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### Authors

TRESEDER, KK  
ALLEN, MF

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Peer reviewed

## Research review

# Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO<sub>2</sub> and nitrogen deposition

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K. K. TRESIEDER\* AND M. F. ALLEN

*Center for Conservation Biology, University of California at Riverside, Riverside, CA 92521, USA*

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### SUMMARY

In this review, we discuss the potential for mycorrhizal fungi to act as a source or sink for carbon (C) under elevated CO<sub>2</sub> and nitrogen deposition. Mycorrhizal tissue has been estimated to comprise a significant fraction of soil organic matter and below-ground biomass in a range of systems. The current body of literature indicates that in many systems exposed to elevated CO<sub>2</sub>, mycorrhizal fungi might sequester increased amounts of C in living, dead and residual hyphal biomass in the soil. Through this process, the fungi might serve as a negative feedback on the rise in atmospheric CO<sub>2</sub> levels caused by fossil fuel burning and deforestation. By contrast, a few preliminary studies suggest that N deposition might increase turnover rates of fungal tissue and negate CO<sub>2</sub> effects on hyphal biomass. If these latter responses are consistent among ecosystems, C storage in hyphae might decline in habitats surrounding agricultural and urban areas. When N additions occur without CO<sub>2</sub> enrichment, effects on mycorrhizal growth are inconsistent. We note that analyses of hyphal decomposition under elevated CO<sub>2</sub> and N additions are extremely sparse but are critical in our understanding of the impact of global change on the cycling of mycorrhizal C. Finally, shifts in the community composition of arbuscular and ectomycorrhizal fungi with increasing CO<sub>2</sub> or N availability are frequently documented. Since mycorrhizal groups vary in growth rate and tissue quality, these changes in species assemblages could produce unforeseeable impacts on the productivity, survivorship, or decomposition of mycorrhizal biomass.

Key words: arbuscular mycorrhizal fungi, ectomycorrhizal fungi, elevated CO<sub>2</sub>, external hyphae, interspecific variation, microbial communities, nitrogen deposition or fertilization, soil carbon sequestration.

### INTRODUCTION

Land-based ecosystems in the northern hemisphere appear to remove, at least temporarily, a substantial portion of anthropogenic CO<sub>2</sub> from the atmosphere (Tans *et al.*, 1990; Ciais *et al.*, 1995; Schimel *et al.*, 1995; Keeling *et al.*, 1996; Fung *et al.*, 1997). The mechanisms behind this C sink are not well understood, even though knowledge of these processes is vital to predict and interpret the responses of ecosystems to global change (Field & Fung, 1999). Changes in plant productivity due to CO<sub>2</sub> enrichment (Friedlingstein *et al.*, 1995; Thompson *et al.*, 1996), nitrogen deposition (Nadelhoffer *et al.*, 1999), land use change (Houghton *et al.*, 1999), and

climatic effects (Dai & Fung, 1993; Malmstrom *et al.*, 1997) have been investigated as potential components (Schimel *et al.*, 1995; Lloyd, 1999). However, the response of microbial communities to these perturbations, and their potential influence on C cycling, have received scarce attention.

Mycorrhizal fungi in particular might play an important role in the sequestration of C in soil under elevated CO<sub>2</sub> and N deposition. This group, which symbiotically colonizes plant roots, forms associations with 80% of plant species and is found in nearly every habitat in the world (Smith & Read, 1997). Plants allocate an estimated 10–20% of net photosynthate to mycorrhizal fungi, although this number can range from 5 to 85% among systems (reviewed by Allen, 1991).

A substantial amount of C allotted to mycorrhizal tissues could be long-lived in the soil. Chitin, which

\*Author for correspondence (fax +1 909 787 4625; e-mail treseder@mail.ucr.edu).

is not readily decomposed (Gooday, 1994), can constitute up to 60% of fungal cell walls (Muzzarelli, 1977). Arbuscular mycorrhizal (AM) fungi are also the sole producers of glomalin, a potentially recalcitrant glycoprotein (Wright *et al.*, 1996; Wright & Upadhyaya, 1996, 1999). AM hyphae in the absorptive hyphal network (nonrunner hyphae) have lifespans of only 5–7 d (Friese & Allen, 1991a), and with each cycle residual hyphal C should remain in the soil. Furthermore, some micro-arthropods prefer to graze on nonmycorrhizal fungi rather than on a variety of AM fungi (Klironomos & Kendrick, 1996; Klironomos & Ursic, 1998; Klironomos *et al.*, 1999), and therefore might not necessarily speed up tissue turnover significantly. As a result, glomalin alone can account for 30–60% of C in undisturbed soils (calculated from data of Wright & Upadhyaya (1996), assuming that the protein is 30% C by weight M. C. Rillig, pers. comm.). Likewise, portions of ectomycorrhizal (ECM) biomass (sheaths, Hartig nets and fruit bodies) were responsible for approx. 15% of soil organic matter in two hardwood forests (Vogt *et al.*, 1982, cited by Vogt *et al.*, 1991). Carbon derived from mycorrhizal tissue can account for a significantly sized pool within ecosystems (Vogt *et al.*, 1982; Fogel & Hunt, 1983; Vogt *et al.*, 1991; O'Neill, 1994; Allen *et al.*, 1995; Rillig & Allen, 1999) and globally.

Because mycorrhizal fungi acquire most or all their C directly from living plants, the nutrient status of foliage strongly affects mycorrhizal growth. As elevated CO<sub>2</sub> generally increases plant growth (Poorter, 1993) and root-to-shoot ratio (Rogers *et al.*, 1996), greater allocation of C to mycorrhizal structures might follow (Norby *et al.*, 1986; O'Neill *et al.*, 1987). Effects of elevated CO<sub>2</sub> on mycorrhizal growth have been reviewed by O'Neill (1994), Diaz (1996), Hodge (1996), and Staddon & Fitter (1998), with an emphasis on changes in percentage root length (or tips) colonized and total root length colonized per plant. These reviews indicate that the percentage of roots with mycorrhizal structures might not necessarily change under elevated CO<sub>2</sub>. However, as root biomass tends to rise, total mycorrhizal biomass per plant might do so as well. This response varies among systems and does not necessarily occur universally. By contrast, increases in N availability through deposition or fertilization tend to reduce root colonization and fruit body production by ECM fungi (reviewed by Arnolds, 1988; Jansen & Dighton, 1990; Arnolds, 1991; Colpaert & van Tichelen, 1996; Wallenda & Kottke, 1998). Effects of CO<sub>2</sub> and N availability on the biomass or production of extraradical hyphae have been less intensively studied or summarized.

In this review, we address the current state of knowledge regarding the potential for mycorrhizal tissue (particularly hyphae) to form a sink or source of C in response to elevated CO<sub>2</sub> or N deposition.

First, we present an overview of processes and pools involved in the cycling of mycorrhizal C and the relevance of various measures of mycorrhizal dynamics (e.g. percentage colonization, hyphal length, vital staining and ergosterol concentration). Inter- and intraspecific variations in traits that could affect C dynamics are considered. Second, we discuss known effects of CO<sub>2</sub> concentration on hyphal biomass, turnover, tissue quality and community composition. Next, we focus on the influence of N availability on these same factors, and finally we address potential interactions between elevated CO<sub>2</sub> and N availability.

