



Title	The Role of Mycorrhiza in Forest Ecosystems under CO ₂ -enriched Atmosphere
Author(s)	Quoreshi, Ali M.; Maruyama, Yutaka; Koike, Takayoshi
Citation	Eurasian Journal of Forest Research, 6(2), 171-176
Issue Date	2003-09
Doc URL	http://hdl.handle.net/2115/22172
Type	bulletin (article)
File Information	6(2)_P171-176.pdf



[Instructions for use](#)

The Role of Mycorrhiza in Forest Ecosystems under CO₂-enriched Atmosphere

QUORESHI Ali. M.^{1*}, MARUYAMA Yutaka² and KOIKE Takayoshi³

¹ Faculté de Foresterie et de Géomatique, Université Laval, Québec, G1K 7P4, Canada

² Forestry and Forest Product Research Institute, Sapporo 062-8516, Japan

³ Hokkaido University Forests, FSC, Sapporo 060-0809, Japan

Abstract

Global atmospheric change and their potential effects on forest ecosystem continue to concern globally. Over the last 150 years, humans have changed the global carbon cycle the most. Consequently, persistent and rapid increase in the levels of CO₂ and other greenhouse gases in the atmosphere continue to occur. These changes have affected all levels of our ecosystems. Elevated CO₂ concentration may affect many biological processes including ecosystem processes by altering carbon allocation pattern in plants and carbon release to soil. Many studies have shown that enhanced atmospheric CO₂ concentration has a significant effect on individual plant growth and photosynthetic rates. However, there is considerable complexity and uncertainty in predicting this effect in terrestrial ecosystems. Part of this uncertainty is probably due to poor knowledge in belowground responses to global increased CO₂ concentration. Although numerous reports suggest that the mid- and high latitude forests in Northern Hemisphere are functioning as a significant sink for carbon, predicting their future role in global carbon budget is still uncertain. Shortage of nutrients and water might limit the long-term response of trees to increased levels of CO₂. A complete understanding of nutrient cycling and extensive research on belowground processes in forest ecosystem under enriched CO₂ conditions are required to predict long-term responses to atmospheric changes. Soil microbial populations play a significant role in regulating global carbon cycles. Mycorrhizas are most probably key components of this regulation. However, reports of research are sparse that addresses the influence of CO₂ on responses of mycorrhizas in forest communities. Therefore, urgent attention of plant scientists is essential for predicting the responses of mycorrhizas to ultimate ecosystem productivity under global environmental changes.

Key words: Global climate change, elevated CO₂, mycorrhizas, rhizosphere, and forest ecosystem

Introduction

The concentration of atmospheric CO₂ has been steadily rising since pre-industrial revolution (Boden *et al.* 1994). This increase in CO₂ concentration is one of the crucial factors in relation to global climate change. Elevated CO₂ concentration may affect many biological processes including ecosystem processes by altering carbon sequestration and changing carbon allocation pattern in plants and carbon release to soil (Diaz 1996). According to a recent report, rising atmospheric CO₂ concentrations may lead to enhanced water availability because water use efficiency of photosynthesis increases with CO₂ in most plant species (Grunzweig *et al.* 2003). Numerous study results demonstrated that many plants increased their photosynthesis and growth when grown under elevated CO₂ concentrations (Rogers *et al.* 1994, Bazzaz 1990). Many plants also show alteration in their carbon distribution pattern, which is mainly greater allocation to the root systems (Rogers *et al.* 1996, Norby 1994). Changes in root growth and its architecture, nutrient uptake pattern, and microbial population have observed in many studies.

However, study results suggests that the ability of plants respond to changing CO₂ condition with greater growth and development may depends on their ability to uptake soil nutrients and water (Berntson and Bazzaz 1996). In a recent well designed FACE experiment in the Duke Forest (North Carolina, USA), reported that enhanced wood growth during first three years of experiment and then return to original state. However, fertilized experimental plot continue to maintain increased growth. They concluded that shortage of water and nutrient might limit long-term response to trees to increase level of CO₂ concentration (Oren *et al.* 2001).

