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Mycorrhizas and global environmental change: research at different scales

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Abstract

Global environmental change (GEC), in particular rising atmospheric CO_2 concentration and temperature, will affect most ecosystems. The varied responses of plants to these aspects of GEC are well documented. As with other key below-ground components of terrestrial ecosystems, the response of the ubiquitous mycorrhizal fungal root symbionts has received limited attention. Most of the research on the effects of GEC on mycorrhizal fungi has been pot-based with a few field (especially monoculture) studies. A major question that arises in all these studies is whether the GEC effects on the mycorrhizal fungi are independent of the effects on their plant hosts. We evaluate the current knowledge on the effects of elevated CO_2 and increased temperature on mycorrhizal fungi and focus on the few available field examples. The value of using long-term and large-scale field experiments is emphasised. We conclude that the laboratory evidence to date shows that the effect of elevated CO_2 on mycorrhizal fungi is dependent on plant growth and that temperature effects seen in the past might have reflected a similar dependence. Therefore, how temperature directly affects mycorrhizal fungi remains unknown. In natural ecosystems, we predict that GEC effects on mycorrhizal fungal communities will be strongly mediated by the effects on plant communities to the extent that community level interactions will prove to be the key mechanism for determining GEC-induced changes in mycorrhizal fungal communities.

Introduction

Global environmental change (GEC) caused by human activities is one of the greatest challenges facing our society (Wyman, 1991). GEC encompasses a wide range of occurrences including rising atmospheric carbon dioxide concentration, leading to global warming, but also increased nitrogen deposition, tropospheric ozone depletion and other impacts. We will focus here on the first two aspects. It is undeniable that atmospheric CO_2 levels are increasing due to fossil fuel burning and land use changes, but a consensus on the role of human activity in global warming has been less forthcoming. However, the Intergovernmental Panel on Climate Change has stated in the last year that human activity is having a measurable effect on the Earth's climate (Kerr, 2001; see also Macilwain, 2000).

Much research into the biological effects of rising atmospheric CO_2 concentrations and temperature has focussed on plant growth and carbon fixation. However, other crucial components of terrestrial ecosystems, especially in the soil, have received less attention. We shall concentrate here on GEC research on mycorrhizal fungi. These fungi form symbiotic associations with plant roots and occur in the vast majority of terrestrial plants (Smith and Read, 1997). In terrestrial ecosystems they can account for a substantial proportion of their hosts photosynthate (e.g. Jakobsen and Rosendahl, 1990) and can mediate competition between plants (Hetrick, 1991). In terms of the global carbon cycle, mycorrhizal fungi could also prove to play a critical role in carbon sequestration in soils.

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Little is known about the external phase of arbuscular mycorrhizal fungi but if the extraradical mycorrhizal hyphal density was stimulated under a warmer climate this could act as a negative feedback to rising atmospheric CO_2.

In this review, we will evaluate the research to date on the effects of elevated CO_2 and increased temperature on mycorrhizal fungi, but will pay particular attention to the different hierarchical levels of the observed effects of elevated CO_2 or temperature on mycorrhizal fungi, i.e. whether the observed effect is direct, independent of host-plant response; indirect, but simply a scale-dependent consequence of the host plant's growth response; indirect, resulting from changes in host physiology independently of host growth response; or mediated by more complex mechanisms (such as interspecific interactions) (see Figure 1). The importance of an hierarchy of organisational levels in mycorrhizal systems (e.g. from individual host to plant community) has been recently discussed by Miller and Kling (2000). Without having such a framework in mind, the chances of reaching erroneous conclusions about impacts of key environmental factors on mycorrhizal functioning in ecosystems could be quite high.

Elevated atmospheric carbon dioxide

At the level of an individual plant-mycorrhizal fungus symbiosis

The response of individual mycorrhizal fungal species (especially arbuscular mycorrhizas) to elevated atmospheric CO_2 has been reviewed several times over the past few years (Fitter et al., 2000; Rillig and Allen, 1999; Staddon and Fitter, 1998; Treseder and Allen, 2000). Here, we shall summarise the main points raised in the previous reviews and consider a few more recent papers. Other types of mycorrhizas will also be discussed where appropriate.

