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Competition between ectomycorrhizal fungi colonizing *Pinus densiflora*

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Abstract Interactive competition of *Pisolithus tinctorius* (Pers.) Coker et Couch with an unidentified species Tanashi 01 and *Suillus luteus* (L.: Fr.) S. F. Gray was investigated using a rhizobox. *Pinus densiflora* Sieb. et Zucc. was used as the host plant and mycelia were distinguished by hyphal color. The speed of mycelial spread differed between the fungi; *P. tinctorius* and Tanashi 01 grew faster than *S. luteus*. A *P. tinctorius* mycorrhizal seedling and a Tanashi 01 mycorrhizal seedling were transplanted on opposite sides of the rhizobox. The mycelia and mycorrhizae of *P. tinctorius* were overgrown by Tanashi 01 hyphae and development of *P. tinctorius* was gradually inhibited. The areas occupied by mycelia and mycorrhiza of *P. tinctorius* decreased by 52% and 37%, respectively, 154 days after transplantation relative to that at 91 days. In the overlap area of *P. tinctorius* and Tanashi 01, the latter fungus infected new root tips emerging from *P. tinctorius* mycorrhiza, which lacked a mantle of *P. tinctorius* hyphae, and formed a composite mycorrhizal structure. *P. tinctorius* mycorrhizae were progressively replaced by Tanashi 01 mycorrhizae. Mycelial spread of *P. tinctorius* and *S. luteus* were naturally inhibited but there was no interaction in mycorrhizal formation.

Key words Ectomycorrhiza · Competition · *Pinus densiflora* · Japanese red pine

Introduction

Individual species of woody plants form ectomycorrhizae with various fungal species in nature. For example, Trappe (1977) estimated that some 2000 species of fungi are potential mycorrhizal associates of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Furthermore, more than one type of mycorrhiza formed by different species of fungi can often be observed on the same root system (Harvey et al. 1980; Fleming 1985). Timonen et al. (1997) recently identified 12 distinct morphological mycorrhizal types on the root system of Scots pine (*Pinus sylvestris* L.) from natural humus microcosms and examined their genotypes using isozyme and molecular fingerprinting techniques. In such cases, ectomycorrhizal fungi may compete with each other, as well as with parasitic or saprophytic fungi and bacteria, for the limited space and nutrients in the soil.

Mycorrhizal types on *Pinus* seedlings from a nursery were completely replaced by indigenous types after transplanting (Benecke and Gobl 1974; Lamb 1979). Likewise, new roots of Douglas-fir seedlings inoculated with *Laccaria laccata* and *Hebeloma crustuliniforme* were all colonized by indigenous mycorrhizal fungi 5 months after transfer to the field (Bledsoe et al. 1982). Fleming (1985) suggested that mycorrhizal fungi colonizing pot-cultured *Betula* spp. could be classified into "early-stage" and "late-stage" fungi. Since the host plant and soil water conditions influence mycorrhizal colonization (Reid 1978; Zambonelli and Morara 1984), the above transitions of ectomycorrhizal types may result from changes in the physiological state of the host and in environmental conditions. However, it is also possible that competition between mycorrhizal fungi is an important factor. Although it is thus necessary to evaluate the competition between mycorrhizal fungi in order to understand ectomycorrhiza succession in forests, this has rarely been reported due to the lack of direct and suitable methods for identification of different mycorrhizal hyphae.

Recently, root windows and rhizoboxes have been successfully employed in research on mycorrhiza (Egli and Kalin 1990; Francis and Read 1994). Also, as a species of mycorrhizal fungi efficient in promoting growth of trees, *Pisolithus tinctorius* is often employed in seed-

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ling culture and afforestation. However, it is often driven out by other species of fungi (Marx 1977). Therefore, investigation of the competition between *Pisolithus tinctorius* and other species of fungi is very important. Therefore, in the present report, we investigated the interaction of *Pisolithus tinctorius* with Tanashi 01 and *Suillus luteus* in a rhizobox using a Pictrostat 330. *S. luteus* and Tanashi 01, an unidentified mycorrhizal isolate from *Pinus densiflora* at the Tanashi Nursery, Tokyo, Japan, both form a white mycelium which is easily distinguishable from the yellow mycelium of *Pisolithus tinctorius*.

