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ORIGINAL PAPER

Transfer of ^{14}C-photosynthate to the sporocarp of an ectomycorrhizal fungus *Laccaria amethystina*

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Abstract Sporocarps of ectomycorrhizal fungi are strong carbon sinks for the source in host trees, but the details of carbon transfer from the host to the sporocarp are unknown. In this study, single seedlings of Japanese red pine (*Pinus densiflora*) colonised by *Laccaria amethystina* were grown on floral foam plates fitted in rhizoboxes, resulting in fruiting on the substrate. The seedlings were photosynthetically labelled with $^{14}CO_2$; ^{14}C-labelled photosynthate transfer from leaves to sporocarps was then chased using a time-course autoradiography technique. ^{14}C was transferred to healthy, fresh sporocarps in a purple colour ranging from primordial to elongate sporocarps, but hardly to senesced ones that had faded to white or grey, or browned. This suggested that C is transferred only to physiologically active sporocarps. Two seedlings associated with a growing sporocarp were labelled again 7 and 16 days after the first labelling, respectively. ^{14}C accumulation in the sporocarps rose in a stepwise manner after the second labelling, indicating that sporocarps mainly used recently rather than previously photosynthesised C.

Keywords ECM fungus · Fruit body · Sporophore · Basidiocarp · ^{14}C-labelling · Autoradiography · Carbohydrate · Translocation

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Introduction

Ectomycorrhizal (ECM) symbioses are commonly found in most forest ecosystems, where ECM mycelia account for the largest proportion of microbial biomass (Read 1984; Allen 1991; Smith and Read 2008). A number of studies have shown that ECM fungi play an ecologically important role in carbon (C) flow through forest ecosystems by mediating C transfer from trees to soil (e.g. Cromack et al. 1979; Vogt et al. 1982; Fogel and Hunt 1983; Read 1984; Söderström and Read 1987; Chapela et al. 2001; Wu et al. 2002; Cairney 2005; Anderson and Cairney 2007; Courty et al. 2010). Vogt et al. (1982) estimated that, in the soil of an *Abies amabilis* forest, 15% of net primary production in the canopy was used by ECM fungi. Söderström and Read (1987) showed that about 30% of total respiration by ECM-associated *Pinus sylvestris* and *Pinus contorta* seedlings can be attributed to fungal mycelia in soil. In forests, carbon transfer from trees to ECM fungi is supported by nutrient barter. The fungi absorb soil mineral nutrients, such as phosphorus and nitrogen, via their extraradical mycelia and transfer them to the trees; in return, the trees provide photosynthetically fixed C to ECM fungi (Smith and Read 2008).

Most ECM fungi belong to the basidiomycota and as such form sporocarps. Sporocarps account for a significant proportion of fungal biomass in forests as ECM mycelia. Sporocarp production per year is estimated to be 8.8 and 380 kg/ha in a 100-year-old Norway spruce forest (Dahlberg et al. 1997) and a 180-year-old *A. amabilis* forest (Vogt et al. 1982), respectively. Fogel and Trappe (1978) also estimate that the annual biomass production of epigeous sporocarps is considered to range 3 to 180 kg/ha in the northern

hemisphere. Since C would be transferred from the tree to the sporocarps developed on the extraradical mycelia in soil as well as the mycelia themselves, such a large amount of sporocarps may represent the importance of C transfer from the host to sporocarps in the whole carbon flow through forest.