Plants grown at elevated CO_2 generally grow faster than when grown at ambient CO_2 (Poorter, 1993). Also, they tend to show an increase in the allocation of carbon to their root system relative to their shoots (Rogers et al., 1996). This could, therefore, result in more carbon being available to symbionts in the roots of plants grown at elevated CO_2 (Díaz et al., 1993). Numerous studies have attempted to demonstrate that this increased below-ground carbon results in the stimulation of mycorrhizal colonisation (see reviews cited above). However, as argued in Staddon and Fitter (1998) and Fitter et al. (2000) much of this research is inconclusive because differential plant growth was not taken into account (a problem inherent to single harvest experiments). Evidence to date shows no plant growth-independent effect of elevated CO_2 on arbuscular mycorrhizal colonisation or extraradical hyphal production. Recent work by Gavito and coworkers (Gavito et al., 2000) also confirms this finding and furthermore shows that mycorrhizal function in terms of phosphorus uptake is unaffected by elevated CO_2, which was previously reported by Staddon et al. (1999). In other words, at elevated CO_2 plants tend to be larger, and their mycorrhizal symbionts are proportionately larger.

Time course studies on ectomycorrhizas (EcM) have shown similar results to those on arbuscular mycorrhizas (AM). For example, Lewis et al. (1994) state that "despite significant effects on root carbohydrate levels, there were generally no significant effects on mycorrhizal colonization" for *Pinus taeda* grown at elevated CO_2. Other research has shown the potential for interspecific variation in the response of both AM (Klironomos et al., 1998) and EcM (Gorissen and Kuyper, 2000) in plants grown at elevated CO_2, although this work was based on a single harvest.

Many contradictions in the reports on the effect of elevated CO_2 on mycorrhizas arise from directly comparing results from pot-based single species plant-mycorrhizal fungus experiments to multispecies systems or by attempting to extrapolate to the field situation. The reason for these contradictions will become clearer in the following sections.

At the multispecies level

The simplest type of mycorrhizal association involves an individual host plant with a single mycorrhizal fungus as discussed above. The next level of complexity is where either several host plant species or more commonly several fungal species are studied. This opens up the possibility for more distal effects of elevated CO_2 on the system; effects which are mediated by interspecific interactions (e.g. competition), which in turn depend on the species-specific responses.

The following scenario can be used to highlight this possibility: a plant in symbiosis with two different mycorrhizal fungal species is grown at elevated CO_2. Assume that it has been previously determined that elevated CO_2 has no effect on the two mycorrhizal fungus species independent of plant growth, when they were grown in individual association with the

