation has been found (35). Modeling simulation results indicate that AMF combined with organic matter and plant roots are key contributors to aggregate formation in soils (15). These studies and others (e.g., 52; 5; 47) confirm the role of AMF in aggregate formation and persistence.

Stimulation of Organic Carbon Decomposition

In contrast to traditional understanding of the effect of residue inputs on soil C, recent field experiments find soil C loss after fresh residues input accompanied by increased hyphae growth (31; 11). However the mechanisms behind these observations are not well described. It has been shown that AMF mycelium can excrete hydrolytic enzymes, such as cellulase, pectinase, and xyloglucanase, but no direct evidence has been presented to show saprotrophic ability (21; 22; 67; 64). Arbuscular mycorrhizal fungi exudates could trigger priming effects, but this is thought to be negligible compared with root exudation and root litter inputs (56). This could suggest that there are indirect mechanisms through which AMF promote organic C decomposition (Fig. 2).

Figure 2. Three proposed pathways via which arbuscular mycorrhizal fungi (AMF) stimulate organic decomposition

114 Alkaline phosphatase activity has been shown to increase in leaf litter and soil in the presence of
 115 AMF (33). Another P - related enzyme phosphomonoesterase shows higher activity in the presence
 116 of AMF vs. in their absence (45). These may be attributed to external hyphae, which can either
 117 directly produce phosphatases or stimulate phosphatase production by other microorganisms (45). In
 118 addition, AMF can also modify the composition of plant - derived organic acids. For example, in
 119 exudates of *Glomus intraradices* inoculated roots, significantly higher concentrations of proline and
 120 isocitrate are observed than in non - colonized roots (40). Further, the community composition of soil
 121 microorganisms could be impacted by AMF through the production of exudates, modification of
 122 rhizodeposition products, and alteration of soil structure (52; 3).

123

124 **OPEN QUESTIONS AND DISCUSSION**

125

126 In the presence of AMF, C loss commonly increases in the short term following new residue inputs
 127 (31; 11), whereas the mycorrhizal influence on C stabilization during litter decomposition is generally
 128 persistent over time (68). Therefore, our below discussion will focus on different C pools potentially
 129 affected by AMF.

130

131 **Different Carbon Pools**

132

133 A comparison of litter decomposition between “fresh” and “old” litters (the old litter had been
 134 incubated for 3 mo and thus had passed through an initial stage of decomposition) shows that the
 135 addition of old residues results in more retention of litter - derived C and N in soils compared with
 136 the application with fresh residues (68). One possible explanation for this observation comes from
 137 model simulation result that suggests that the application of mycorrhizal fungi (mixed
 138 ectomycorrhizal and AMF) leads to the increased storage of particulate organic C over the long -

139 term (43). This may indicate that the role of AMF in soil C balance may depend on them affecting
140 different C pools (4). However, the role of nutrients, particularly P, in the litter and soil is rarely
141 considered in these simulation exercises.

142 The increase in the activity of alkaline phosphatase in soil following plant litter application often
143 leads to the suppression of the activity of alkaline phosphatase occurs in the absence of fresh litter,
144 despite the presence of mycorrhiza (33). A recent forest study found that the presence of AMF
145 mycelia increases the activity of phosphomonoesterase in an ingrowth core without leaf litter addition,
146 but not in the presence of new/fresh leaf litter (45). In addition to the change in enzyme activity, AMF
147 can also alter soil microbial community composition during litter decomposition (64). The
148 competition for C and nutrients can occur between AMF and saprotrophs and between
149 ectomycorrhizal and saprotrophic fungi known as the “Gadgil effect” (19). The presence of AMF
150 leads to a reduction in plant - C release to soil (20) followed by a reduction in nutrient availability to
151 saprotrophs due to the intensified competition for C and nutrients by AMF (55). Other studies support
152 this observation that AMF suppresses the growth of microbes by competing for nutrients which can
153 lead to the overall slowing of decomposition activity (31; 6). For example, AMF can suppress Gram -
154 positive and Gram - negative bacteria, and the actinomycetes (27). Further, AMF can prolong
155 decomposition by negatively affecting decomposers overall through competition for limited resources
156 (27). These results suggest that AMF stimulate the decomposition of fresh residue, while suppressing
157 the decomposition of old residue and soil C (Fig. 3).

Figure 3. Conceptual diagram of the differential roles of arbuscular mycorrhizal fungi (AMF) in organic decomposition of different carbon pools: fresh residue, old residue, and soil organic matter (SOM).