A number of studies revealed that photosynthetic status of the host tree strongly influences sporocarp formation (e.g. Last et al. 1979; Godbout and Fortin 1990, 1992; Lamhamedi et al. 1994; Högberg et al. 2001; Kuikka et al. 2003). By means of a large-scale stem-girdling experiment in a boreal Scots pine (*P. sylvestris*) forest in northern Sweden, Högberg et al. (2001) found that the number of sporocarps and their total dry biomass significantly decreased in girdling plots. Kuikka et al. (2003) found that sporocarp numbers decreased more than 60% by artificial defoliation in a *P. sylvestris* forest. In the study by Last et al. (1979), when seedlings of *Betula pendula* collected from three widely spaced locations with different latitude were grown in a nature stand, total numbers of sporocarps were inversely related to rates of foliar yellowing. They also found that sporocarp production ceased immediately after seedlings had been defoliated. Lamhamedi et al. (1994) demonstrated a positive correlation between the photosynthetic rate of *Pinus strobus* seedlings and the growth rate of colonising *Laccaria bicolor* sporocarps, and a cessation of furthermore sporocarp development at a very low photon flux density. These studies suggest that most of the C supplied to the sporocarp is newly synthesised by the host. However, in a recent study by Pestaña and Santolamazza-Carbone (2011), although ECM colonisation was significantly reduced by a treatment of 75% defoliation accompanied with a decline in species richness and diversity, sporocarp biomass and abundance were not affected by foliage loss. This indicates that it is unclear whether C is supplied to the sporocarp from newly synthesised or stored photosynthates. Direct analysis of C transfer from the host plant to the sporocarp would be necessary to understand the process of carbon transfer from the host to the sporocarp in detail.

Tracer experiments, especially pulse-chase ones, have allowed C transfer processes to be studied on a finer scale. In those experiments, a radioactive tracer (^{14}C) has been used as an efficient tool for direct measurement of C transfer from host trees to ECM mycelia (Reid and Woods 1969; Brownlee et al. 1983; Finlay and Read 1986; Leake et al. 2001; Wu et al. 2001, 2002; Teste et al. 2010). Finlay and Read (1986) used autoradiography to clearly demonstrate that ^{14}C is transferred from the host to the extraradical mycelia of ECM fungi (*Suillus bovinus* and *Suillus granulatus*) radiating from the roots of ECM-associated pine seedlings (*P. sylvestris* and *P. contorta*). In a time-course autoradiography study, Wu et al. (2002) showed that photosynthetically fixed ^{14}C in the leaves of *Pinus densiflora* seedlings is translocated to an overall network of extraradical mycelia within 1 day and immobilised 3 days after labelling. These results clearly demonstrate that ECM extraradical mycelia in the soil acts as strong C sinks, and that transferred C to the mycelia is mainly composed of the recently synthesised photosynthate.

Such effective techniques, however, have not been applied to the analysis of C transfer from the host to the sporocarps. One reason why it has not been investigated is derived from the difficulty in forming sporocarps in an experimental system. In our rhizobox experiments for a different purpose, we found that ECM pine seedlings colonised by *Laccaria amethystina* formed sporocarps during the seedling cultivation in the rhizobox. This experimental system led us to tracer experiments for the detailed analysis of C transfer from the host to the sporocarp.

Here, we describe the process of C transfer from the host shoot to the sporocarp using time-course and quantitative autoradiography on ^{14}C-labelled Japanese red pine (*P. densiflora* Sieb. et Zucc.) seedlings associated with *L. amethystina* (Bolt. ex Hooker) Murr. sporocarps on the extraradical mycelia. Our objective is to know (1) to what type of sporocarp C is transferred from the host and (2) when C transferred to sporocarps is photosynthesised.

Materials and methods

Preparation of rhizoboxes for sporocarp formation

An isolate of *L. amethystina* (Bolt. ex Hooker) Murr. provided by Dr. K. Nara (Graduate School of Frontier Sciences, The University of Tokyo, Japan) was used as the inoculum. *L. amethystina* mycelium was cultured at 23°C for 2 weeks on cellophane film - covered plates of modified Melin-Norkrans agar medium (Marx 1969).

Seeds of *P. densiflora* Sieb. et Zucc. were sown on a mixture (1:1, *v*/*v*) of soil from the Koishikawa Arboretum (black sandy loam, pH 5.3) and Shibanome soil (volcanic sand, pH 5.8–6.0; Setogahara, Gunma, Japan), both of which had been autoclaved at 121°C for 90 min. Two-month-old seedlings of *P. densiflora* were transplanted to rectangular flat rhizoboxes (140×205×15 mm) filled with the autoclaved soil mixture and inoculated with *L. amethystina* by placing pieces of the cultured mycelium on the roots. The seedlings were cultivated in a growth chamber under a regimen of 16 h of light (350–500 μmol m^{-2} s^{-1} of photosynthetically active radiation, PAR) at 25°C and 8 h of darkness at 23°C.