#### MYCORRHIZAL CARBON CYCLING

##### *Major fluxes and pools of carbon*

Processes involved in the cycling of mycorrhizal C include production, survivorship and decomposition rates of tissue. As mycorrhizal tissue grows, C is transferred from the atmosphere via plants to the pool of live hyphae. Micro-arthropods might graze a fraction of live hyphae, but grazing on AM hyphae should be low, as in feeding trials mites and collembola appear to prefer nonmycorrhizal fungi (Klironomos & Kendrick, 1996; Klironomos & Ursic, 1998; Klironomos *et al.*, 1999). When grazing of AM fungal hyphae does occur, animals often only clip the hyphae, severing connections to the root but not ingesting mycelial mass (Klironomos & Ursic, 1998). Thus changes in micro-arthropod numbers might not have a major impact on C flux from AM hyphae to soil organic matter. Instead, death rates of live hyphae determine the flux of C from the live to the dead hyphal pool. At this point, dead tissue is distributed between active and slow soil organic matter pools as a function of tissue quality (following Parton *et al.*, 1988). Active soil organic matter includes sugars and other metabolites that are processed relatively quickly (in days to a few years) by decomposers; slow soil organic matter consists of recalcitrant components such as chitin and glomalin, and might last from years to decades in the soil. In plant tissues, higher N content generally speeds decomposition rates (Melillo *et al.*, 1982). Finally, as soil organic matter decomposes, a portion of C remains in decomposer tissues, and the rest returns to the atmosphere. Each of these fluxes and pools might be affected directly by elevated CO<sub>2</sub> and N deposition, or indirectly through changes in the composition of the mycorrhizal community.

##### *The role of inter- and intraspecific variation*

Groups of mycorrhizal fungi differ in several factors, including growth rate, that could influence C cycling. For example, isolates of ECM fungi vary markedly

in productivity, both within species (Wallander *et al.*, 1999; reviewed by Cairney, 1999) and among species (Wallander *et al.*, 1999). In AM fungi, Sanders *et al.* (1998) observed significant differences in hyphal biomass (after 18 wk growth on *Prunella vulgaris*) among three *Glomus* species. In addition, after 16 wk growth, total hyphal lengths of *Acaulospora denticulata* and *Scutellospora calospora* were significantly greater than those of two *Glomus* species in a glasshouse experiment with *Artemisia tridentata* (Klironomos *et al.*, 1998). If mycorrhizal communities are altered by climate change, then variation in growth and biomass among groups could affect the amount of atmospheric C that is initially drawn into the pool of live hyphae.

Mycorrhizal groups also differ in tissue qualities that might affect the rate at which this mycorrhizal C is returned to the atmosphere. Wallander *et al.* (1997) found that five morphotypes of ECM fungi on field-grown *Pinus sylvestris* varied more than twofold in chitin concentration. Likewise, glomalin content in AM hyphae differed between *Gigaspora* and *Glomus* (approx. 20 and 60  $\mu\text{g}$  protein  $\text{mg}^{-1}$  hyphae, respectively; Wright *et al.*, 1996), and significantly between *Glomus caledonium* and *Glomus intraradices* (Wright & Upadhyaya, 1999). In addition, mean N concentrations in the hyphae of four isolates of *Paxillus involutus* (an ECM fungus) ranged from 5 to 9% when grown in culture (Wallander *et al.*, 1999). Nitrogen content might be related to decomposability of fungal tissue (see 'Major fluxes and pools of carbon'). These results suggest that the identity, as well as the amount, of mycorrhizal fungi might be important in soil C dynamics.

#### *Measures of mycorrhizal response to environmental changes*

As most mycorrhizal structures are relatively delicate and often below ground, measurements of mycorrhizal biomass, growth rate or turnover present some challenges. Most mycorrhizal studies under elevated  $\text{CO}_2$  or N deposition have quantified changes in mycorrhizal colonization (percentage root length colonized by AM, or percentage root tips colonized by ECM). This measure might be an appropriate index for nutrient transfer to the host plant (in AM fungi the presence of internal structures such as arbuscules implies transfer of P). However, because extraradical hyphae account for a large portion of fungal biomass (30–87% of ECM fungi; Colpaert *et al.*, 1992; Wallander & Nylund, 1992, cited by Ekblad *et al.*, 1995), direct measures of hyphal length are a valuable indicator of the mycorrhizal C pool (Rillig & Allen, 1999). Furthermore, root colonization does not necessarily increase linearly with hyphal biomass, and environmental changes might alter relationships between the two variables. For instance, the ratio of AM

hyphal length : total root length colonized by AM varied nearly twofold among  $\text{CO}_2$  and N treatments in *Gutierrezia sarothrae* (Rillig & Allen, 1998), and was nearly three times greater under ambient versus elevated  $\text{CO}_2$  in a serpentine grassland (Rillig *et al.*, 1999a). In an additional study, Staddon *et al.* (1999) noted a decrease in this ratio with elevated  $\text{CO}_2$  in *Plantago lanceolata* and *Trifolium repens*. For this reason we focus primarily on hyphal length or biomass in this review. We emphasize that hyphal length per unit soil area is a particularly meaningful variable in field studies, and might be used eventually to scale biomass to the ecosystem or regional level.

The life stage of hyphae is also an important consideration when measuring fungal productivity. Few  $\text{CO}_2$  or N studies have made the distinction between live and dead hyphae when determining hyphal length. The size of this combined pool is a function of productivity, survival rate and initial decomposition rate, and therefore changes in any combination of these factors might influence the results. Although the magnitude of these two pools provides useful information regarding immobilization of C, the influence of underlying mechanisms must be interpreted with caution. To draw conclusions about productivity, the growth rate of live hyphae must be directly followed. Several techniques enable us to focus on this live pool. For example, ergosterol concentrations are thought to indicate relative amounts of living fungal cytoplasm (Salmanowicz & Nylund, 1988; Martin *et al.*, 1990; Nylund & Wallander, 1992), and are an appropriate measure when no nonmycorrhizal fungi are present. In addition, stains such as fluorescein diacetate, differential fluorescent stain and immunofluorescent antibodies (Friese & Allen, 1991b; Morris *et al.*, 1997) can distinguish between live and dead hyphae. Immunofluorescent antibodies are also specific to different genera and can be used to characterize the community composition of hyphae (Egerton-Warburton & Allen, 2000). This information, together with live and dead hyphal biomass, can be critical in analyses of mycorrhizal C dynamics.

#### EFFECTS OF ELEVATED $\text{CO}_2$

##### *Hyphal biomass and productivity*

Mycorrhizal fungi might provide a negative feedback on anthropogenic  $\text{CO}_2$  emissions by responding to rising concentrations of this trace gas. Overall, elevated  $\text{CO}_2$  tends to increase or produce no change in hyphal biomass or growth on both ECM and AM fungi (Table 1). These variables are determined independently of plant growth or biomass, and are therefore not an indication of relative allocation between plant and fungal tissue. Studies have reported variation among mycorrhizal species, plant