Materials and methods

Preparation of mycorrhizal seedlings

One short side of a sterile rectangular plate (230 mm × 80 mm × 15.5 mm; Eiken Kizai Co., Tokyo, Japan) was cut off and the plate was filled with an autoclaved (121 °C, 1 h) 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 Co., Gunma, Japan.). One-month-old *Pinus densiflora* Sieb. et Zucc. seedlings were transplanted into the plate and inoculated with *Pisolithus tinctorius* (Pers.) Coker et Couch, *S. luteus* (L.: Fr.) S. F. Gray or an unidentified species (Tanashi 01) as described previously (Nara and Hogetsu 1996). The fungal inocula were cultured at 25 °C for 3 months in a mixture (3:1, v/v) of vermiculite and peat moss watered with liquid MMN medium (Marx 1969). Inoculated seedlings were cultivated for mycorrhizal formation in a temperature-regulated greenhouse at 25 °C day/23 °C night for 3 months.

Rhizobox set-up

Rhizoboxes (350 mm × 250 mm × 17 mm) were constructed with the lid part of a plastic box (Sanplatec Co., Tokyo, Japan) and a cover of 4-mm-thick glass. One of the long edges of the lid was removed for plant growth. Boxes were filled with the autoclaved soil mixture described as above.

Pisolithus tinctorius mycorrhizal seedlings were placed on the soil 2.5 cm from the left side of each box, and *S. luteus* or Tanashi 01 mycorrhizal seedlings were placed 2.5 cm from the right side of the box. The yellow mycelia and mycorrhiza of *Pisolithus tinctorius* could be easily distinguished from the white Tanashi 01 and *S. luteus* hyphae. Five 1-month-old nonmycorrhizal seedlings were placed at 5-cm intervals between two mycorrhizal seedlings (Fig. 1). As a control, each kind of mycorrhizal seedlings was also placed in a rhizobox opposite a nonmycorrhizal seedling. Treatments were designated as Pt vs T1 (*Pisolithus tinctorius* mycorrhizal seedling and Tanashi 01 mycorrhizal seedling placed in the same rhizobox), Pt vs Sl (*Pisolithus tinctorius* mycorrhizal seedling and *S. luteus* mycorrhizal seedling in a rhizobox), Pt (*Pisolithus tinctorius* mycorrhizal seedling in a control rhizobox), T1 (Tanashi 01 mycorrhizal seedling in a control rhizobox) and Sl (*S. luteus* mycorrhizal seedling in a control rhizobox). Each treatment was repeated three times. All rhizoboxes, shaded with a black plastic plate, were placed in the greenhouse and watered with tap water twice a week.

Measurements of mycelial spread and mycorrhizal formation

The soil surface of each rhizobox was photographed using a Pictrostat 330 (Fujifilm Co., Tokyo) after 15, 32, 91 and 154 days. Each image was covered by a transparent OHP sheet on which a lattice of 5 × 5 mm was printed. The number of 5 mm squares in which mycelia or mycorrhizae were observed under a dissecting microscope was recorded (Fig. 2). Mycorrhizae in the rhizoboxes were observed directly under a dissecting microscope or were fixed (formalin 3.7%; nonidet P-40 0.1%; dimethyl sulfoxide 10%) for several hours, cryosectioned and examined under a light microscope.

