Chapter 12

Respiratory Costs of Mycorrhizal Associations

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Summary

Mycorrhizal fungi form symbiotic and often mutually beneficial relationships with the roots of most terrestrial plants. In this chapter we review current literature concerned with plant respiratory requirements for supporting this important plant-fungal association, and its effect on the overall plant carbon economy. Controlled studies indicate that mycorrhizal respiratory costs are considerable, consuming between 2 to 17% of the photosynthate fixed daily, varying depending on the host and fungal species involved, the stage of colonization, and the environmental conditions. Respiratory energy is required by the mycobiont for construction of new intraradical

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and extraradical fungal tissue (including reproductive structures), for maintenance and repair of existing fungal tissue, and for cellular processes in the fungal tissue associated with the absorption, translocation and transfer of nutrients from the soil to the host. Additional respiration is also required by the host plant for stimulated root cellular processes, and potentially for increased production of root biomass. Field studies of these important processes will eventually lead us to better understand how significant mycorrhizal fungi are to the total carbon budgets of natural and managed plant communities.

I. Introduction

It is difficult to estimate the actual costs of root respiration in natural soils without considering the role of mycorrhizal fungi. These fungi are an integral part of nearly all plant communities (Van der Heijden et al., 1998). They are ubiquitous in most natural and agricultural soils, and are capable of forming close symbiotic associations with the roots of nearly 90% of the terrestrial plant species investigated thus far (Newman and Reddell, 1987; Trappe, 1987). Like many pathogenic soil fungi, mycorrhizal fungi penetrate living roots of plants to acquire energy-rich carbohydrates needed for their growth, maintenance, and function. However, unlike the pathogens, external hyphae produced by mycorrhizas absorb soil nutrients and translocate them to the fungal-plant interface where they are transferred to root epidermal and cortical cells. In effect, these fungi act as extensions of the plant's root system, increasing uptake of many soil-derived nutrients, and in some cases, even water, thereby improving the host plant's productivity (Smith and Read, 1997) and reproductive fitness (Koide and Dickie, 2002). Thus, mycorrhizal fungi incur both costs and benefits to the overall carbon economy of the host plant (Koide and Elliott, 1989; Tinker et al., 1994; Douds et al., 2000).

In this chapter, we focus on the respiratory costs of mycorrhizal associations, particularly with regard to growth, maintenance, and ion uptake by both the fungus and the host root system colonized by the fungus. While mycorrhizal fungi may be beneficial during at least some stage of a plant's development, studies indicate that below-ground carbohydrate costs are often higher when plants are associated with these fungi than when plants are not. In fact, under conditions where soil resources are non-limiting and the fungi are providing little or no benefit to the plant, carbon consumption by mycorrhizal fungi can actually reduce plant growth (Buwalda and Goh, 1982; Molina and Chamard, 1983; Koide, 1985; Ingestad et al, 1986; Modjo and Hendrix, 1986; Rousseau and Reid, 1991; Peng et al., 1993; Taylor and Harrier, 2000). The total amount of carbon required by the association is the sum of several component costs, including direct export of carbon from the host to the fungus (for growth and metabolism), as well as additional carbon use such as increased plant respiratory and non-respiratory (exudation, cell death, etc.) requirements (Finlay and Söderström, 1992). Controlled studies using whole-plant ^{14}C-labeling techniques suggest that the total cost of the association ranges from 3 to 36% of the carbon fixed daily by photosynthesis, with the largest proportion of the carbon allocated to respiration (Table 1).

The two most common and well studied types of mycorrhizal associations, categorized according to symbiont morphology and host-taxon relationships, are arbuscular (previously called vesicular-arbuscular) mycorrhizas and ectomycorrhizas. Arbuscular mycorrhizal fungi occur on many different species of herbaceous and woody plants including most crop plants and tropical trees. They are obligatorily dependent on the host plant for their source of carbohydrate energy, and form, within the root cortical cells of the host, characteristic branched haustorical structures known as arbuscules, which are likely sites for significant transfer of carbohydrate and nutrients between the host and fungus. Other distinguishing features sometimes found, depending on the fungal species, include large hyphal coils (also likely sites for carbohydrate and nutrient transfer), usually located within the epidermal cells, and terminal and intercalary swellings known as vesicles (likely storage organs containing abundant lipids) formed within and between the cortical cells. Arbuscular mycorrhizas are most noted for their ability to enhance plant uptake of diffusion-limited inorganic ions such as phosphate, copper and zinc. Ectomycorrhizal fungi, on the other hand, occur mainly on forest trees of temperate and boreal regions. They are characterized by a dense sheath or mantle of fungal tissue that encloses the colonized root, and by a plexus of

Abbreviations: PPFD – photosynthetic photon flux density; Q_{10} – temperature coefficient of respiration

Table 1. Amount of carbon required by arbuscular and ectomycorrhizal fungi associated with various host plants. Values were estimated using whole-plant ^{14}C pulse-chase labeling techniques.

Host species	Fungal species	Percentage of C fixed by photosynthesis			Reference
		Fungal Biomass	Fungal respiration	Total to fungus	
Arbuscular mycorrhizas					
Allium porrum	*Glomus mosseae*	2	5	7	Snellgrove et al. (1982)
Citrus aurantium	*G. intraradices*	n.d.	n.d.	6	Koch and Johnson (1984)
Cucumis sativus	*G. caledonium*	2	7	9	Pearson and Jakobsen (1993)
C. sativus	*G. fasciculatum*	5	15	20	Jakobsen and Rosendahl (1990)
C. sativus	*G. sp.*	9	8	17	Pearson and Jakobsen (1993)
C. sativus	*Scutellospora calospora*	2	17	19	Pearson and Jakobsen (1993)
Glycine max	*G. fasciculatum*	3	5-14	8-17	Harris et al. (1985)
Poncirus trifoliate x *C. aurantium*	*G. intraradices*	n.d.	n.d.	6-8	Douds et al. (1988)
P. trifoliate x *C. aurantium*	*G. intraradices*	n.d.	n.d.	11	Koch and Johnson (1984)
Vicia faba	*G. mosseae*	n.d.	n.d.	10	Pang and Paul (1980)
V. faba	*G. mosseae*	1	3	4	Paul and Kucey (1981); Kucey and Paul (1982)
Ectomycorrhizas					
Pinus ponderosa	*Hebeloma crustuliniforme*	2-3	5-8	7-11	Anderson and Rygiewicz (1995)
P. ponderosa	*H. crustuliniforme*	3	4	7	Rygiewicz and Anderson (1994)
Pinus taeda	*Pisolithus tinctorius*	n.d.	n.d.	6-36	Reid et al. (1983)
Salix viminalis	*Thelephora terrestris*	1-8	2-4	3-12	Durall et al. (1994)

n.d. – not determined.