**Table 1.** Effects of elevated CO<sub>2</sub> on growth or biomass of mycorrhizal hyphae

Reference	Host plant or system	Mycorrhizal species	Growth environment*	Duration	CO <sub>2</sub> concentrations	Growth or biomass response (elevated: ambient CO <sub>2</sub> )
<b>Ectomycorrhizal fungi</b>						
Ineichen <i>et al.</i> (1995)	<i>Pinus sylvestris</i> seedlings	<i>Pisolithus tinctoris</i>	Petri dishes, GC	25 d 56 d 91 d	350/600 ppm	NS NS ~ 2.0
Tingey <i>et al.</i> (1995)	<i>Pinus ponderosa</i> seedlings	Mixed (mostly <i>Thelephora terrestris</i> )	OTC	2.5 yr	Ambient/ambient +175 ppm/ambient +350 ppm	Increase across three N levels (Table 2)†
Godbold <i>et al.</i> (1997)	<i>Betula papyrifera</i> saplings <i>Pinus strobus</i> saplings	Mixed	GH	25 wk 35 wk	Ambient/700 ppm	1.6 NS
Rouhier & Read (1998a)	<i>Pinus sylvestris</i> seedlings	<i>Suillus bovinus</i> <i>Paxillus involutus</i>	Plexiglass observation chambers	87 d 55 d	350/700 ppm	2.3 4.4
<b>Arbuscular mycorrhizal fungi</b>						
Klironomos <i>et al.</i> (1996)	<i>Artemisia tridentata</i> seedlings	Mixed	Pots, GC	12 wk	350/700 ppm	~2.3‡
Klironomos <i>et al.</i> (1997)	<i>Populus tremuloides</i> saplings	Mixed	OTC	14 months	350/700 ppm	1.8 (low N; Table 2) NS (high N)
Klironomos <i>et al.</i> (1998)	<i>Artemisia tridentata</i> seedlings	<i>Glomus intraradices</i> <i>G. etunicatum</i> <i>Acaulospora denticulata</i> <i>Scutellospora calospora</i>	Pots, GC	16 wk	350/700 ppm	NS NS ~1.4 ~1.5
Lussenhop <i>et al.</i> (1998)	<i>Populus × euramericana</i> saplings (constructed ecosystem)	Mixed (inoculum from high fertility soil)	OTC	5 months	34.5/69.3 Pa	NS (low N; Table 2) NS (high N)
Rillig & Allen (1998)	<i>Gutierrezia sarothrae</i>	Mixed	Pots, GC	4 months	Ambient/750 ppm	~2.1 (low N; Table 2) NS (high N)
Rouhier & Read (1998b)	<i>Plantago lanceolata</i>	Mixed (inoculum from dune turf roots)	Pots, GH	41, 76, 104 d	350/540 ppm	NS at any harvest
Sanders <i>et al.</i> (1998)	<i>Prunella vulgaris</i>	<i>Glomus</i> isolates Bassle Pi and BEG 19	Pots, GC	20 wk	350/600 ppm	3.8 (1–2 cm from root) 3.9 (6.5–7.5 cm) 5.2 (13–14 cm)
Rillig <i>et al.</i> (1999a)	Serpentine grassland Sandstone grassland	Mixed	OTC	5.25 yr	Ambient/ambient+350 ppm	1.9 NS
Staddon <i>et al.</i> (1999)	<i>Plantago lanceolata</i> <i>Trifolium repens</i>	<i>Glomus mosseae</i>	Pots, OTC	37–71 d 42–75 d	400/650 ppm	Up to 1.7 Up to 2.3 (varied with harvest)

\*GC, growth chamber; GH, glasshouse; OTC, open-top chamber. †Could include some nonmycorrhizal species. ‡Used DFS staining to measure hyphal biomass.

communities, N treatments or harvest dates; however none has detected a significant decrease in hyphal length or growth. This trend suggests a possible increase in global mycorrhizal biomass as atmospheric CO<sub>2</sub> levels rise, although the magnitude of this response might vary regionally and among species.

Long-term field-based studies of mycorrhizal biomass under elevated CO<sub>2</sub> are rare but critical in predicting responses of natural systems. Rillig *et al.* (1999a) found increases in AM hyphal biomass in a serpentine grassland (but no significant change in a sandstone grassland) after >5 yr CO<sub>2</sub> treatment. This change could be due to indirect effects of shifts in plant or fungal communities, or direct effects on plant C status. A similar increase occurred in AM fungi associated with trembling aspen after 14 months (Klironomos *et al.*, 1997). Likewise, Tingey *et al.* (1995) noted a rise in the presence of ECM root tips and visible hyphae after 2.5 yr enrichment. With the exception of the sandstone grassland, these results are not consistent with the hypothesis that hyphal lengths in soils are already at a maximum under ambient CO<sub>2</sub> and will not increase as CO<sub>2</sub> levels rise (O'Neill, 1994; Allen *et al.*, 1995). Each of these studies focused on changes in the incidence of live and dead hyphae combined.

Additional field studies have indicated that the quantity of soil organic matter derived from mycorrhizal tissue might rise under CO<sub>2</sub> enrichment. Rillig *et al.* (1999b) reported an increase in glomalin concentrations in soil from a chaparral system exposed to elevated CO<sub>2</sub> for 3 yr. In large macroaggregates (1–2 mm diameter) from the same ecosystem, the length of live AM hyphae increased 10-fold as CO<sub>2</sub> treatments varied from 250 to 650 ppm CO<sub>2</sub> (K. Treseder, unpublished). This increase in mycorrhizal biomass was accompanied by a 30-fold rise in C allocation to these macroaggregates. These field-based studies suggest that the combined influences of elevated CO<sub>2</sub> on mycorrhizal C dynamics (including community changes, productivity and decomposition) could ultimately produce an increase in the amount of C sequestered in intact hyphae and their residual components. However, many more studies of this nature are required before we can make general statements with any certainty. In addition, it is not clear whether these increases in hyphal biomass or residues will be maintained at equilibrium levels after the system has adjusted to the sudden rise in CO<sub>2</sub> that occurred at the onset of the experiment.

Controlled, smaller-scale experiments provide insights into the mechanisms underlying the increase in hyphal biomass in field systems. For example, Rouhier & Read (1998a) directly followed hyphal growth of two ECM fungi and noted a positive response in both under CO<sub>2</sub> enrichment. These measurements of actual growth rates are rare.

Most investigations have been conducted in growth chambers or glasshouses for periods from several weeks to months (Table 1). Many of these have reported augmentation of hyphal length under CO<sub>2</sub> enrichment. However, the duration and scale of these experiments impose some limitations in scaling up to ecosystem-level dynamics or in assessing underlying mechanisms (Allen, 1996). As the plants and fungi were not grown in an intact community, they were not necessarily subject to competition or interactions from higher trophic levels. In addition, the bacterial community might not have been representative of those found in natural systems. Decomposition might also be a factor in experiments lasting more than a few weeks, and could introduce some unknown degree of error into interpretation of growth rates. Klironomos *et al.* (1996) used differential fluorescent staining to restrict biomass measurements to live hyphae, and found a more than twofold increase with elevated CO<sub>2</sub>. This response might also have been affected somewhat by changes in lifespan of the fungi. Nevertheless, the general trend toward increases in hyphal biomass (usually associated with increasing plant biomass) under elevated CO<sub>2</sub> in pot experiments indicates that the abundance of mycorrhizal hyphae could rise in a number of AM and ECM fungal species and, potentially, ecosystems. Notably, the hyphal lengths of ECM fungi do not appear to demonstrate a greater frequency or magnitude of response to CO<sub>2</sub> than do hyphae of AM fungi, as suggested by O'Neill (1994).

#### *Shifts in the mycorrhizal community*

Mycorrhizal groups vary in the magnitude of their responses to elevated CO<sub>2</sub> (Table 1), resulting in shifts in the mycorrhizal community structure (O'Neill, 1994; Cairney & Meharg, 1999). In AM fungi, hyphal lengths of *Acaulospora denticulata* and *Scutellospora calospora* increased in response to CO<sub>2</sub> enrichment, while those of two *Glomus* species did not (Klironomos *et al.*, 1998). These genera were each grown separately in pots (with *Artemisia tridentata*) and did not compete for resources. In a complementary chaparral-based field experiment, the abundance of hyphae from four AM genera (*Acaulospora*, *Gigaspora*, *Glomus* and *Scutellospora*) was evenly distributed in chambers exposed to CO<sub>2</sub> concentrations of 250–350 ppm, but *Acaulospora* and *Scutellospora* dominated at 450–650 ppm (K. Treseder, unpublished). The results of these two studies indicate that *Acaulospora* and *Scutellospora* might become more prevalent as CO<sub>2</sub> levels rise.