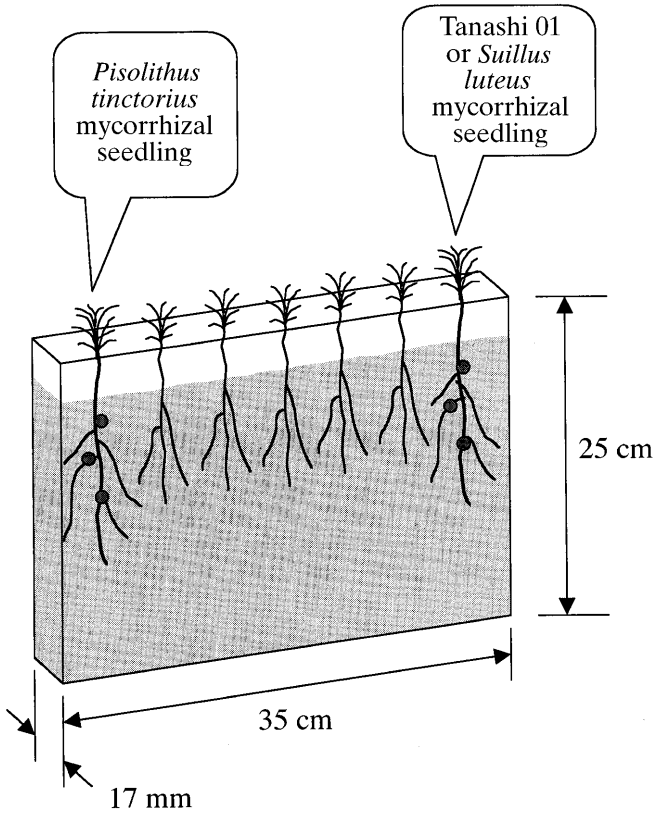

Fig. 1 Rhizobox used in the experiment. Intervals between seedlings were 5 cm

Results

Mycelial spread and mycorrhizal formation of three fungi without the competitive counterpart

Mycelial spread and mycorrhizal formation are shown in Figs. 3 and 4. The mycelia of the three ectomycorrhizal fungi had different styles and speeds of extension (Fig. 3). The mycelia of *Pisolithus tinctorius* formed well-developed rhizomorphs. Tanashi 01 formed even emanating mycelia but the mycelia of *S. luteus* produced several mycelial zones of different density. Tanashi 01 and *S. luteus* had linear extension rates during 154 days of culture, while spread of *Pisolithus tinctorius* became slower after 91 days (Fig. 4). Mycelial spread and mycorrhizal formation of *Pisolithus tinctorius* and Tanashi 01 were faster than *S. luteus*. *Pisolithus tinctorius* formed many rhizomorphs and areas uncolonized by hyphae were observed. Tanashi 01 spread evenly without gap areas in the hyphal area. Although the rhi-