hyphae known as the Hartig net, which penetrates the root intercellularly and surrounds the epidermal and cortical cells. Most ectomycorrhizal fungi are also obligate symbionts, but some may be able to act as saprotrophs (Haselwandter et al., 1990). They can hydrolyze proteins and organic phosphates, and increase plant uptake of both organic and inorganic forms of nitrogen and phosphorus (Tinker and Nye, 2000). Other distinctive groups of mycorrhizas that are less common and not as well studied include ericoid and ectendomycorrhizas, which are formed in association with ericaceous plant families, and orchid mycorrhizas (Wilcox, 1996). Thus far, only the carbohydrate requirements of arbuscular and ectomycorrhizas have been examined in detail, which restricts our discussion to these two groups of fungi.

II. Total Respiratory Costs

The total respiratory costs of mycorrhizal associations are a considerable component of the overall carbon economy of the host plant. Of those studies listed in Table 1, where respiration attributed to the fungus was separated from other fungal carbohydrate requirements, 47 to 89% of the carbon allocated to the mycorrhizal association was consumed by respiration. Respiration in these studies varied depending on the host plant and fungal species, the stage of mycorrhizal development, and the environmental conditions under which the host plant and fungus were grown.

A. Variation among Plant and Fungal Species

Root respiration varies among plant species (Lambers et al., 2002). Respiration also appears to vary among mycorrhizal fungal species associated with a particular host. In cucumber (*Cucumis sativus*), for example, the proportion of assimilated ^{14}C allocated to below-ground respiration in plants colonized by the arbuscular mycorrhizal fungus *Scutellospora calospora* was 16.5% higher than that in non-colonized plants, but only 6.5 or 7.6% higher when plants were colonized by two other arbuscular species, *Glomus caledonium* or an unclassified *Glomus* sp., respectively (Pearson and Jakobsen, 1993). Bidartondo et al. (2001) observed that of four ectomycorrhizal fungi they examined, *Paxillus involutus* produced the fewest mycorrhizal connections to its host plant and respired less carbohydrates per unit biomass than

did the other fungi. Variability in respiration among species may be due to differences in 1) the amount and quality (e.g., number of arbuscules and vesicles) of fungal biomass produced and maintained by the mycobiont both within the host's root system and in the surrounding rhizosphere (Graham et al., 1982b; Giovannetti and Hepper, 1985; Estaún et al., 1987; Lioi and Giovannetti, 1987; Wong et al., 1989; 1990; Jakobsen et al., 1992; Burgess et al., 1994; Lerat et al., 2003), 2) the metabolic activity of the fungus (Lewis and Harley, 1965a,b,c; Söderström and Read, 1987; Bago et al., 2002), 3) the level of stimulation of cellular activities (e.g., cell wall and cytoplasmic invertases) and changes in carbohydrate metabolism (e.g., sucrose synthase) in the epidermal and cortex regions of the colonized roots (Wright et al., 1998, 1999), and/or 4) the extent of growth promotion (or depression) of the root system (Krishna et al., 1985; Bryla and Koide, 1990).

B. Changes with Mycorrhizal Development and Plant Age

Respiratory costs are expected to be especially high during early stages of colonization when most of the new fungal tissue is being produced, but decrease as the association matures, much in the same way that root respiratory costs decline with root age (Bouma et al., 2000, 2001). Carbohydrate substrates and respiratory energy are required during this period for construction of new intra- and extraradical fungal components, and for modifications in the cellular structures of the host (Graham and Eissenstat, 1994). Table 2 shows that although intraradical fungal biomass in soybean (*Glycine max*) roots colonized by *Glomus fasciculatum* increased from 115 mg per plant at 6 weeks to 266 mg per plant at 9 weeks, the specific rate of ^{14}C incorporation into fungal biomass was, in fact, lower at 9 weeks than at 6 weeks. The distribution of assimilated carbon to fungal respiration also decreased during this 3-week period from 18.2 mg ^{14}C plant^{-1} to 9.7 mg ^{14}C plant^{-1}, consequently lowering the plant's cost of supporting the association.

Further evidence that mycorrhizal cost decreases with age can be found in the ectomycorrhizal literature. Cairney et al. (1989) found in *Eucalyptus pilularis* roots colonized by *Pisolithus tinctorius* that young mycorrhizas accumulated more ^{14}C than older mycorrhizas, with much of the carbon transfer occurring during the first few weeks after inoculation. By 90 days after inoculation, all ^{14}C translocation to mycorrhizas had stopped. This information led them to hypothesize that in mature root systems only a small portion of the roots would require significant amounts of photosynthate to support mycorrhizal associations at any one time, which appeared to be the case when Cairney and Alexander (1992) compared allocation of ^{14}C with younger and older mycorrhizas of *Tylospora fibrillose* on *Picea sitchensis*. In this later study, they measured the ratio of activity in young to older mycorrhizas, and found that the ratio progressively increased from 2:1, when newly colonized seedlings were first transferred to a peat substrate, to 54:1 by 38 weeks after transfer. Similarly, Durall et al. (1994) examined carbon allocation in *Salix viminalis* inoculated with *Thelephora terrestris*, and found that the proportion of ^{14}C allocated to mycorrhizal respiration decreased as the plants aged from 50 to 98 days.

C. Impact of Environmental Conditions

Respiration associated with mycorrhizas is usually influenced by a combination of environmental factors that either directly affect the symbiosis by altering fungal growth and metabolism, or indirectly affect it by influencing photosynthesis and supply of carbohydrates provided by the host. Factors that have received some attention in the literature and will be discussed here include soil nutrient availability, soil temperature and moisture, light intensity, elevated atmospheric CO_2 concentrations, and ozone pollution.

