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ORIGINAL PAPER

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Spatiotemporal transfer of carbon-14-labelled photosynthate from ectomycorrhizal *Pinus densiflora* seedlings to extraradical mycelia

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Abstract Seedlings of *Pinus densiflora* colonized by an unidentified ectomycorrhizal fungus (T01) were labelled photosynthetically with ^{14}C. Movement of ^{14}C-labelled photosynthates within the underground part of the seedlings was investigated by temporal autoradiography using an imaging plate. Within 1 day, ^{14}C was transferred from the shoot to the underground part that included roots, mycorrhizae, and the extraradical mycelium; within 3 days, the ^{14}C in the underground part reached its maximum density. Mycorrhizae and actively growing root tips were large C sinks. Three days after ^{14}C labelling, counts of ^{14}C radioactivity in the underground part of the mycorrhizal seedlings were 2.6 times those of nonmycorrhizal seedlings. The mycorrhizae of mycorrhizal plants accumulated 5.2 times the ^{14}C counts in the short-root tips of nonmycorrhizal plants. ^{14}C counts in various areas of the extraradical mycelium demonstrated that all ^{14}C-photosynthate transfer from the host root to the extraradical mycelium occurred within 3 days after ^{14}C labelling, and that there was only a short lag of <1 day between ^{14}C accumulation in the basal and distal parts of the mycelium. Although more ^{14}C accumulated in the distal than in the basal parts, ^{14}C counts per unit hyphal biomass were similar between the two. These results suggest that ^{14}C spread rapidly throughout the entire mycelium. Thirteen days after ^{14}C labelling, we estimated ^{14}C allocation to extraradical mycelia by taking autoradiographs after removing host roots. About 24% of ^{14}C counts in the underground part of the mycorrhizal seedlings had been allocated to extraradical mycelia in this system, indicating that the fugal mycelium is an important sink for photosynthates.

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Introduction

Ectomycorrhizal fungi play an important role in the C cycle of forest ecosystems (Smith and Read 1997). Studies have shown that ectomycorrhizal fungi in symbiosis with trees stimulate photosynthesis in host trees and benefit from the organic compounds produced by them (Ekwebelam and Reid 1983; Reid et al. 1983; Dosskey et al. 1990; Nara and Hogetsu 1996). The stimulation of photosynthesis in host trees is caused by the increased C sink strength created by the fungal colonization (Smith and Read 1997).

The extraradical mycelium is a dominant component of soil microbial biomass in the forest ecosystem (Finlay and Söderström 1992), where it plays important roles in N, P and C cycles (Smith and Read 1997). Söderström and Read (1987) demonstrated that approximately 30% of total respiration was attributable to the mycorrhizal mycelium, and when mycelial connections to the roots were severed the respiration rate decreased considerably. Rygiewicz and Andersen (1994) also showed that respiration by mycorrhizal roots and mycelium led to an increase in the amount of C allocated below ground. Estimating the amount of C allocated by the plant to support the growth and maintenance of its ectomycorrhizal mycelium is important when determining C and nutrient cycles (Smith and Read 1997).

Several researchers have studied how photosynthates are allocated to the underground parts of mycorrhizal and nonmycorrhizal plants using ^{14}C-tracer experiments. They have shown that more ^{14}C accumulated in ectomycorrhizal roots than in nonmycorrhizal roots (Bevege et al. 1975; Reid et al. 1983; Cairney et al. 1989). Using *Salix viminalis*, either colonized by *Thelephora terrestris* or grown in nonmycorrhizal conditions, Jones et al. (1991) reported that the amount of C allocated below ground was consistently greater in mycorrhizal than in

nonmycorrhizal plants during a 98-day growth period. In a more recent study using microautoradiography, it was shown that the ectomycorrhizal fungus had a high capacity to attract ^{14}C-labelled photosynthates (Bücking and Heyser 2001). Although the amount of C allocation to extraradical mycelium has been measured by scintillation counting in previous studies (Miller et al. 1989; Rygiewicz and Andersen 1994), the timing and spatial allocation of fixed ^{14}C to the shoots, roots, mycorrhizae and extraradical mycelia remains uncertain. In the present study, imaging-plate autoradiography (Nara and Hogetsu 1998; Wu et al. 2001) was used to examine the spatiotemporal transfer of ^{14}C-labelled photosynthate from mycorrhizal *Pinus densiflora* seedlings to extraradical mycelia.