Concerns on the increase in atmospheric CO₂ concentration, its effects on forest ecosystem and global carbon balance have resulted in numerous experiments on trees both at greenhouse and ecosystem levels. However, most of this study is focused on the above ground part of the plant with little effort being designed for belowground processes. These studies show CO₂ enhancement generally increases tree growth through increase in net photosynthesis. Consequently, increased

carbon sequestration within forest ecosystem, where carbon can be stored in plants and soils. These results suggest increased sequestration might partly offset emissions from fossil-fuel combustion, industries and deforestation. Although many studies have reported increased photosynthesis and plant growth in response to elevated CO₂, the whole process is not that simple. There is considerable complexity and uncertainty in predicting this effect in terrestrial ecosystem.

The interaction between C and N as well as belowground microbial processes and mycorrhizal components are much more complicated. Understanding rhizosphere processes to elevated CO₂ is necessary in estimating the response of forest ecosystem to global climate changes because belowground processes are closely related to nutrient, carbon cycling and organic matter decomposition. Of the various types of soil organisms, mycorrhiza, the symbiotic association of plant roots with fungi constitutes a crucial link at the root-soil interface considered as a key group. Mycorrhizal fungi depend on their host plants for carbon and hence mycorrhizas are strong sink for host carbon (Staddon 1998).

Mycorrhizas are most probably the single largest consumers of net primary production (Allen 1991). Carbon transfer to the soil can be mediated directly via plant roots or indirectly via many soil biota including mycorrhizas. Carbon consumption to mycorrhizal fungi can be 10-20% of photosynthetically fixed carbon (Staddon *et al.* 1999, Jakobsen and Rosendahl 1990). If elevated CO₂ supports more C being fixed by forest plants then greater C should be available for mycorrhizal association. This assumption suggests that mycorrhizas would be responsible for greater sink for photosynthesis and consequently their role as a pathway for C flow to the soil might be increased. The predicted alterations in plant C distribution by plant-mycorrhizal system might have positive effects of increased atmospheric CO₂ concentration. The focus of this article is to review of current concern on CO₂ concentration that affects forest ecosystem, importance of belowground processes and the carbon balances with an emphasis on role of mycorrhizas.

Global Scenario

There is no doubt that CO₂ concentration is increasing. Human induced changes that prompted steady increase in atmospheric CO₂ concentration includes fossil-fuel combustion and deforestation. Fossil-fuel combustion and global deforestation has increased the atmospheric concentration by 30% in the past three centuries. However, more than half of this increase occurred in the past 40 years (Chaplin *et al.* 2000). Intensive clear cutting and logging of forests, industrial emission, automobile exhausts, forest fires – all these factors have contributed to sharp increase in CO₂ concentration in our atmosphere. According to literature, about 7 billion tones of carbon released annually by fossil fuel consumption and land use changes (Staddon 1998). In a report by Dixon *et al.* 1994, estimates for annual emission of CO₂ by fossil fuel combustion and land use change are about 5.4 Gt

and 1.6 Gt of C per year, respectively. In this total C emission, oceans are estimated to sequester 2 Gt of C annually, about 2 Gt or so of C per year sequestered by terrestrial ecosystems, and about 3 Gt of C per year remains in the atmosphere (Staddon 1998). The ratio between the rate of at which oceans and terrestrial ecosystems absorb C and the rate of emissions decides the total change of atmospheric CO₂ concentration. According to global carbon budget, the mid- and high latitude forests in Northern Hemisphere are functioning as a significant terrestrial sink for carbon (Tans *et al.* 1990, Denning *et al.* 1995). The part of responses may be driven by belowground processes and mediated by responses of soil microorganisms and mycorrhizas to CO₂ enrichment. It is uncertain whether the presumed net terrestrial sink for carbon will sustain under climate change. This uncertainty will remain unless we fully understand belowground processes well. Therefore, to predict accurate global carbon budget requires extensive research on belowground processes, which might explain the “missing sink”.