1. Soil Nutrient Availability

Mycorrhizal respiration in many plant-fungal combinations is likely very dependent on soil nutrient availability, as this can affect the total amount of fungal biomass produced by the symbiosis, and also the proportion of biomass allocated to various fungal structures (some of which may have higher or lower respiratory requirements than others). Typically, mycorrhizas develop more readily under nutrient-poor conditions than under nutrient-rich or heavily fertilized conditions (Hayman, 1970; Chambers et al., 1980; Amijee et al., 1989; de Miranda et al., 1989; Jones et al., 1990; Koide and Li, 1990; Wallander and Nylund, 1991; 1992; Henry and Kosola, 1999, Nilsson and Wallander, 2003), and should therefore require proportionally more photosynthates for growth and metabolism when soil nutrients are limited. This was the case in a study by Baas and Lambers (1988) that examined the effect of increasing soil phosphorus on

Table 2. Dry weights, mycorrhizal colonization, distribution of assimilated ^{14}C, and specific rate of ^{14}C incorporation in *Glycine max – Rhizobium japonicum – Glomus fasciculatum* associations at six and nine weeks after emergence (from Harris et al., 1985).

Component	Six weeks	Nine weeks
Dry weights (g)		
Shoot	4.90	11.28
Roots	1.75	3.37
Nodules	0.14	0.41
Mycorrhiza		
Intraradicle	0.12	0.27
Extraradicle	0.16	0.24
Mycorrhizal colonization (%)		
Root length	68	76
Root mass	6.6	7.9
Distribution of assimilated ^{14}C (%)		
Biomass		
Shoot	51.0	61.2
Roots	9.7	9.4
Nodules	2.0	1.7
Mycorrhiza	2.7	2.8
Respiration		
Shoot	6.3	3.9
Roots + soil	5.2	6.5
Nodules	9.4	9.8
Mycorrhiza	13.7	4.7
Specific rate of ^{14}C incorporation (mg ^{14}C g^{-1} d. wt. day^{-1})		
Shoot	13.9	11.4
Roots	5.4	5.3
Nodules	18.8	8.7
Mycorrhiza	15.6	10.9

root respiration of *Plantago major* spp. *pleiosperma* grown with or without *G. fasciculatum*. At 38 days after transplanting, although plant growth was mostly unresponsive to colonization at any level of phosphorus, both colonized root length and root respiration of plants grown with the fungus decreased with increasing soil phosphorus availability, while root respiration of uncolonized plants remained unchanged (Fig. 1). Likewise, Lu et al. (1998) speculated that depression of soil respiration after the addition of nitrogen fertilizers to ectomycorrhizal Douglas-fir (*Pseudotsuga menziesii*) seedlings, grown in relatively fertile soil, was probably due to reduced root and mycorrhizal mycelial growth. Soil nutrient status will especially reduce mycorrhizal colonization and its corresponding respiration when conditions, such as irradiance or temperature, limit carbohydrate assimilation and transport below ground (Graham et al. 1982a; Son and Smith, 1988).

Soil nutrient status also affects the rate of nutrient acquisition by both the fungus and the host, the nutritional status of the host, and the responsiveness of the host to colonization, all of which will impact respiration associated with the symbiosis. Plants that are deficient in a particular nutrient tend to use less of the nutrient to produce a unit of biomass than plants with adequate levels of the nutrient in their tissues (Eissenstat et al., 1993). As mentioned previously, mycorrhizal fungi are most commonly found to increase plant uptake of phosphorus. However, improved plant phosphorus status tends to reduce plant allocation to roots and reduce mycorrhizal colonization (Smith and Read, 1997). Specific rates of mycorrhizal root respiration likely diminish with an increase in plant phosphorus concentration. For example, root respiration in mycorrhizal *Citrus volkameriana* seedlings grown in high-phosphorus soil was only 72% of that in mycorrhizal seedlings grown

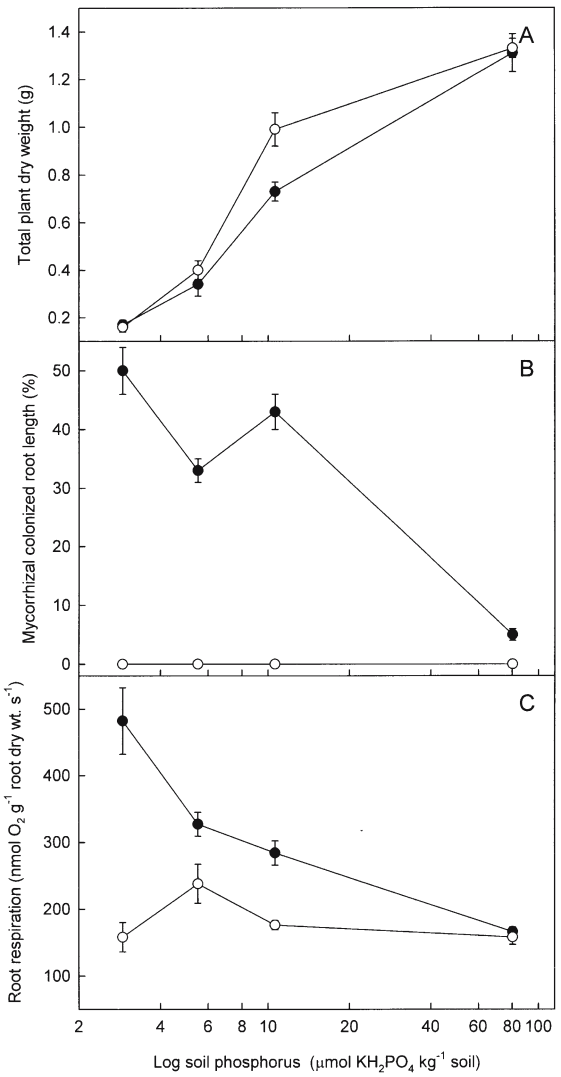

Fig. 1. (A) Total plant dry weight, (B) colonized root length, and (C) root respiration rate of mycorrhizal (●) and non-mycorrhizal (○) *Plantago major* spp. *pleiosperma* grown at four soil phosphorus levels. Vertical bars are SE. Data from Baas and Lambers (1988).

in low-phosphorus soil (Peng et al., 1993). Reduced respiration was primarily due to fewer lipid-rich vesicles of *Glomus intraradices* in high-phosphorus seedlings, and to lower maintenance requirements. It should be noted that some of the faster respiration rates in low-phosphorus mycorrhizal plants may also be a result of lower phosphorus nutrition, and not increased colonization and activity of the mycorrhizal fungus.

