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

3

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Abstract

34

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

53

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56

57 **Abbreviations:** AMF, arbuscular mycorrhizal fungi.

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

69

70 **THE ROLE OF ARBUSCULAR MYCORRHIZAL FUNGI IN ORGANIC** 71 **DECOMPOSITION**

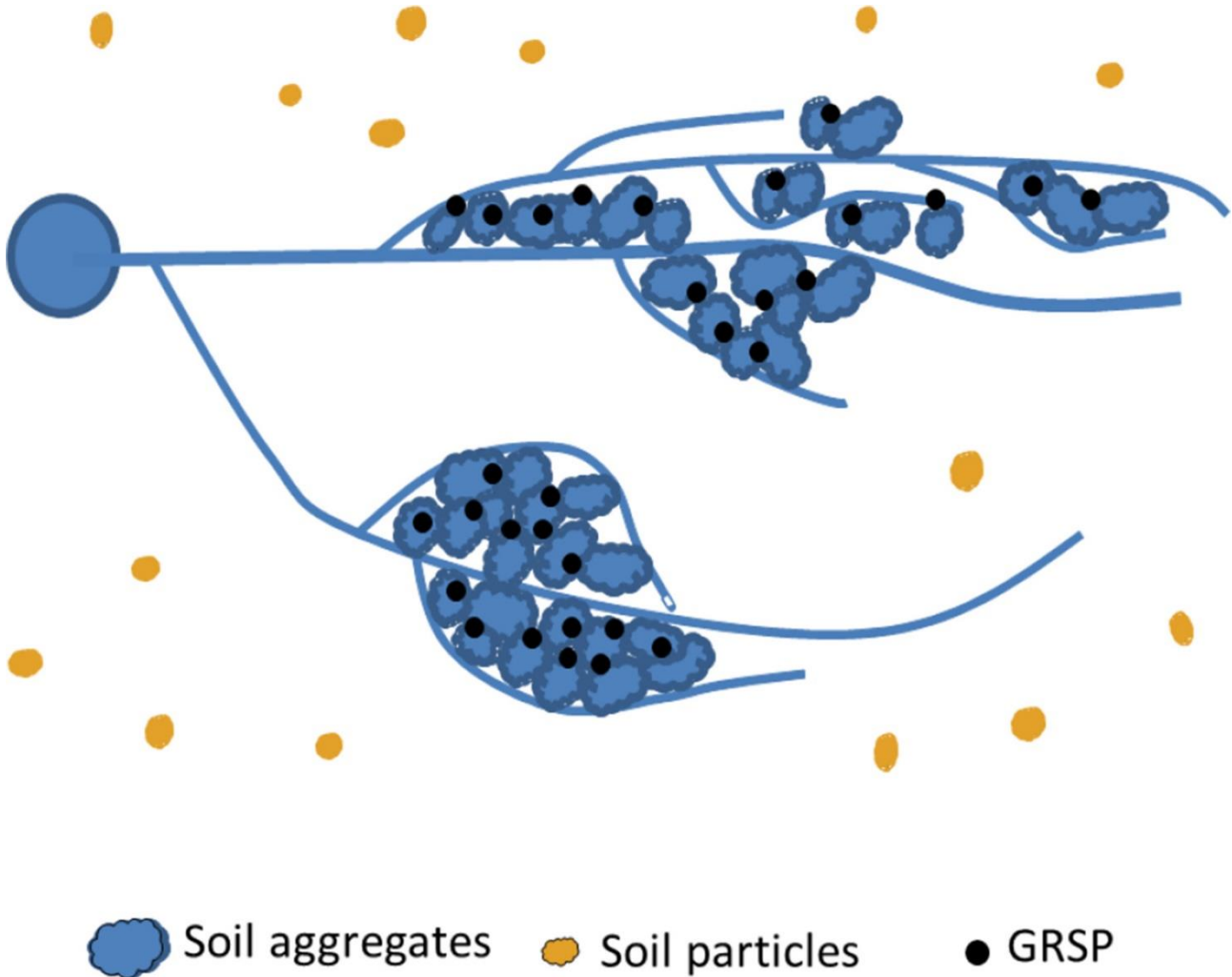
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73 **Contribution to Soil Aggregation**