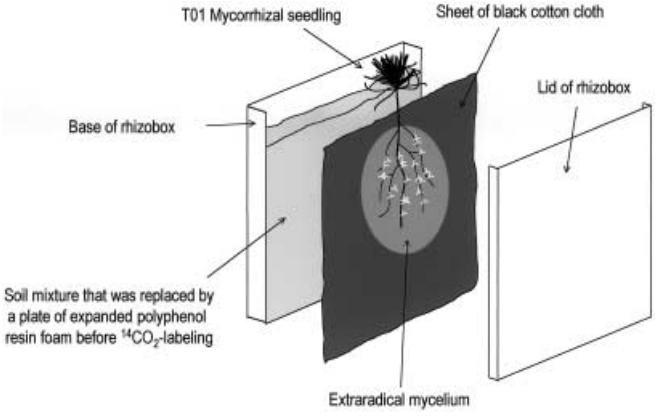

Fig. 1 Diagram of the rhizobox

Materials and methods

Mycorrhiza synthesis and preparation of observation rhizoboxes

Seeds of *Pinus densiflora* Sieb. et Zucc. were sown in a plastic pot filled with a mixture (1:1, v/v) of Tanashi nursery soil (black sand loam, pH 5.65) and Shibanome soil (volcanic sand, pH 5.8–6.0; Setogahara, Gunma, Japan) that had been autoclaved at 121°C for 1 h. An unidentified basidiomycete fungal species (T01), isolated from an ectomycorrhiza of *P. densiflora* grown in a nursery of the University of Tokyo (Nara and Hogetsu 1996; Wu et al. 1999), was used as the fungal symbiont. The fungal internal transcribed spacer (ITS) sequence of the fungus did not match with ITS sequences of ectomycorrhizal fungi of species which formed sporocarps in the nursery and those registered in the GenBank database. Axenic fungal inocula were cultured in flasks at 25°C for 3 months in an autoclaved mixture of peat moss and vermiculite (1:3, v/v) moistened with modified Melin-Norkrans' medium (Marx 1969). About 2 g inoculum was added to the centre of a rectangular flat plate (230×80×15 mm; Eiken Kizai, Tokyo) filled with the autoclaved soil mixture described above. One-month-old pine seedlings were transplanted, one per plate, for inoculation of the roots. Nonmycorrhizal seedlings were also prepared by planting seedlings in plates lacking the inoculum. The seedlings were cultivated for 8 months in a temperature-regulated greenhouse at 25°C day/23°C night for mycorrhizal formation and development.

Flat rhizoboxes (140×205×15 mm) (Fig. 1) were each filled with the autoclaved soil mixture and covered with a sheet of black cotton cloth (140×195 mm) that had been sterilized with 70% ethanol, as described by Wu et al. (2001). Either a mycorrhizal or nonmycorrhizal seedling grown for 8 months in the rectangular flat plate was transferred onto each cloth sheet. The lid and base of each rhizobox were held together using rubber bands. All boxes were wrapped with aluminium foil, placed in the greenhouse, and watered with tap water twice a week. After 4–5 weeks of cultivation, we selected three mycorrhizal seedling samples growing in rhizoboxes for $^{14}CO_2$ labelling, in which fungal hyphae extended far from mycorrhizae and formed advanced extraradical mycelia on the surface of the cloth. The white mycelia grew preferentially along, and contrasted with, the black cloth surface, facilitating observation of mycelial growth. Three nonmycorrhizal seedlings growing in rhizoboxes were also chosen from among those cultivated without the fungus for $^{14}CO_2$ labelling.

$^{14}CO_2$ labelling

Each seedling was photographed using a Pictrostat 330 machine (Fuji Film, Tokyo) as described by Wu et al. (2001). The Pictrostat produces full-size, high-resolution colour photographs of materials placed on its upper, flat window, like an ordinary photocopier. The seedlings and cloth sheets were then carefully transferred together to an expanded polyphenol resin foam plate (Oasis Slab P-5770; Smithers-Oasis, Tokyo) fitted into an empty rhizobox. A nutrient solution (Hyponex; Hyponex Japan, Osaka), diluted 1,000-fold, was added to the foam. Contamination of soil with ^{14}C is prohibited in the radioisotope laboratory of our university, and before ^{14}C labelling, plant materials had to be transferred onto a nonsoil substrate.

