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CARBON ALLOCATION TO ECTOMYCORRHIZAL FUNGI CORRELATES WITH BELOWGROUND ALLOCATION IN CULTURE STUDIES

ERIK A. HOBBIE¹

Complex Systems Research Center, University of New Hampshire, Durham, New Hampshire 03824 USA

Abstract. Ectomycorrhizal fungi form symbioses with most temperate and boreal tree species, but difficulties in measuring carbon allocation to these symbionts have prevented the assessment of their importance in forest ecosystems. Here, I surveyed allocation patterns in 14 culture studies and five field studies of ectomycorrhizal plants. In culture studies, allocation to ectomycorrhizal fungi (NPP_f) was linearly related to total belowground net primary production (NPP_b) by the equation $NPP_f = 41.5\% \times NPP_b - 11.3\%$ ($r^2 = 0.55$, $P < 0.001$) and ranged from 1–21% of total net primary production. As a percentage of NPP, allocation to ectomycorrhizal fungi was highest at lowest plant growth rates and lowest nutrient availabilities. Because total belowground allocation can be estimated using carbon balance techniques, these relationships should allow ecologists to incorporate mycorrhizal fungi into existing ecosystem models. In field studies, allocation to ectomycorrhizal fungi ranged from 0% to 22% of total allocation, but wide differences in measurement techniques made intercomparisons difficult. Techniques such as fungal in-growth cores, root branching-order studies, and isotopic analyses could refine our estimates of turnover rates of fine roots, mycorrhizae, and extraradical hyphae. Together with ecosystem modeling, such techniques could soon provide good estimates of the relative importance of root vs. fungal allocation in belowground carbon budgets.

Key words: *belowground NPP; carbon flux; culture vs. field studies; ectomycorrhizae; forest ecosystems; fungal C allocation; net primary production; nutrient limitation; Pinus spp.; root C allocation.*

INTRODUCTION

Ectomycorrhizal fungi are obligate symbionts of many economically and ecologically important tree taxa in temperate, boreal, and tropical regions, including *Eucalyptus* (Myrtaceae), Pinaceae, Betulaceae, Salicaceae, Fagaceae, and Dipterocarpaceae. They are necessary for survival of their plant hosts because they provide much of the plant nutrient supply (Read and Perez-Moreno 2003). Carbon allocation from trees to ectomycorrhizal fungi appears to be sensitive to anthropogenic influences such as elevated nitrogen deposition, ozone, and carbon dioxide (Rillig et al. 2002). Difficulties in estimating allocation to these symbionts have prevented the incorporation of mycorrhizal fungi into system-scale models of carbon and nitrogen cycling. This limits predictions of soil carbon storage and ecosystem responses to various stresses. One solution is to calibrate allocation to mycorrhizal fungi to other measurable quantities in field studies, such as total belowground allocation. Total belowground allocation can be estimated using the carbon balance approach (Raich and Nadelhoffer 1989, Davidson et al. 2002, Giardina and Ryan 2002), in which respiration derived from aboveground litter decay is subtracted from total

soil CO₂ efflux. Here, I compiled data from published field and culture studies to search for underlying relationships between total belowground allocation and relative allocation to ectomycorrhizal fungi. In addition, to examine how nutrient availability correlates with allocation to ectomycorrhizal fungi, I used culture studies to estimate the effect of mycorrhizal colonization on plant growth at different rates of nutrient supply.

METHODS

I surveyed all available literature on allocation to ectomycorrhizal fungi in culture studies or in field studies. Seedlings in culture studies were generally grown in semihydroponic systems composed of perlite, brick pellets, or sand to which nutrients were added. Additional substrates included peat, sandy soil, peat-vermiculite, peat-sandy loam, or a soil-sand mix. Culture studies were analyzed for distributions of either biomass or carbon. In most cases, biomass distributions were taken from final harvest measurements, with allocation to mycorrhizal hyphae extending beyond the root (extraradical hyphae) assessed by increases in mass, ergosterol concentrations, or chitin assays. Partitioning in mycorrhizal roots between plants and fungi was assessed using concentrations of ergosterol, glucosamine, or nitrogen. A few of the studies included estimates of plant and fungal respiration. Allocation in some studies was determined by tracer studies using

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¹ E-mail: erik.hobbie@unh.edu

