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REVIEW

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What is the role of arbuscular mycorrhizal fungi in plant-to-ecosystem responses to Elevated atmospheric CO_2?

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Abstract We advocate the concept of an arbuscular mycorrhiza (AM) as a temporally and spatially complex symbiosis representing a suite of hosts and fungi, as against the more traditional "dual organism" view. We use the hierarchical framework presented in Fig. 1 as a basis for organizing many unanswered questions, and several questions that have not been asked, concerning the role of AM in responses to elevated atmospheric CO_2. We include the following levels: plant host, plant population, plant community, functional group and ecosystem. Measurements of the contributions of AM fungi at the various levels require the use of different response variables. For example, hyphal nutrient translocation rates or percent AM root infection may be important measures at the individual plant level, but hyphal biomass or glomalin production and turnover are more relevant at the ecosystem level. There is a discrepancy between our knowledge of the multifaceted role of AM fungi in plant and ecosystem ecology and most of the current research aimed at elucidating the importance of this symbiosis in global-change scenarios. Our framework for more integrated and multifactorial research on mycorrhizal involvement in regulating CO_2 responses may also serve to enhance communication between researchers working at different scales on large global-change ecosystem projects.

Key words Arbuscular mycorrhiza · Elevated CO_2 · Microorganisms · Rhizosphere · Soil Fungi · Global change

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Introduction

The increasing atmospheric concentration of carbon dioxide is one of the most significant factors of global change, both with respect to the empirical evidence supporting its occurrence (e.g., Keeling et al. 1995) and the number of studies aimed at describing its effect on ecosystems. As a general trend, a large proportion of the additionally fixed carbon in terrestrial ecosystems is channeled below ground, to roots (Rogers et al. 1994) and soil (e.g., Jones et al. 1998). Growth in the number of reviews on the topic of soil microbial limitations and responses to elevated CO_2 (e.g., Zak et al. 1993; O'Neill 1994; Díaz 1996; Hodge 1996; Sanders 1996; Sadowsky and Schortemeyer 1997; Paterson et al. 1997) is therefore not surprising.

Arbuscular mycorrhizae (AM), ubiquitous symbioses between fungi in the Glomales and roots of higher plants, constitute a crucial link at the root-soil interface. The mineral nutritional aspects of AM symbioses are widely appreciated (Smith and Read 1997). Consequently, the vast majority of studies on the role of AM fungi in global-change scenarios involving elevated atmospheric CO_2 concentrations have taken on this aspect of the symbiosis as their main focus (e.g., Hodge 1996).

We challenge this mineral-nutrition centered approach in this paper, and advocate a more multifaceted view of the role of AM fungi in mediating ecosystem responses to CO_2. O'Neill et al. (1991) and Allen (1991, 1996) have argued that a hierarchical view (MacMahon et al. 1978; O'Neill et al. 1986) is warranted in research that tries to ascertain the importance of small-scale processes to large-scale perturbations. In this paper, we use a hierarchically structured conceptual framework to organize our discussion of research on mycorrhizae and elevated CO_2.

Arbuscular mycorrhiza: a different view

A mycorrhiza is a mutualistic symbiosis between plants and fungi localized in the root or rhizoid (e.g., Allen 1991). To most ecologists, this implies a symbiosis between a microorganism (a fungus) and a macroorganism (a plant). This view has led to the large bias that the relationship can be studied virtually exclusively at the scale of an individual plant with a response to a single fungus. However, we know that a single plant will form mycorrhizae with many fungi as the roots encounter different patches. Just as important, a single mycelium can extend across multiple plants. We do not know the limit of that spread, but labeling studies demonstrate that carbon and nutrients can be transported by AM hyphae to many surrounding plants (e.g., Chiarello et al. 1982). It is also important to note that an individual plant may die and become replaced by a new seedling (of the same or different species). The fungus will likely remain (unless, for example, there is severe disturbance) and form a mycorrhiza with the replacement. Similarly, a patch of an individual mycelium of a fungus may die and be replaced while the plant remains, again re-forming mycorrhizae. Thus, an AM is not always best represented as a "dual organism" that can be studied as an entity, but as a suite of plants and fungi whose organization is spatiotemporally complex, transient, and extensive. Therefore, we argue that research on mycorrhizal aspects of global-change biology is most appropriately hierarchically structured.