Carbon/Nitrogen Ratio of Organic Residue

The quality of plant residues is a controversial topic in describing factors affecting decomposition. The widely accepted view is that the ratio of C/N and/or the labile to recalcitrant fraction is a crucial regulator of decomposition (12; 28). Commonly, studies find that AMF stimulation of plant residue decomposition applies both to leaf or fine - root sources (31; 3; 36; 11). However, an increase in soil aggregation and C retention was demonstrated for woody plant litter decomposition compared to leaf litter (35). A likely explanation for the results is that a higher proportion of recalcitrant compounds such as cellulose and lignin in the woody structures compared to leaf litter (42) could contribute to the occluded particulate fraction within aggregates. In addition, microorganism uses the labile

fraction more efficiently than the recalcitrant fraction (56) preferentially leaving recalcitrant soil and plant residue C sources alone. Therefore, the fate of plant residue C in the presence of AMF also depends on whether fresh organic residues have the opportunity to be decomposed or to be incorporated into soil aggregates. Recalcitrant residues slow the decomposition rate in the absence of available soil resources and allows for a greater probability of occluding particulate C within aggregates (70).

Some modeling studies indicate that recalcitrant materials are not necessary for soil organic matter formation (18). These studies indicate that some fast - cycling fractions of soil organic matter are comprised of a mixture of plant compounds that include plant lignin and carbohydrates (16). There has no clear explanation for this phenomenon, but it may be related to the high N demand of AMF (32). Experimental work has increasingly demonstrated that AMF hyphae preferentially colonize decomposing organic patches and to acquire N directly from the decomposing materials (31; 3; 36). The N acquisition from organic materials can account for up to 31% of fungal N (32). In support of high N demand, it is shown that arginine - N transport in the mycelium (23) and a mycorrhiza - specific ammonium transporter are preferentially activated in AMF hyphae (26). More recent evidence indicates that the N needed by AMF can be used preferentially before being transferred to its plant host (32). Accordingly, hyphae may stimulate decomposition irrespective of the ratio of labile to recalcitrant residues when N is limiting. For example, a lignin - degrading enzyme was found to be positively correlated with mycorrhizal biomass and AMF may promote lignin degradation to access N (39).

These results are supported partly by the observation that high soil N availability reduces the development of AMF extraradical hyphae (41). This can be associated with the obligate need for C from associated plant roots, which allows mycorrhizal fungi to forego the need for C from soils to build their own biomass (59). This has led to the acceptance and conclusion that C - rich and nutrient - poor compound, such as cellulose, would not to be degraded by mycorrhizal fungi. This is

also supported by the negative correlation of AMF spore density with the activity of β - glucosidase (which is involved in cellulose decomposition) and the content of soil organic C (14). A decline in mycorrhizal mycelial abundance and an increase in free - living saprotrophic fungi when hyphal connections to roots are severed suggest that mycorrhizae have the ability to repress C availability to free - living microbes that can compete with ectomycorrhizal fungi (38). However, the relationship between AMF and cellulose decomposition vary with AMF species. Cellulose can increase the amount of external mycelium of *G. intraradices* and *G. mosseae* but conversely the decrease in hyphal growth and P uptake by *G. intraradices* was also found (49). The decomposition of cellulose is time dependent. Cellulose reduces the growth of AMF initially, then increases growth over a longer time period (25). The increased AMF growth with cellulose amendment may be related to a priming effect of saprotrophic microorganisms that solubilize inorganic nutrients, which is essential for AMF hyphal growth (71). Secondary metabolites produced by microorganisms during decomposition of cellulose can also be a contributor to AMF growth (24). These synergistic decomposer/resource availability outcomes influence the maintenance and growth of the entire microbial community and are often overlooked in microbial interaction studies. Future research should address these dependencies of resource availability of different microbial groups during the decomposition process.

Elevated Carbon Dioxide Effects

The effects of eCO₂ on microbial processes have attracted a lot of interest from researchers. Many studies have looked into the growth and proliferation of AMF under eCO₂, and found a consistent positive response of AMF to eCO₂ despite the varied responses among different genera of AMF (53; 65; 11). The AMF response to eCO₂ is often the production of a significantly higher number of spores, development of significantly longer hyphal lengths, and increasing colonization of roots (34). Some genera show higher spore number and hyphal lengths but not an increase in the colonization rate (34).

222 Comparatively, total mycorrhizal biomass may be a stronger indicator for eCO₂ effect than
 223 colonization rate, because colonization rate is related both with mycorrhizal fungi and root length
 224 which can be increased proportionally under eCO₂ (65). A meta - analysis indicates that total biomass
 225 of AMF can be increased approximately 50% under eCO₂ (65). Carbon dioxide enrichment strongly
 226 affects external hyphae compared to the internal hyphae, indicating that it promotes C allocation to
 227 the external AMF hyphal biomass (54; 61; 2). Therefore, it is expected that eCO₂ will likely affect
 228 AMF outcomes in controlling soil C dynamics.