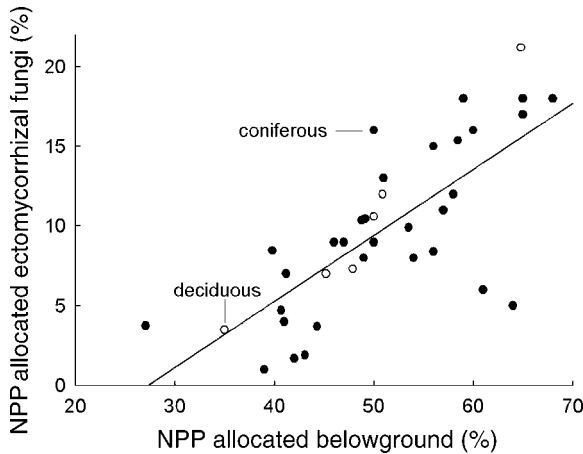


FIG. 1. Net primary production (NPP) allocated to ectomycorrhizal fungi correlates with relative belowground allocation in culture studies ($n = 37$, $r^2 = 0.55$, $P < 0.001$). Deciduous host trees are shown with open circles, evergreen conifers with solid circles. Studies and study conditions are listed in the Appendix.

^{14}C measurements. Study duration varied from 45 to 300 days. Studies were not included in which only respiratory carbon was assessed (e.g., Söderström and Read 1987) or in which fungal colonization of ectomycorrhizae was not explicitly assessed (e.g., Ineichen et al. 1995).

To compare plant growth rates and allocation to ectomycorrhizal fungi, I used data from four studies that grew plants under conditions of exponential growth either with or without mycorrhizal fungi. In exponential growth, plants are supplied daily with nutrients at a fixed percentage of the existing plant nutrient stock, e.g., 3% per day (Ingestad and Ågren 1992). Under these conditions, nutrient supply rates match plant uptake rates, and stable plant nutrient concentrations are established.

Estimates of allocation to ectomycorrhizal fungi in five field studies were also examined. The four main components of ectomycorrhizal allocation are respiration, fruit bodies, the fungal portion of ectomycorrhizae, and fungal structures beyond the root. These last structures include extraradical hyphae, as well as specialized structures such as sclerotia and rhizomorphs. Most studies did not account for all four components.

RESULTS

Culture studies

In culture studies, allocation of carbon to ectomycorrhizal fungi by plants ranged from 1% to 21% of total net primary production (NPP), whereas belowground allocation ranged from 27% to 68% of NPP (Fig. 1 and Appendix). As shown in Fig. 1, the relationship between the percentage of NPP allocated below ground (NPP_b) was linearly related to the per-

centage allocated to ectomycorrhizal fungi (NPP_f) by the following equation:

$$\text{NPP}_f = 41.5\% \times \text{NPP}_b - 11.3\%. \quad (1)$$

Thus, increased belowground allocation was positively correlated with increased allocation to ectomycorrhizal fungi.

Nutrient availability is a major control on patterns of belowground allocation in plants. Reduced nutrient supply of nitrogen, phosphorus, or sulfur increases belowground allocation, whereas reduced nutrient supply of magnesium or potassium decreases belowground allocation (Ericsson 1995). Plant growth rate declines with reduced nutrient supply (Ågren and Bosatta 1996). Given the clear increase in allocation to ectomycorrhizal fungi with increased belowground allocation shown in Fig. 1, it is plausible to assume that carbon allocation to ectomycorrhizal fungi can substantially reduce plant growth if mycorrhizal colonization does not improve the plant acquisition of nutrients. When plants are grown with mycorrhizal fungi at exponentially increasing rates of nutrient addition (termed exponential growth), plant growth adjusts to match nutrient application rates. Under these conditions, plants cannot derive nutritional benefit from mycorrhizal colonization, allowing the carbon cost of colonization to be readily calculated (Ingestad et al. 1986).