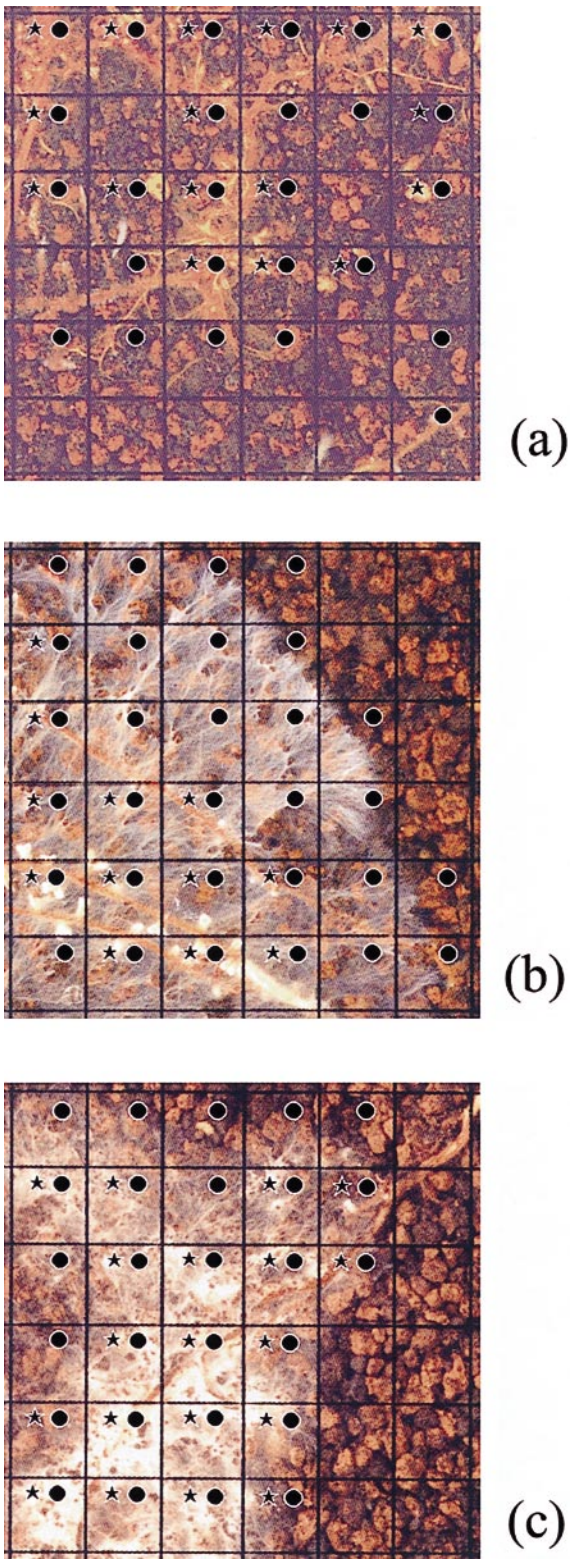

Fig. 2a–c Examples of mesurement method of mycelia and mycorrhizae. Images were overlaid by a 5-mm lattice-printed (5×5 mm), transparent sheet and the presence of mycelia and mycorrhizae in each 5-mm square was determined under a dissecting microscope. Squares marked with '●' were counted as mycelia, and those marked with '★' as mycorrhiza. Mycelia and mycorrhiza of *Pisolithus tinctorius* (**a**), Tanashi 01 (**b**) and *Suillus luteus* (**c**)

zomorphs of *Pisolithus tinctorius* spread rapidly, mycorrhizal formation was relatively late. For example, at 154 days in Pt treatment, mycorrhizal formation had reached about 18 cm (4 th seedling) from the left side of the rhizobox while the mycelia had reached the right side (Fig. 3). Tanashi 01 and *S. luteus* formed mycorrhizae even in areas close to the front line of their extending mycelia. Thus, mycelial spread of Tanashi 01 and *S. luteus* was associated with immediate mycorrhizal formation.

Competition characteristics on mycelial spread and mycorrhizal formation

The mesh graphs and Pictrostat photographs of Pt vs T1, Pt and T1 was shown in Fig. 5. In Pt vs T1, the mycelia of *Pisolithus tinctorius* spread more rapidly than Tanashi 01 before encountering the mycelia of Tanashi 01. After the meeting of the two fungi, the mycorrhizae and mycelia of *Pisolithus tinctorius* were overgrown by Tanashi 01 hyphae (see also Fig. 6a) and were obviously inhibited (Figs. 3, 4, 5). Generally, healthy rhizomorphs and hyphae of *Pisolithus tinctorius* have a shiny, yellow color. However, after overgrowth by Tanashi 01 hyphae, they lost their sheen to become a dull dark brown (Fig. 6b) and finally disappeared. After 91 and 154 days, when *Pisolithus tinctorius* hyphae had already encountered and been overlapped by their counterpart, the square counts of *Pisolithus tinctorius* mycelia decreased by 41% and 77%, respectively, relative to the Pt treatment (Fig. 4). Mycelia and mycorrhizae of *Pisolithus tinctorius* overgrown by Tanashi 01 were gradually replaced by their counterpart. From 91 to 154 days, mycelia and mycorrhizae of *Pisolithus tinctorius* decreased by 52% and 37%, respectively (Fig. 3). However, mycelial spread and mycorrhizal formation of Tanashi 01 continued without any inhibition by *Pisolithus tinctorius* mycelia.

In the treatment Pt vs Sl, some interference apparently occurred in the mycelial spread between *Pisolithus tinctorius* and *S. luteus*. After 91 and 154 days, the square counts of *Pisolithus tinctorius* mycelia decreased by 17% and 14%, and the square counts of *S. luteus* mycelia decreased by 31% and 19%, respectively, relative to the treatments Pt and Sl (Fig. 4). However, no interaction was found in mycorrhizal formation. Furthermore, the mycelia of the two fungi were not mutually overgrown after encounter.

Composite mycorrhiza formation

It was easy to distinguish *Pisolithus tinctorius* and Tanashi 01 in mantle hyphae by their diameter and color. *Pisolithus tinctorius* hyphae were yellowish-brown with a diameter of 5–6 μm; whereas Tanashi 01 hyphae were transparent with a diameter of 2–3 μm (Fig. 9b, c). *Pisolithus tinctorius* hyphae overgrown by Tanashi 01 hy-