229 Elevated CO₂ effects on the decomposition of fresh litters vary mainly with litter quality and soil
 230 nutrient regimes (13; 7). A meta - analysis including the data from field experiments shows no
 231 consistent pattern in either mass loss or respiration rates from litter produced under eCO₂ compared
 232 to litter from ambient CO₂ conditions (44). Whatever positively or negatively affects fresh litter
 233 decomposition by eCO₂, the increased rhizodeposits under eCO₂ could lead to an acceleration of soil
 234 microbial growth and decomposition of older soil organic C fractions (i.e., “the priming effect”)
 235 regardless of nutrient availability (1; 8; 69). In the presence of AMF, both short - term microcosm
 236 experiment and field studies show that eCO₂ enhances the decomposition of soil organic C with varied
 237 responses among different AMF species (11). These studies also find that eCO₂ significantly
 238 increases AMF colonization with fine roots and their hyphae in bulk soil, resulting in a considerable
 239 reduction of total N within hyphae - ingrowth bags and cores and a synchronal increase in plant N,
 240 which may be because by the eCO₂ effects, namely the scavenging of N by AMF (11). Therefore, the
 241 amount of available soil N is likely a major outcome in mediating belowground C turnover under the
 242 interactive effects of eCO₂ on AMF.

243 When mineral nutrients are available, eCO₂ can reduce priming effects, because soil
 244 microorganisms shift from consuming older soil organic C pools to utilizing easily degraded
 245 rhizodeposits (7). The presence of AMF enhance the suppression of eCO₂ on the decomposition of
 246 soil organic C, but such suppression is reduced when AMF community is absent (9), indicating that

the AMF influence under eCO₂ promotes C storage. When soil C pools are partitioned into particulate organic matter and mineral - bound C pools, eCO₂ significantly enhances the breakdown of soil particulate organic matter and increases mineral - bound C pools (7). Due to lack of the studies that partition soil C pools into particulate organic matter and mineral - bound C pools in the presence of AMF, how AMF interactively affect with eCO₂ on these soil C pools is not well characterized, which warrants further investigation. Overall, eCO₂ could enhance fresh residue decomposition, priming effect, and soil aggregate formation through promoting AMF growth and their colonization (Fig. 4).

Figure 4. The hypothetical relationships between elevated CO₂, arbuscular mycorrhizal fungi (AMF), priming effect or soil aggregation. (The CO₂ curve was cited from the Scripps Institution of Oceanography at the Mauna Loa Observatory in Hawaii; The conceptual framework of soil aggregation was modified from 58).

258

CONCLUSIONS

260

261 The role of AMF in regulation of soil C dynamics is C pool dependent. Stimulation of fresh residue
 262 decomposition occurs only in the short term following in the presence of labile or N - rich fresh
 263 residues, whereas in the longer term, AMF tend to promote the retention of organic C into soil
 264 aggregates. It should be noted that our discussion does not include the effect of the turnover of AMF
 265 hyphae. The turnover of extra - radical mycelium of AMF is commonly rapid (live only 5 - 6 d; 62),
 266 thereby mycorrhizae may act as a substantial pathway of C flow to the soil. Despite potential to
 267 sequester soil C by AMF, studies show that most of the C in the hyphae is rapidly recycled back to
 268 the atmosphere (62). Therefore, this C loss can be underestimated. To quantify the specific
 269 contributions of AMF in soil C dynamics, we strongly suggest that studies on organic C
 270 decomposition should take into account the time scales, the proximate constituent, and N content of
 271 plant residues. Finally, synergistic outcomes of decomposer/resource availability influences AMF
 272 biomass and colonization through affecting the maintenance and growth of the entire microbial
 273 community. Future research should address the effect of resource availability on the performance of
 274 different microbial groups during the decomposition process that affect AMF.

275

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277

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280

281 **REFERENCES**

282

283 1 Allard, V., Robin, C., Newton, P.C.D., Lieffering, M., and Soussana, J.F.. 2006. Short and long-
 284 term effects of elevated CO₂ on *Lolium perenne* rhizodeposition and its consequences on soil organic