After 6 months, mycorrhizal seedlings with well-developed ectomycorrhizae were individually transplanted

to rhizoboxes equipped with a floral foam plate (Smithers-Oasis, Tokyo) containing 40 ml of a 1,000-fold-diluted nutrient solution (Hyponex Japan, Osaka). Seedlings were cultivated in a natural-light biotron (25°C during the day/23°C at night) until sporocarps had formed.

Once primordial sporocarps began to form on the foam, the rhizobox was scanned with a scanner (ES-10000 G, EPSON) every 3–4 days until the end of the experiment. In this study, we defined sporocarps less and more than 10 mm in length as primordial and elongate ones, respectively. Longitudinal lengths and projected areas of sporocarps were measured from the scanned images. The distribution of the size at an interval of 1 mm was drawn from lengths of 363 sporocarps formed in three randomly selected rhizoboxes.

$^{14}CO_2$ labelling

Labelling was carried out in an illuminated draft chamber (23–25°C, PAR=150–200 μmol m^{-2} s^{-1}) using a method described by Wu et al. (2002). The aboveground part of the seedling was covered with a polyethylene bag, inside of which a silicon-plugged microtube containing 925 kBq of ^{14}C-$NaHCO_3$ (36.39 μg) was attached with double-faced tape. The bag was sealed around the stem with Plasticine to prevent air leakage. $^{14}CO_2$ was produced by injecting 10% lactic acid (200 μl) with a syringe through the silicon plug into the microtube and released inside the bag by removing the plug. For photosynthetic ^{14}C labelling, the seedling was exposed to light for 2 h in the draft chamber. The bag was then removed, and extra $^{14}CO_2$ was trapped using 1 N NaOH. For two labelled sporocarp that was still growing after the first labelling, their host seedlings were labelled again after 7 and 16 days with $^{14}CO_2$ as described above.

Autoradiography and radioactivity counting

An autoradiograph was obtained by exposing the labelled seedling on the surface of the foam plate in each rhizobox for 90 min in the dark to an imaging plate (BAS-SR2040, Fuji Film). The surface of rhizobox was covered with wrapping film (Asahi Kasei, Tokyo) to prevent ^{14}C contamination. The radioactivity recorded on the imaging plate was then visualised with an imaging analyzer (FLA-2000, Fuji Film). For quantitative standard, a set of three small circles (6 mm in diameter) of filter paper containing 1.24, 7.4 and 37 kBq of [^{14}C(U)]-sucrose, respectively, was exposed simultaneously with each sample to the imaging plate. Photo-stimulated luminescence on the autoradiographs was counted using Multi Gauge V 3.1 software (Fuji Film) and converted to the absolute radioactivity (Bq) by comparing with the standards as Wu et al. (2002). Time-course autoradiographs were repeatedly taken from the same rhizobox until the targeted sporocarps had stopped growing and faded.

In the autoradiographs, black images of some sporocarps could be easily distinguished from the background, and those of the other could not because of overlapping with other radioactive parts of rhizosphere. Thus, only the former ones were used for radioactive analysis. In single-labelling experiments, 23 primordial and 3 elongate sporocarps that were fresh and purple, and 7 elongate sporocarps that were white, grey or brown were chosen from 11 rhizoboxes of the labelled seedlings, and their radioactivity densities in projected area (becquerel per millimetre square) were calculated. Growing sporocarps in the double-labelling experiments were chosen from different two rhizoboxes, and their total radioactivity within the projected area (becquerel) were used for the time-course analyses.

Results

Sporocarp formation and growth

Sporocarps in various sizes and appearances (primordial and elongate; fresh purple, white, grey and withered brown) sporadically developed on the surface of the foam plate in each rhizobox in which an ECM-associated seedling was cultivated (Fig. 1). In examined 11 rhizoboxes, primordial sporocarps began to form about 2 weeks after the transplantation of ECM-associated seedlings. Most of them stopped growing and remained small; about 80% of the sporocarps did not exceed 3 mm in length. Within a rhizobox, only one or two sporocarps grew to a large size, and the largest sporocarp was 48 mm long (Fig. 2). Several days after growth had stopped, the purple colour of the sporocarps faded to white or grey. Thereafter, they browned and wilted (Fig. 3c).