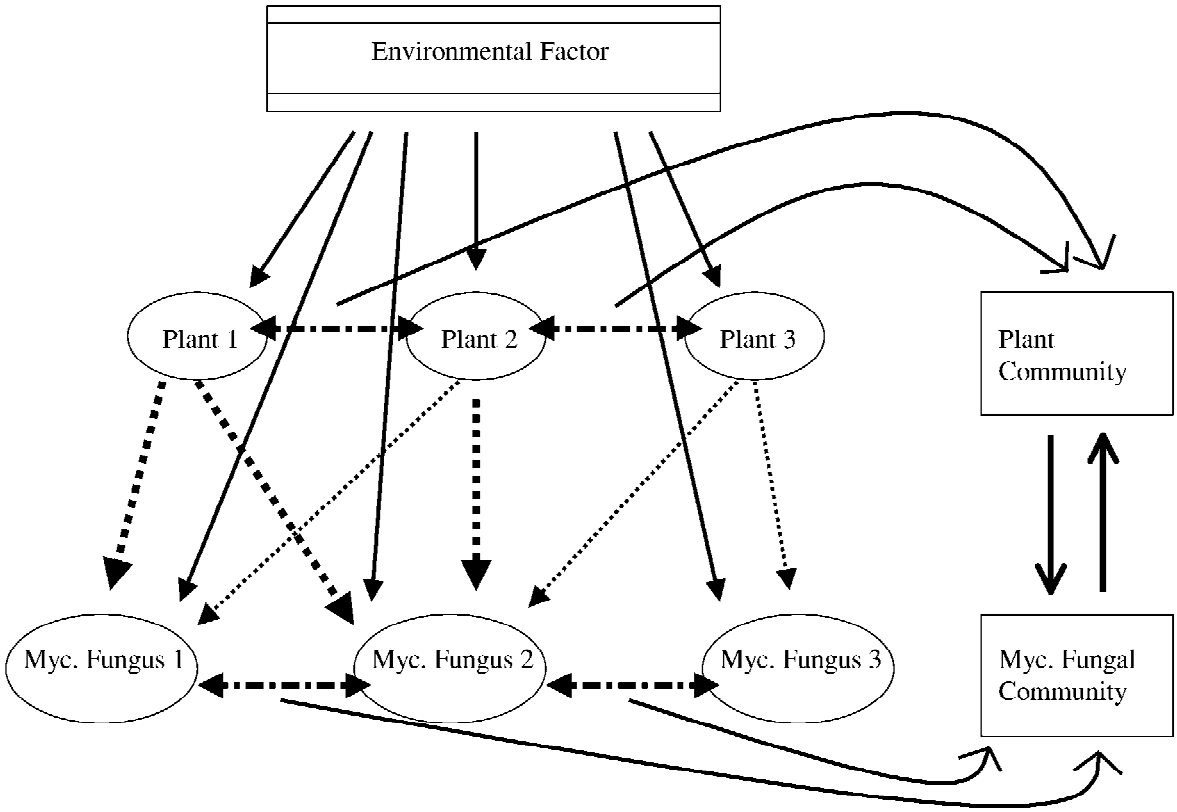

Figure 1. The direct and indirect impacts of an environmental factor on a simplified mycorrhizal fungal community. An environmental factor can have direct effects on both plants and their associated mycorrhizal fungi (→). It can also affect mycorrhizal fungi indirectly via impacts on the host plants; these effects may vary in magnitude depending on the level of association between the host-plant and the mycorrhizal fungus (⇢, the thicker the arrow, the stronger the effect). Interspecific interactions (←·→), at the level of the plants and the mycorrhizal fungi will determine plant and mycorrhizal fungal community structure (↷). Furthermore, the plant and the mycorrhizal fungal communities both influence each other (⇄).

host plant. The *a priori* prediction would be that there would also be no plant-independent effect of elevated CO_2 on the dual mycorrhizal colonisation. However, it could easily be envisaged that the altered carbohydrate availability in the roots of the host plant might result in a shift in the competitive balance of the two mycorrhizal fungal species if, for example, one has a slightly greater intrinsic growth rate than the other. This could occur even if the same change in carbohydrate availability had no effect on either fungus on its own.

Changes in mycorrhizal fungal species community structure in plants grown at elevated CO_2 have been shown for ectomycorrhizas (EcM) in *Betula papyrifera* (Godbold and Berntson, 1997). Furthermore, changes in the relative proportion of EcM to AM colonisation in *Tsuga canadensis* have also been reported (Godbold et al., 1997). There is also the potential for plant species-specific effects to elevated CO_2 induced changes in mycorrhizal community assemblages (Rillig et al., 1998).

At the community level

There are two crucial points relating to the study of the effects of elevated CO_2 on mycorrhizas at the community level. Firstly, only community level studies (preferably in the field) can reflect what will happen in the 'real world', because we lack the understanding to extrapolate from single-species studies to the community. Secondly, community level studies will reveal an overall effect (e.g. a change in community composition) and can not unambiguously reveal the mechanisms behind any changes in ecosystem structure or function. Based on a few recent papers, we shall concentrate here on what can be achieved from research on the effects of elevated CO_2 at the com-

munity level and the inherent difficulties in explaining the mechanisms behind these effects.

There are primarily two types of experimental situation where the effect of elevated CO_2 can be studied at the community level in the field: free-air CO_2 enrichment (FACE) (Prior et al., 1994) or open top chamber (OTC) (Curtis et al., 1989) experiments, where the CO_2 concentration is artificially increased, and natural CO_2 vents or springs (Raschi et al., 1997), which in some cases may have resulted in exposure to elevated CO_2 over several decades or longer. The advantage of the latter is obvious for the length of time involved but the history of the site may not be known. Some FACE experiments (e.g. Schlesinger and Lichter, 2001) have now been running continuously for several years and have generated a great deal of data, especially concerning the response of vegetation (especially agricultural crops and plantation trees) to elevated CO_2. The main advantages of FACE over OTC technology are that under FACE no other environmental parameter is (directly) altered by the set-up and that FACE experiments are much larger in scale. OTCs are, however, much cheaper to set up and operate.