- 285 matter turnover and plant N yield. *Soil Biol. Biochem.* 38 (6): 1178– 1187. doi:
 286 <https://doi.org/10.1016/j.soilbio.2005.10.002>
- 287 2 Antoninka, A., Reich, P.B., and Johnson, N.C.. 2011. Seven years of carbon dioxide enrichment,
 288 nitrogen fertilization and plant diversity influence arbuscular mycorrhizal fungi in a grassland
 289 ecosystem. *New Phytol.* 192 (1): 200– 214. doi: <https://doi.org/10.1111/j.1469-8137.2011.03776.x>
- 290 3 Atul-Nayyar, A., Hamel, C., Hanson, K., and Germida, J.. 2009. The arbuscular mycorrhizal
 291 symbiosis links N mineralization to plant demand. *Mycorrhiza* 19 (4): 239– 246. doi:
 292 <https://doi.org/10.1007/s00572-008-0215-0>
- 293 4 Ball, B.A., Carrillo, Y., and Molina, M.. 2014. The influence of litter composition across the litter–
 294 soil interface on mass loss, nitrogen dynamics and the decomposer community. *Soil Biol. Biochem.*
 295 69: 71– 82. doi: <https://doi.org/10.1016/j.soilbio.2013.10.048>
- 296 5 Bedini, S., Avio, L., Sbrana, C., Turrini, A., Migliorini, P., Vazzana, C., and Giovannetti, M.. 2013.
 297 Mycorrhizal activity and diversity in a long-term organic Mediterranean agroecosystem. *Biol. Fertil.*
 298 *Soils* 49 (7): 781– 790. doi: <https://doi.org/10.1007/s00374-012-0770-6>
- 299 6 Brooks, D.D., Chan, R., Starks, E.R., Grayston, S.J., and Jones, M.D.. 2011. Ectomycorrhizal
 300 hyphae structure components of the soil bacterial community for decreased phosphatase production.
 301 *FEMS Microbiol. Ecol.* 76: 245– 255. doi: <https://doi.org/10.1111/j.1574-6941.2011.01060.x>
- 302 7 Cardon, Z.G., Hungate, B.A., Cambardella, C.A., Chapin, F.S. III, Field, C.B., Holland, E.A., and
 303 Mooney, H.A.. 2001. Contrasting effects of elevated CO₂ on old and new soil carbon pools. *Soil Biol.*
 304 *Biochem.* 33 (3): 365– 373. doi: [https://doi.org/10.1016/S0038-0717\(00\)00151-6](https://doi.org/10.1016/S0038-0717(00)00151-6)
- 305 8 Carney, K.M., Hungate, B.A., Drake, B.G., and Megonigal, J.P.. 2007. Altered soil microbial
 306 community at elevated CO₂ leads to loss of soil carbon. *Proc. Natl. Acad. Sci. USA* 104 (12): 4990–
 307 4995. doi: <https://doi.org/10.1073/pnas.0610045104>

- 308 9 Carrillo, Y., Dijkstra, F.A., Le Cain, D., and Pendall, E.. 2016. Mediation of soil C decomposition
309 by arbuscular mycorrhizal fungi in grass rhizospheres under elevated CO₂. *Biogeochemistry* 127 (1):
310 45– 55. doi: <https://doi.org/10.1007/s10533-015-0159-3>
- 311 10 Cavagnaro, T.R., Bender, S.F., Asghari, H.R., and van der Heijden, M.G.A.. 2015. The role of
312 arbuscular mycorrhizas in reducing soil nutrient loss. *Trends Plant Sci.* 20 (5): 283– 290. doi:
313 <https://doi.org/10.1016/j.tplants.2015.03.004>
- 314 11 Cheng, L., Booker, F.L., Tu, C., Burkey, K.O., Zhou, L., and Shew, H.D. et al 2012. Arbuscular
315 mycorrhizal fungi increase organic carbon decomposition under elevated CO₂. *Science* (Washington,
316 DC) 337 (6098): 1084– 1087. doi: <https://doi.org/10.1126/science.1224304>
- 317 12 Cornwell, W.K., Cornelissen, J.H., Amatangelo, K., Dorrepaal, E., Eviner, V.T., and Godoy, O.
318 et al 2008. Plant species traits are the predominant control on litter decomposition rates within biomes
319 worldwide. *Ecol. Lett.* 11 (10): 1065– 1071. doi: <https://doi.org/10.1111/j.1461-0248.2008.01219.x>
- 320 13 Cotrufo, M.F., Briones, M.J.I., and Ineson, P.. 1998. Elevated CO₂ affects field decomposition
321 rate and palatability of tree leaf litter: Importance of changes in substrate quality. *Soil Biol. Biochem.*
322 30 (12): 1565– 1571. doi: [https://doi.org/10.1016/S0038-0717\(98\)00032-7](https://doi.org/10.1016/S0038-0717(98)00032-7)
- 323 14 Delelegn, Y.T., Purahong, W., Blazevic, A., Yitaferu, B., Wubet, T., Göransson, H., and Godbold,
324 D.L.. 2017. Changes in land use alter soil quality and aggregate stability in the highlands of northern
325 Ethiopia. *Sci. Rep.* 7 (1):article 13602. doi: <https://doi.org/10.1038/s41598-017-14128-y>
- 326 15 Daynes, C.N., Field, D.J., Saleeba, J.A., Cole, M.A., and McGee, P.A.. 2013. Development and
327 stabilisation of soil structure via interactions between organic matter, arbuscular mycorrhizal fungi
328 and plant roots. *Soil Biol. Biochem.* 57: 683– 694. doi: <https://doi.org/10.1016/j.soilbio.2012.09.020>
- 329 16 Derrien, D., and Amelung, W.. 2011. Computing the mean residence time of soil carbon fractions
330 using stable isotopes, impacts of the model framework. *Eur. J. Soil Sci.* 62: 237– 252. doi:
331 <https://doi.org/10.1111/j.1365-2389.2010.01333.x>