Interspecific variation and shifts in community composition have also been documented in ECM fungi. For example, Rouhier & Read (1998a) reported that the biomass of *P. involutus* responded more strongly to a doubling of CO<sub>2</sub> concentrations than did that of *Suillus bovinus*. Likewise, in

mycorrhizal root tips of *Betula pendula* seedlings *Leccinum* dominated at elevated CO<sub>2</sub>, but at ambient CO<sub>2</sub> species were more evenly distributed (Rey & Jarvis, 1997). In addition, in *Betula papyrifera* the relative abundance of ECM morphotypes changed significantly under elevated CO<sub>2</sub> (Godbold *et al.*, 1997), with a shift toward morphotypes with higher numbers of associated hyphae and rhizomorphs (Godbold & Berntson, 1997). Finally, in young *Pinus sylvestris* trees, CO<sub>2</sub> enrichment reduced by half the presence of the dominant (dichotomous) morphotype (Kasurinen *et al.*, 1999), although this response could have been strictly morphological. As mycorrhizal groups vary in tissue quality and growth rate, these shifts in the mycorrhizal community might feed back to affect several processes involved in the cycling of mycorrhizal C.

#### *Life span and decomposition of mycorrhizal tissue*

The effects of elevated CO<sub>2</sub> on the life span or turnover of individual mycorrhizal hyphae (ECM or AM) are not known. Rygielwicz *et al.* (1997) used minirhizotrons to track the length of time between formation and disappearance of mycorrhizal root tips on seedlings of *Pinus ponderosa* and found that elevated CO<sub>2</sub> had no significant effect. Moreover, as high CO<sub>2</sub> increased production of new root tips, a greater C flux through mycorrhizas was implied. Single hyphae might respond in a similar manner, and studies of their dynamics are required. Additionally, nutrient concentrations might be related to decomposition rates in mycorrhizal tissue (as in plant tissue), and P concentrations in ECM tips of *P. involutus* and *S. bovinus* declined significantly with CO<sub>2</sub> enrichment (Rouhier & Read, 1998a). Nitrogen content also decreased in *P. involutus*. Finally, we note that elevated CO<sub>2</sub> can increase fine-root mortality (Pregitzer *et al.*, 1995), which might be followed by a decrease in the life span of relatively long-lived ECM root tips and rhizomorphs.

#### *Summary of CO<sub>2</sub> effects*

Although approaches and scopes have varied widely among studies of elevated CO<sub>2</sub> on mycorrhizal dynamics, several lines of evidence indicate that pools of mycorrhizal C might increase as CO<sub>2</sub> levels rise. With exceptions, growth rate and biomass of total live and dead hyphae tend to increase for both AM and ECM fungi both at plant and ecosystem level. This response is probably related to concurrent increases in plant biomass (Staddon & Fitter, 1998) or to changes in plant or fungal community composition. Hyphal length rarely, if ever, decreases. In addition, preliminary evidence indicates that soil organic matter associated with mycorrhizal hyphae might become more prevalent. However, few data exist regarding changes in life span or decomposition rate under CO<sub>2</sub> enrich-

ment, and these processes have strong controls over the long-term accumulation of soil organic matter pools over time. In addition, shifts in community composition of mycorrhizal fungi with CO<sub>2</sub> concentration might affect all aspects of mycorrhizal C cycling in an unforeseeable manner. Additional research on ecosystem-level responses and underlying mechanisms is critical.

#### EFFECTS OF NITROGEN DEPOSITION

##### *Biomass and productivity*

Elevated CO<sub>2</sub> often occurs concurrently with several other aspects of global change, including widespread N deposition. Increasing N availability might reduce investment by plants in mycorrhizal fungi. This response is especially likely for ECM fungi, as this group acts as an important mechanism of N acquisition for plants (Read, 1991). The decline in abundance of fruiting bodies of ECM fungi in European forests has been well documented (Arnolds, 1988, 1991; Jansen & Dighton, 1990; Colpaert & van Tichelen, 1996; Wallenda & Kottke, 1998; Cairney & Meharg, 1999), and N deposition is considered a major contributing factor. Nitrogen fertilization has often been used to simulate effects of N deposition, and usually produces decreases in mushroom production (Menge & Grand, 1978; Ruhling & Tyler, 1991; Termorshuizen, 1993). This decline in fruiting bodies might in itself represent a noteworthy decrease in ECM fungal biomass, but might not necessarily be accompanied by a decrease in the presence of below-ground tissue (Termorshuizen, 1993).

Extraradical hyphae can also account for a substantial portion of mycorrhizal biomass, and ecosystem-level responses of hyphae to N fertilization vary (Table 2). For example, the incidence of ECM biomass (including hyphae) in root tips was not affected by long-term fertilization in *P. ponderosa* seedlings (Tingey *et al.*, 1995) or in a *Picea abies* forest (Karen & Nylund, 1997). In AM fungi, Klironomos *et al.* (1997) reported a significant reduction in hyphal length associated with *Populus tremuloides* saplings after 14 months of N additions, but Eom *et al.* (1999) observed an increase in biomass in a tallgrass prairie fertilized for 10 yr. Of these four studies, all but Karen & Nylund (1997) included both live and dead hyphae in their measurements of biomass. These inconsistencies in N response could be attributable to the initial N status of the systems, and to varying influences of alterations in growth rate, decomposition, life span or community structure.

Nitrogen treatments also have inconsistent effects on hyphal growth rate (Table 2). Arnebrant (1994) documented significant decreases in growth with increasing N availability in five ECM isolates.

**Table 2.** Effects of nitrogen availability on growth or biomass of mycorrhizal hyphae

Reference	Host plant or system	Mycorrhizal species	Growth environment*	Duration	Nitrogen additions	Growth or biomass response (N addition: control)
<b>Ectomycorrhizal fungi</b>						
Wallander & Nylund (1992)	<i>Pinus sylvestris</i> seedlings	<i>Laccaria bicolor</i> <i>Suillus bovinus</i>	Semi-hydroponic	6–9 wk	NH <sub>4</sub> Cl in 1–10 or 100–200 mg N l <sup>-1</sup>	~0.3† ~0.1
Arnebrant (1994)	<i>Pinus contorta</i> seedlings <i>P. contorta</i> seedlings <i>P. sylvestris</i> seedlings <i>P. sylvestris</i> seedlings <i>P. sylvestris</i> seedlings	<i>Paxillus involutus</i> isolate 1 <i>P. involutus</i> isolate 2 <i>S. bovinus</i> Unidentified Unidentified	Microcosms	2–4 months	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> , NaNO <sub>3</sub> , NH <sub>4</sub> <sup>+</sup> + NO <sub>3</sub> <sup>-</sup> in 1, 2, or 4 mg N g <sup>-1</sup> peat	0.8 0.4 0.3 0.5 0.3
Wallander <i>et al.</i> (1994)	<i>P. sylvestris</i> seedlings	<i>Hebeloma crustuliniforme</i>	Semi-hydroponic	5 wk	75 mg l <sup>-1</sup> type of N not given	Decrease†
Ekblad <i>et al.</i> (1995)	<i>P. sylvestris</i> seedlings <i>Alnus incanta</i> seedlings	<i>P. involutus</i>	Pots, GC	13 wk 10 wk	NH <sub>4</sub> NO <sub>3</sub> in 6 or 54 mg kg <sup>-1</sup>	~1.5
Tingey <i>et al.</i> (1995)	<i>P. ponderosa</i> seedlings	Mixed (mostly <i>Thelephora terrestris</i> )	OTC	2.5 yr	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> in 0, 100 or 200 kg ha <sup>-1</sup> yr <sup>-1</sup>	NS in three CO <sub>2</sub> levels (Table 1)
Karen & Nylund (1997)	<i>Picea abies</i> adults	Mixed	Forest	4 yr	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> in 0 or 100 kg ha <sup>-1</sup> yr <sup>-1</sup>	NS (biomass in root tips)†
Wallander <i>et al.</i> (1999)	<i>Pinus sylvestris</i> seedlings	<i>P. involutus</i> 1 (low-N habitat) <i>P. involutus</i> 2 (moderate N) <i>P. involutus</i> 3 (high N) <i>P. involutus</i> 4 (moderate N)	Microcosms	3–8 wk	(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> in 1, 2, or 4 mg N per g peat	NS
<b>Arbuscular mycorrhizal fungi</b>						
Klironomos <i>et al.</i> (1997)	<i>Populus tremuloides</i> saplings	Mixed (soil inoculum)	OTC	14 months	Soil with high (348 µg g <sup>-1</sup> d <sup>-1</sup> ) or low (45 µg g <sup>-1</sup> d <sup>-1</sup> ) N mineralization	0.3 across CO <sub>2</sub> levels (Table 1)
Lussenhop <i>et al.</i> (1998)	<i>Populus × euramericana</i> saplings (constructed ecosystem)	Mixed (inoculum from high-fertility soil)	OTC	5 months	High-(15.1 g N kg <sup>-1</sup> ) or low-(4.6 g N kg <sup>-1</sup> ) N soil	2.3 across CO <sub>2</sub> levels (Table 1)
Rillig & Allen (1998)	<i>Gutierrezia sarothrae</i>	Mixed	Pots, GC	4 months	CaNO <sub>3</sub> + NH <sub>4</sub> NO <sub>3</sub> in 100 kg N ha <sup>-1</sup> yr <sup>-1</sup>	NS (ambient CO <sub>2</sub> ; Table 1) ~0.5 (elevated CO <sub>2</sub> )
Bethenfalvay <i>et al.</i> (1999)	Soybean	Mixed (soil)	GH	9 wk	1 mM NH <sub>4</sub> NO <sub>3</sub> , 3 mM Ca(NO <sub>3</sub> ) <sub>2</sub> or 4 mM urea-[CO(NH <sub>2</sub> ) <sub>2</sub> ]	NS
Eom <i>et al.</i> (1999)	Tallgrass prairie	Mixed	Prairie	10 yr	NH <sub>4</sub> NO <sub>3</sub> in 10 g N m <sup>-2</sup> yr <sup>-1</sup>	1.2