Mycorrhizas, root growth and elevated CO₂

Mycorrhizas are symbiotic association between plant roots and fungi, which represent an intimate interface between roots and rhizosphere microorganisms. These unique relationships provide a critical linkage between soil resources and roots and can affect carbon balance of trees. At least seven types of mycorrhizal association recognized in terrestrial vegetation system (Smith and Read 1997). These are vesicular-arbuscular mycorrhizas (VAM), Ectomycorrhiza (ECM), Ectoendomycorrhiza, Arbutoid, Monotropoid, Ericoid, and Orchid mycorrhiza. The most important associations are ectomycorrhizae (ECM) (Fig. 1) and VAM associated with forest ecosystems. Arbuscular mycorrhizas are most common type of mycorrhizas and are found in most plant species (Smith and Read 1997).

Mycorrhizal association increases plant nutrient uptake and water supply resulting in greater plant growth. Many mycorrhizal fungi have the capacity to utilize organic N and breakdown of phenolic compounds (Smith and Read 1997, Quoreishi *et al.* 1995). Mycorrhiza provides protection from parasitic fungi and nematodes. Mycorrhizal hyphal networks are likely having important role in nutrient cycling processes. Mycorrhizal fungi play an important role in carbon sequestration into forest soil. As a carbon sink, mycorrhizae play an essential role in C allocation (Rygiewick and Anderson 1994) and can affect nutrient cycling of ecosystem. Mycorrhizal fungi are pioneer biota in soil, which obtain photosynthate from host plants. They have direct influences on both sequestration and emission of carbon. Numerous experiments have shown that elevated CO₂ stimulated plant growth (on leaves, stems, and branches) by increased photosynthesis (Staddon *et al.* 1999, Rogers *et al.* 1994, Körner 1993, Rozema *et al.* 1993). Fewer studies have focused on the effect of elevated CO₂ on fine roots and root processes (Norby 1994). Recently, Stulen and den Hertog (1993) and Rogers *et al.* (1994) reviewed thoroughly on root responses. However, in

general, there is a tendency of shifting C allocation pattern in terrestrial ecosystem, mainly in favor of the roots under elevated CO₂ condition (Stullen and den Hertog 1993). Plants responds to increasing atmospheric CO₂ with increased growth also partly depends upon their ability to uptake soil nutrients and water. O'Neill *et al.* (1987) suggested that enhanced CO₂ stimulated mycorrhizal associations increasing nutrient acquisition. Greater C allocated to below-ground may be used to support higher colonization by mycorrhizal fungi.

A few studied demonstrated that elevated CO₂ enhanced fine root and produces more highly branched root system, allowing plants to exploit a larger soil volume (Curtis *et al.* 1994, Norby 1994, Pregitzer *et al.* 1995). In a study by our group observed increased root growth and fine-root production of *Picea glehnii* seedlings under enriched CO₂ (Fig. 2). Total seedling dry mass also enhanced in response to elevated CO₂ (result not shown). When these seedlings are transplanted into forest soil to see outplanting performances, increased seedling growth continue with seedling grown under elevated CO₂, suggesting positive effect of elevated CO₂ on seedling growth through well developed root system. (Fig. 3)