- 17 Drigo, B., Pijl, A.S., Duyts, H., Kielak, A.M., Gamper, H.A., and Koutekamer, M.J. et al 2010. Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO₂. *Proc. Natl. Acad. Sci. USA* 107: 10938– 10942. doi: <https://doi.org/10.1073/pnas.0912421107>
- 18 Dungait, J.A.J., Hopkins, D.W., Gregory, A.S., and Whitmore, A.P.. 2012. Soil organic matter turnover is governed by accessibility not recalcitrance. *Glob. Change Biol.* 18 (6): 1781– 1796. doi: <https://doi.org/10.1111/j.1365-2486.2012.02665.x>
- 19 Fernandez, C.W., and Kennedy, P.G.. 2016. Revisiting the ‘Gadgil effect’: Do interguild fungal interactions control carbon cycling in forest soils? *New Phytol.* 209 (4): 1382– 1394. doi: <https://doi.org/10.1111/nph.13648>
- 20 Fitter, A.H., Graves, J.D., Watkins, N.K., Robinson, D., and Scrimgeour, C.. 1998. Carbon transfer between plants and its control in networks of arbuscular mycorrhizas. *Funct. Ecol.* 12: 406– 412. doi: <https://doi.org/10.1046/j.1365-2435.1998.00206.x>
- 21 García-Romera, I., García-Garrido, J.M., Martínez-Molina, E., and Ocampo, J.A.. 1991. Production of pectolytic enzymes in lettuce root colonized by *Glomus mosseae*. *Soil Biol. Biochem.* 23 (6): 597– 601. doi: [https://doi.org/10.1016/0038-0717\(91\)90118-4](https://doi.org/10.1016/0038-0717(91)90118-4)
- 22 García-Garrido, J.M., García-Romera, I., and Ocampo, J.A.. 1992. Cellulase production by the vesicular–arbuscular mycorrhizal fungus *Glomus mosseae* (Nicol. & Gerd.) Gerd. and Trappe. *New Phytol* 121 (2): 221– 226. doi: <https://doi.org/10.1111/j.1469-8137.1992.tb01107.x>
- 23 Govindarajulu, M., Pfeffer, P.E., Jin, H., Abubaker, J., Douds, D.D., and Allen, J.W. et al 2005. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. *Nature (London)* 435: 819– 823. doi: <https://doi.org/10.1038/nature03610>
- 24 Gryndler, M., Hřelová, H., Cajthaml, T., Havráňková, M., Řezáčová, V., Gryndlerová, H., and Larsen, J.. 2009. Influence of soil organic matter decomposition on arbuscular mycorrhizal fungi in

- terms of asymbiotic hyphal growth and root colonization. *Mycorrhiza* 19 (4): 255– 266. doi: <https://doi.org/10.1007/s00572-008-0217-y>
- 25 Gryndler, M., Vosátka, M., Hřelová, H., Chvátalová, I., and Jansa, J.. 2002. Interaction between arbuscular mycorrhizal fungi and cellulose in growth substrate. *Appl. Soil Ecol.* 19: 279– 288. doi: [https://doi.org/10.1016/S0929-1393\(02\)00004-5](https://doi.org/10.1016/S0929-1393(02)00004-5)
- 26 Guether, M., Neuhäuser, B., Balestrini, R., Dynowski, M., Ludewig, U., and Bonfante, P.. 2009. A mycorrhizal-specific ammonium transporter from *Lotus japonicus* acquires nitrogen released by arbuscular mycorrhizal fungi. *Plant Physiol.* 150: 73– 83. doi: <https://doi.org/10.1104/pp.109.136390>
- 27 Gui, H., Purahong, W., Hyde, K.D., Xu, J., and Mortimer, P.E.. 2017. The arbuscular mycorrhizal fungus *Funneliformis mosseae* alters bacterial communities in subtropical forest soils during litter decomposition. *Front. Microbiol.* 8:article 1120. doi: <https://doi.org/10.3389/fmicb.2017.01120>
- 28 Hättenschwiler, S., Coq, S., Barantal, S., and Handa, I.T.. 2011. Leaf traits and decomposition in tropical rainforests: Revisiting some commonly held views and towards a new hypothesis. *New Phytol.* 189 (4): 950– 965. doi: <https://doi.org/10.1111/j.1469-8137.2010.03483.x>
- 29 Heimann, M., and Reichstein, M.. 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature (London)* 451: 289– 292. doi: <https://doi.org/10.1038/nature06591>
- 30 Helfrich, M., Ludwig, B., Potthoff, M., and Flessa, H.. 2008. Effect of litter quality and soil fungi on macroaggregate dynamics and associated partitioning of litter carbon and nitrogen. *Soil Biol. Biochem.* 40 (7): 1823– 1835. doi: <https://doi.org/10.1016/j.soilbio.2008.03.006>
- 31 Hodge, A., Campbell, C.D., and Fitter, A.H.. 2001. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature (London)* 413: 297– 299. doi: <https://doi.org/10.1038/35095041>
- 32 Hodge, A., and Fitter, A.H.. 2010. Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *Proc. Natl. Acad. Sci. USA* 107: 13754– 13759. doi: <https://doi.org/10.1073/pnas.1005874107>