In Fig. 2, data from four culture studies under exponential growth were used to compare how much mycorrhizal colonization reduced growth of *Pinus sylvestris* relative to nonmycorrhizal controls at different rates of nutrient supply. Growth rate was normalized vs. plant biomass. Plant growth rates are primarily determined by the rate of nutrient supply (Ingestad and Ågren 1992). Here, growth decreased dramatically with

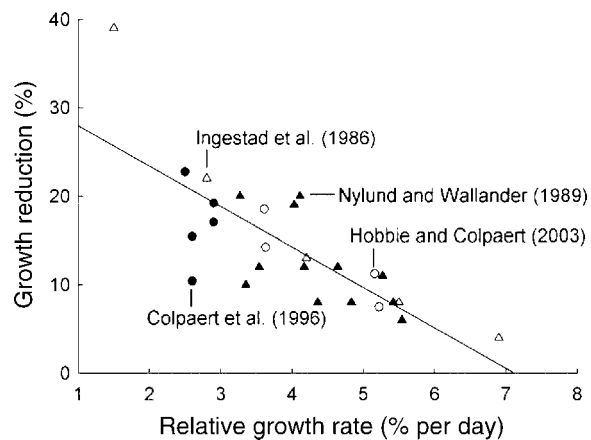


FIG. 2. The carbon cost (equivalent to growth reduction on graph) of mycorrhizal colonization in *Pinus sylvestris* is greater at low relative growth rates ($n = 26$, $r^2 = 0.60$, $P < 0.001$). Data were taken from the four studies cited on figure. The carbon cost was calculated by comparing biomass of plants with or without mycorrhizal colonization grown at comparable nutrient addition rates. The relative growth rate is the daily percentage increase in biomass.

TABLE 1. Field-based estimates of carbon allocation to ectomycorrhizal fungi as a percentage of net primary production (NPP), gross primary production (GPP), or total uptake.

Dominant species	Allocation (%) [†]		Total flux (kg C·ha ⁻¹ ·yr ⁻¹)	Reference
	EMC	Belowground		
<i>Abies amabilis</i>				
23-yr-old stand	13.9 ^{‡,§,}	72.6	10 584 (NPP)	Vogt et al. (1982)
180-yr-old stand	15.0 ^{‡,§,}	81.7	11 191 (NPP)	Vogt et al. (1982)
<i>Pseudotsuga menziesii</i>				
Drought year [¶]	20.8 ^{§,#}	67.5	18 724 (uptake)	Fogel and Hunt (1983)
Normal year	13.7 ^{§,#}	68.0	25 460 (uptake)	Fogel and Hunt (1983)
<i>Pinus sylvestris</i>	14–15 ^{††}	63	5800 (NPP)	Finlay and Söderström (1992)
<i>Pinus radiata</i>				
Control	22.2 ^{‡‡}	51.2	24 140 (GPP)	Ryan et al. (1996)
Irrigated	15 ^{‡‡}	46.3	25 310 (GPP)	Ryan et al. (1996)
Irrigated and fertilized	0 ^{‡‡}	26.8	34 380 (GPP)	Ryan et al. (1996)
<i>Betula nana</i>	7–16 ^{§§}	unknown	1800 (GPP)	J. Hobbie and E. A. Hobbie, <i>unpublished manuscript</i>

Notes: If biomass values were given, they were converted to carbon values, assuming that biomass averages 45% carbon. ECM, ectomycorrhizal fungi.

[†] As a percentage of total flux (GPP, NPP, or uptake).

[‡] No allocation to extraradical hyphae.

[§] Based on biomass harvests and sequential coring.

^{||} Mycorrhizae assumed to be 40% fungal by the authors.

[¶] 45% of normal precipitation.

[#] Soil hyphae not differentiated between mycorrhizal and saprotrophic fungi, mycorrhizae only included in plant totals. I assumed that 20% of mycorrhizae were fungal, and that 50% of soil and litter hyphae were of mycorrhizal origin. A value of 50% appears reasonable based on similar decreases in soil respiration following tree girdling in Höglberg et al. (2001).

^{††} Roots <2 mm diameter assumed to be 40% fungal.

^{‡‡} “Unknown” allocation in Ryan et al. (1996) invoked to close mass balance was interpreted by Waring and Running (1998) as allocation to mycorrhizal fungi and exudates.