The framework

The entities to be included are host plant, plant population, plant community, functional group, and ecosystem (Fig. 1). We use the host plant as the basic unit, because an individual organism is the basic unit of selection (MacMahon et al. 1978). From this basic unit, two hierarchical lines are pursued, population to community, and functional group to ecosystem ('population-community' versus 'process-functional' according to O'Neill et al. 1986; or 'coevolutionary' versus 'matter-energy exchange' according to MacMahon et al. 1978). Thus far, the development of conceptual models (Andersen and Rygiewicz 1991; Berntson and Bazzaz 1996) and mycorrhizal research on elevated CO_2 (O'Neill 1994; Sanders 1996; Klironomos et al. 1996; Díaz 1996) have concentrated on the individual plant. The ways in which mycorrhizal fungi can potentially influence responses to CO_2 at the various levels include: (a) influencing the homeostatic adjustment of individual host plants to elevated CO_2, (b) altering the variability of responses to CO_2 within a plant population, (c) differentially responding and providing feedbacks to different plant species within a plant community and to different plant functional assemblages in an ecosystem,

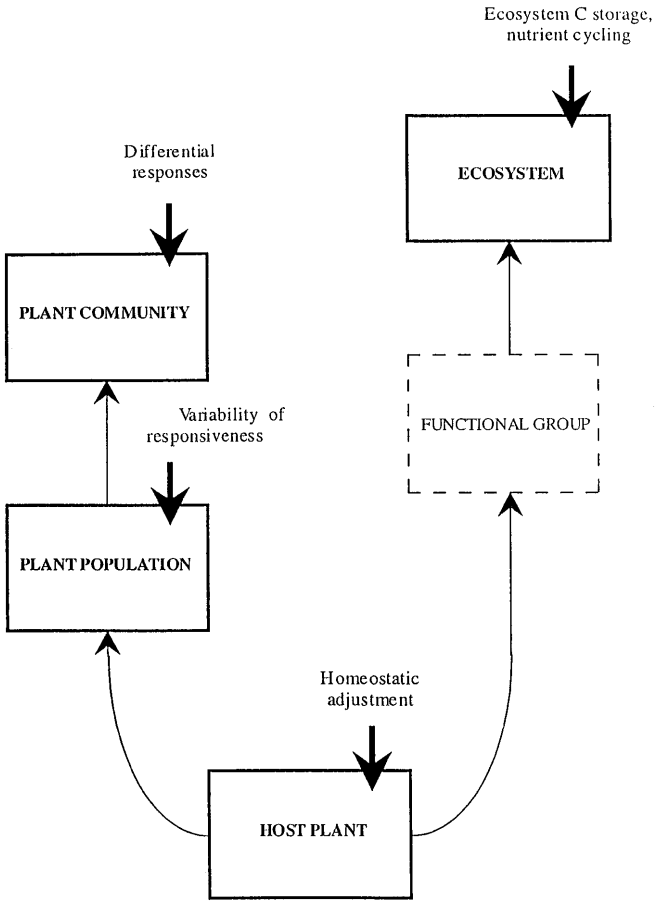

Fig. 1 Framework for the discussion of arbuscular mycorrhizal (AM) fungal contributions to responses to elevated atmospheric CO_2 at the levels of individual host plant, plant population, plant community and the ecosystem. 'Ecosystem' as defined here belongs to the process-functional branch, and 'community' to the 'population-community' branch of the hierarchy (see text). The *bold arrows* signify the different ways in which AM fungi can influence CO_2 responses at the respective levels. It will be necessary to eventually introduce the level of the functional group response group, once sufficient data have been collected to identify suitable groupings

(d) providing an increased ecosystem sink of carbon in the soil, and influencing nutrient cycling patterns. For example, because 'community' and 'ecosystem' belong to different hierarchies, it follows that changes in plant community composition mediated by AM fungi do not necessarily have to lead to ecosystem ('process') changes, and vice versa. It is necessary to consider which response variables are most meaningful at each level of organization (MacMahon et al. 1978). For example, percent root infection by AM fungi may yield desirable information for studying P uptake in an individual plant (e.g., Smith and Read 1997). However, percent infection may be a less important measure of ecosystem soil carbon storage, for which AM extraradical hyphal length, biomass or glomalin turnover may be more crucial.