^{14}C labelling was performed in an illuminated growth chamber (25–28°C, photosynthetically available radiation, 500 µmol m^{-2} s^{-1}). $^{14}CO_2$ was produced by adding 10% lactic acid with a syringe to 0.5 µmol $Na_2{}^{14}CO_3$ containing 925 kBq ^{14}C in a silicon-plugged microtube. The microtube was then glued to the inside of a transparent polyethylene bag. Each seedling shoot was enclosed in the polyethylene bag, containing about 100 ml air, and the silicon plug was removed to release the $^{14}CO_2$ into the bag. After 2 h, unused $^{14}CO_2$ was removed using a trap containing 1 N NaOH, and the bags were removed from the shoots. These seedlings were cultivated in the growth chamber at 15 h light/9 h dark during the experiment.

^{14}C radioactivity counting of autoradiography image

After removing the lid of each rhizobox and covering its surface with Riken Wrap (Riken Vinyl, Tokyo) to prevent ^{14}C contamination of the imaging plate, it was exposed to an overlaid imaging plate (BAS-SR2040; Fuji Film, Tokyo) for 90 min to produce an autoradiography image. An image analyser (FLA-2000; Fuji Film) was used to visualize radioactivity recorded on each exposed imaging plate. Photo-stimulated luminescence (PSL) on the audioradiography image was counted using MacBas V2.52 software (Fuji Film). Filter paper circles (6 mm in diameter) containing 0, 1.45, 2.89, 5.78, 11.56 and 23.13 KBq of D-[^{14}C(U)]-glucose, respectively, were simultaneously exposed together with each sample to the imaging plate. The PSL counts of filter paper circles were used to correct the errors of PSL counts between images and to confirm if the PSL counts were linearly related to the disintegrations per second (DPS).

Each rhizobox was repeatedly autoradiographed at intervals of up to 13 days after labelling. After autoradiographic exposure at 13 days, each seedling was carefully removed from the cloth sheet, retaining as much of the extraradical mycelium as possible. Another autoradiograph was taken of each to determine ^{14}C allocation in the extraradical mycelium.

Determination of hyphal density

The Pictrostat photograph of each rhizobox was analysed using MacBas V2.52 software. Relative hyphal density [auto unit mm^{-2} (AU mm^{-2})] in the extraradical mycelium was calculated from white pixel density. Hyphal quantity (AU mm^{-2}), density of ^{14}C counts (PSL mm^{-2}), and the relation between the two were determined for 12 places (21.28 mm^2 each) in the extraradical mycelium of one rhizobox.

Results

Time course of ^{14}C transfer from shoot to the underground part of seedlings

Figure 2 shows the time course of fixed ^{14}C movement in a nonmycorrhizal seedling (Fig. 2a) and a mycorrhizal seedling (Fig. 2b) up to 13 days after ^{14}C labelling. Fixed ^{14}C was confined to the shoot immediately (1 h) after ^{14}C labelling. A considerable amount of fixed ^{14}C was transferred from the shoot to the underground part within 1 day. After 2 days, ^{14}C radioactivity in the underground part increased.

The ^{14}C detected in filter paper circles as PSL by autoradiography using an imaging plate was directly proportional to the DPS (DPS=0.314×PSL, r^2=0.998, n=6, P<0.001). Temporal changes in the radioactivity of the shoot and the underground part are shown in Fig. 3. Mycorrhizal seedlings photosynthetically fixed 3.5 times more ^{14}C than nonmycorrhizal seedlings immediately after ^{14}C labelling. ^{14}C reduction in the shoot and the increase in the underground part occurred mostly within 3 days after ^{14}C labelling. In the underground part of mycorrhizal seedlings, 33.5±9.6%, 43.2±8.1%, and 46.5±8.6% of the total counts of ^{14}C radioactivity were present 1, 2, and 3 days after ^{14}C labelling, respectively. From 3 to 13 days after ^{14}C labelling, almost no net shoot-to-root ^{14}C transfer occurred in either mycorrhizal or nonmycorrhizal seedlings. Much more ^{14}C was transferred from the shoot to the underground part in mycorrhizal seedlings than in nonmycorrhizal seedlings; for example, underground ^{14}C counts (including those in roots, mycorrhizae, and extraradical mycelia) in mycorrhizal seedlings were 2.6 times those in nonmycorrhizal seedlings 3 days after ^{14}C labelling.