Transfer of ^{14}C-photosynthate to the sporocarp

Eleven ECM pine seedlings in rhizoboxes were labelled with $^{14}CO_2$. In the rhizoboxes, a total of 2,514 primordial (<10 mm in length) and 12 elongate (≥10 mm in length) sporocarps were formed until ^{14}C labelling. Of all 2,526 sporocarps, 948 primordial and 5 elongate ones were coloured in purple and the other in white, grey or brown. The transfer of ^{14}C incorporated into pine leaves to 23 primordial and 10 elongate sporocarps was chased by autoradiography (Fig. 3). These sporocarps had stopped growing at the labelling. All purple-coloured sporocarps ranging from primordial (Fig. 3a) to elongate ones (Fig. 3b) accumulated ^{14}C radioactivity, but white, grey or brown sporocarps hardly did (Fig. 3c). The radioactivity accumu-

Fig. 1 An ECM *P. densiflora* seedling in the rhizobox. Primordial and elongate sporocarps in fresh purple, white, grey and withered brown sporadically developed on the surface of the foam plate. The *arrow* shows a healthy sporocarp with a fresh purple colour. *Scale bar* 5 cm

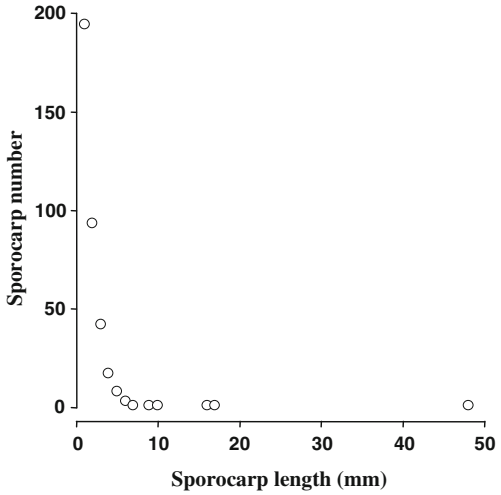

Fig. 2 Frequency distribution of the size of 363 primordial and elongate sporocarps formed in three rhizoboxes

lation in the purple sporocarps was detected at day 1 after labelling. ^{14}C radioactivity densities (becquerel per millimetre square) reached the maximum (7.6 and 2.2 Bq mm^{-2}) within primordial and elongate purple sporocarps 3 days after labelling (Fig. 4). Both ^{14}C-accumulation and mycelial biomass in the extraradical mycelium including the growing margin were less than in purple sporocarps.

Two sporocarps in different rhizoboxes used for the twice-labelling experiments kept growing at the first $^{14}CO_2$ labelling. One of the sporocarps grew from 10.5 to 25.2 mm in length, and from 24.4 to 98.3 mm^2 in projected area until day 7 after the first labelling. By day 10, growth had stopped and the colour had faded to white (Fig. 5a). A second round of labelling was performed at day 7 after the first labelling. Radioactivity in the sporocarp increased until day 3 after the first labelling, reaching a constant value (0.36 kBq), and remained constant until the second labelling (Figs. 5a and 6). After the second labelling, ^{14}C radioactivity immediately increased, reaching a maximum (0.61 kBq) at day 9 after the first labelling and then remained constant (Fig. 6).

Another sporocarp was a primordial one at the first labelling and begun to grow at day 7 after the first labelling. It grew to a length of 48 mm and reached a projected area of 103.3 mm^2 at day 21 after the first labelling, i.e. 5 days after the second labelling (Fig. 5b). ^{14}C accumulated slowly in the sporocarp until day 16 after the first labelling and reached a low value of 0.11 kBq just before the second round of $^{14}CO_2$ labelling (Figs. 5b and 6). After the second labelling, however, radioactivity in the sporocarp remarkably and continuously accumulated up to day 22, i.e. 6 days after the second labelling, reaching 1.72 kBq (Fig. 6).