Plant homeostatic adjustment: the individual

Among the most important factors determining the extent of down-regulation of photosynthesis are availability of nutrients and sinks. Further, factors that affect growth and not necessarily photosynthesis are going to be important. We discuss mineral nutrition, water relations, physiological carbon sink, and interactions with saprophytic and parasitic fungi.

Response variables (and mineral nutrition)

AM fungi can clearly play an important role in the mineral nutrition of their host (George et al. 1992; Smith and Read 1997), and nutrients can limit photosynthesis when not supplied at adequate rates concomitant with elevated CO_2. The response variable most commonly measured to reflect AM status of plants grown in CO_2 (and in general) has been percent colonized root or colonized root length. While there may be a direct correlation for a few systems between colonized root length and nutrient flow to roots via the mycobionts, this is not always (or even often) true (Smith and Read 1997). This assumption becomes even more questionable when imposed treatments (like CO_2 or water) may cause changes in the composition of AM fungi colonizing roots (Klironomos et al. 1998), leading to different average nutrient translocation rates per colonized root length. In the shrub *Gutierrezia sarothrae*, the presence of arbuscules (structures largely responsible for carbon and nutrient exchange) increased more than 14-fold in elevated CO_2, with no significant changes in percent AM infection or AM-colonized root length (Rillig and Allen 1998). In the same study, extraradical hyphal length per AM infected root length also increased in elevated CO_2, again with no change in percent AM root infection. We also found an increase with elevated CO_2 in the number of hyphae within an individual root ('intensity' of infection) in two different species (Rillig and Allen 1998; Rillig et al. 1998), without changes in percent AM fungal colonization or changes in colonized root length.

These results clearly illustrate that AM percent infection measurements are often insufficient in capturing mycorrhizal responses to elevated CO_2 when used as the only indicator. Measurements of AM fungal hyphal nutrient translocation (George et al. 1992) in elevated CO_2 are needed to test if nutrient translocation rates change on a hyphal length basis (either as a function of changed fungal isolate composition or altered single isolate physiology in elevated CO_2).

Most studies on the individual plant level have been conducted as single-time harvest experiments. This design has the disadvantage that, potentially, plants of different phenological stages and sizes are compared, if the phytobiont responds to the treatment with increased growth. Rouhier and Read (1998), using three sequential harvests, showed that some mycorrhizal parameters (colonized root length, arbuscular and vesicular colonization) may only respond to the CO_2 enrichment later in the plant's life cycle. Hence, a single-time harvest may miss potential significant responses. Staddon et al. (1998, 1999ab), in a series of experiments, showed that significant responses of percent root infection and extraradical hyphal length (Staddon et al. 1999a) to the CO_2 treatment can disappear when plant growth parameters are included in the analysis as covariates. Hence, Staddon and co-workers concluded that there is no direct effect of the CO_2 treatment on the mycorrhiza, but that the fungi respond simply to the fact that plants grow larger. Although this important effect has been demonstrated for a variety of hosts (Staddon et al. 1999b), it was only shown for a single fungal isolate in growth chamber experiments with a highly artificial growth medium. The wider relevance of the results is questionable, particularly given the known biodiversity and potential functional specialization of AM fungi (Giovannetti and Gianinazzi-Pearson 1994; Morton and Bentivenga 1994), and isolate-specific response to CO_2 (Klironomos et al. 1998) of the mycobionts. Following the model experiment of Staddon et al., studies containing different or several fungal species should be carried out to test the validity of this conclusion. In a growth chamber experiment with soil containing several mycobionts and involving 11 sequential harvests, we could not confirm the findings of Staddon and coworkers (Rillig, Luo, and Field; unpublished data).

Water relations

While AM fungi can improve plant water relations (e.g. Allen and Allen 1986; George et al. 1992; but see e.g., Bryla and Duniway 1997), in water-limited ecosystems elevated atmospheric CO_2 often improves plant water-use efficiency (e.g., Bazzaz 1990). Mycorrhizae appear primarily to increase water throughput, thereby presumably maximizing plant carbon uptake for subsequent translocation to the fungus itself (Allen et al. 1981). If AM fungi rarely or minimally improve water-use efficiency, important interactions, warranting further study, could result when plants are grown in elevated CO_2, particularly in arid ecosystems. Further studies on plant water relations in elevated CO_2 atmospheres should, therefore, not ignore mycorrhizal aspects.