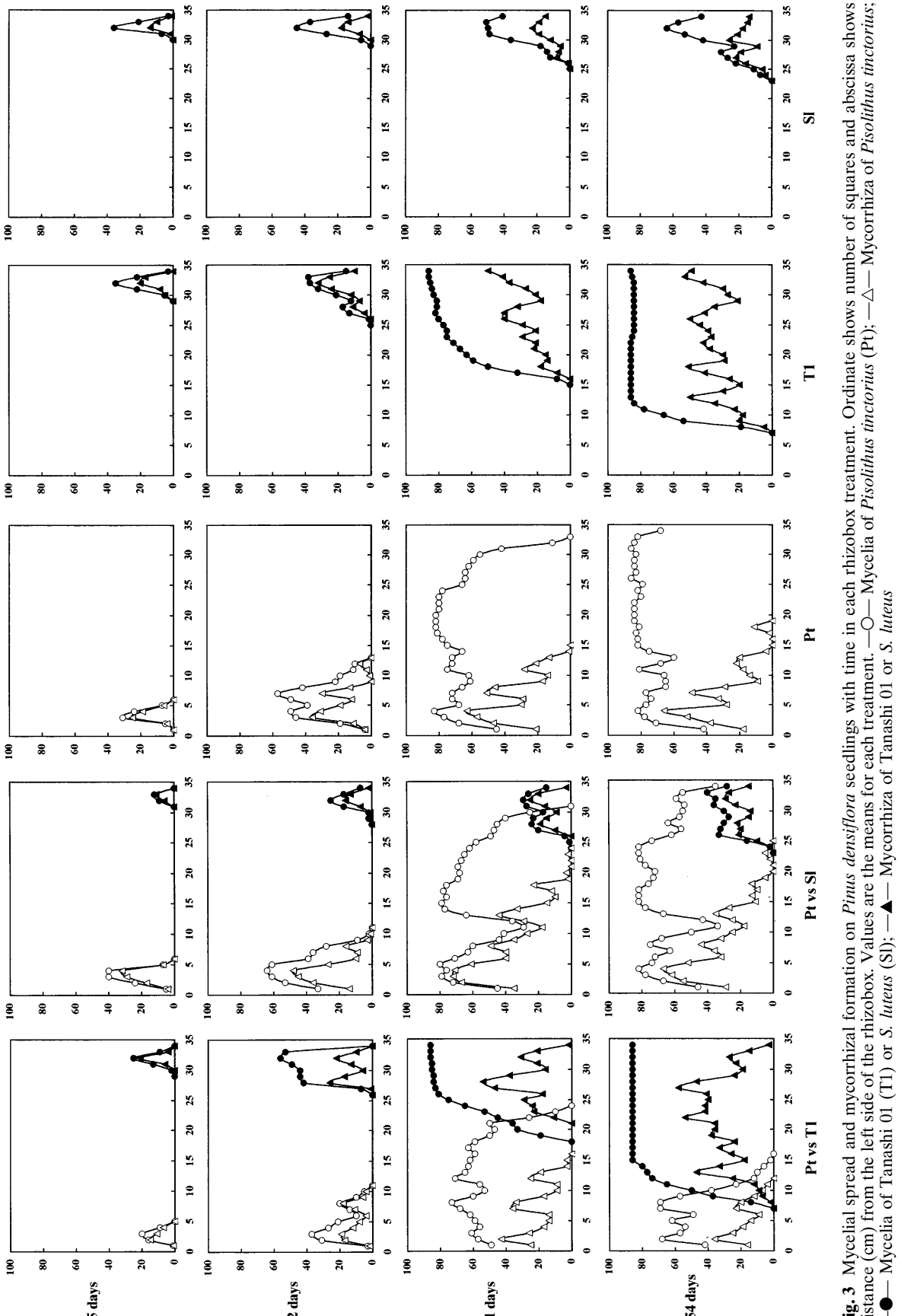

Fig. 3 Mycelial spread and mycorrhizal formation on *Pinus densiflora* seedlings with time in each rhizobox treatment. Ordinate shows number of squares and abscissa shows distance (cm) from the left side of the rhizobox. Values are the means for each treatment. —○— Mycelia of *Pisolithus tinctorius* (Pt); —△— Mycorrhiza of *Pisolithus tinctorius*; —●— Mycelia of Tanashi 01 (T1) or *S. luteus* (Sl); —▲— Mycorrhiza of Tanashi 01 or *S. luteus*

phae failed to form new mycorrhizae on fine roots. However, Tanashi 01 hyphae infected not only nonmycorrhizal but also mycorrhizal roots of *Pisolithus tinctorius* to form Pt-T1 composite mycorrhizae (Figs. 8a, 9a). We also observed that the root tip sometimes emerged from the mantle of *Pisolithus tinctorius* mycorrhiza (Fig. 7). Tanashi 01 probably infected such bare root tips to form the composite mycorrhiza. Overgrowth of *Pisolithus tinctorius* mycorrhizae by Tanashi 01 mycelia led to the original mantle of *Pisolithus tinctorius* becoming dark brown and gradually disappearing (Fig. 8b).