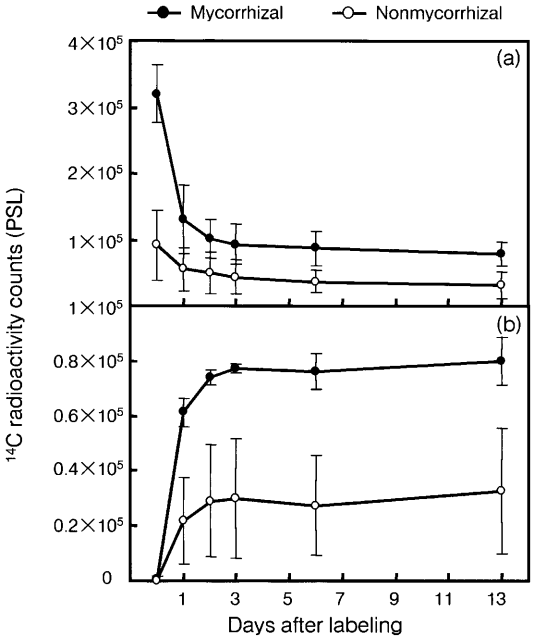

Fig. 3 Temporal variation in counts of ^{14}C radioactivity in the shoot (**a**) and the underground part (**b**) of nonmycorrhizal and T01 mycorrhizal *P. densiflora* seedlings up to 13 days after $^{14}CO_2$ labelling. *Values* are means±SD; n=3. m Nonmycorrhizal seedling; l mycorrhizal seedling

^{14}C in the extraradical mycelium was estimated by measuring ^{14}C counts in the autoradiograph taken after carefully removing roots from the cotton cloth. After removal, 31.1±9.4% and 6.7±0.4%, respectively, of the ^{14}C counts in the underground parts of mycorrhizal and nonmycorrhizal seedlings remained on the cloth sheet. Thus, the ^{14}C remaining after mycorrhizal seedling removal was mostly accounted for by the allocation of ^{14}C to the extraradical mycelium.