- 33 Joner, E.J., and Jakobsen, I.. 1995. Growth and extracellular phosphatase activity of arbuscular mycorrhizal hyphae as influenced by soil organic matter. *Soil Biol. Biochem.* 27: 1153– 1159. doi: [https://doi.org/10.1016/0038-0717\(95\)00047-I](https://doi.org/10.1016/0038-0717(95)00047-I)
- 34 Klironomos, J.N., Ursic, M., Rillig, M., and Allen, M.F.. 1998. Interspecific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO₂. *New Phytol.* 138 (4): 599– 605. doi: <https://doi.org/10.1046/j.1469-8137.1998.00141.x>
- 35 Leifheit, E.F., Verbruggen, E., and Rillig, M.C.. 2015. Arbuscular mycorrhizal fungi reduce decomposition of woody plant litter while increasing soil aggregation. *Soil Biol. Biochem.* 81: 323– 328. doi: <https://doi.org/10.1016/j.soilbio.2014.12.003>
- 36 Leigh, J., Hodge, A., and Fitter, A.H.. 2009. Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. *New Phytol.* 181 (1): 199– 207. doi: <https://doi.org/10.1111/j.1469-8137.2008.02630.x>
- 37 Lehmann, J., and Kleber, M.. 2015. The contentious nature of soil organic matter. *Nature (London)* 528: 60– 68.
- 38 Lindahl, B.D., de Boer, W., and Finlay, R.D.. 2010. Disruption of root carbon transport into forest humus stimulates fungal opportunists at the expense of mycorrhizal fungi. *ISME J.* 4: 872– 881. doi: <https://doi.org/10.1038/ismej.2010.19>
- 39 Lindahl, B.D., and Tunlid, A.. 2015. Ectomycorrhizal fungi– potential organic matter decomposers, yet not saprotrophs. *New Phytol.* 205 (4): 1443– 1447. doi: <https://doi.org/10.1111/nph.13201>
- 40 Lioussanne, L., Jolicœur, M., and St-Arnaud, M.. 2008. Mycorrhizal colonization with *Glomus intraradices* and development stage of transformed tomato roots significantly modify the chemotactic response of zoospores of the pathogen *Phytophthora nicotianae*. *Soil Biol. Biochem.* 40: 2217– 2224. doi: <https://doi.org/10.1016/j.soilbio.2008.04.013>

- 404 41 Liu, A., Hamel, C., Hamilton, R.I., and Smith, D.L. 2000. Mycorrhizae formation and nutrient
405 uptake of new corn (*Zea mays* L.) hybrids with extreme canopy and leaf architecture as influenced
406 by soil N and P levels. *Plant Soil* 221 (2): 157– 166. doi: <https://doi.org/10.1023/A:1004777821422>
- 407 42 McLellan, T.M., Aber, J.D., Martin, M.E., Melillo, J.M., and Nadelhoffer, K.J.. 1991.
408 Determination of nitrogen, lignin, and cellulose content of decomposing leaf material by near infrared
409 reflectance spectroscopy. *Can. J. For. Res.* 21 (11): 1684– 1688. doi: <https://doi.org/10.1139/x91-232>
- 410 43 Moore, J.A., Jiang, J., Patterson, C.M., Mayes, M.A., Wang, G., and Classen, A.T.. 2015.
411 Interactions among roots, mycorrhizas and free-living microbial communities differentially impact
412 soil carbon processes. *J. Ecol.* 103: 1442– 1453. doi: <https://doi.org/10.1111/1365-2745.12484>
- 413 44 Norby, R.J., Cotrufo, M.F., Ineson, P., O'Neill, E.G., and Canadell, J.G.. 2001. Elevated CO₂, litter
414 chemistry, and decomposition: A synthesis. *Oecologia* 127 (2): 153– 165. doi:
415 <https://doi.org/10.1007/s004420000615>
- 416 45 Nottingham, A.T., Turner, B.L., Winter, K., Chamberlain, P.M., Stott, A., and Tanner, E.V.. 2013.
417 Root and arbuscular mycorrhizal mycelial interactions with soil microorganisms in lowland tropical
418 forest. *FEMS Microbiol. Ecol.* 85: 37– 50. doi: <https://doi.org/10.1111/1574-6941.12096>
- 419 46 Oades, J.M. 1984. Soil organic matter and structural stability, mechanisms and implications for
420 management. *Plant Soil* 76: 319– 337. doi: <https://doi.org/10.1007/BF02205590>
- 421 47 Peng, S., Guo, T., and Liu, G.. 2013. The effects of arbuscular mycorrhizal hyphal networks on
422 soil aggregations of purple soil in southwest China. *Soil Biol. Biochem.* 57: 411– 417. doi:
423 <https://doi.org/10.1016/j.soilbio.2012.10.026>
- 424 48 Poirier, V., Angers, D.A., and Whalen, J.K.. 2014. Formation of millimetric-scale aggregates and
425 associated retention of ¹³C–¹⁵N-labelled residues are greater in subsoil than topsoil. *Soil Biol.*
426 *Biochem.* 75: 45– 53. doi: <https://doi.org/10.1016/j.soilbio.2014.03.020>