74

75 Arbuscular mycorrhizal fungi can facilitate soil aggregation and contribute to soil stability through
76 their extensive hyphae system (50; 51; 37). A hypothetical framework based on the aggregate
77 hierarchy hypothesis (63; 46) in coupled with a “life cycle” conceptual model (58) describes the
78 involvement of AMF hyphae in the soil aggregation process. Namely, macro-aggregates (250–2500
79 μm in diameter) are formed first and hyphal enmeshment helps to stabilize the macro-aggregates (50;
80 51; 37; Fig. 1). This is followed by the formation of micro-aggregates (<250 μm) within macro-
81 aggregates with the aid of biological binding agents, including glomalin-related soil proteins which
82 is produced by the hyphal of AMF (58; 57; 15; Fig. 1). Using a stable isotope-tracing technique, an

83 incubation study provided direct evidence to confirm the process of residue retention within macro-
 84 aggregates (48). The study shows that macro-aggregates are formed initially and enriched in ^{13}C and
 85 ^{15}N when ^{13}C - ^{15}N -labeled corn residues applied, and then the accumulation of ^{13}C and ^{15}N continued
 86 throughout the incubation. The results show micro-aggregates are enmeshed within macro-aggregates
 87 and become highly persistent due to the protection created by spatial effects of occlusion (58, 57; 48).



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

90

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

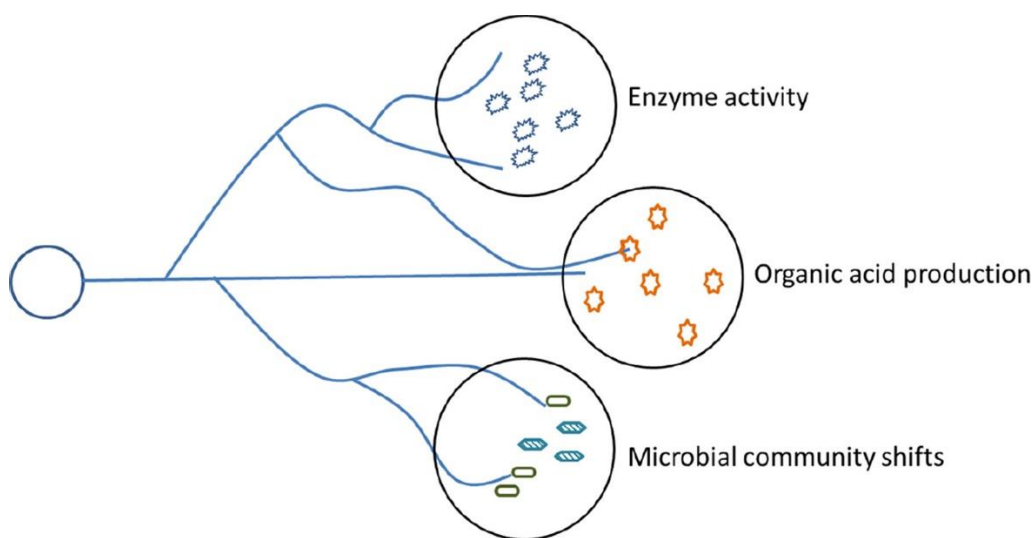
95 are tightly correlated with the abundance of AMF in multispecies prairie communities (72). By using
 96 a root experiment, a direct positive effect of AMF hyphae on soil aggregate formation has been found
 97 (35). Modeling simulation results indicate that AMF combined with organic matter and plant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

100

101 **Stimulation of Organic Carbon Decomposition**

102

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



111

112 Figure 2. Three proposed pathways via which arbuscular mycorrhizal fungi (AMF) stimulate organic
 113 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