^{§§} Based on ¹⁵N distributions, nitrogen budgets, and C:N stoichiometry. Arctic tundra site.

mycorrhizal colonization at slower growth rates and lower nutrient supply rates (Eq. 2), with the relative growth rate (RGR) expressed as percentage increase in biomass per day:

$$\text{growth reduction (\%)} = -4.57 \times \text{RGR} + 32.5\% \quad (2)$$

Growth reduction may be considered equivalent to allocation diverted to ectomycorrhizal fungi. Accordingly, the variability in allocation to ectomycorrhizal fungi for a given growth rate may reflect corresponding variability in the carbon demands of different fungal species. Increasing growth reduction presumably indicates carbon allocated to fungal respiration rather than to biomass accumulation. Thus, according to Eq. 2, supplying plants at a high nutrient supply rate of 5% per day relative to existing nutrient stocks reduced growth by 9.7% in mycorrhizal plants vs. nonmycorrhizal plants, whereas supplying plants with nutrients at a low rate of only 2% per day reduced growth by 23.4% in mycorrhizal plants vs. nonmycorrhizal plants.

Field studies

The few studies that have estimated allocation to ectomycorrhizal fungi in the field are listed in Table 1. These studies are difficult to compare directly because carbon budgets were calculated in various ways. Estimated allocation to ectomycorrhizal fungi in different studies ranged from 0% to 22% of GPP (gross primary

production), from 14% to 15% of NPP, and from 14% to 21% of total carbon uptake. Of these studies, only Vogt et al. (1982) and Fogel and Hunt (1983) attempted complete ecosystem budgets with explicit measurements of different fungal components of allocation, although they did not estimate carbon flux through extraradical ectomycorrhizal hyphae. Finlay and Söderström (1992) compiled production estimates of fruit bodies, mycorrhizae, and extraradical hyphae from a variety of studies to derive a composite estimate for Swedish *Pinus sylvestris* forests. A study in *Pinus radiata* plantations in Australia inventoried carbon stocks and fluxes thoroughly and estimated that up to 22% of GPP was unaccounted for (Ryan et al. 1996). This unknown flux was later interpreted by Waring and Running (1998) as allocation to ectomycorrhizal fungi and exudates. Most recently, estimates for ecosystem-scale carbon and nitrogen fluxes have been combined with fungal C:N ratios and a nitrogen isotope mass balance model to estimate that 7–16% of GPP was allocated to fungal symbionts at an Arctic tundra site (J. Hobbie and E. A. Hobbie, *unpublished manuscript*). In northern hardwoods, allocation to mycorrhizal fungi plus exudates was estimated, using carbon balance approaches, at 17% of total belowground allocation (Fahey et al. 2005). This field study included an unknown proportion of arbuscular mycorrhizae. Exudation appears to be a quite minor percentage of belowground NPP in ecto-

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mycorrhizal systems, >0.5% of total NPP (Norby et al. 1987).

DISCUSSION

The simple relationship between allocation to ectomycorrhizal fungi and belowground allocation shown in Fig. 1 and Eq. 1 should enable estimates of allocation to ectomycorrhizal fungi in many forests, facilitate modeling the impact of ectomycorrhizal fungi on forest processes, and help to constrain field-based estimates of allocation to ectomycorrhizal fungi. Although we lack a comprehensive theory on scaling up allocation from culture studies to the field, patterns of total belowground allocation appear similar between the culture studies cited here and ecosystem budgets derived from field studies (Raich and Nadelhoffer 1989). The pattern from culture studies shown in Fig. 2 indicates that relative allocation to mycorrhizal fungi increases at reduced growth rates. Given that growth rates will be slow when belowground allocation is high and nutrient availability is low (Ingestad and Ågren 1992, Beets and Whitehead 1996), both Figs. 1 and 2 suggest that the importance of ectomycorrhizal fungi to plant carbon balance increases at low nutrient availability.

What do these patterns imply for ecosystems dominated by ectomycorrhizal plants? Gower et al. (2001) reported that deciduous trees in boreal sites generally allocated a lower percentage of NPP below ground than did evergreen conifers. In addition, deciduous stands tend to have higher nutrient availability relative to coniferous stands (Reichle 1981), again suggesting a tendency toward lower belowground allocation. Application of Eq. 1 to these relationships gives insight to the differences in the probable ectomycorrhizal allocation between stand types; a high allocation to ectomycorrhizal fungi is expected in low-nutrient coniferous stands. Thus, I predict that a lower percentage of total NPP is allocated to ectomycorrhizal fungi in deciduous forests than in coniferous forests. Anthropogenic increases in nutrient availability are associated with decreased fruiting of ectomycorrhizal fungi, decreased production of extraradical hyphae, and decreased colonization intensity of ectomycorrhizal roots (Wallenda and Kottke 1998).