\*GC, growth chamber; GH, glasshouse; OTC, open-top chamber. †Used ergosterol as index of hyphal biomass.



However, in another ECM experiment Wallander *et al.* (1999) found no significant N effect on growth rates of four isolates of *P. involutus* collected from regions exposed to varying levels of N deposition. Aside from these two studies, few direct assessments of N effects on ECM or AM growth rates are reported in the literature. In experiments that have measured ECM biomass after weeks or months of growth, decreases (Wallander & Nylund, 1992; Wallander *et al.*, 1994); lack of response (Wallander & Nylund, 1992); or increases (Ekblad *et al.*, 1995) under higher N availability have each been observed. Likewise, the responses of AM biomass to N concentration have been positive (Lussenhop *et al.*, 1998), negative (Rillig & Allen, 1998), or not significant (Rillig & Allen, 1998; Bethlenfalvay *et al.*, 1999).

Much of the inconsistency in N effects among and within studies might be due to variation in responses among mycorrhizal groups or among plant/fungal combinations. Wallander and Nylund (1992) reported that *S. bovinus* was more sensitive to N additions than was *Laccaria bicolor* when both were grown on *Pinus sylvestris* in a semi-hydroponic medium. In a microcosm experiment conducted by Arnebrant (1994), two isolates of *P. involutus*, one isolate of *S. bovinus*, and two additional unidentified species of ECM fungi were exposed to increasing N availability. The growth rate of *S. bovinus* and one unknown species declined markedly, while one *P. involutus* isolate was only slightly affected. In a separate study by Wallander *et al.* (1999), four isolates of *P. involutus* and two of *S. bovinus* grown in culture (as a complement to the seedling experiment summarized in Table 2) also displayed different sensitivities to N additions. One *P. involutus* isolate from a low-N deposition site, another from a moderate-N site, and an isolate of *S. bovinus* from a low-N site each grew significantly more slowly when supplied with excess N. Additional isolates from moderate- to high-N (or unknown) sites had no significant response. These N effects were not consistent with those of the seedling experiment, in which hyphal growth rates were not affected in any group. Nevertheless, these three studies suggest that ECM fungi might differ in productivity under N deposition, and that *S. bovinus* appears particularly susceptible. It remains to be seen whether AM groups might vary as well.

#### *Shifts in community composition*

Several studies have detailed changes caused by N deposition or fertilization in the species assemblage of mushrooms (Menge & Grand, 1978; Arnolds, 1988, 1991; Termorshuizen, 1993). However, as the community composition of ECM fruiting bodies can differ from that of below-ground ECM structures (Gardes & Bruns, 1996), and below-ground biomass

could be a substantial C pool, this review focuses on the species composition of fungal structures in the soil. In both a Swedish *Picea abies* forest (Karen & Nylund, 1997) and a Scottish Sitka spruce plantation (Taylor & Alexander, 1989), frequencies of ECM morphotypes on root tips shifted upon long-term N fertilization. Likewise, in *Pinus sylvestris* forests in Sweden, colonization of 'bait' seedlings by one particular morphotype was less frequent in N-fertilized than in control plots (Arnebrant & Soderstrom, 1992).

Composition of AM communities can also shift with N availability. In a natural N deposition gradient in southern California coastal sage scrub, spores of *Scutellospora* and *Gigaspora* species became less prevalent with increasing deposition. Conversely, spores of certain *Glomus* species (e.g. *G. aggregatum*, *G. leptotichum* and *G. geosporum*) proliferated under the same conditions (Egerton-Warburton & Allen, 2000). In addition, in tallgrass prairie the abundance of spores from *Gigaspora gigantea* and *Glomus mosseae* increased with N fertilization, while that of *Entrophospora infrequens* declined significantly (Eom *et al.*, 1999). Johnson (1993) noted an increase in the presence of *Gigaspora gigantea*, *Gigaspora margarita*, *Scutellospora calospora* and *Glomus occultum*, and a decrease in *Glomus intraradix* after 8 yr fertilization with a suite of nutrients including N and P. Alterations in the species assemblage of mycorrhizal fungi, either directly through N availability or indirectly through shifts in plant communities, appear to be a likely outcome of widespread N deposition.

#### *Life span and decomposition of mycorrhizal tissue*

Nitrogen effects on the survivorship and decomposition of mycorrhizal hyphae have received little attention. Using minirhizotrons, Majdi & Nylund (1996) found that N fertilization significantly reduced the life span of ectomycorrhizal short roots from 240 to 210 d in a 30-yr-old Norway spruce stand in southwest Sweden. The authors did not speculate on mechanisms underpinning this change, but we suggest that alterations of the ECM community could have been one factor. In another minirhizotron experiment, Rygielwicz *et al.* (1997) recorded no effect of N fertilization on the length of time between appearance and disappearance of ECM tips. This latter result includes both life span and decomposition rate of the fungal tissue. These studies present valuable information on the dynamics of mycorrhizal root tips. However, alterations in turnover of extraradical ECM and AM hyphae by N additions have yet to be reported in the literature. Nitrogen concentrations of hyphae from one *P. involutus* isolate were reported to increase with higher N availability in a culture experiment

(Wallander *et al.*, 1999), with possible shifts in decomposition rate. Additionally, root turnover can increase with N fertilization (Pregitzer *et al.*, 1995; Majdi & Nylund, 1996), and this response could produce a corresponding decrease in the life span of ECM structures such as mycorrhizal root tips and rhizomorphs.