Carbon flow to the soil can occur through the plants root or indirectly through soil microorganisms including mycorrhizas. It has been estimated that about 10 to 20% of photosynthetically fixed carbon can be allocated to mycorrhizal fungi (Harris and Paul 1987, Jakobsen and Rosendahl 1990). Therefore, in terms of global carbon cycle, mycorrhizas can account for huge proportion of the carbon fixed by the plants, which is up to 20% in some association. If more C being fixed by the plants under elevated CO₂ then more C might be allocated to belowground for increased mycorrhizal association. Therefore, it assumed that plant responses to increased CO₂ concentration could lead to enhanced C storage in soils. By changing C inputs from plant to soil, elevated CO₂ may affect plant biomass and root symbionts (Diaz 1996). In a recent study, Tingey *et al.* (1997) documented that elevated CO₂ concentration increases root growth, root life span and root zone activity of *Pinus ponderosa* forest. Rygielwicz *et al.* (1997) found substantially more carbon enters to the soil via mycorrhizal fungi than previously thought and greatest in the high CO₂ treatment. Hence, mycorrhizal fungi play an important role in carbon sequestration into forest soil.

Increased mycorrhizal colonization also increases respiration rates. It means mycorrhizas have direct influence on both sequestration and emissions of carbon. Several reports indicate that ectomycorrhizal association often stimulates by elevated CO₂ although this might not be always the case. However, three times more mycorrhizal root cluster and twice more external hyphal production on Scots pine were reported under increased CO₂ (Ineichen *et al.* 1995). Unfortunately, a few studies have examined external hyphal production at elevated CO₂ possibly because of methodological problem. Godbold *et al.* (1997) found distinct changes in the ectomycorrhizal morphotypes assemblage of

Betula papyrifera. The morphotype changes lead to increase in ectomycorrhizal infection levels with a higher incidence of emanating hyphae and rhizomorphs under enriched CO₂. The importance of mycorrhizal external hyphae should not be ignored, because considerable amount of carbon can consume by hyphal system, particularly under elevated atmospheric CO₂ condition. Based on all these hypotheses and published results a schematic presentation can be drawn for possible effect of elevated CO₂ on plants roots and mycorrhizae (Fig. 4).

Mycorrhizas and extraradical hyphal network

The extensive mycorrhizal hyphal network in the soil is essentially an important avenue for the transport of fixed carbon from roots to soil (Staddon 1998). As stated earlier, several ecosystem modeling studies have indicated that the mid- and high latitude forests in northern hemisphere are functioning as a significant sink for carbon (Oren *et al.* 2001). The responses may be driven by belowground processes particularly ectomycorrhiza to CO₂ enrichment. Consequently, they may affect ectomycorrhizal functioning, such as infection rates and extra radical hyphal production in response to elevated CO₂. Since most of the plants in this region are heavily infected with ectomycorrhizal fungi. As we know elevated CO₂ often increase the rates of ectomycorrhizal infection, it might cause considerable amount of carbon drain to produce greater extraradical mycelial net work. In return, mycorrhizae benefit their host by increased nutrient and water uptake via tremendous hyphal proliferation. An example of mycorrhizal and non-mycorrhizal seedlings is shown in Figure 5. It is evident that mycelial network capture almost completely the growing substrate, increased plant growth observed despite the cost of carbon. As extra C derived from enhanced photosynthesis under elevated CO₂ enters the rhizosphere via the fine-root production and greater root turn over. The possibility of increased colonization of ectomycorrhizal fungi even cost of carbon increased. At the same time, respiration rates of both roots and mycorrhizal fungi might increase.

According to the recent investigation, increased demand of nutrient and water under enhanced CO₂ condition observed in order to sustain long-term response of trees to increased CO₂ (Oren *et al.* 2001). In their experiment, in both moderate-fertility and infertile sites elevated CO₂ alone had no significant effect. However, fertilizing in ambient CO₂ showed a significant effect. Fertilization under elevated CO₂ had significantly greater effects than sum of the single CO₂ and N effect. In this situation, ectomycorrhizas might play an essential role in carbon sequestration and emission in most forests, particularly in boreal forests.