Discussion

The present results indicate that mycelial extension and mycorrhizal formation of *Pisolithus tinctorius* colonizing *Pinus densiflora* roots were inhibited by Tanashi 01. Such inhibition may be due to differences in mycelial structure between *Pisolithus tinctorius* and Tanashi 01. *Pisolithus tinctorius* formed extensive rhizomorphs which facilitate transport of nutrients and water to the root and the growing front of the mycelium (Brownlee et al. 1983; Kammerbauer et al. 1989; Agerer 1991). Rhizomorphs, however, seem to be disadvantageous to mycorrhizal colonization. In the present study, Tanashi 01 formed mycorrhizae on roots even near the mycelial front but *Pisolithus tinctorius* only on roots far behind the mycelial front. Raidl (1997) found that fine hyphae of some ectomycorrhizal fungi degraded when rhizomorphs were formed. In the present study, the fine hyphae of *Pisolithus tinctorius* distributed between rhizomorphs may also be degraded, leaving areas in the soil free of *Pisolithus tinctorius* hyphae, thus providing Tanashi 01 hyphae with space and roots to colonize.

The result of the competition between *Pisolithus tinctorius* and Tanashi 01 may also be caused by difference in affinity for *Pinus densiflora* between the fungi. The affinity of Tanashi 01 may be higher than that of *Pisolithus tinctorius*.

Interaction between mycorrhizal fungi may also depend on growth conditions. The Tanashi nursery soil used in the present experiment, from which Tanashi 01 was isolated, might be more suitable for this fungus. Since *Pisolithus tinctorius* prefers soils with low organic matter to form mycorrhizae on *Pinus* trees, the relationship between *Pisolithus tinctorius* and Tanashi 01 might be reversed, if soil with less organic matter were used. Therefore, it is of interest to investigate further competition between fungi in different soil types.

Some ectomycorrhizal fungi have been shown to produce and excrete antibiotics which inhibit infection by pathogenic fungi (Marx and Davey 1969; Krywolap 1971). The possibility that Tanashi 01 produces such substances and inhibits the growth of *Pisolithus tinctorius* hyphae should also be considered.

Tanashi 01 infected not only nonmycorrhizal roots but also the tips of mycorrhizae previously formed by