Discussion

Sporocarp formation and growth

Although a number of primordial sporocarps formed in the rhizoboxes during the experiment, most did not grow and only one or two grew to form large sporocarps. Even among growing sporocarps, variances in growth period and growth rate were relatively large. Since physiological and physical conditions are known to influence sporocarp development, the heterogeneity of the physiological (e.g. C storage and translocation of the host and fungi, availability of other micronutrients) and physical (e.g. temperature, moisture, contact with other roots) environment on the oasis plate might have contributed to these results (Godbout and Fortin 1990; Kües and Liu 2000). However, since in our set-up aqueous solutions were able to diffuse through the foam plate relatively freely, restricted nutrient availability does not fully

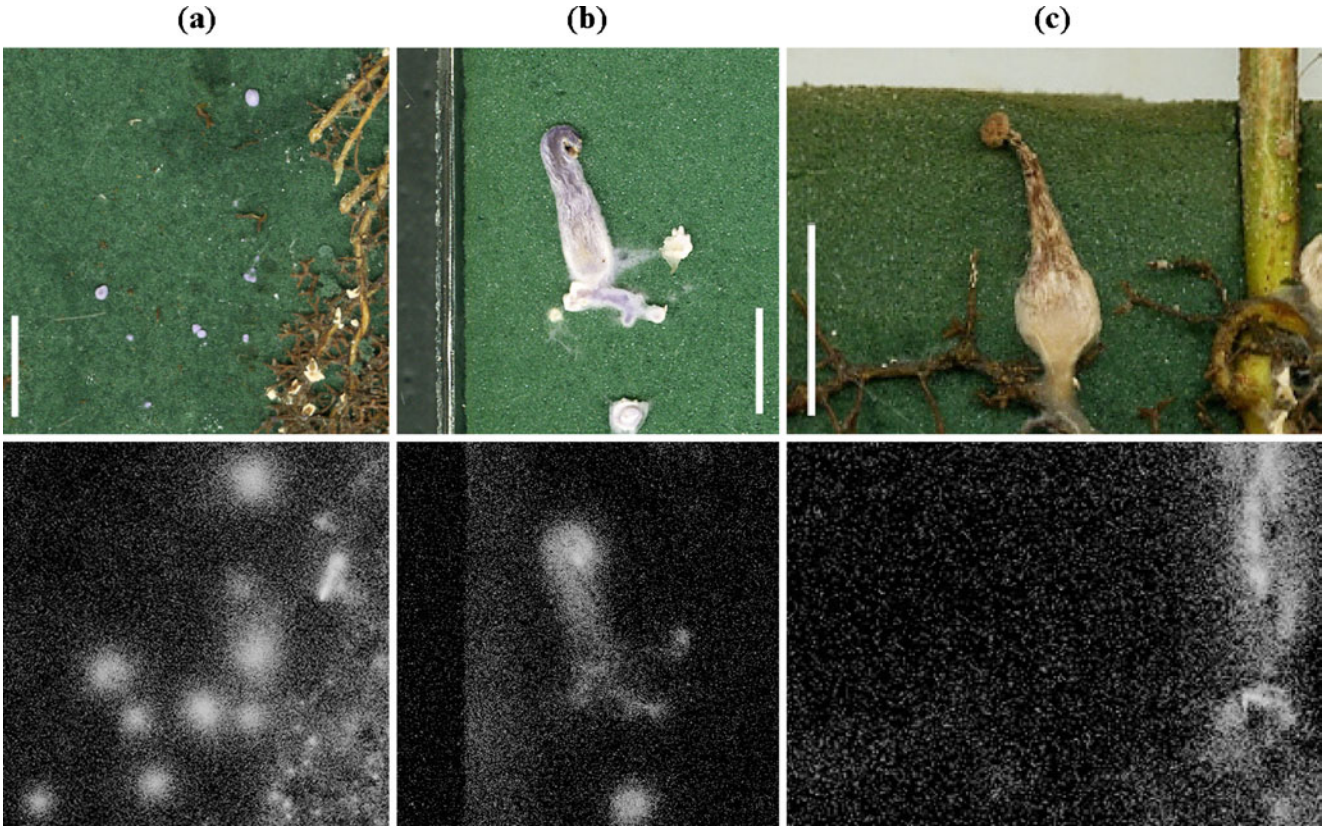

Fig. 3 Photographs (*upper*) and autoradiographs (*below*) of primordial sporocarps (**a**), an elongate sporocarp that stopped growing but retained its fresh purple colour (**b**), and an elongate sporocarp that faded (**c**). The autoradiographs were taken 3 days after $^{14}CO_2$ labelling. *Scale bar* 1 cm