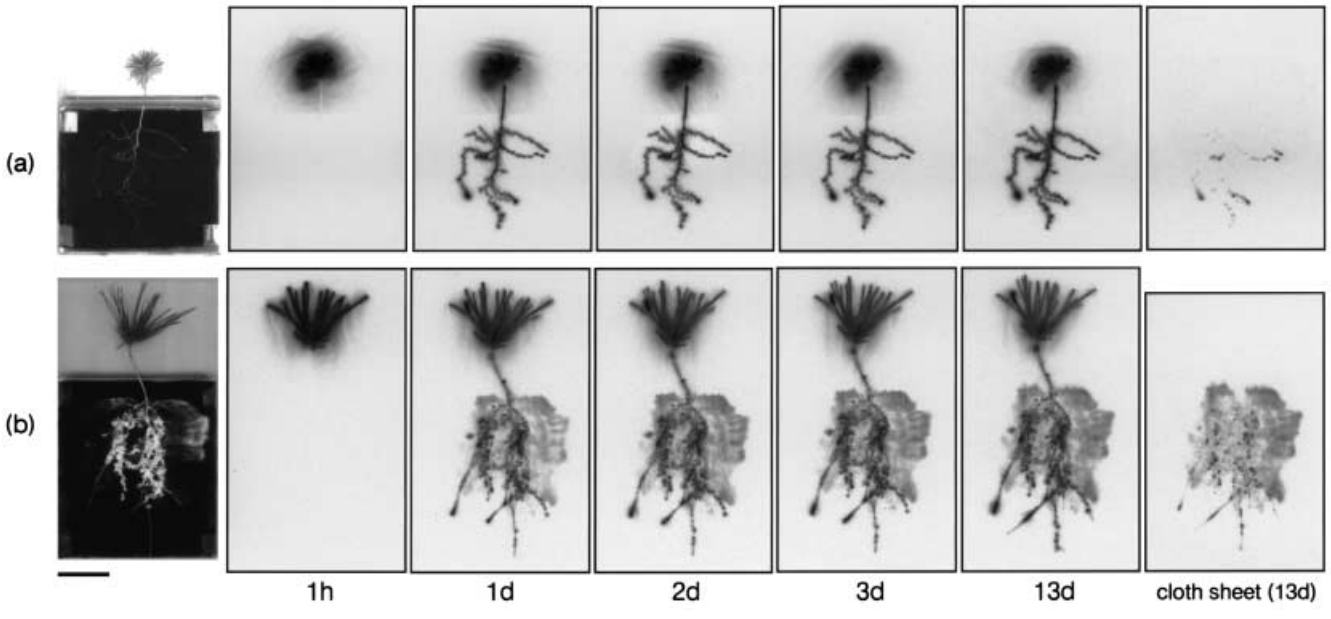

Fig. 2 Time course of ^{14}C distribution in *Pinus densiflora* seedlings grown in rhizoboxes after feeding shoots with $^{14}CO_2$. Pictrostat photos (*left*) and autoradiographs (*right*) show a nonmycorrhizal seedling (**a**) and a T01 mycorrhizal seedling (**b**). *Scale bar* 5 cm

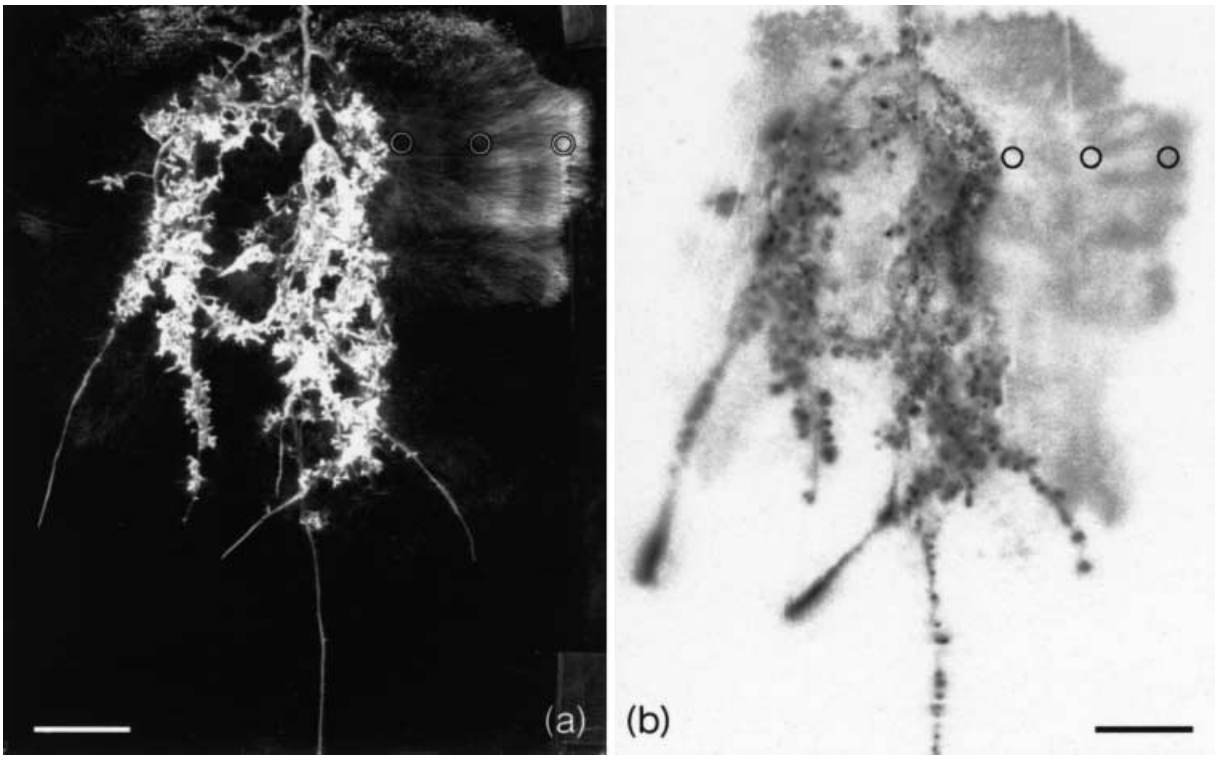

Fig. 4 **a** Pictrostat photo of the underground part of a mycorrhizal *P. densiflora* seedling. **b** Autoradiograph of area shown in **a** 3 days after ^{14}C labelling. *Circles* show the places for measuring hyphal density and counts of ^{14}C radioactivity. *Scale bars* 2 cm

Table 1 Density of ^{14}C counts (photo-stimulated luminescence mm^{-2}) of different parts within the underground part of mycorrhizal and nonmycorrhizal *Pinus densiflora* seedlings 3 days after $^{14}CO_2$ labelling