#### *Summary of N effects*

Increases in N availability inconsistently affect hyphal dynamics (especially growth and biomass). In field studies, this variation in response could be partially attributable to the initial N status of the ecosystem; N-limited systems might respond differently from systems in which another factor (e.g. P or water) limits primary productivity. Nutrient limitation of plants is an important consideration because mycorrhizal fungi derive the majority of their C from the host. However, this possibility has not been explicitly tested. At this point we can only suggest that C storage in living and recently dead mycorrhizal tissue might only be affected (e.g. augmented or reduced) in certain systems exposed to N deposition. Furthermore, in glasshouse or culture studies the use of different fungal species or isolates might contribute to conflicting responses of hyphal growth or biomass. Even isolates of the same species can vary in response to N availability (Arnebrant, 1994; Wallander *et al.*, 1999).

Overall, alteration in the community composition of mycorrhizal fungi (probably due to differences among groups in sensitivity to N) appears to be the most general response to N addition. Because mycorrhizal groups can vary in chitin content and growth rate, these shifts could have important consequences for C immobilization in live hyphal tissue or its residual soil organic matter. However, a more complete understanding of differences in tissue quality and physiology among groups is necessary in order to predict their influence on C dynamics.

#### *Interactions between elevated CO<sub>2</sub> and N deposition*

Effects of elevated CO<sub>2</sub> and N availability can interact to influence hyphal biomass. In a 14-month experiment on *P. tremuloides* seedlings, AM hyphal lengths increased with CO<sub>2</sub> in the low-N but not the high-N treatment (Klironomos *et al.*, 1997). Arbuscular mycorrhizal hyphae associated with *Gutierrezia sarothrae* responded in a similar manner after 4 months' exposure to high and low treatments of CO<sub>2</sub> and N (Rillig & Allen, 1998). Apparently, N additions can negate CO<sub>2</sub> effects on mycorrhizal biomass in some systems. This interaction is not universal, however. Lussenhop *et al.* (1998) noted no significant CO<sub>2</sub> by N effects in AM biomass of a constructed ecosystem of *Populus × euramericana* seedlings. Tingey *et al.* (1995) also found no CO<sub>2</sub> and

N interaction on the presence of ECM root tips and hyphae on *P. ponderosa* seedlings. Further investigations of this interaction and its effects on processes including turnover will be of interest. Unlike elevated CO<sub>2</sub>, which is a global phenomenon, N deposition is greatest near regions with dense human populations. Therefore interactions between these two elements of global change will be factors primarily in ecosystems surrounding urban and agricultural areas, and investigations should focus on these habitats.

#### CONCLUSION

The potential for mycorrhizal fungi to influence the sequestration of soil C under various aspects of global change has been frequently suggested in the literature, although rarely directly addressed. The current body of work on mycorrhizal dynamics suggests that elevated CO<sub>2</sub> might augment global pools of C in living, dead and residual mycorrhizal tissue by increasing productivity in numerous habitats. By contrast, the (smaller-scale) influence of N deposition on ecosystem-level responses is less general than that of CO<sub>2</sub>, and might rely on several factors, including the initial N status of the vegetation. Preliminary evidence that N fertilization increases turnover rates of hyphae indicates that C sequestration in hyphal biomass might decrease in areas exposed to N deposition. Elevated CO<sub>2</sub> and N deposition could therefore have conflicting influences on mycorrhizal C.

Shifts in the community composition of AM and ECM fungi with CO<sub>2</sub> and N enrichment could have important influences on mycorrhizal C dynamics. For instance, since *Scutellospora* and *Acaulospora* species appear to proliferate under elevated CO<sub>2</sub>, and *Glomus* species can be more abundant with N deposition, predictions of the community structure under both disturbances are challenging. Nevertheless, our understanding of these changes is important; AM genera and species can vary in tissue quality and therefore affect C transformations. ECM fungi present similar issues. Compared with *Suillus bovinus*, *P. involutus* can respond more strongly to elevated CO<sub>2</sub> and can be less sensitive to N addition, with potential consequences for species composition and C storage. However, these patterns are derived from very few studies. Our knowledge indicates that the influence of mycorrhizal fungi on C dynamics under global change remains largely unknown, but could be a significant factor in soil C sequestration.