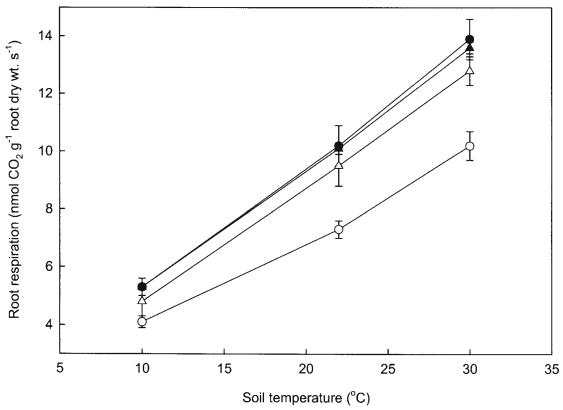

Fig. 2. Root respiration of mycorrhizal (●, ▲) and non-mycorrhizal (○, △) *Picea abies* seedlings exposed to various soil temperatures. Seedlings were grown in semi-hydroponic sand culture supplied with $(NH_4)_2SO_4$ (●, ○) or KNO_3 (▲, △) nutrient solution. Vertical bars are SE. Data from Eltrop and Marschner (1996).

2. Soil Temperature and Moisture

The respiratory response of mycorrhizas to changes in soil temperature was investigated by Eltrop and Marschner (1996). *Picea abies* seedlings were grown with or without *P. tinctorius*, and fertilized with either ammonium sulfate or potassium nitrate. They found that root respiration was significantly faster in mycorrhizal than in non-mycorrhizal plants when supplied with ammonium, but not when supplied with nitrate (Fig. 2). However, regardless of the treatment effects, the response to soil temperature was similar. Whether plants were mycorrhizal or not, or fertilized with NH_4-N or NO_3-N, the temperature coefficients of respiration, Q_{10}, from 10 to 30 °C were similar, ranging from 1.58 to 1.64. Burton et al. (2002) further demonstrated that the average Q_{10} for roots of arbuscular and ectomycorrhizal tree species were nearly identical. These few results suggest that the respiratory response of plant roots and mycorrhizal fungi to soil temperature is alike, although more research is required before any generalizations can be made.

One might also expect mycorrhizas to have little effect on the change in respiration with soil moisture; exposure to dry soil leads to a gradual decline in root respiration in many plant species (Palta and Nobel, 1989a,b; Bryla et al., 1997; Burton et al., 1998; Bouma and Bryla, 2000). In isolated fine roots of mature *C. volkameriana* trees, Espeleta and Eissenstat (1998) observed that respiration was similar between

mycorrhizal and non-mycorrhizal roots exposed to 8 weeks of localized drought. After 15 weeks of drought, however, mycorrhizal roots exhibited 34% slower respiration and 21% less mortality than non-mycorrhizal roots did. *Citrus* is apparently capable of suppressing mycorrhizal root respiration after prolonged exposure to dry soil, thereby preventing excessive carbon expenditure in maintenance respiration. Thus, the ability of mycorrhizal associations to reduce root respiration under drought may delay root shedding, and serve as a way by which the fungus guarantees survival under hostile environmental conditions.

3. Light Conditions

On an absolute basis, low light availability reduces root respiration (Lambers et al., 2002) and also limits mycorrhizal respiration if photoassimilation is appreciably reduced (Bücking and Heyser, 2003). In addition, low light can reduce the percentage of root length colonized by mycorrhizal fungi (Tester et al., 1986), especially under high phosphorus conditions (Son and Smith, 1988), which would also tend to reduce mycorrhizal root respiration.

Compared with plants grown under high-light conditions, shaded plants have proportionally less root biomass which indicates that shaded plants have proportionally less total below-ground carbon expenditure than plants exposed to full light. This observation has been used to support theories of optimality in shoot and root growth, where shading leads to greater allocation of photosynthate to leaf production so that light is less limiting to overall plant growth (Brouwer, 1983; Bloom et al., 1985). However, evidence in support of this preferential allocation to shoots for shaded plants often involves comparisons between small, shaded plants and larger, non-shaded plants (Reich, 2002). Proportional allocation to roots and shoot changes continuously with plant size, making such comparisons misleading. When ontogenetic effects of plant size are taken into account using an allometric approach, most studies found no evidence of an allocation shift towards leaf production at low light (reviewed by Reich, 2002).

While biomass allocation may not be affected by light regime, there is some evidence that proportionally more photosynthate is typically allocated to maintain the metabolism of mycorrhizal root tissues when plants are grown under lower light conditions. Gansert (1994) used a PC-controlled cuvette system to measure respiration in situ of individual fine roots on 10-year-old beech saplings growing in the shaded understory and in a natural light gap of a mature beech forest. Roots were colonized by the hyphae of several ectomycorrhizas including *Xerocomus chrysenteron*, *Lactarius subdulcis* and *Russula ochroleuca*, and the rate of root respiration was correlated with colonization (expressed as percent dry weight of the total root biomass) at both sites. Although net CO_2 assimilation and mycorrhizal root respiration throughout the season was much faster in saplings growing in the light gap than in those growing in the understory, the ratio of respiration to net CO_2 assimilation, both measured on a unit dry weight basis, was substantially higher in the understory saplings (Table 3), indicating a higher relative cost of below-ground respiration when light conditions were low.

Low light may also increase the relative cost of mycorrhizal associations. At 990 μmol m^{-2} s^{-1}, mycorrhizal colonization with *P. tinctorius* increased the proportion of assimilated carbon allocated to root respiration in *Picea abies* by only 0.6 to 3.4% at soil temperatures ranging from 10 to 30°C, while at a PPFD of 290 μmol m^{-2} s^{-1}, the proportion was increased by 1.8 to 7.4% (Fig. 3). This indicates that, regardless of soil temperature, proportionally more carbon was required to support the symbiosis when plants were grown under low-light conditions than when they were grown under higher-light conditions.

4. Elevated Atmospheric CO_2 and Ozone Pollution

Rising atmospheric CO_2 concentrations and increasing levels of air pollutants, such as ozone, are expected to impact considerably the respiration associated with roots, mycorrhizas and other soil microorganisms over this century (Andrews et al., 1999; Ball and Drake, 1998; Hungate et al., 1997).