- 427 49 Ravnskov, S., Larsen, J., Olsson, P.A., and Jakobsen, I.. 1999. Effects of various compounds on
 428 growth and phosphorus uptake of an arbuscular mycorrhizal fungus. *New Phytol.* 141: 517– 524. doi:
 429 <https://doi.org/10.1046/j.1469-8137.1999.00353.x>
- 430 50 Rillig, M.C. 2004. Arbuscular mycorrhizae, glomalin, and soil aggregation. *Can. J. Soil Sci.* 84:
 431 355– 363. doi: <https://doi.org/10.4141/S04-003>
- 432 51 Rillig, M.C., Mardatin, N.F., Leifheit, E.F., and Antunes, P.M.. 2010. Mycelium of arbuscular
 433 mycorrhizal fungi increases soil water repellency and is sufficient to maintain water-stable soil
 434 aggregates. *Soil Biol. Biochem.* 42: 1189– 1191. doi: <https://doi.org/10.1016/j.soilbio.2010.03.027>
- 435 52 Rillig, M.C., Mummey, D.L., Ramsey, P.W., Klironomos, J.N., and Gannon, J.E.. 2006.
 436 Phylogeny of arbuscular mycorrhizal fungi predicts community composition of symbiosis-associated
 437 bacteria. *FEMS Microbiol. Ecol.* 57 (3): 389– 395. doi: [https://doi.org/10.1111/j.1574-](https://doi.org/10.1111/j.1574-6941.2006.00129.x)
 438 [6941.2006.00129.x](https://doi.org/10.1111/j.1574-6941.2006.00129.x)
- 439 53 Rillig, M.C., Treseder, K.K., and Allen, M.F.. 2002. Global change and mycorrhizal fungi In:
 440 M.G.A. Heijden, and I. Sanders, editors, *Mycorrhizal ecology*. Springer, Berlin, Germany. p. 135–
 441 160. doi: https://doi.org/10.1007/978-3-540-38364-2_6
- 442 54 Sanders, I.R., Streitwolf-Engel, R., Van der Heijden, M.G.A., Boller, T., and Wiemken, A.. 1998.
 443 Increased allocation to external hyphae of arbuscular mycorrhizal fungi under CO₂ enrichment.
 444 *Oecologia* 117 (4): 496– 503. doi: <https://doi.org/10.1007/s004420050685>
- 445 55 Schimel, J.P., and Bennett, J.. 2004. Nitrogen mineralization: Challenges of a changing paradigm.
 446 *Ecology* 85: 591– 602. doi: <https://doi.org/10.1890/03-8002>
- 447 56 Shahzad, T., Chenu, C., Genet, P., and Barot, S.. 2015. Contribution of exudates, arbuscular
 448 mycorrhizal fungi and litter depositions to the rhizosphere priming effect induced by grassland
 449 species. *Soil Biol. Biochem.* 80: 146– 155. doi: <https://doi.org/10.1016/j.soilbio.2014.09.023>