Among the role of ectomycorrhizae, a study by Simard *et al.* (1997), Read (1997) showed an interesting result. In forest ecosystem, different plant species can be connected with the same species of mycorrhizal fungi and can form a common mycelial network (Fig. 6). They expressed considerable amounts of carbon can transfer through the hyphae of shared

fungal symbionts between the trees. These mycelial networks can connect many plants and travel greater areas into the soil. This result encouraged plant scientist to study forest ecosystem from a new perspective (Read 1997). They also suggested that increased mycorrhization might result an equalization of resource availability that might induce greater biodiversity rather than reduced biodiversity. Numerous studies have shown the fundamental importance of mycorrhizae not just the growth and nutritional aspects of individual plants, but the essential ecosystem processes depend on mycorrhizal fungi and associated microorganisms.

Therefore, it is important to study changes in mycorrhizal colonization as well as lifetime and temporal occurrence of mycorrhizal assemblage with different morphotypes to understand the mycorrhizal symbiosis and function under elevated CO₂.

Conclusion

Mycorrhizal association plays an essential role in forest ecosystem. Roots and mycorrhizal fungi may be substantially affected by changes in CO₂ concentration. Although forests are functioning as significant carbon sink, accurate prediction of their role needs extensive research on belowground processes. Mycorrhizas can respond in varied ways under elevated CO₂ that might affect plant growth, nutrient uptake, altering soil-plant carbon allocation patterns. The evidence suggests that elevated CO₂ is possibly having an effect on forest systems, mediated by altered C inputs from plants. Assessment of future carbon sequestration should consider the interactions between enhanced C inputs and N limitations as well as increased mycorrhizal functions with greater resource acquisition capacity. In term of both increased internal colonization and extraradical hyphal production, mycorrhizal fungi could be performing as larger sink for photosynthate and could be adding more C to the soil than they are currently.

Reference

- Allen, M. F. (1991) The ecology of Mycorrhizae. Cambridge University Press, New York.
- Bazzaz, F.A. (1990) The response of natural ecosystems to the raising global CO₂ levels. *Annu. Rev. Ecol. Syst.*, 21: 167-196.
- Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C. and Diaz, S. (2000) Consequences of changing biodiversity. *Nature* 405: 234-242.
- Curtis, P. S., O'Neill, E. G., Teeri, J. A., Zak, D. R. and Pregitzer, K. S. (1994) Belowground responses to atmospheric CO₂: implications for plants, soil biota and ecosystem processes. *Plant and Soil* 165: 1-6.
- Diaz, S. (1996) Effects of elevated [CO₂] at the community level mediated by root symbionts. *Plant and Soil* 187: 309-320.
- Dixon, R. K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M. C. and Wisniewski, J. (1994) Carbon pools and flux of global forest ecosystems. *Science* 263: 185-190.
- Godbold, D. L., Berntson, G. M. and Bazzaz, F. A. (1997) Growth and mycorrhizal colonization of three North American tree species under elevated atmospheric CO₂. *New Phytol.*, 137: 433-440.
- Grunzweig, J.M., Lin, T., Rotenberg, E., Schwartz, A., and Yakir, D. (2003) Carbon sequestration in arid-land forest. *Global Change Biol.* 9: 791-799.
- Haris, D. and Paul, E. A. (1987) Carbon requirements of vesicular-arbuscular mycorrhizae. *In* *Ecophysiology of VA mycorrhizal plants*. Eds. G. R. Safir. CRC Press, Boca Raton, FL. Pp. 93-105.
- Ineichen, K., Wiemken, V. and Wiemken, A. (1995) Shoots, roots, and ectomycorrhiza of pine seedlings at elevated atmospheric carbon dioxide. *Plant Cell Environ.*, 18: 703-707.
- Jakobsen, I. and Rosendahl, L. (1990) Carbon flow into soil and external hyphae from roots of mycorrhizal cucumber plants. *New Phytol.*, 115: 77-83.
- Klironomos, J. N., Ursic, M., Rillig, M. and Allen, M. F. (1998) Interspecific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO₂. *New Phytol.*, 138: 599-605.
- Körner, C (1993) Fertilisation: the great uncertainty in future vegetation development. *In: Vegetation Dynamics and Global Change*. Eds. A.M. Solomon and H.H. Shugart. Chapman and Hall, New York, USA, pp 53-70.
- Norby, R. J. (1994) Issues and perspective for investigating root responses to elevated atmospheric carbon dioxide. *Plant and soil* 165: 9-20.
- O'Neill, E. G., Luxmoore, R. J. and Norny, R. J. (1987) Increases in mycorrhizal colonization and seedling growth in *Pinus echinata* and *Quercus alba* in an enriched CO₂ atmosphere. *Can. J. For. Res.* 17: 878-883.
- Oren, R., Ellsworth, D. S., Johnsen, K. H., Phillips, N., Ewers, B. E., Maier, C., Schafer, K. V. R., Mccarthy, H., Hendrey, G., McNulty, S.G. and Katul, G. G. (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature* 411: 469-472.
- Pregitzer, K. S., Zak, D.R., Curtis, P. S., Kubiske, M. E., Teeri, J. A. and Vogel, C. S. (1995) Atmospheric CO₂, soil nitrogen and turn over of fine roots. *New Phytol.*, 129: 579-585.
- Quoreshi, A. M., Ahamad, I., Malloch, D. and Hellebust, J. A. (1995) Nitrogen metabolism in the ectomycorrhizal fungus *Hebeloma crustuliniforme*. *New Phytol.*, 131: 263-271.
- Read, D. (1997) The ties that bind. *Nature* 388: 517-518.
- Rogers, H. H., Prior, S. A., Runion, G. B. and Mitchell, R. J. (1996) Root to shoot ratio of crops as influenced by CO₂. *Plant and Soil* 187: 229-248.
- Rogers, H. H., Runion, G. B. and Krupa, S. V. (1994) Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environ. Pollut.*, 83: 155-189.
- Rozema, J., Lambers, H. and van de Geijn, S C., (1993).