Elevated [CO_2] can increase mycorrhizal development and associated respiration by stimulating host photosynthesis, and thereby enhancing carbon allocation to the fungus (Ineichen et al., 1995; Sanders, 1996; Jifon et al., 2002). Photosynthesis of *Plantago lanceolata* was stimulated by elevated [CO_2] (600 μl l^{-1}) far more than plant growth, especially when plants were associated with *Glomus mosseae* (Staddon et al., 1999). Based on plant dry mass measurements, most of the extra carbon fixed by photosynthesis at elevated CO_2 appeared to be respired by the mycorrhizal fun-

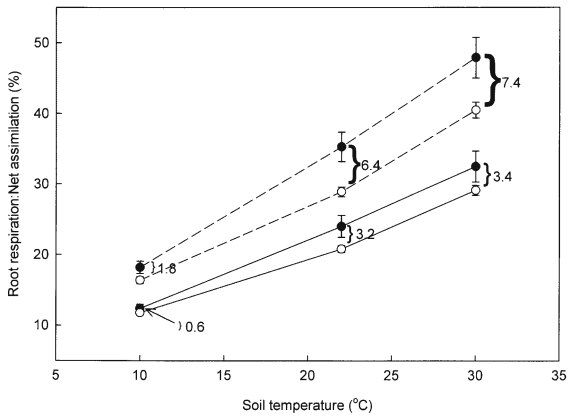

Fig. 3. Root respiration:net CO_2 assimilation ratio of mycorrhizal (●) and non-mycorrhizal (○) *Picea abies* seedlings exposed to various soil temperatures. Seedlings were grown in semi-hydroponic sand culture at a PPFD of 290 μmol m^{-2} s^{-1} (- - - -) or at 990 μmol m^{-2} s^{-1} (——). Vertical bars are SE. Data from Eltrop and Marschner (1996).

gus and the roots, which suggests that mycorrhizal fungi may increase carbon transfer through the system at elevated [CO_2] in addition to altering soil carbon pools, as shown by others (Rillig et al., 1998; Rouhier and Read, 1998; Sanders et al., 1998).

Ozone pollution, on the other hand, often reduces the formation of mycorrhizas (Ho and Trappe, 1981; Reich et al., 1986; Stroo et al., 1988; Simons and Kelly, 1989; Meier et al., 1990), and can affect the respiratory activity of the association (McCool and Menge, 1983; Gorissen et al., 1991; Scagel and Anderson, 1997; Anderson, 2003). Anderson and Rygiewicz (1995) studied the allocation and metabolism of carbon in *Pinus ponderosa* seedlings inoculated with *Hebeloma crustuliniforme* under ozone stress. Seedlings were grown in root 'mycocosms' that enabled them to measure carbon fluxes through the root system as well as through a portion of intact extramatrical hyphae, while maintaining symbiotic integrity (Rygiewicz and Anderson, 1994). Ozone reduced hyphal respiration and carbon accumulation by the fungus in mycorrhizal plants, although mycorrhizal seedlings exhibited greater biomass-weighted respiration rates than non-mycorrhizal controls (Table 4). Ozone tended to shift allocation patterns in mycorrhizal seedlings, making them more similar to non-mycorrhizal seedlings grown without ozone. Reductions in carbon allocation to mycorrhizas caused by increasing levels of air contaminants may eventually reduce vigor of the association, thus affecting any plant-derived benefits associated with forming the symbiosis.

III. Components of Mycorrhizal Respiration

As mentioned in previous chapters, root respiration depends on three major energy-requiring processes: root growth, maintenance of root biomass, and uptake of mineral nutrients. Respiration of roots associated with mycorrhizas has additional processes specifically related to the symbiosis. These include growth and maintenance of the fungal tissue, and ion uptake by the fungus (as well as transport and transfer of the ions to the host plant).

A. Construction Costs and Growth Respiration

Mycorrhizal growth respiration depends both on the amount of root and fungal tissue produced, and on the chemical composition of each tissue. Tissue containing high quantities of lipids and proteins, for example, will have higher respiratory costs of construction than tissue with more carbohydrates.

Table 3. Net CO_2 assimilation rate (C_{in}) and fine root respiration rate (C_{out}) measured on 10-year-old *Fagus sylvatica* saplings growing in the understory and in a natural gap of a mature beech forest (from Gansert, 1994).

	Understory			Gap		
	Net CO_2 assimilation (mg C $plant^{-1}$ day^{-1})	Root respiration (mg C $plant^{-1}$ day^{-1})	C_{in} : C_{out}	Net CO_2 assimilation (mg C $plant^{-1}$ day^{-1})	Root respiration (mg C $plant^{-1}$ day^{-1})	C_{in} : C_{out}
May	56 ± 15	5 ± 1	10	548 ± 95	20 ± 5	28
June	111 ± 19	7 ± 1	17	560 ± 113	30 ± 3	19
July	55 ± 21	9 ± 1	6	740 ± 141	48 ± 2	15
August	51 ± 22	7 ± 1	8	494 ± 113	54 ± 4	9
September	0 ± 17	6 ± 1	0	262 ± 100	39 ± 4	7
October	–2 ± 18	6 ± 0	0	241 ± 140	33 ± 2	7

Table 4. Biomass-weighted retention and respiratory loss of ^{14}C in mycorrhizal and non-mycorrhizal *Pinus ponderosa* seedlings exposed to two levels of ozone (from Anderson and Rygiewicz, 1995).

Ozone exposure ($\mu mol\ mol^{-1}\ h^{-1}$)	Mycorrhizal status	Retained					Respired				
		Needle	Stem	Coarse roots	Fine roots	Fungus	Shoot	Root	Fungus	Root + fungus	Total
0	Mycorrhizal	39.5	27.9	20.9	25.1	18.7	45.8	15.1	52.5	20.3	31.4
	SE	4.0	2.4	2.8	2.8	2.0	11.0	2.4	15.4	2.5	3.8
0	Non-myco.	34.2	19.2	12.8	15.8	0.0	30.4	9.5	0.0	9.5	20.4
	SE	4.8	2.1	2.8	4.9	0.0	7.3	1.7	0.0	1.7	4.2
39.3	Mycorrhizal	39.8	24.6	17.2	24.2	11.2	52.9	16.8	31.2	18.6	32.6
	SE	6.7	1.4	1.5	7.9	2.3	11.3	2.7	5.1	2.1	5.7
39.3	Non-myco.	32.2	19.8	10.5	18.7	0.0	25.5	8.7	0.0	8.7	17.6
	SE	7.2	3.7	1.8	2.9	0.0	4.4	0.6	0.0	0.6	2.1

Allocation values were biomass-weighted to normalize for differences in plant component fraction size. Units are percent allocated divided by tissue component dry weight.