explain the observed variation. Godbout and Fortin (1990) found that only one of the *L. bicolor* primordial sporocarps that colonised a white pine seedling developed into a mature sporocarp, which suggests that the other primordia were used as nutrient pools for the growth of the developing one. This type of interaction among primordial sporocarps might also have been present in our system.

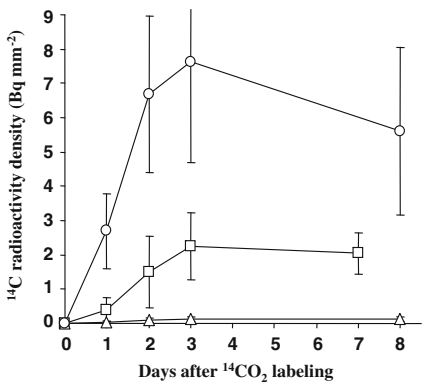

Fig. 4 Time-course of ^{14}C radioactivity density in the primordial and elongate sporocarps. Results are the mean±SE. *Open circles*, primordial sporocarps (23 sporocarps in six rhizoboxes, n=6) that stopped growing but retained their fresh purple colour, as shown in Fig 3a. *Squares*, elongate sporocarps (three sporocarps in three rhizoboxes, n=3) that stopped growing but retained their fresh purple colour, as shown in Fig. 3b. *Triangles*, faded sporocarps (seven sporocarps in six rhizoboxes, n=6), as shown in Fig. 3c

C transfer from the host seedling to the sporocarp

Growing and non-growing sporocarps with a purple colour were shown to act as strong C sinks, in contrast to non-growing sporocarps in white, grey or brown, which did not accumulate ^{14}C-labelled photosynthates. This result suggests that the strength of the C sink is linked to the purple colour, i.e. that some physiological activities causing the C sink strength are probably lost during senescence. The physiological activities that give rise to the mycelial C sink are as yet undetermined.

In the twice-labelling experiments, ^{14}C was transferred to sporocarps in a stepwise manner. This result indicated that although the transfer of previously fixed ^{14}C to the sporocarp ceased within a few days after labelling, purple sporocarps maintained their C-sink activity as long as their physiological activities were high. Thus, recently photosynthesised C strongly contributed to sporocarp growth and metabolic activities. Using sporocarps of *L. bicolor* at different developmental stages, Lamhamedi et al. (1994) showed that a lowering of net photosynthesis by the host plant resulted in the failure of growing young sporocarps to