CO₂ and biosphere. Eds. M. L. Cambridge, Kluwer, Boston.

Rygiewich, P. T., Johnson, M. G., Ganio, L. M., David, T. T. and Storm, M. J. (1997) Lifetime temporal occurrence of ectomycorrhizae on ponderosa pine (*Pinus ponderosa* Laws.) seedlings grown under varied atmospheric CO₂ and nitrogen levels. *Plant and Soil* 198: 275-287.

Ryzewicz, P. T. and Andersen, C. P. (1994) Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature* 369: 58-60.

Simard, S. W., Perry, D.F.A., Jones, M. D., Myrold, D. D., Durall, D. M. and Molina Randy. (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388: 579-582.

Smith, S. E. and Read, D. J. (1997) Mycorrhizal symbiosis. 2nd edition. Academic Press Inc., London and New York.

Staddon, P. L. (1998) Insights into mycorrhizal

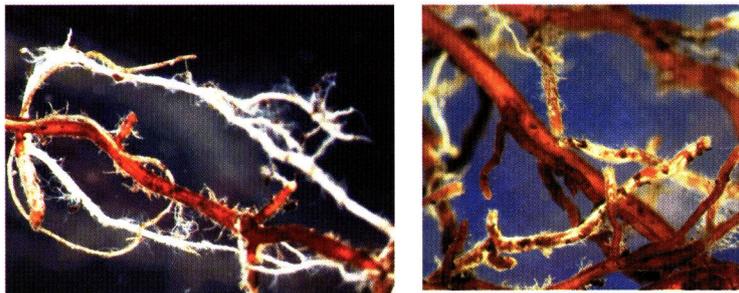
colonization at elevated CO₂: a simple carbon partitioning model. *Plant and Soil* 205: 171-180.