By using daily construction costs and subtracting the carbon retained in new root growth, Peng et al. (1993) estimated that daily growth respiration accounted for 16% of the total root and soil respiration associated with mycorrhizal colonization in *C. volkameriana* (Fig. 4; Table 5). Respiratory energy is required during colonization for growth of new internal and external fungal structures, as well as for any cellular modifications and changes in carbon allocation to the host root.

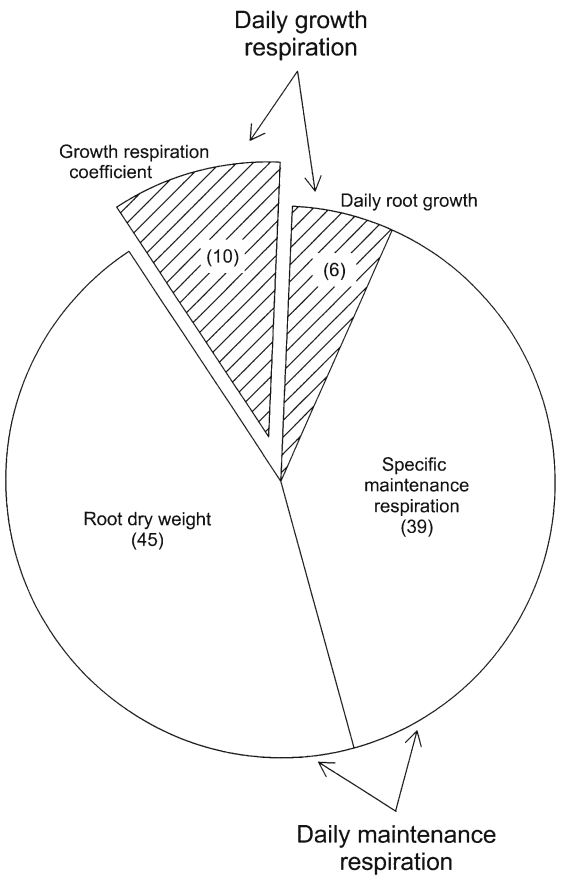

Fig. 4. Differences in total root and soil respiration between mycorrhizal and non-mycorrhizal *Citrus volkameriana* seedlings grown in high-phosphorus soil. Data from Peng et al. (1993).

1. The Host Root

Mycorrhizas tend to increase root:shoot partitioning in some species (Bryla and Koide, 1990, Eissenstat et al., 1993), but not in others (Fredeen and Terry, 1988; Thomson et al., 1986; Berta et al. 1991, 1996). Increased root biomass and root growth rate accounted for one-third of the difference in growth respiration between mycorrhizal and non-mycorrhizal *C. volkameriana* plants (Fig. 4); the other two-thirds was attributed to building more expensive roots and fungal structures (see below). Baas et al. (1989) suggested that mycorrhizal plants might have higher relative root growth rates than uncolonized plants of equal size, because of a shift in the carbon balance during the development of the symbiosis. For the most part, plants colonized by mycorrhizas do not necessarily allocate biomass to roots and shoots in the same proportion as nutritionally equivalent uncolonized plants. This altered pattern of allocation will profoundly influence plant productivity, and, consequently, any respiratory costs associated with the symbiosis. Thus, the possibility exists that faster instantaneous relative growth rates of the host root system result in faster rates of respiration for growth by mycorrhizal plants.

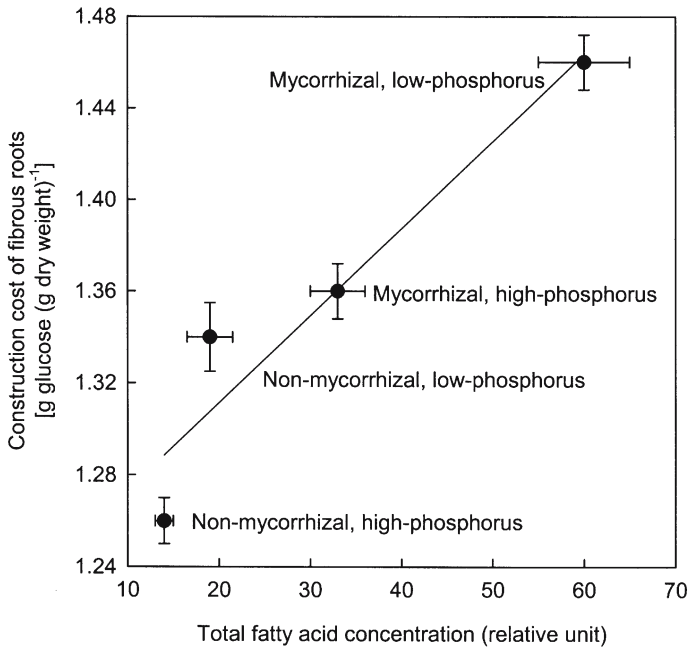

Fig. 5. Relationship between construction cost and relative total fatty acid content of fibrous roots from mycorrhizal and non-mycorrhizal *Citrus volkameriana* seedlings grown in low- and high-phosphorus soil. Data from Peng et al. (1993).

2. Intraradical Hyphae and Fungal Organelles

Carbon demand for the development of mycorrhizal hyphae and other fungal structures appears to be quite considerable in the few species examined so far (Table 1). Jakobsen and Rosendahl (1990) estimated that 16% of the photosynthetic carbon fixed daily was allocated to intraradical hyphae, arbuscules and vesicles in 22-day-old cucumber seedlings heavily colonized by *G. fasciculatum*. Histological and chemical analyses of arbuscular mycorrhizas reveal abundant amounts of lipids in the fungal tissue, particularly in the vesicles (Cox et al., 1975; Nagy and Nordby, 1980; Pacovsky & Fuller, 1988; Graham et al., 1995; Olsson and Johansen, 2000). Mycorrhizal colonization in *C. volkameriana* increased root lipid content by 227% in high-phosphorus soil and by 307% in low-phosphorus soil (Fig. 5), and may have accounted for up to 60% of the growth respiration (Fig. 4).