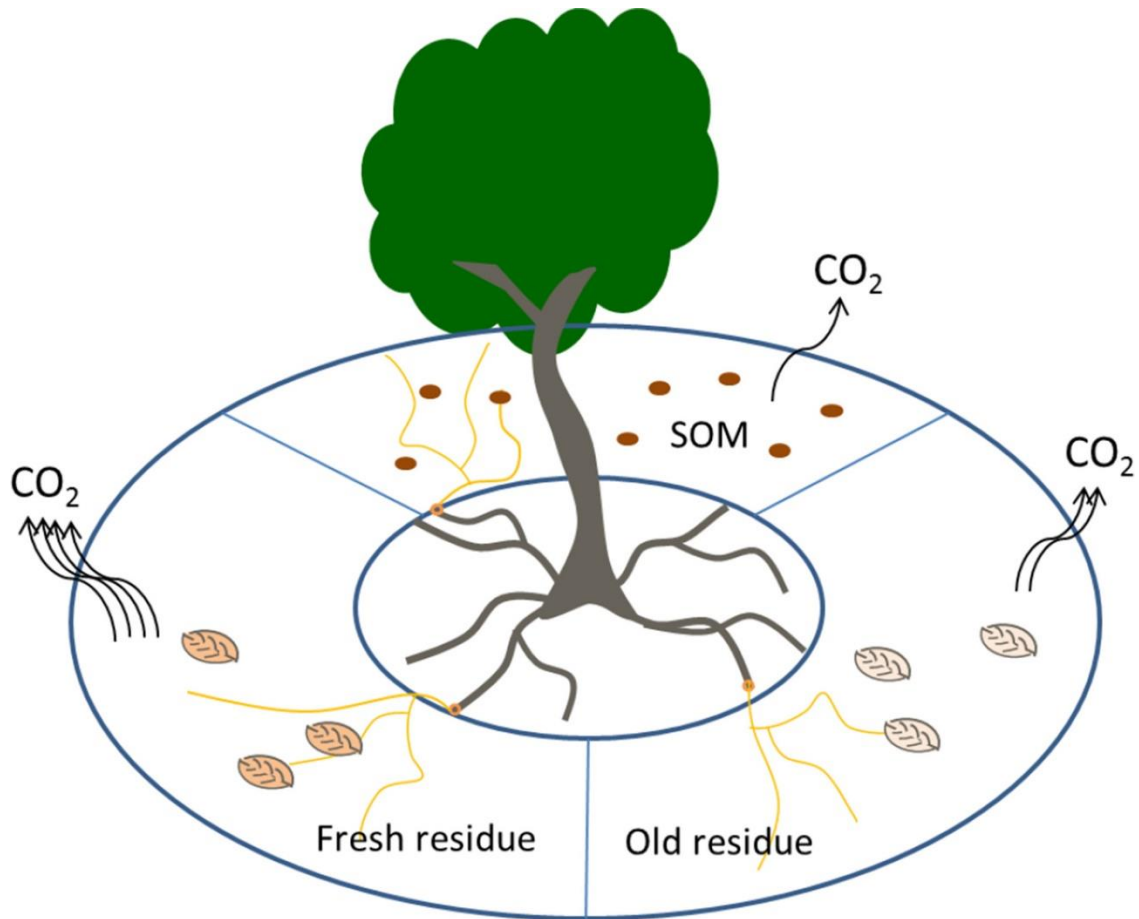
131 **Different Carbon Pools**

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).



158

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

161

162 **Carbon/Nitrogen Ratio of Organic Residue**

163

164 The quality of plant residues is a controversial topic in describing factors affecting decomposition.

165 The widely accepted view is that the ratio of C/N and/or the labile to recalcitrant fraction is a crucial

166 regulator of decomposition (12; 28). Commonly, studies find that AMF stimulation of plant residue

167 decomposition applies both to leaf or fine - root sources (31; 3; 36; 11). However, an increase in soil

168 aggregation and C retention was demonstrated for woody plant litter decomposition compared to leaf

169 litter (35). A likely explanation for the results is that a higher proportion of recalcitrant compounds

170 such as cellulose and lignin in the woody structures compared to leaf litter (42) could contribute to