One of the first pieces of research which attempted to look at the effects of elevated CO_2 on mycorrhizas in the field was performed as part of a FACE experiment on cotton (Runion et al., 1994): no difference in mycorrhizal colonisation was detected. On a subsequent FACE experiment at the same site, but this time on sorghum, an increase in extraradical mycorrhizal hyphal length density was reported at elevated CO_2, but there was unfortunately no data for root length density, which could explain this effect (Rillig et al., 2001). Both studies were monocultures, highlighting the lack of funding available for ecological/environmental research when compared with agricultural (and sylvicultural) science. In the next few years, studies are likely to focus on the effect of elevated CO_2 on the below ground component, including mycorrhizas, in FACE experiments in more natural settings such as those located in a desert scrub (Jordan et al., 1999), in a tall grass prairie (Luscher et al., 1998) or in a sheep-grazed pasture (Edwards et al., 2001).

There has also been surprisingly little mycorrhizal work carried out with OTCs apart from that by Rillig and co-workers. In one OTC study, they report an increase in arbuscular mycorrhizal colonisation at elevated CO_2 (Rillig et al., 1999b) and in a second study they report that mycorrhizal colonisation was stimulated in some plant species but not in others (Rillig et al., 1999a). Unfortunately no measure of vegetation response to elevated CO_2 was obtained. It is known that elevated CO_2 may cause changes in ecosystem productivity, plant community structure and species composition (Bazzaz, 1990), and that changes in the plant community are linked to changes in the mycorrhizal fungal community (van der Heijden et al., 1998). Therefore, a change in mycorrhizal colonisation, such as those seen by Rillig and co-workers, could be a consequence of unknown changes in the plant community.

Natural CO_2 springs such as those in New Zealand (Newton et al., 1996) or Italy (van Gardingen et al., 1995) have the potential to reveal how natural terrestrial ecosystems respond to increasing atmospheric CO_2. They also have the advantage of possessing CO_2 gradients. As far as we are aware, only a single study (Rillig et al., 2000) has to date reported on mycorrhizal data from communities near CO_2 vents. They report increasing root colonisation and extraradical hyphal density with increasing CO_2 level. However, as with the OTC data discussed above, there was no quantitative survey of plant species composition, nor measurements of plant productivity or biomass or of root density. Without some attempt to determine the effect of increased atmospheric CO_2 (or any other environmental variable for that matter) on the vegetation, research solely on the mycorrhizal fungal component of an ecosystem is of strictly limited value.

Increased temperature

At the level of an individual plant-mycorrhizal fungus symbiosis

Research investigating temperature effects on the arbuscular mycorrhizal (AM) symbiosis has been reviewed by Daniels Hetrick (1984). However, in most of these studies, effects on the plant could not be separated from those on the fungus as only a single harvest was used (Table 1). Increased fungal growth was possibly due to increased plant growth. Also, treatments were mostly applied at the inoculation stage (Table 1). Fungal growth responses might, therefore, reflect impacts on spore germination and growth of initial infection units (Schenk et al., 1975; Tinker, 1975; Daniels Hetrick, 1984). The fungus itself might respond to temperature directly independently of any plant responses (Fitter et al., 2000). There is an obvi-

Table 1. Effect of temperature on arbuscular mycorrhizal colonisation (percentage root length colonised, RLC) and its external phase in various plant species

Plant species	Fungus species	Location of study	Duration of study	Harvest numbers/ Temperature	Percentage RLC at elevated temperature	Plant responses to elevated temperature	References
Allium cepa	GM?	Gr. ch.[a]	17 wk	9/ 16, 21, 26 °C, d1 treat[g]	increase	increase	Furlan and Fortin (1973)
Sorghum sp.	GF	Gr. hs.[b]	6 wk	1/ (soil temp.) 25, 30, 35 °C, d1 treat.	increase	increase under medium P	Graham and Leonard (1982)
Hordeum vulgare	GH GMa	Gr. hs.	7–9 wk	1/ (soil temp.) ca 11, 26 °C, d1 treat.	increases but low magn[f]	no change	Grey (1991)
Trifolium repens	GC GE	Gr. hs.	18 wk	3/ d1 treat. 18 °C & 150 μmol m^{-2} s^{-1} or 27 °C & 300 μmol m^{-2} s^{-1}	increase	increase	Jensen (1984)
Pascopyrum smithii	(from prairie soil)	Gr. ch.	2 & 4 yr	1 each/ ambient & +4 °C, d1 treat.	decrease but low magn.	not avail[e]	Monz et al. (1994)
Allium cepa	GM?	Gr. ch.	10 wk	1/ ca 14, 23 °C, d1 treat.	increase in RLC_{arb}[c]	increase	Hayman (1974)
Trifolium subterraneum	GC GiC AL	Gr. ch.	15 wk	4-6/ 7 temperatures: 5–37 °C, d1 treat.	not avail. but increase in EMH[d]	not avail.	Tommerup (1983)
T. subterraneum, Medicago truncatula	from field soil, >GM?	Gr. ch.	12 days	5/ 4 temperatures: 12–25 °C, d1 treat.	increased number of entry points, depended on root length	increased root length	Smith and Bowen (1979)