In comparison, ectomycorrhizas also contain abundant lipids (Olsson, 1999) as well as considerable amounts of sterols (Antibus and Sinsabaugh, 1993) and insoluble polysaccharides (Ling-Lee et al., 1977, Piché et al., 1981) in the fungal tissue, but produce considerably more fungal biomass than arbuscular mycorrhizas. While arbuscular mycorrhizal fungi usually represent less than 10% of the colonized root mass (but see Hepper, 1977), values representing 20 to 40% of the root mass are more common in ectomycorrhizas due to the large amount of hyphae associated with the mantle and the Hartig net (Vogt et al., 1982; 1991). Thus, construction costs and growth respiration associated with ectomycorrhizas are expected to represent a substantial host expense.

3. Extraradical Hyphae

Growth of the extraradical hyphae begins soon after root penetration, and can total more than 10 m of hyphae cm^{-3} of soil in arbuscular mycorrhizas (Sanders et al., 1977; Tisdall and Oades, 1979; Jakobsen and Rosendahl, 1990; Jakobsen et al., 1992), with hyphal diameters ranging from 2-30 μm (Read, 1992). In one case, Miller et al. (1995) calculated arbuscular hyphal lengths and dry weights as high as 81 m cm^{-3} and 339 μg cm^{-3}, respectively, in a pasture soil, and 111 m cm^{-3} and 457 μg cm^{-3}, respectively, in a tall grass prairie soil located in mid-western U.S. If we assume a mean hyphal radius of 5 μm, then about 0.08% of the soil volume is occupied by hyphae in soil containing 10 m cm^{-3} of hyphae. In contrast, root length density is

Table 5. Below-ground respiratory components in mycorrhizal and non-mycorrhizal *Citrus volkameriana* seedlings grown in low- or high-phosphorus soil (from Peng et al., 1993).

	Low-phosphorus		High-phosphorus	
	Mycorrhizal	Non-mycorrhizal	Mycorrhizal	Non-mycorrhizal
Root dry weight (mg)	134	78	273	230
Root growth (mg day^{-1})	9.62	3.90	14.8	13.4
Daily cost (μmol CO_2 day^{-1})				
Construction cost	468	174	671	563
Root growth (carbon) [a]	356	135	518	446
Total respiration [b]	555	234	820	600
Growth respiration [c]	114	40	153	117
Maintenance respiration [d]	330	138	558	372
Ion uptake respiration [e]	111	56	109	111
Cost per unit root dry weight [mmol CO_2 (g new root)$^{-1}$]				
Construction cost	48.7	44.7	45.3	42.0
Growth respiration coefficient	11.8	10.1	10.3	8.7
Specific respiration rates [mmol CO_2 (g whole-root system)$^{-1}$ d^{-1}]				
Total respiration	4.14	3.00	3.00	2.61
Maintenance + ion uptake respiration	3.33	2.51	2.44	2.10

[a] Calculated based on ash content, N content, and heat of combustion. [b] Measured by gas exchange. [c] Construction cost – root growth. [d] Total respiration – (growth + ion uptake respiration). [e] Estimated based on the change in whole-plant N content.

typically about 0.1 m cm^{-3} of soil near the soil surface (Marschner, 1995), although in pastures root length density can exceed 1 m cm^{-3} of soil (Newman et al., 1989). If we assume an average root radius of 0.2 mm, then roots with a root length density of 0.1 m cm^{-3} of soil would occupy about 1.3% of the soil volume, or 16 times more soil volume than external hyphae. If we further assume similar tissue densities of fungal biomass and plant biomass, then fine root biomass is about 16-fold greater than hyphal biomass outside the root. Extraradical hyphae produced by arbuscular mycorrhizas would therefore have considerably less carbon costs associated with their construction than the same length of fine roots produced by the host. Theoretical explorations have emphasized the efficiency of mycorrhizal hyphae based on their very small diameter (Yanai et al., 1995).

Mean hyphal length produced by ectomycorrhizal fungi associated with seedlings of *Pinus sylvestris*, *Pinus taeda*, and *S. viminalis* can reach 3-80 m cm^{-1} of root (Read and Boyd, 1986; Jones et al., 1990; Rousseau et al., 1994), and in *P. sylvestris*, extraradical hyphae accounted for 15% of root dry weight with *Laccaria laccata* and 123% of root dry weight with *Paxillus involutus* (Colpaert et al., 1992). Likewise, in ectomycorrhizal *Pinus pinaster* with *Hebeloma cylindrosporum*, extraradical hyphae accounted for up to 20% of root dry weight (Plassard et al., 1994). Under field conditions, the total amount of hyphal biomass produced in forest soils by ectomycorrhizal fungi (i.e. 1.25 to 2.0 kg m^{-2}) was nearly equivalent to the fine root biomass production (Högberg et al., 2001; Wallander et al., 2001; Högberg and Högberg, 2002). Thus, extraradical hyphal biomass in ectomycorrhizal plants can greatly exceed that found in arbuscular mycorrhizal plants, and should consequently have even faster rates of respiration for growth than the arbuscular fungi.

B. Maintenance Respiration

Mycorrhizal associations require respiratory energy to maintain existing fungal structures and activities, as well as any host cellular activities linked to the presence of the symbiont. Eighty-four percent of the difference in daily total root and soil respiration between mycorrhizal and non-mycorrhizal *C. volkameriana* seedlings was considered maintenance respiration (Fig. 4; Table 5). Higher maintenance respiration in the mycorrhizal seedlings was attributed to both a larger root system and to apparently greater specific rates of maintenance respiration (which, in

this case, also included respiration associated with ion uptake, microbial respiration, and growth respiration of the extraradical hyphae). Increased maintenance respiration also appeared to account for most of the respiration associated with mycorrhizal colonization in common bean (*Phaselous vulgaris*) (Nielsen et al., 1998).

Assuming maintenance respiration represents most of the respiratory costs associated with mycorrhizal fungi, maintenance respiration of mycorrhizal tissue appears to be considerable. Per unit biomass, mycelial respiration by mycorrhizal fungi is several orders of magnitude faster than host root respiration (Martin et al., 1987; Rygiewicz and Anderson, 1994; Eltrop and Marschner, 1996). Per unit length, however, the fungi cost considerably less to maintain than roots. Coupled with lower construction costs, mycorrhizal associations enable the host plant to explore more soil volume per unit of carbon invested, and increase the efficiency of nutrient capture when soil resources are limited (Eissenstat and Volder, in press).