Physiological carbon sink

Plants may respond to elevated CO_2 initially with increased photosynthesis, but if there are sink limitations complete homeostatic adjustment of an individual plant may occur (e.g. Bazzaz 1990). AM fungi can constitute a physiologically important carbon sink (Wright et al. 1998). Roots with AM fungi receive about 4–20% more

photosynthate than comparable non-mycorrhizal (NM) roots (Smith and Read 1997). Jakobsen and Rosendahl (1990) estimated that AM fungi could use up to 20% of the total fixed $^{14}CO_2$ in young plants. The importance of this sink to plants grown in elevated CO_2 has been recognized (Jongen et al. 1996). However, upon measuring total non-structural carbon pools of mycorrhizal and NM plants in ambient and elevated CO_2, no change in the C-sink was found (Jongen et al. 1996). Pools are just one representation of sinks, as turnover and respiration rates may also change. For young *Vicia faba* plants, Paul and Kucey (1981) estimated that AM fungi respired about 3% of the host photosynthate, while incorporating only ca. 1%. It is conceivable that respiration rates of AM hyphae change when plants are exposed to elevated CO_2, because carbon supply may be altered. To date, hyphal respiration rates have never been measured directly for AM fungi, and consequently no data exist for rates under elevated CO_2 conditions.

Parasitic and facultatively parasitic/ saprophytic fungi

Specific root length often increases in elevated CO_2 for many plant species (Rogers et al. 1994), and hence surface area for potential fungal attack. Also, just as roots may become richer sources of carbon per root length (Rouhier et al. 1996; Paterson et al. 1997), roots may also become more attractive to NM fungi growing on or inside roots. Therefore, it appears possible that protection of roots against saprophytic or parasitic fungi could increase in importance in elevated CO_2.

Mycorrhizal infection can reduce root infection by parasitic fungi probably by a range of mechanisms including direct AM fungus – pathogen interactions (St. Arnaud et al. 1995), or improvement of host nutritional status (Newsham et al. 1995). If the functioning of AM fungi with respect to these nutrient translocation or inter-fungus interaction processes increases in elevated CO_2, because of increased carbon supply from the host, this protection mechanism may become increasingly important. Clearly, root-inhabiting parasitic fungi represent a carbon drain on the plant, can cause disease, promote homeostatic adjustment, and reduce fitness.

Facultatively parasitic/saprophytic fungi are typically common on plant root surfaces, but our knowledge of the biology of these fungi is still poorer than that of mycorrhizal or pathogenic fungi. Nevertheless, these fungi derive carbon from the root and represent a sink. Unlike AM fungi, this group of fungi typically does not have direct root tissue access, but depends on rhizodeposits. Therefore, AM fungi can potentially protect roots from this group simply by carbon preemption. It has been hypothesized that AM fungi can take up host extra carbon before it is rhizodeposited and available to all rhizosphere inhabitants (Diaz et al. 1993; Diaz 1996).

Runion et al. (1994) have shown a trend towards increased infection of rice by *Rhizoctonia* in elevated CO_2. Klironomos et al. (1996) found increased levels of NM root infection in high-nutrient conditions in elevated CO_2, but no change in low nutrient conditions, using *Artemisia*. We found decreased NM fungal infection in elevated CO_2 in several arbuscular mycorrhizal plant species from an annual grassland. This unexpected result was obtained when plants were grown in monoculture in pots for one growing season (Rillig et al. 1998), and when grown in the field for 6 years (Rillig, Field, and Allen, in press). Why did root infection by NM fungi decrease? Were there direct effects of roots on NM fungi (mediated by qualitative changes in rhizodeposition, or changes in plant susceptibility to NM infection)? Did competition for nutrients and/or carbon between mycorrhizal fungi and NM fungi intensify, with conditions favoring AM fungi? Did the root-inhabiting AM fungal community more aggessively protect roots against NM fungal colonization? These questions highlight the strong need for more experiments in this neglected and important area.

Plant population: spatial heterogeneity of AM fungi

Although variability within populations in response to CO_2 will not have very large effects on an ecosystem's response to CO_2, it may be important to a mechanistic understanding of longer-term trends. Interest in plant population level responses has increased with the realization that variability within a population in CO_2-responsiveness may be the key to potential evolutionary adaptations to elevated CO_2 (e.g. Curtis et al. 1996). Also, it is not experimentally obtained statistical means that respond to CO_2, but the breadth represented by a population in a natural setting, as influenced for example by phenotypic plasticity (Curtis et al. 1996; Schmid et al. 1996). Can mycorrhizae contribute to this variability in CO_2 responses within a population, and do mycorrhizal plants have a greater breadth of CO_2 responses than NM plants? We hypothesize that AM fungi increase the range of plant responses to CO_2 in a population and that they play an important role in microevolutionary physiological adaptations to CO_2.