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## REFERENCES

- Allen MF. 1991. *The ecology of mycorrhizae*. Cambridge, UK: Cambridge University Press.
- Allen MF. 1996. The ecology of arbuscular mycorrhizas: a look back into the 20th century and a peek into the 21st. *Mycological Research* **100**: 769–782.
- Allen MF, Morris SJ, Edwards F, Allen EB. 1995. Microbe–plant interactions in Mediterranean-type habitats: shifts in fungal symbiotic and saprophytic functioning in response to global change. In: Moreno JM, Oechel WC, eds. *Global change and Mediterranean-type ecosystems*. New York, USA: Springer Verlag, 287–305.
- Arnebrant K. 1994. Nitrogen amendments reduce the growth of extramatrical ectomycorrhizal mycelium. *Mycorrhiza* **5**: 7–15.
- Arnebrant K, Soderstrom B. 1992. Effects of different fertilizer treatments on ectomycorrhizal colonization potential in two Scots pine forests in Sweden. *Forest Ecology and Management* **53**: 77–89.
- Arnolds E. 1988. The changing macromycete flora in the Netherlands. *Transactions of the British Mycological Society* **90**: 391–406.
- Arnolds E. 1991. Decline of ectomycorrhizal fungi in Europe. *Agriculture, Ecosystems and Environment* **35**: 209–244.
- Bethlenfalvay G, Cantrell I, Mihara K, Schreiner R. 1999. Relationships between soil aggregation and mycorrhizae as influenced by soil biota and nitrogen nutrition. *Biology and Fertility of Soils* **28**: 356–363.
- Cairney JWG. 1999. Intraspecific physiological variation: implications for understanding functional diversity in ectomycorrhizal fungi. *Mycorrhiza* **9**: 125–135.
- Cairney JWG, Meharg AA. 1999. Influences of anthropogenic pollution on mycorrhizal fungal communities. *Environmental Pollution* **106**: 169–182.
- Ciais P, Tans PP, Trolier M, White JWC, Francey RJ. 1995. A large northern-hemisphere terrestrial CO<sub>2</sub> sink indicated by the <sup>13</sup>C/<sup>12</sup>C ratio of atmospheric CO<sub>2</sub>. *Science* **269**: 1098–1102.
- Colpaert JV, van Assche JA, Luijckens K. 1992. The growth of the extramatrical mycelium of ectomycorrhizal fungi and the growth response of *Pinus sylvestris* L. *New Phytologist* **120**: 127–135.
- Colpaert JV, van Tichelen KK. 1996. Mycorrhizas and environmental stress. In: Frankland JC, Magan N, Gadd GM, eds. *Fungi and environmental change*. Cambridge, UK: Cambridge University Press, 109–128.
- Dai A, Fung IY. 1993. Can climate variability contribute to the “missing” CO<sub>2</sub> sink? *Global Biogeochemical Cycles* **7**: 599–609.
- Diaz S. 1996. Effects of elevated [CO<sub>2</sub>] at the community level mediated by root symbionts. *Plant and Soil* **187**: 309–320.
- Egerton-Warburton LM, Allen EB. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* **10**: 484–496.
- Ekblad A, Wallander H, Carlsson R, Huss-Danell K. 1995. Fungal biomass in roots and extramatrical mycelium in relation to macronutrients and plant biomass of ectomycorrhizal *Pinus sylvestris* and *Alnus incana*. *New Phytologist* **131**: 443–451.
- Eom A-H, Hartnett DC, Wilson GWT, Figge DAH. 1999. The effect of fire, mowing and fertilizer amendment on arbuscular mycorrhizas in tallgrass prairie. *American Midland Naturalist* **142**: 55–70.
- Field CB, Fung IY. 1999. The not-so-big US carbon sink. *Science* **285**: 544–545.
- Fogel R, Hunt G. 1983. Contribution of mycorrhizae and soil fungi to nutrient cycling in a Douglas-fir ecosystem. *Canadian Journal of Forest Research* **13**: 219–232.
- Friedlingstein P, Fung I, Holland E, John J, Brasseur G, Erickson D, Schimel D. 1995. On the contribution of CO<sub>2</sub> fertilization to the missing biospheric sink. *Global Biogeochemical Cycles* **9**: 541–556.
- Friese CF, Allen MF. 1991a. The spread of VA mycorrhizal fungal hyphae in the soil: inoculum types and external hyphal architecture. *Mycologia* **83**: 409–418.
- Friese CF, Allen MF. 1991b. Tracking the fates of exotic and local VA mycorrhizal fungi: methods and patterns. *Agriculture, Ecosystems and Environment* **34**: 87–96.
- Fung I, Field CB, Berry JA, Thompson MV, Randerson JT, Malmstrom CM, Vitousek PM, Collatz GJ, Sellers PJ, Randall DA, Denning AS, Badeck F, John J. 1997. Carbon 13 exchanges between the atmosphere and biosphere. *Global Biogeochemical Cycles* **11**: 507–533.
- Gardes M, Bruns TD. 1996. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. *Canadian Journal of Botany* **74**: 1572–1583.
- Godbold DL, Berntson GM. 1997. Elevated atmospheric CO<sub>2</sub> concentration changes ectomycorrhizal morphotype assemblages in *Betula papyrifera*. *Tree Physiology* **17**: 347–350.
- Godbold DL, Berntson GM, Bazzaz FA. 1997. Growth and mycorrhizal colonization of three North American tree species under elevated atmospheric CO<sub>2</sub>. *New Phytologist* **137**: 433–440.
- Gooday GW. 1994. Physiology of microbial degradation of chitin and chitosan. In: Ratledge C, ed. *Biochemistry of microbial degradation*. Dordrecht, The Netherlands: Kluwer Academic, 279–312.
- Hodge A. 1996. Impact of elevated CO<sub>2</sub> on mycorrhizal associations and implications for plant growth. *Biology and Fertility of Soils* **23**: 388–398.
- Houghton RA, Hackler JL, Lawrence KT. 1999. The US carbon budget: contributions from land-use change. *Science* **285**: 574–578.
- Ineichen K, Wiemken V, Wiemken A. 1995. Shoots, roots and ectomycorrhiza formation of pine seedlings at elevated atmospheric carbon dioxide. *Plant, Cell & Environment* **18**: 703–707.
- Jansen AE, Dighton J. 1990. Effects of air pollutants on ectomycorrhiza. A review. *Air Pollution Research Report* **30**: 1–58.
- Johnson NC. 1993. Can fertilization of soil select less mutualistic mycorrhizae? *Ecological Applications* **3**: 749–757.
- Karen O, Nylund JE. 1997. Effects of ammonium sulfate on the community structure and biomass of ectomycorrhizal fungi in a Norway spruce stand in southwestern Sweden. *Canadian Journal of Botany* **75**: 1628–1642.
- Kasurinen A, Helmisaari HS, Holopainen T. 1999. The influence of elevated CO<sub>2</sub> and O<sub>3</sub> on fine roots and mycorrhizas of naturally growing young Scots pine trees during three exposure years. *Global Change Biology* **5**: 771–780.
- Keeling RF, Piper SC, Heimann M. 1996. Global and hemispheric CO<sub>2</sub> sinks deduced from changes in atmospheric O<sub>2</sub> concentration. *Nature* **381**: 218–221.
- Klironomos JN, Bednarczuk EM, Neville E. 1999. Reproductive significance of feeding on saprobic and arbuscular mycorrhizal fungi by the collembolan, *Folsomia candida*. *Functional Ecology* **13**: 756–761.
- Klironomos JN, Kendrick WB. 1996. Palatability of microfungi to soil arthropods in relation to the functioning of arbuscular mycorrhizae. *Biology and Fertility of Soils* **21**: 43–52.
- Klironomos JN, Rillig MC, Allen MF. 1996. Below-ground microbial and microfaunal responses to *Artemisia tridentata* grown under elevated atmospheric CO<sub>2</sub>. *Functional Ecology* **10**: 527–534.
- Klironomos JN, Rillig MC, Allen MF, Zak DR, Kubiske M, Pregitzer KS. 1997. Soil fungal–arthropod responses to *Populus tremuloides* grown under enriched atmospheric CO<sub>2</sub> under field conditions. *Global Change Biology* **3**: 473–478.
- Klironomos JN, Ursic M. 1998. Density-dependent grazing on the extraradical hyphal network of the arbuscular mycorrhizal fungus, *Glomus intraradices*, by the collembolan, *Folsomia candida*. *Biology and Fertility of Soils* **26**: 250–253.
- Klironomos JN, Ursic M, Rillig M, Allen MF. 1998. Interspecific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated CO<sub>2</sub>. *New Phytologist* **138**: 599–605.
- Lloyd J. 1999. Current perspectives on the terrestrial carbon cycle. *Tellus Series B – Chemical and Physical Meteorology* **51**: 336–342.
- Lussenhop J, Treonis A, Curtis PS, Teeri JA, Vogel CS. 1998. Response of soil biota to elevated atmospheric CO<sub>2</sub> in poplar model systems. *Oecologia* **113**: 247–251.