To apply Eq. 1 to estimate allocation to ectomycorrhizal fungi, we must estimate total belowground allocation. The best method currently available for estimating this allocation appears to be the carbon balance approach, in which total belowground allocation is estimated as CO₂ flux from the decomposition of aboveground litter subtracted from total soil CO₂ efflux. Although soil C accumulation is a potentially confounding factor, it appears unimportant because of the relatively slow rate at which soil organic carbon accumulates (Giardina and Ryan 2002, Fahey et al. 2005).

Several difficulties exist in attempting to measure allocation in field studies. All field studies to date are confounded by uncertainties about turnover rates of

roots, mycorrhizal hyphae, and fungal sclerotia, and by uncertainties about the percentage of fungal matter on mycorrhizal root tips. For example, Vogt et al. (1982) used sequential coring in *Abies amabilis* stands and estimated very high allocation to fine roots and *Cenococcum* sclerotia. A review of methods to estimate root allocation concluded that sequential coring dramatically overestimates flux through the root system (Nadelhoffer and Raich 1992). This suggests that belowground NPP and allocation to ectomycorrhizal fungi are overestimated in studies using sequential coring, such as Vogt et al. (1982) and Fogel and Hunt (1983). Höglberg et al. (2002) concluded that root allocation was overestimated in the budget of Persson (1978) for Scotch pine forests, as the estimates of Persson (1978) required an unrealistically high value of 90% for the efficiency with which photosynthate was converted into biomass. Because Finlay and Söderström (1992) estimated the fungal component in fine roots as a fixed fraction of the root biomass given in Persson (1978), they probably overestimated this component of fungal allocation. Careful work with minirhizotrons and radiocarbon measurements may determine life spans of relatively long-lived belowground components such as some fine roots and ectomycorrhizae (Tierney and Fahey 2002, Treseder et al. 2004), whereas life spans of extraradical hyphae may require combining isotopic tracer studies and minirhizotrons.

Many root studies probably underestimate the contribution of the finest roots to carbon budgets because roots of different branch orders are commonly combined (Guo et al. 2004). Exciting recent work suggests that fine roots of the lowest branching orders (i.e., the most distal roots) contribute disproportionately to total root carbon flux because of relatively rapid turnover, and that disregarding their contribution may account for many of the discrepancies in turnover reported using different methods (R. Mitchell, *personal communication*). In light of these findings, it appears probable that the contribution of fine roots to carbon budgets may be underestimated in the Ryan et al. (1996) study cited in Table 1. The hypothesized contribution of mycorrhizal fungi to ecosystem carbon balance, as calculated by difference for that study, may accordingly be overestimated.

A second difficulty is to estimate accurately the percentage of fungal matter in fine roots or mycorrhizae. The contribution of fungal matter to fine roots appears to be highly variable, depending on the intensity of mycorrhizal development of the root system, the percentage of mycorrhizae consisting of fungal biomass, and the operational definition of fine roots used. Early morphological work with *Fagus* mycorrhizae reported that mycorrhizae were 39% fungal matter (Harley and McCready 1952). This value (rounded to 40%) has been subsequently propagated through numerous review articles (e.g., Harley 1971) and several field studies. For example, Finlay and Söderström (1992) assumed that

40% of root matter >2 mm in diameter was of fungal origin in a Swedish pine forest, and Vogt et al. (1982) assumed a similar value of 40% for mycorrhizae in *Abies amabilis* stands. Although individual mycorrhizae occasionally may be composed of 40% fungal matter, scaling up this value to ecosystem estimates of fine-root production probably overestimates fungal biomass.