Notes:: [a]growth chamber, [b]green house, [c] arbuscular RLC, [d]extraradical mycorrhizal hyphae, elongation only, [e]not available, [f] used very low magnification, [g] treatment started on the day when inoculated with AM fungus, GM (*Glomus mosseae*), GF (*G. fasciculatum*), GH (*G. hoi*), GMa (*G. macrocarpum*), GC (*G. caledonium*), GE (*G. epigaeus*), GiC (*Gigaspora calospora*), AL (*Acaulospora laevis*). ? means possibility of the isolate (inoculum) to be (mainly) *G. mosseae* (i.e. *Endogone* sp.).

ous need of time-course data, allowing allometric analysis (Staddon and Fitter, 1998) to determine whether the response is due to altered plant growth. The only study incorporating plant growth effects on root colonisation of AM fungi was that of Smith and Bowen (1979), but the temperature treatment was imposed at the time of inoculation (Table 1).

Most studies investigating temperature responses of the AM symbiosis have been performed under highly artificial conditions (e.g. high levels of nutrients and in growth chambers) and used only one AM fungus, mostly *Glomus mosseae* or *G. fasciculatum* (Table 1). These conditions do not represent natural conditions, where a root system is often colonized by more than one AM fungus (Merryweather and Fitter, 1998) and where environmental conditions vary both temporally and spatially. Nutrient levels might also influence overall root colonisation responses to temperature as reported for CO_2 (Klironomos et al., 1996). Furthermore, the most commonly used AM fungal species might not reflect the ecologically important species in the field (Helgason et al., 1999).

The need to test temperature effects under field conditions has often been called for (e.g. Miller and Kling, 2000). Yet the only study using a natural AM fungal community was that of Monz et al. (1994). It was also the first published research on the effects of the increase in temperature of the range predicted for global warming on mycorrhizas. Monz et al. (1994) reported a decrease in mycorrhizal colonisation in *Pascopyrum smithii* as a result of a 4 °C increase in temperature but no change in *Bouteloua gracilis*. However, no data was provided on the effect on the host plant, so it could simply be, as for elevated CO_2, a plant-mediated effect.

Nearly all research has focused on intra-radical colonization, yet it is the external phase of the AM fungus which is more likely to respond to temperature (Gavito et al., 2000) as it experiences a wider variation in soil temperatures. Little is known about the nature and dynamics of the EMH (Miller et al., 1995). The only study testing temperature effects on the EMH of a mycorrhizal fungus was carried out by Tommerup (1983). However, only mean hyphal elongation data was given, and there was no data for percent root length colonised (Table 1). If the EMH were to respond directly to temperature their functioning might be changed, possibly leading to altered carbon input into the soil. Furthermore, if EMH respiration acclimated to rising soil temperatures a positive growth response of the EMH might then lead to carbon accumulation in soils under a warmer climate. We do not know whether the EMH might also respond to temperature changes independently of effects on internal hyphal growth. EMH might show less sensitivity to temperature than does internal colonisation, since colonisation can be measured at high levels in natural ecosystems in winter (Merryweather and Fitter, 1995). Compartment studies (Dodd, 1994), commonly used for investigating impacts on ion uptake by the EMH of phosphorus (Jakobsen et al., 1992; Schweiger and Jakobsen, 2000) or nitrogen (Hodge et al., 2001; Mäder et al., 2000) could offer a valuable tool to detect direct temperature responses of the AM fungus.