- Majdi H, Nylund J-E. 1996. Does liquid fertilization affect fine root dynamics and lifespan of mycorrhizal short roots? *Plant and Soil* **185**: 305–309.
- Malmstrom CM, Thompson MV, Juday GP, Los SO, Randerson JT, Field CB. 1997. Interannual variation in global-scale net primary production: testing model estimates. *Global Biogeochemical Cycles* **11**: 367–392.
- Martin F, Delaruelle C, Hilert J-L. 1990. An improved ergosterol assay to estimate fungal biomass in ectomycorrhizas. *Mycological Research* **94**: 1059–1064.
- Melillo JM, Aber JD, Muratore JM. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**: 621–626.
- Menge JA, Grand LF. 1978. Effect of fertilization on production of epigeous basidiocarps by mycorrhizal fungi in loblolly pine plantations. *Canadian Journal of Botany* **56**: 2357–2362.
- Morris SJ, Zink T, Connors K, Allen MF. 1997. Comparison between fluorescein diacetate and differential fluorescent staining procedures for determining fungal biomass in soils. *Applied Soil Ecology* **6**: 161–167.
- Muzzarelli RAA. 1977. *Chitin*. New York, USA: Pergamon.
- Nadelhoffer KJ, Emmett BA, Gundersen P, Kjonaas OJ, Koopmans CJ, Schlei P, Tietemal A, Wright RF. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Science* **398**: 145–147.
- Norby RJ, O'Neill EG, Luxmoore RJ. 1986. Effects of atmospheric CO<sub>2</sub> enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. *Plant Physiology* **82**: 83–89.
- Nylund J-E, Wallander H. 1992. Ergosterol analysis as a means of quantifying mycorrhizal biomass. In: Norris JR, Read DJ, Varma AK, eds. *Methods in microbiology*. London, UK: Academic Press, 24.
- O'Neill EG. 1994. Responses of soil biota to elevated atmospheric carbon dioxide. *Plant and Soil* **165**: 55–65.
- O'Neill EG, Luxmoore RJ, Norby RJ. 1987. Increases in mycorrhizal colonization and seedling growth in *Pinus echinata* and *Quercus alba* in an enriched CO<sub>2</sub> atmosphere. *Canadian Journal of Forest Research* **17**: 878–883.
- Parton WJ, Stewart JWB, Cole CV. 1988. Dynamics of C, N, P, and S in grassland soils: a model. *Biogeochemistry* **5**: 109–131.
- Poorter H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO<sub>2</sub> concentration. *Vegetatio* **140**: 77–97.
- Pregitzer KS, Zak DR, Curtis PS, Kubiske ME, Teeri JA, Vogel CS. 1995. Atmospheric CO<sub>2</sub>, soil nitrogen and turnover of fine roots. *New Phytologist* **129**: 579–585.
- Read DJ. 1991. Mycorrhizas in ecosystems – nature's response to the 'Law of the Minimum'. In: Hawksworth DL, ed. *Frontiers in mycology. Honorary and general lectures from the Fourth International Mycological Congress, Regensburg, Germany, 1990*. Wallingford, UK: CAB International, 101–130.
- Rey A, Jarvis PG. 1997. Growth response of young birch trees (*Betula pendula* Roth.) after four and a half years of CO<sub>2</sub> exposure. *Annals of Botany* **80**: 809–816.
- Rillig MC, Allen MF. 1998. Arbuscular mycorrhizae of *Gutierrezia sarothrae* and elevated carbon dioxide: evidence for shifts in C allocation to and within the mycobiont. *Soil Biology and Biochemistry* **30**: 2001–2008.
- Rillig MC, Allen MF. 1999. What is the role of arbuscular mycorrhizal fungi in plant-to-ecosystem responses to elevated atmospheric CO<sub>2</sub>? *Mycorrhiza* **9**: 1–8.
- Rillig MC, Field CB, Allen MF. 1999a. Soil biota responses to long-term atmospheric CO<sub>2</sub> enrichment in two California annual grasslands. *Oecologia* **119**: 572–577.
- Rillig MC, Wright SF, Allen MF, Field CB. 1999b. Rise in carbon dioxide changes soil structure. *Nature* **400**: 628.
- Rogers HH, Prior SA, Runion GB, Mitchell RJ. 1996. Root to shoot ratio of crops as influenced by CO<sub>2</sub>. *Plant and Soil* **187**: 229–248.
- Rouhier H, Read DJ. 1998a. Plant and fungal responses to elevated atmospheric carbon dioxide in mycorrhizal seedlings of *Pinus sylvestris*. *Environmental and Experimental Botany* **40**: 237–246.
- Rouhier H, Read DJ. 1998b. The role of mycorrhiza in determining the response of *Plantago lanceolata* to CO<sub>2</sub> enrichment. *New Phytologist* **139**: 367–373.
- Ruhling A, Tyler G. 1991. Effects of simulated nitrogen deposition to the forest floor on the macrofungal flora of a beech forest. *Ambio* **20**: 261–263.
- Rygiewicz PT, Johnson MG, Ganio LM, Tingey DT, Storm MJ. 1997. Lifetime and temporal occurrence of ectomycorrhizae on ponderosa pine (*Pinus ponderosa* Laws.) seedlings grown under varied atmospheric CO<sub>2</sub> and nitrogen levels. *Plant and Soil* **189**: 275–287.
- Salmanowicz B, Nylund J-E. 1988. High performance liquid chromatography determination of ergosterol as a measure of ectomycorrhizal infection in Scots pine. *European Journal of Forest Pathology* **18**: 291–298.
- Sanders IR, Streitwolf-Engel R, van der Heijden MGA, Boller T, Wiemken A. 1998. Increased allocation to external hyphae of arbuscular mycorrhizal fungi under CO<sub>2</sub> enrichment. *Oecologia* **117**: 496–503.
- Schimel D, Enting IG, Heimann M, Wrigley TML, Raynaud D, Alves D, Siegenthaler U. 1995. CO<sub>2</sub> and the carbon cycle. In: Houghton JT, Meira Filho LG, Bruce J, Lee J, Callander BA, Haties E, Harris N, Maskell K, eds. *Climate change 1994. Radiative forcing of climate change and an evaluation of the IPCC IS92 emission scenarios*. Cambridge, UK: Cambridge University Press, 39–71.
- Smith SE, Read DJ. 1997. *Mycorrhizal symbiosis*. San Diego, CA, USA: Academic Press.
- Staddon PL, Fitter AH. 1998. Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? *Trends in Ecology and Evolution* **13**: 455–458.
- Staddon PL, Fitter AH, Graves JD. 1999. Effect of elevated atmospheric CO<sub>2</sub> on mycorrhizal colonization, external mycorrhizal hyphal production and phosphorus inflow in *Plantago lanceolata* and *Trifolium repens* in association with the arbuscular mycorrhizal fungus *Glomus mosseae*. *Global Change Biology* **5**: 347–358.
- Tans PP, Fung IY, Takahashi T. 1990. Observational constraints on the global atmospheric CO<sub>2</sub> budget. *Science* **247**: 1431–1438.
- Taylor AFS, Alexander IJ. 1989. Demography and population dynamics of ectomycorrhizas of Sitka spruce fertilized with N. *Ecosystems and Environment* **28**: 493–496.
- Termorshuizen AJ. 1993. The influence of nitrogen fertilizers on ectomycorrhizas and their fungal carpophores in young stands of *Pinus sylvestris*. *Forest Ecology and Management* **57**: 179–189.
- Thompson MV, Randerson JT, Malmstrom CM, Field CB. 1996. Change in net primary production and heterotrophic respiration – how much is necessary to sustain the terrestrial carbon sink? *Global Biogeochemical Cycles* **10**: 711–726.
- Tingey DT, Johnson MG, Phillips DL, Storm MJ. 1995. Effects of elevated CO<sub>2</sub> and nitrogen on ponderosa pine fine roots and associated fungal components. *Journal of Biogeography* **22**: 281–287.
- Vogt KA, Grier CC, Meier CE, Edmonds RL. 1982. Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. *Ecology* **63**: 370–380.
- Vogt KA, Publicover DA, Vogt DJ. 1991. A critique of the role of ectomycorrhizas in forest ecology. *Agriculture, Ecosystems and Environment* **35**: 171–190.
- Wallander H, Arnebrant K, Dahlberg A. 1999. Relationships between fungal uptake of ammonium, fungal growth and nitrogen availability in ectomycorrhizal *Pinus sylvestris* seedlings. *Mycorrhiza* **8**: 215–223.
- Wallander H, Massicotte HB, Nylund J-E. 1997. Seasonal variation in protein, ergosterol and chitin in five morphotypes of *Pinus sylvestris* L. ectomycorrhizae in a mature Swedish forest. *Soil Biology and Biochemistry* **29**: 45–53.
- Wallander H, Nylund JE. 1992. Effects of excess nitrogen and phosphorus starvation on the extramatrical mycelium of ectomycorrhizas of *Pinus sylvestris* L. *New Phytologist* **120**: 495–503.
- Wallander H, Nylund J-E, Sundberg B. 1994. The influence of IAA, carbohydrate and mineral concentration in host tissue on ectomycorrhizal development on *Pinus sylvestris* L. in relation to nutrient supply. *New Phytologist* **127**: 521–528.

**Wallenda T, Kottke I. 1998.** Nitrogen deposition and ecto-mycorrhizas. *New Phytologist* **139**: 169–187.

**Wright SF, Franke-Snyder M, Morton JB, Upadhyaya A. 1996.** Time-course study and partial characterization of a protein on hyphae of arbuscular mycorrhizal fungi during active colonization of roots. *Plant and Soil* **181**: 193–203.

**Wright SF, Upadhyaya A. 1996.** Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. *Soil Science* **161**: 575–586.

**Wright SF, Upadhyaya A. 1999.** Quantification of arbuscular mycorrhizal fungi activity by the glomalin concentration on hyphal traps. *Mycorrhiza* **8**: 283–285.