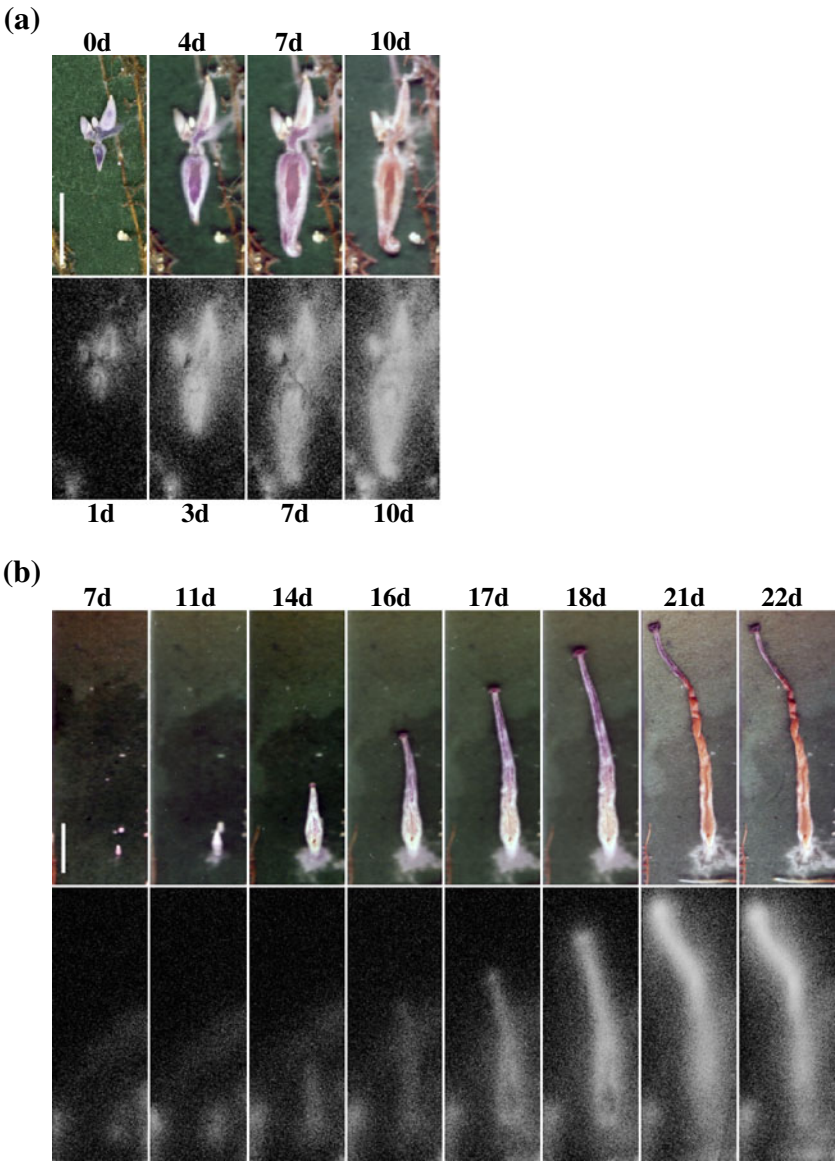

Fig. 5 Photographs (*upper*) and autoradiographs (*below*) of two growing sporocarps (**a** and **b**) that were subjected to a second round of $^{14}CO_2$ labelling at day 7 (**a**) and day 16 (**b**), respectively. *Numbers above* and *below the figures* indicate the days after the first $^{14}CO_2$ labelling (*0d* means the labelling day). *Scale bar* 1 cm

continue their development, suggesting that sporocarps make use of the current supply of host photosynthates. Our results, which show that recently photosynthesised C is mainly transferred to the sporocarps of *L. amethystina*, substantiate their observations. However, Pestaña and Santolamazza-Carbone's (2011) study showed that sporocarp biomass and abundance of 16 ECM fungal species were not affected by foliage loss. This suggests that C transfer style may be different between fungal species.

The present study provided direct evidence for photosynthetic C transfer from the host plant to ECM sporocarps. Our results lead to the following conclusion: (1) C is only transferred to primordial and elongate sporocarps having physiological activity, which is represented by the purple colour; and (2) recently rather than previously photosynthesised C is transferred to the *L. amethystina* sporocarps.

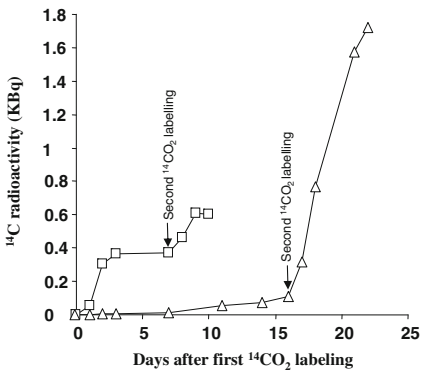

Fig. 6 Time-course of ^{14}C radioactivity in the growing sporocarps shown in Fig. 5. *Squares*, the sporocarp shown in Fig. 5a. *Triangles*, the sporocarp shown in Fig. 5b. Sporocarps shown in Fig. 5a and b were subjected to a second round of $^{14}CO_2$ labelling 7 and 16 days after the first round of $^{14}CO_2$ labelling, respectively, as shown by the *arrows*

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