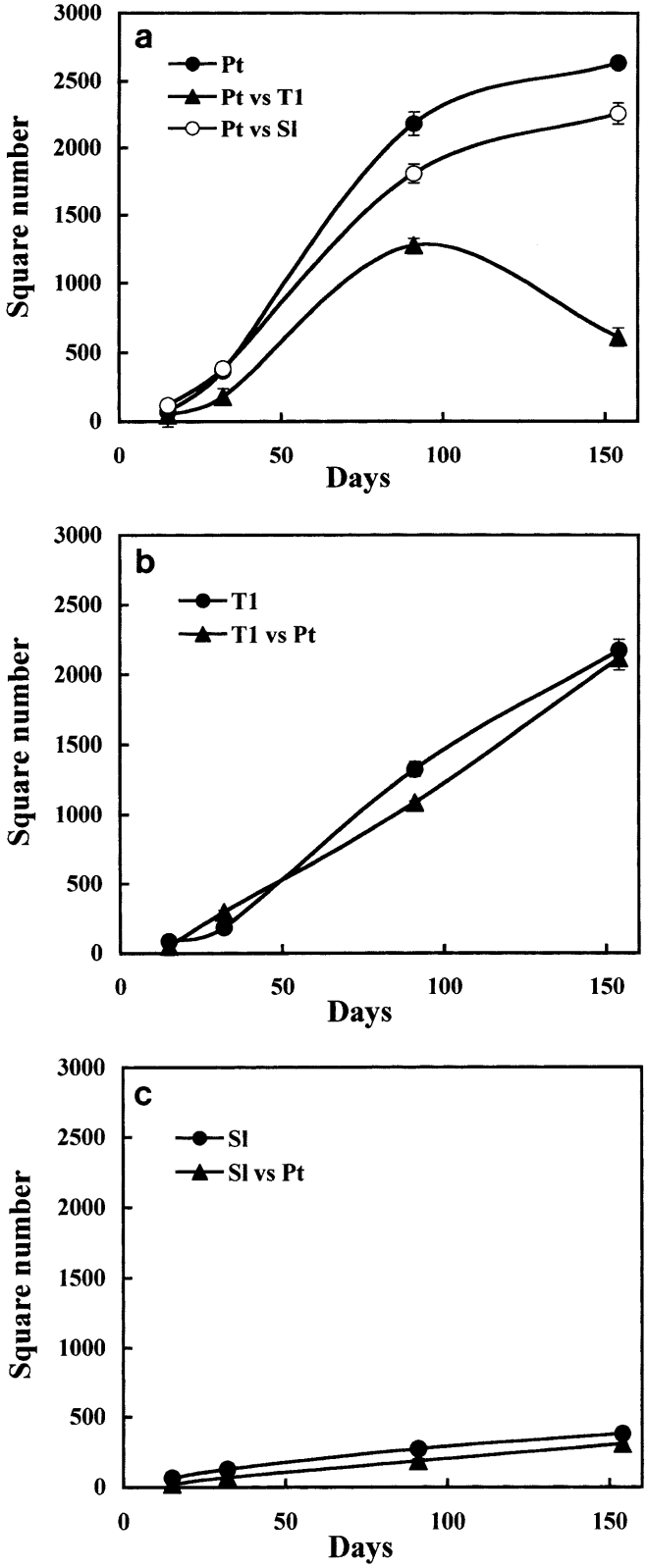

Fig. 4 Mycelial spread of *Pisolithus tinctorius* (**a**), Tanashi 01 (**b**) and *S. luteus* (**c**) colonizing *Pinus densiflora* seedlings during 154 days of culture. Vertical bars represent least significant difference at $P=0.05$, $n=3$