C. Ion Uptake Respiration

Mycorrhizal fungi often increase the ability of many plants to acquire soil nutrients, and therefore, may increase the energy demand required for ion uptake. Baas et al. (1989) attributed 13% of the increased respiration associated with mycorrhizal colonization in *Plantago major* to increased nutrient uptake. However, in many cases, mycorrhizas do not tend to appreciably enhance plant uptake of mobile soil ions including nitrate (Tinker and Nye, 2000), which quantitatively is the most important ion associated with uptake respiration (Veen, 1981). Thus, the importance of mycorrhizas on ion uptake respiration may be somewhat limited. Hawkins et al. (1999), for example, found no increase in ion uptake respiration due to colonization by *G. mosseae* in wheat when plants were grown hydroponically under non-limiting nutrient conditions. Colonization by *G. intraradices* also had no effect on ion uptake respiration in *C. volkameriana* seedlings grown under high-phosphorus soil conditions, but did increase ion uptake respiration when plants were grown under low-phosphorus conditions (Table 5). This was likely due to the fact that under low-phosphorus conditions, seedlings colonized by the fungi were larger and had faster rates of ion uptake by roots and hyphae than uncolonized seedlings.

Ectomycorrhizal fungi can also utilize organic forms of nitrogen by producing extracellular proteinases (Abuzinadah and Read, 1986; Zhu et al., 1990; Maijala et al., 1991), thereby providing the host plant access to nitrogen sources that would otherwise be unavailable. Respiratory costs associated with nitrogen uptake by this process are unknown.

IV. Other Respiratory Costs

There are other respiratory costs associated with mycorrhizal fungi that are potentially important to the carbon economy of the host plant, but these costs have received relatively little attention in the literature. They include respiration associated with fungal reproduction, respiration of microorganisms residing in the region of soil surrounding the extraradical hyphae, termed the mycorrhizosphere, and respiration associated with forming hyphal links with neighboring plants.

A. Fungal Reproduction

Most mycorrhizal studies have been done with young plants under laboratory or glasshouse conditions, and therefore provide no information on the carbon requirements of the mycorrhizal fruiting bodies or spores typically associated with mature vegetation in the field. The development of spores and sporocarps by mycorrhizal fungi represents significant production of fungal biomass in a relatively short time, capable of exceeding several kg m^{-2} yr^{-1} (e.g., Sieverding et al., 1989; Johnson, 1994), and depends on current assimilate from the host (Last et al., 1979; Lamhamedi et al., 1994; Högberg et al., 2001). Mycorrhizal spores are especially rich in lipids and fatty acids which comprise more than 45 to 95% of their carbon pool (Jabaji-Hare, 1988; Bago et al., 1999; Olsson and Johansen, 2000). Reproduction by the fungi thus will require large amounts of carbon for respiration and structural build-up, particularly when conditions are most favorable for sporulation such as late in the growing season (Menge, 1984; An et al., 1993; Smith and Read, 1997).

B. Microorganisms Associated with the Mycorrhizosphere

Mycorrhizas strongly influence rhizosphere microbial populations by altering the nutrient and carbon physiology of the host plant, and by changing the

chemical and physical properties of the soil environment (Azcón-Aguilar and Barea, 1992; Linderman, 1992). Several microorganisms also influence the establishment of mycorrhizal fungi (Garbaye, 1994; Perotto and Bonfante, 1997), and facilitate the release of soil nutrients prior to mycorrhizal uptake (Toro et al., 1997). It is expected that most or even all of the energy required by these microorganisms, which may include both beneficial and non-beneficial species, is derived from host assimilates. However, their greatest impact on respiratory costs is probably through their direct and indirect effects on mycorrhizal associations.

C. Hyphal Links between Plants

Many mycorrhizas have low host specificity and are capable of forming inter- and intraspecific hyphal connections between neighboring plants. A number of studies have reported a net transfer of carbon between plants linked by these connections (e.g., Francis and Read, 1984; Grime et al., 1987; Simard et al., 1997), although the quantitative significance of this transfer to the carbon status of the host and recipient plants remains questionable (Fitter et al., 1998; Robinson and Fitter, 1999). Using imaging plate autoradiography, Wu et al. (2001) recorded continual movement of ^{14}C-labeled photosynthetic products between *Pinus densiflora* seedlings linked by extraradical hyphae of *Pisolithus tinctorius* or by an unidentified ectomycorrhizal fungus. Regardless of the mycorrhizal species, within 3 days of labeling, ^{14}C was detected in the extraradical hyphae and the colonized roots of the unlabeled 'receiver' seedling. Reverse-labeling demonstrated that carbon also moved from the 'receiver' seedling to the extraradical hyphae. However, carbon movement between the plants themselves by way of interlinking hyphae was not detected. Therefore, although evidence for carbon transfer between plants (for tissue growth and maintenance) was lacking in this study, the data do illustrate that hyphal links between plants may help reduce the costs associated with supporting the mycorrhiza. In fact, two other reports indicate that as much as 10% of the carbon of an arbuscular mycorrhizal root can be derived from another plant when linked by fungal hyphae (Watkins et al., 1996; Graves et al., 1997). Hyphal links might also reduce respiratory costs associated with ion uptake if nitrogen and other nutrients are transferred between plants (e.g., Frey and Schüepp, 1992).

V. Conclusions

Ever since mechanistic evidence for the dependence of mycorrhizal fungi on host carbon was first presented 30 years ago (Ho and Trappe, 1973), a fair amount of research has been devoted to elucidating the host energy demands for supporting mycorrhizal associations. We now know from laboratory and greenhouse studies that a considerable amount of photosynthate is required by mycorrhizas, and at least half of it is used for respiratory processes. However, there are still many questions about mycorrhizal respiration that remain unanswered. Respiratory costs of ericaceous and orchid mycorrhizas, for example, are entirely unknown, despite the growing realization of their importance in many ecosystems. We also have very little understanding of mycorrhizal respiratory costs on mature plants. Only recently have studies shown the significance of mycorrhizal fungi as important pathways of carbon flux from plants to soil to atmosphere under field conditions (Johnson et al., 2002a, b). New techniques need to be developed to measure respiration of mycorrhizal roots under field conditions (e.g., Espeleta et al., 1998; Bryla et al., 2001; Kutsch et al., 2001; Johnson et al., 2002a,b), and provide answers to the relevance of this symbiosis to overall carbon economy of associated plants.

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