171 the occluded particulate fraction within aggregates. In addition, microorganism uses the labile

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

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

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

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

213

214 **Elevated Carbon Dioxide Effects**

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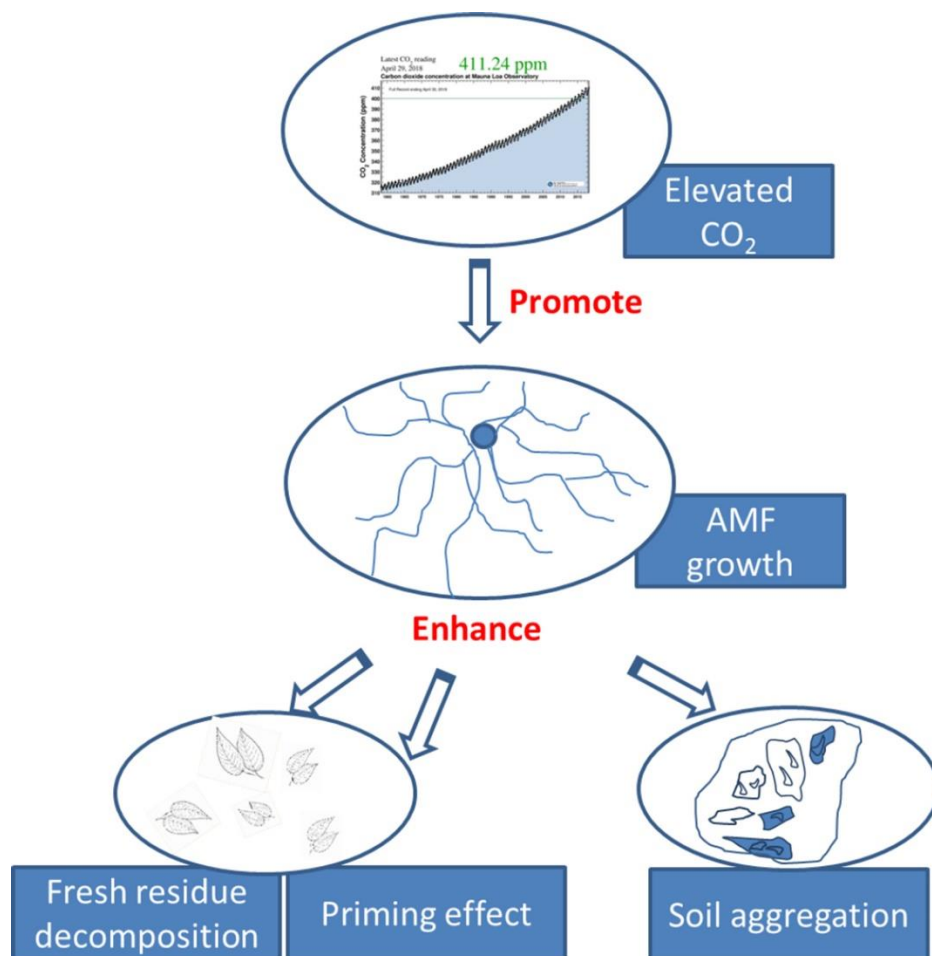
216 The effects of eCO₂ on microbial processes have attracted a lot of interest from researchers. Many
217 studies have looked into the growth and proliferation of AMF under eCO₂, and found a consistent
218 positive response of AMF to eCO₂ despite the varied responses among different genera of AMF (53;
219 65; 11). The AMF response to eCO₂ is often the production of a significantly higher number of spores,
220 development of significantly longer hyphal lengths, and increasing colonization of roots (34). Some
221 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

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



254
 255 Figure 4. The hypothetical relationships between elevated CO₂, arbuscular mycorrhizal fungi (AMF), priming
 256 effect or soil aggregation. (The CO₂ curve was cited from the Scripps Institution of Oceanography at the Mauna
 257 Loa Observatory in Hawaii; The conceptual framework of soil aggregation was modified from 58).

258

259 **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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