AM fungal inoculum potential (e.g., Koide and Mooney 1987; Allen 1991) and AM fungal species (Bever et al. 1996) are non-uniformly distributed in the environment, even on a local scale of a few square meters (Bever et al. 1996). This means that plants from the same population can have quantitatively (percent infection) and qualitatively (subset of the AM fungal community) different AM fungal root colonization. AM fungal species are known to have different effects on the growth of a host plant species (e.g., Ravnskov and Jakobsen 1995). AM fungal isolates present in the same soil can also differentially influence plant clonal growth patterns (Streitwolf-Engel et al. 1997).

There is also a strong possibility that AM fungi change the amount of phenotypic plasticity in a plant population, e.g., in the case of leaf endophytic fungi (Cheplick 1997). Thus, plant populations with and without mycorrhizal fungi may differ in the amount of intrapopulation variability of response to CO_2. This is a hypothesis that deserves further attention.

Differential responses and feedbacks at the plant community level

It is known that AM fungi can influence the composition of plant communities (Allen and Allen 1990; Zobel et al. 1997; van der Heijden et al. 1998), but do AM fungi have an important role in determining CO_2 responses at the plant community level? The first question to be addressed is: will mycorrhizal fungi differentially respond to this ecosystem perturbation as a function of plant species? And, more importantly, will they subsequently also provide different feedbacks to plant physiology and growth as a function of plant species (by mechanisms discussed in the previous section)? Monz et al. (1994), Sanders (1996) and Rillig et al. (1998) showed that mycorrhizal percent infection of plant roots from the same communities showed differential responses among the plant species examined. These results suggest that AM fungi can respond to CO_2 as a function of plant species.

Possible approaches to examine the feedback of this response to plant communities could include extracting mycorrhizal spores and/ or hyphae from soils of elevated CO_2 plots, and comparing plant growth responses to these fungi and the fungal community extracted from 'ambient' treatment soils. Alternatively, plant communities could be grown in mesocosms with a completely factorial combination of mycorrhizal inoculum presence and CO_2 concentration. Because of the plant species dependence of symbiotic responses to CO_2, it is important to realize that a scaling-up of responses from an observation made on an individual plant species to the plant community or ecosystem level is problematic.

Functional groups and response groups

The previous section mentioned host plant species-specific fungus and symbiotic responses to elevated CO_2. The next step needs to be the identification of suitable functional groups, because not all species from an ecosystem can be examined. Will mycorrhizal fungi be more beneficial to certain plant functional assemblages than to others in elevated CO_2? Díaz (1996) discussed how AM fungi may become important in tipping the balance between mycorrhizal and NM plant species growing in the same ecosystem when exposed to elevated CO_2. It is also important to study how mycorrhizal fungi can influence nitrogen fixation in tripartite systems, and to what extent AM fungi can be responsible for frequently observed increases in N-fixation in elevated CO_2 (e.g., Zanetti et al. 1996; Zanetti and Hartwig 1997; Bandara et al. 1998). Other important pairs to consider are C3 versus C4 plants (see Monz et al. 1994), and early successional versus late successional plants. However, to date not nearly enough data exist to make generalizations.

With respect to the identification of response groups, i.e. groupings of organisms responding in similar ways to a disturbance (Lavorel et al. 1997), it is interesting to ask whether those plants that respond strongly to elevated CO_2 also typically derive a large benefit from being mycorrhizal. In other words, will plants with the highest responsiveness to the presence of mycorrhizae under ambient conditions also be the ones to which mycorrhizae confer the greatest benefit in elevated CO_2? Or will plants with little or no response to mycorrhizae under ambient CO_2 show the greatest benefit from mycorrhizae under elevated CO_2?

Ecosystem level: carbon storage in the soil

Pool size of AM fungi in ecosystems

It is often overlooked that not only ectomycorrhizal fungi but also AM fungi can constitute a sizable pool of carbon in the soils of many terrestrial ecosystems (Allen 1991).