At the multispecies level

As far as we are aware, only a single paper (Rygiewicz et al., 2000) has been published where the effect of temperature on mycorrhizal community structure has been studied. They report that an increase in temperature by 4 °C above ambient results in the maintenance of a greater number of EcM morphotypes compared to the control. Unfortunately, this paper gives no data on the host plant response. Nonetheless, these results would point to changes in mycorrhizal community structure as a result of global warming.

At the community level

As with elevated CO_2, there is also little work on the effects of temperature on mycorrhizal communities in the field. Similarly, many of the field warming experiments have concentrated on the effects on the vegetation, in particular the above-ground component (e.g. Grime et al., 2000). As with FACE experiments, there is the possibility to use these relatively long-term warming experiments to study below ground aspects including mycorrhizas. Despite the limitations in their design (the soil being warmed directly) they are the best available tools for the study of ecosystem response to climate change.

At the community level, competitive abilities of host plants change with AM fungal colonisation (Fitter, 1977; Hetrick et al., 1992) and this results in plant community changes (van der Heijden et al., 1998). The impact of environmental factors on mycorrhizal fungi at the community level (i.e. temperature and light) is little understood (Abbot and Robson, 1984; Miller 1987; Fitter et al., 2000). To predict the impact of GEC on ecosystem functioning and carbon flow to the soil, we must pay more attention to the ubiquitous mycorrhizal fungi. Future research should determine whether temperature affects internal colonisation, and extraradical mycelium growth and if any temperature responses are independent from effects on the vegetation. Also, the role of AM fungi in carbon flow to the soil under soil warming must be addressed as they are likely to play a key role in determining soil carbon sink capacity under a warmer and CO_2 enriched world.

Conclusions

There is no evidence that elevated atmospheric CO_2 affects mycorrhizal fungi other than by affecting the growth of the host-plants. The potential of indirect effects, mediated for example by increases in soluble carbohydrates in roots has not been clearly demonstrated. Syvertsen and Graham (1999) measured carbohydrate pools in mycorrhizal and non-mycorrhizal citrus plants at ambient and elevated CO_2. There was no effect of elevated CO_2 on mycorrhizal colonisation, but the presence of mycorrhizal fungi decreased

root carbohydrate stores; more so at elevated CO_2 than at ambient CO_2, but this was linked to a greater mycorrhizal stimulation of net carbon assimilation at elevated CO_2.

At the ecosystem level, effects of elevated CO_2 on mycorrhizas can be mediated by numerous factors, both biotic (e.g. plant interspecific interactions) and abiotic (e.g. nitrogen availability). As the effects of elevated CO_2 on plants are species-specific, plant community structure is altered, and this in turn will lead to changes in the mycorrhizal fungi community at elevated CO_2. We believe that the overriding factor involved in any effect of elevated CO_2 on mycorrhizas in natural ecosystems will be due to altered plant community structure which inherently leads to changes in all other aspects of the ecosystem.

On the other hand, there is increasing evidence that temperature can have direct effects on mycorrhizal fungi. This is not surprising as all organisms have temperature optima in some sense. Temperature dependence of enzymatic activity is well known and is one obvious reason why temperature can directly affect mycorrhizal fungi. Of course, as temperature also impacts on plants it will also affect mycorrhizal fungi via its effects on their plant hosts. Temperature effects can also be indirect via effects on other environmental factors (e.g. soil moisture). So, as for elevated CO_2, we may find that in natural ecosystems the effects of temperature on mycorrhizas will be, in the main, due to temperature induced changes to plant communities.

Many other aspects of GEC will also impact on mycorrhizas, in some cases direct effects may be evident, but mostly, we predict that the main changes to mycorrhizas in natural ecosystems will result from changes in plant community structure. For example, cloudiness is expected to increase in many areas as a result of climate change (Coughlan and Nyenzi, 1991). The resulting lower photosynthetically available radiation (PAR) will clearly impact on plant productivity and below-ground carbon economy (Fitter et al., 1998) thus leading to altered plant communities, but it would have no foreseeable direct effect on mycorrhizas. Also, it must not be overlooked that the numerous changing environmental factors will also interact with one another and with other factors such as the physico-chemical properties of soils. Predicting any detailed impacts of GEC on terrestrial ecosystems, let alone mycorrhizal communities, therefore becomes increasingly problematic. The only certainty is that GEC will change mycorrhizal fungal community structure primarily as a result of changes in plant community structure.

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