Staddon, P. L., Fitter, A.H. and Graves, Jonathan, D. (1999) Effect of elevated CO₂ on mycorrhizal colonization, external mycorrhizal hyphal production and phosphorus inflow in *Plantago lanceolata* and *Trifolium repens* in association with arbuscular mycorrhizal fungus *Glomus mosseae*. *Global Change Biol.*, 5: 347-358.

Stolen, I. and Hertog, D. (1993) Root growth and functioning under atmospheric CO₂ enrichment. *Vegetatio* 104/105: 99-115.

Tans, P. P. and White, J. W. C. (1998) In balance, with a little help from the plants. *Science* 281: 183-184.

Tingey, D. T., Phillips, D. L., Johnson, M. G., Storm, M. J. and Ball, J. T. (1997) Effects of elevated CO₂ and N fertilization on fine root dynamics and fungal growth in seedlings *Pinus ponderosa*. *Env. Exp. Bot.*, 37: 73-83.



ECM roots of *Picea glehnii* with rhizomorph and mycelial strand

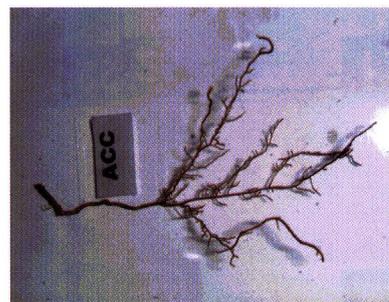


Ectomycorrhizal short roots

Fig. 1. An example of typical ectomycorrhizal roots covered with mycelia and presence of mycelial strands and rhizomorphs.



Elevated



Ambient

Fig. 2. Growth and architecture of *Picea glehnii* roots grown under elevated (ECEL) and ambient (ACC) CO₂ condition.



Fig. 3. Effect of elevated CO₂ on shoot growth of *Picea glehnii* seedlings after transplanting into forest soil. ECEL, represent exponential nutrient loading (high N) grown under elevated CO₂ condition and ACC, represent control (low N) seedlings grown under ambient CO₂ condition.

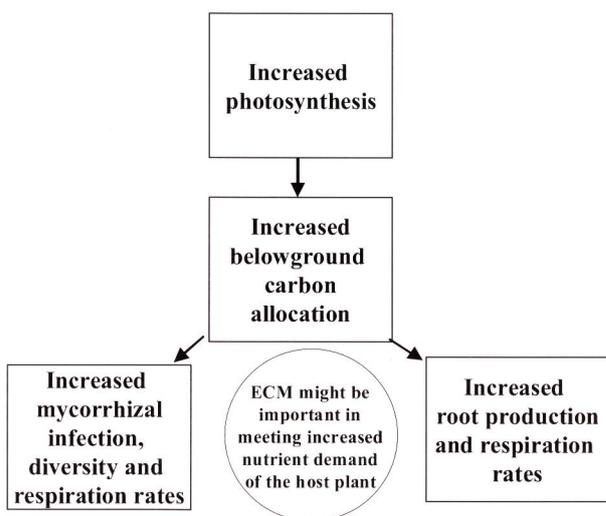


Fig. 4. Schematic representation of possible effect of elevated CO₂ on plant roots and mycorrhizas.



Fig. 5. Photographic representation of Mycorrhizal vs non-mycorrhizal larch seedling, an example of greater absorptive are of seedling infected with ectomycorrhizal fungus.



Figure 1 The roots of up to 90 per cent of the trees in a forest can be colonized by many fungal species, the mycelia of which form ectomycorrhizal networks. These networks, shown above linking two conifer species, provide channels for the transfer of nutrients. Simard *et al.* have now shown that considerable amounts of carbon can be transferred in either direction between trees through these networks.

Fig. 6. Illustrated are the ectomycorrhizal networks in which considerable amounts of carbon can be transferred in either direction between the trees and showing these mycelial networks can capture and travel greater area into soil.

Reprinted by permission from Nature (Read, D. (1997) The ties that bind. Nature 388: 517-518.) copyright (2003). Macmillan Publishers Ltd.