Estimates of extraradical hyphal lengths in the field vary widely. Reports range from 0.02 m g^{-1} soil in a poplar monoculture (Lussenhop et al. 1998), to 38 m ml^{-1} (Allen and Allen 1986) in a shrub-steppe, to a peak length of 111 m ml^{-1} of soil for a prairie community (Miller et al. 1995). For the latter estimate, an external hyphal dry weight of 457 μg ml^{-1} was calculated. This fungus carbon pool may also be a slow-turnover pool, because soil microarthropods seem to preferentially feed on saprophytic hyphae rather than on AM fungal hyphae (Klironomos and Kendrick 1996). Currently, we have no information concerning a potential change in the nutritional value of AM fungal hyphae in global-change scenarios.

The far more significant pool of AM-fungus-related carbon in soil is probably the recently discovered glycoprotein glomalin (Wright and Upadhyaya 1996). Glomalin occurs in a wide variety of soils in the order of several mg per g of dry soil (Wright and Upadhyaya 1998) and is apparently only produced in significant amounts by AM fungus hyphae (Wright et al. 1996). It thus represents a pool of carbon (glomalin is approximately 20–30% carbon; S.F. Wright, personal communication) in soil that should be considered directly related to AM fungi. Very little is known about the turnover of this protein.

Potential for AM fungus carbon pool increase

Does this AM-fungi-related carbon pool have the potential for increase in elevated CO_2? Or are natural ecosystems already mycorrhiza-saturated (Allen et al. 1995)? This question must be answered in the field, after long-term CO_2 exposure in order to allow for all feedbacks to act upon the external hyphae and their products: grazers, litter input and quality, change in other soil microbes, change in glomalin production or decomposition rates, etc.

Lussenhop et al. (1998) found no significant difference in AM hypha biomass in high and low nitrogen soils in response to CO_2 exposure, whereas Klironomos et al. (1997) documented an increase in hyphal length under low-nutrient conditions with *Populus tremuloides*. Preliminary results from an experiment in an annual grassland in northern California indicate a potential for large increases in AM fungus biomass: approximately a 70% increase of AM fungus hyphal length after 6 years of CO_2 enrichment in the field (Rillig, Field and Allen 1999). Increases in AM fungus biomass constitute an ecosystem sink for carbon, providing a negative feedback to the atmospheric CO_2 concentration. In addition to carbon pool size, it is also necessary to examine carbon pool turnover of AM fungus hyphae; however, methodological limitations currently inhibit progress.

Glomalin concentration in soils has been shown to decrease when the soil and AM fungus mycelium is disturbed (Wright and Upadhyaya 1998). As more hyphae can be produced under elevated CO_2, it is, therefore, possible that glomalin concentrations in soil increase after long-term CO_2 enrichment, or even in short-term experiments. If carbon allocation to the mycobiont increases, we speculate that AM fungi produce more of the protein (per hyphal length). Due to the unusually recalcitrant nature of the protein (it requires autoclaving for its extraction from soil; Wright and Upadhyaya 1996), it is interesting to speculate whether the carbon pathway ending in glomalin represents a bypass of the labile soil carbon pool to a slower turnover (more stable) carbon pool.

AM fungus effects on decomposition, and on carbon and nutrient cycling

AM hyphae are not involved in litter decomposition processes, but they take up nutrients (including nitrogen) and translocate them to the plant root. High AM fungus biomass may therefore, impose nutrient limitations on decomposer fungi in nutrient-limited ecosystems (Allen 1991). So far, only ectomycorrhizal fungi have been postulated to suppress decomposition by this mechanism (Gadgil and Gadgil 1971; but see Zhu and Ehrenfeld 1996). It is not known whether AM fungi can inhibit decomposition in similar ways, and whether this effect can be magnified by elevated CO_2. In case AM fungi prove to be important in this context, they would modify carbon cycling and retard the release of CO_2 back to the atmosphere, thereby increasing the system carbon sink.

Conclusion

Structuring research within the framework used in this paper has heuristic value (MacMahon et al. 1978) in formulating questions for mycorrhizal contributions to ecosystem responses in elevated CO_2. Because global-change research also greatly depends on interdisciplinary collaboration because of the high investment necessary to maintain long-term CO_2 enrichment experiments, a structuring of research like this may also improve communication between researchers working at different scales.

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