- 450 57 Six, J., Bossuyt, H., Degryze, S., and Denef, K.. 2004. A history of research on the link between
 451 (micro) aggregates, soil biota, and soil organic matter dynamics. *Soil Tillage Res.* 79 (1): 7– 31. doi:
 452 <https://doi.org/10.1016/j.still.2004.03.008>
- 453 58 Six, J., Elliott, E.T., and Paustian, K.. 2000. Soil macroaggregate turnover and microaggregate
 454 formation, a mechanism for C sequestration under no-tillage agriculture. *Soil Biol. Biochem.* 32:
 455 2099– 2103. doi: [https://doi.org/10.1016/S0038-0717\(00\)00179-6](https://doi.org/10.1016/S0038-0717(00)00179-6)
- 456 59 Smith, S.E., and Read, D.J.. 2010. *Mycorrhizal symbiosis*. Academic Press, San Diego, CA.
- 457 60 Soudzilovskaia, N.A., Heijden, M.G.A., Cornelissen, J.H.C., Makarov, M.I., Onipchenko, V.G.,
 458 and Maslov, M.N. et al 2015. Quantitative assessment of the differential impacts of arbuscular and
 459 ectomycorrhiza on soil carbon cycling. *New Phytol.* 208 (1): 280– 293. doi:
 460 <https://doi.org/10.1111/nph.13447>
- 461 61 Staddon, P.L., Gregersen, R., and Jakobsen, I.. 2004. The response of two *Glomus* mycorrhizal
 462 fungi and a fine endophyte to elevated atmospheric CO₂, soil warming and drought. *Glob Chang Biol.*
 463 10 (11): 1909– 1921. doi: <https://doi.org/10.1111/j.1365-2486.2004.00861.x>
- 464 62 Staddon, P.L., Ramsey, C.B., Ostle, N., Ineson, P., and Fitter, A.H.. 2003. Rapid turnover of
 465 hyphae of mycorrhizal fungi determined by AMS microanalysis of ¹⁴C. *Science (Washington, DC)*
 466 300: 1138– 1140. doi: <https://doi.org/10.1126/science.1084269>
- 467 63 Tisdall, J.M., and Oades, J.M.. 2006. Organic matter and water stable aggregates in soil. *Eur. J.*
 468 *Soil Sci.* 33 (2): 141– 163. doi: <https://doi.org/10.1111/j.1365-2389.1982.tb01755.x>
- 469 64 Toljander, J.F., Lindahl, B.D., Paul, L.R., Elfstrand, M., and Finlay, R.D.. 2007. Influence of
 470 arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure. *FEMS*
 471 *Microbiol. Ecol.* 61: 295– 304. doi: <https://doi.org/10.1111/j.1574-6941.2007.00337.x>
- 472 65 Treseder, K.K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and
 473 atmospheric CO₂ in field studies. *New Phytol.* 164: 347– 355. doi: <https://doi.org/10.1111/j.1469->
 474 [8137.2004.01159.x](https://doi.org/10.1111/j.1469-8137.2004.01159.x)

- 475 66 van der Heijden, M.G.A., Martin, F.M., Selosse, M.A., and Sanders, I.R.. 2015. Mycorrhizal
 476 ecology and evolution, the past, the present, and the future. *New Phytol.* 205 (4): 1406– 1423. doi:
 477 <https://doi.org/10.1111/nph.13288>
- 478 67 Varma, A. 1999. Hydrolytic enzymes from arbuscular mycorrhizae, the current status. *Mycorrhiza*.
 479 Springer, Berlin. p. 373– 389. doi: https://doi.org/10.1007/978-3-662-03779-9_15
- 480 68 Verbruggen, E., Jansa, J., Hammer, E.C., and Rillig, M.C.. 2016. Do arbuscular mycorrhizal fungi
 481 stabilize litter-derived carbon in soil? *J. Ecol.* 104 (1): 261– 269. doi: [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2745.12496)
 482 [2745.12496](https://doi.org/10.1111/1365-2745.12496)
- 483 69 Vestergård, M., Reinsch, S., Bengtson, P., Ambus, P., and Christensen, S.. 2016. Enhanced
 484 priming of old, not new soil carbon at elevated atmospheric CO₂. *Soil Biol. Biochem.* 100: 140– 148.
 485 doi: <https://doi.org/10.1016/j.soilbio.2016.06.010>
- 486 70 von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E.,
 487 and Marschner, B.. 2007. SOM fractionation methods: Relevance to functional pools and to
 488 stabilization mechanisms. *Soil Biol. Biochem.* 39 (9): 2183– 2207. doi:
 489 <https://doi.org/10.1016/j.soilbio.2007.03.007>
- 490 71 Welc, M., Ravnskov, S., Kieliszewska-Rokicka, B., and Larsen, J.. 2010. Suppression of other soil
 491 microorganisms by mycelium of arbuscular mycorrhizal fungi in root-free soil. *Soil Biol. Biochem.*
 492 42: 1534– 1540. doi: <https://doi.org/10.1016/j.soilbio.2010.05.024>
- 493 72 Wilson, G.W.T., Rice, C.W., Rillig, M.C., Pringer, A., and Hartnett, D.C.. 2009. Soil aggregation
 494 and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi,
 495 results from long-term field experiments. *Ecol. Lett.* 12 (5): 452– 461. doi:
 496 <https://doi.org/10.1111/j.1461-0248.2009.01303.x>