Realistic estimates of the fungal contribution to mycorrhizae have been derived from measurements of the volume of fungal tissue in mycorrhizae or from measuring proxies for fungal biomass such as ergosterol concentrations. In cultures of *Picea sitchensis*–*Lactarius rufus*, Alexander (1981) suggested that 20% of root system mass might be from fungal matter. Mycorrhizae in this system were 250 μm in radius, with a sheath thickness of 15–30 μm , so treating the mycorrhizae as perfect cylinders meant that fungi comprised 12–23% of mycorrhiza volume. Harley and Smith (1983) indicated that mycorrhizae of *Fagus* and *Nothofagus* had sheath thicknesses of 39 μm and 30 μm , respectively, whereas Lewis and Harley (1965) found that sheath tissue was 32% of the total mass of *Fagus* mycorrhizae. In *Pinus sylvestris* cultures, *Thelephora terrestris* mycorrhizae were ~22% fungal matter, regardless of the level of nitrogen availability, whereas *Suillus luteus* mycorrhizae were 14% and 20% fungal matter at high and low nitrogen availabilities, respectively (Hobbie and Colpaert 2003). Nitrate-supplied *Pinus pinaster* roots colonized by *Hebeloma cylindrosporum* consisted of 20% fungal matter (Plassard et al. 1994). In a culture study in which *Pinus sylvestris* and *Alnus incana* were grown together, ectomycorrhizal fungi averaged 9.8% by mass on *Pinus* roots and 3.6% by mass on *Alnus* roots (calculated graphically from Ekblad et al. 1995). In *Picea abies* colonized by *Pisolithus tinctorius*, the percentage of fungal matter in roots was only 1.55% for ammonium-supplied plants and 0.96% for nitrate-supplied plants (Eltrop and Marschner 1996). These small values contrast with results for *Picea abies* ectomycorrhizae in a field study, in which the fungal mantle comprised 18–28% of the cross-sectional area of mycorrhizae (Ostonen and Löhmus 2003).

I conclude that the published studies in Table 1 have methodological discrepancies. These issues weaken the confidence with which we can compare results from the field studies with culture studies. Thus, the validity of estimating allocation to ectomycorrhizal fungi from belowground allocation as given in Eq. 1 remains unclear. However, as discussed in the preceding paragraphs, the estimates of mycorrhizal and fine-root turnover, root branching-order demographics, and the fungal contribution to ectomycorrhizae could be improved using current techniques.

Several new methods appear promising for helping to estimate allocation to ectomycorrhizal fungi in field studies, including using in-growth cores to estimate new fungal growth (Wallander et al. 2001), estimating

existing ectomycorrhizal biomass by measuring its degradation after incubating field cores in the laboratory (Bååth et al. 2004, Wallander et al. 2004), and studying the system response to large-scale tree girdling (Högberg et al. 2001). A recent modification of the girdling technique will permit belowground allocation patterns to be studied repeatedly by chilling tree stems to restrict belowground carbon flux (R. Waring, *personal communication*). The challenge now for ecologists is how best to extrapolate estimates derived from these new techniques to ecosystem-scale budgets. These new methods should be compared as part of complete ecosystem budgets. In addition, promising techniques in scaling microbial and animal metabolism based on network theory potentially could provide similar insights into fungal metabolism in plant–mycorrhizal symbioses. For example, network theory predicts that respiration will scale as the three-fourths power of mass (Enquist et al. 2003). This would suggest that mycorrhizal hyphae with an average diameter of 10 μm will respire 32 times faster than a fine root of 100 μm diameter, assuming that hyphae are metabolically active throughout their length.

The available evidence suggests that a large proportion of the missing carbon sink in the global carbon budget is located in temperate and boreal forest regions (House et al. 2003) where ectomycorrhizal fungi are the dominant mycorrhizal type. Allocation to ectomycorrhizal fungi may be an important conduit for carbon from plants to the belowground community, and ultimately to storage as stable soil carbon (Treseder and Allen 2000). If transfers to stable soil carbon are favored by allocation to mycorrhizal fungi, then much of the carbon sink in northern latitudes may derive from carbon flux through mycorrhizal fungi, particularly in coniferous forests. The relationships discussed here will be useful in efforts to generalize allocation patterns to ectomycorrhizal fungi in ecosystem models and across landscapes, and consequently will aid in assessing the role of ectomycorrhizal fungi in many ecosystems at different scales. Given the growing confidence with which total belowground allocation can now be estimated using carbon balance approaches (Raich and Nadelhoffer 1989, Davidson et al. 2002, Giardina and Ryan 2002), Eq. 1 may help to partition belowground allocation between roots and mycorrhizal fungi in forests dominated by ectomycorrhizal species.

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APPENDIX

Table showing carbon or biomass allocation in culture studies of ectomycorrhizal plants (*Ecological Archives* XXXXXXXXXXXX).