	Mycorrhizal	Nonmycorrhizal
Lateral root	6.61±4.19	4.19±0.13
Short root tip		25.09±0.59
Growing root tip	129.25±8.13	124.50±0.71
Mycorrhiza	129.80±22.63	–
Mycelium	0.33~15.00	–

Within nonmycorrhizal seedlings, relatively large ^{14}C counts were accumulated in actively growing root tips and short roots. In mycorrhizal seedlings, ^{14}C was detected throughout extraradical mycelia, as well as in actively growing root tips and mycorrhizae (Table 1). Mycorrhizae accumulated 5.2 times more ^{14}C counts than did short root tips in nonmycorrhizal seedlings. Extraradical mycelia accumulated 0.33–15 PSL mm^{-2} of ^{14}C counts.

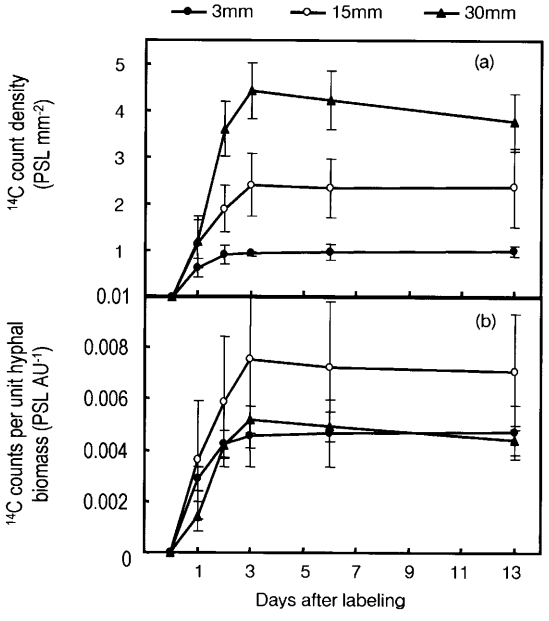

Fig. 5 Temporal variation in density of ^{14}C counts (**a**) and ^{14}C counts per unit hyphal biomass (**b**) at various places in the extraradical mycelium up to 13 days after $^{14}CO_2$ labelling. We took measurements at 3 mm (l), 15 mm (m), and 30 mm (s) from mycorrhizae. *Values* are means±SD; *n*=3

Temporal change in radioactivity within the mycelium

More ^{14}C was detected in the dense hyphal front of extraradical mycelia than in the more basal parts (Fig. 4). Figure 5 shows that the mycelial front (30 mm from mycorrhizae) accumulated more ^{14}C than the middle or basal parts (15 and 3 mm from mycorrhizae, respectively). One and 2 days after ^{14}C labelling, ^{14}C counts density at 3, 15, and 30 mm came to 59.7±12.9%, 41.1±12.2% and 26.5±9.3% and 88.0±10.2%, 69.9±10.51% and 81.0±4.0% of their maximal values, respectively. How-

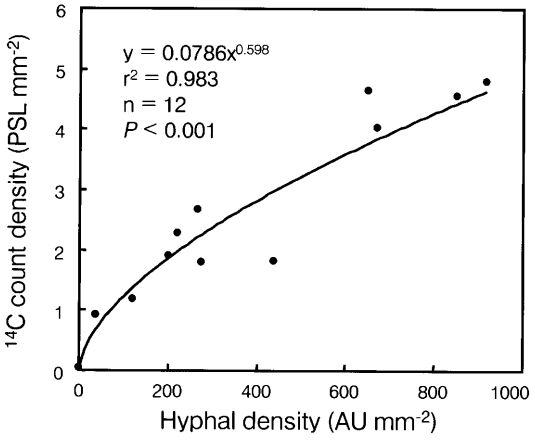

Fig. 6 Relationship between hyphal density and density of ^{14}C counts of extraradical mycelia 3 days after $^{14}CO_2$ labelling

ever, radioactivity throughout the mycelia reached or approached the maximum 3 days after ^{14}C labelling. The density of ^{14}C counts tended to diminish in the mycelial front 3–13 days after ^{14}C labelling (Fig. 5a), perhaps because of hyphal respiration. ^{14}C counts per unit hyphal biomass did not differ significantly among regions (Fig. 5b). The density of ^{14}C counts in extraradical mycelia was positively correlated with hyphal density, as shown in Fig. 6; mycelial regions with higher hyphal density accumulated more ^{14}C counts.

Discussion

Autoradiography using an imaging plate enabled the spatiotemporal allocation of ^{14}C-labelled photosynthate from seedlings to ectomycorrhizal mycelia to be simultaneously visualized and quantified. The method is quite similar to that used in a recent study by Leake et al. (2001) using instant digital autoradiography, and has significantly improved spatiotemporal allocation of ^{14}C compared with previous studies using either liquid scintillation counting (Reid et al. 1983; Cairney et al. 1989; Miller et al. 1989; Rygiewicz and Andersen 1994) or X-ray film autoradiography (Brownlee et al. 1983; Finlay and Read 1986; Cairney et al. 1989; Bending and Read 1995). Images which showed good resolution of ^{14}C in the mycelial system were captured by imaging plates with an exposure of only 90 min.

The result showed that ^{14}C was transferred to the root, mycorrhiza, and extraradical mycelium within 3 days, after which no net ^{14}C transfer to the root system occurred. An explanation for this could be that ^{14}C loss by respiration in the mycelium is the same or more than its input, although the respiration of the fungal mycelium was not measured in our experiment. However, because ^{14}C counts in the shoot and underground part did not reduce significantly from 3 to 13 days, ^{14}C may not be metabolized by respiration after 3 days, but may be incorporated into structural compounds. A model of ^{14}C partitioning after pulse labelling (Swinnen et al. 1994) showed that ^{14}C fixed in spring wheat shoots was incorporated entirely into structural compounds within 5 days, and the transfer of ^{14}C from shoot to root was complete at this time. Since several studies have reported that ectomycorrhizal hyphae often contain abundant insoluble polysaccharides (Ling-Lee et al. 1977; Piché et al. 1981), ^{14}C transferred to fungal hyphae in our study may also have been transformed to such insoluble compounds, thus halting further ^{14}C transfer.

The ratio of the mean density of ^{14}C counts in mycorrhizal versus nonmycorrhizal short roots was 5.2:1 in this study (Table 1), smaller than other reported ratios of 15:1 for *Pinus radiata* infected with *Rhizopogon roseolus* (Bevege et al. 1975) and 18.8:1 for *Eucalyptus pilularis* infected with *Pisolithus tinctorius* (Cairney et al. 1989). These data suggest that the photosynthate-attracting capacity of a fungal partner may be according to the host and fungal symbiont species. There was only a brief lag in the accumulation of ^{14}C counts between the basal and middle parts and between the middle and distal parts of extraradical mycelia, indicating that ^{14}C moves rapidly from the base to the front of mycelia. Although fronts with mycelial fans of higher hyphal density received more ^{14}C, ^{14}C counts per unit hyphal biomass were independent of position in the mycelium. This makes sense, given the rapid spread of ^{14}C compounds throughout the whole mycelium.

Seedling removal left 31.1±9.4% of ^{14}C counts in the underground part of mycorrhizal seedlings on the cloth sheet. Even after nonmycorrhizal seedlings were removed, a small amount of ^{14}C counts (6.7±0.4% of the ^{14}C counts in the underground part), considered root exudates, remained on the cloth sheet. Assuming that mycorrhizal seedlings excrete the same amount of ^{14}C on the cloth as nonmycorrhizal seedlings, we estimate that about 24% of the ^{14}C counts in the underground part remained in the extraradical mycelia. This value, however, would be an overestimate of the real value. Because of quenching of the ^{14}C signal in the plant and fungal tissues, the counting efficiency of ^{14}C detected by the imaging-plate method varies in a tissue-specific manner. Leake et al. (2001) measured the counting efficiency of radioactivity in pine roots and mycorrhizal hyphae. According to their measurements, although the counting efficiency of ^{14}C radioactivity in plant tissue varies considerably from tissue to tissue, the counting efficiency in fungal hyphae is approximately 1.5 times higher than that in plant roots. Given the same situation of counting efficiency in our system, about 17% of total radioactivity in the underground part was calculated to be present in fungal mycelia. The result indicates that the fungal mycelium is an important sink for photosynthates besides mycorrhiza. Although the results from experimental symbiotic systems do not necessarily reflect the true situation in nature, the present results suggest that C flow to the extaradical mycelium cannot be ignored in investigations on C allocation in ectomycorrhizal plants.

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