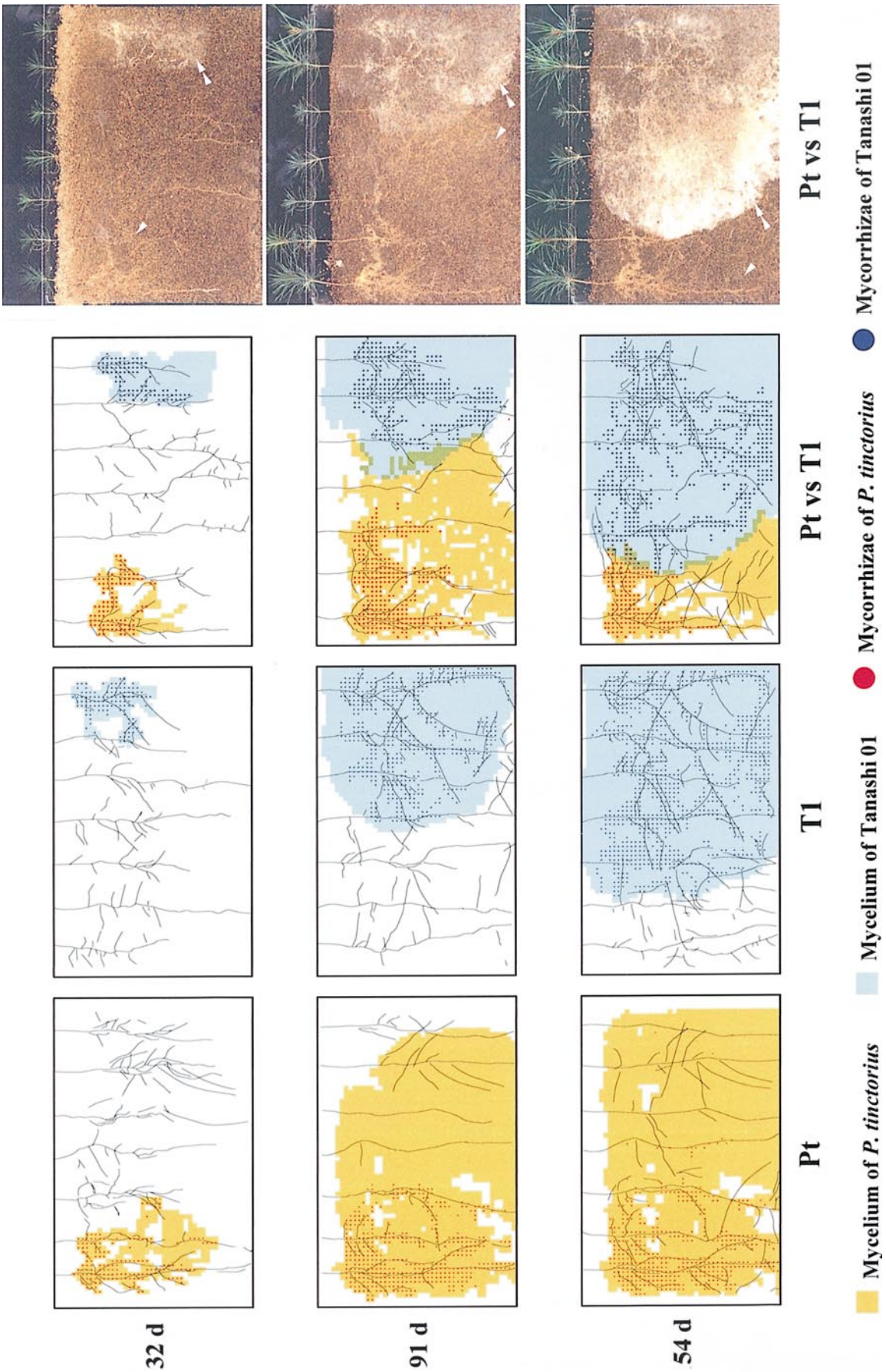

Fig. 5 Mesh graphs of one set of Pt, T1, and Pt vs T1 rhizoboxes and Pictrostat photographs of the Pt vs T1 rhizobox. *Single arrow*, mycelium of *Pisolithus tinctorius*, *double arrow*, mycelia of Tanashi 01

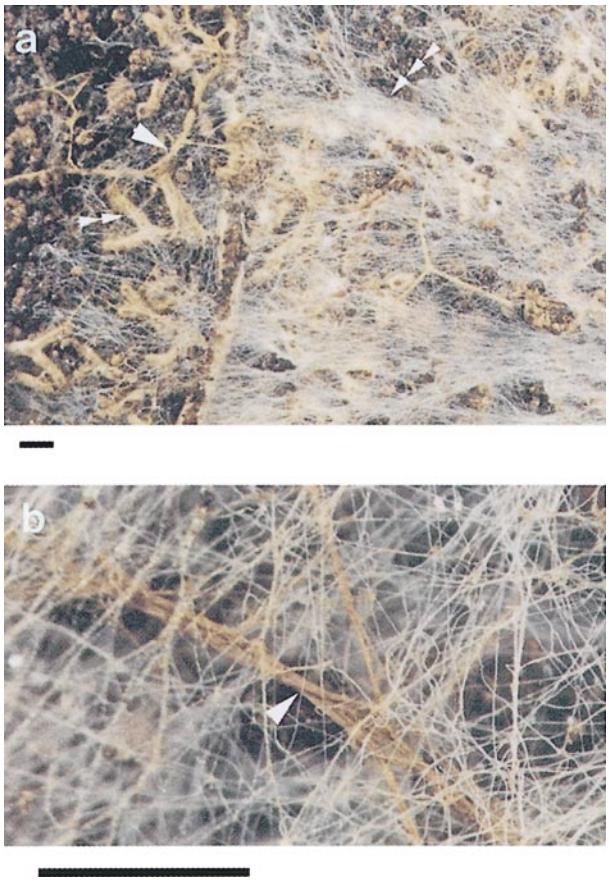

Fig. 6a,b Photographs of the overlap between *Pisolithus tinctorius* and Tanashi 01 mycelia. The mycelia (*single arrow*) and mycorrhizae (*double arrow*) of *Pisolithus tinctorius* were overgrown by Tanashi 01 hyphae (*triple arrow*) (**a**). The hyphae of *Pisolithus tinctorius* (*single arrow*) overgrown by Tanashi 01 hyphae became dark brown (**b**); *bars* 1 mm

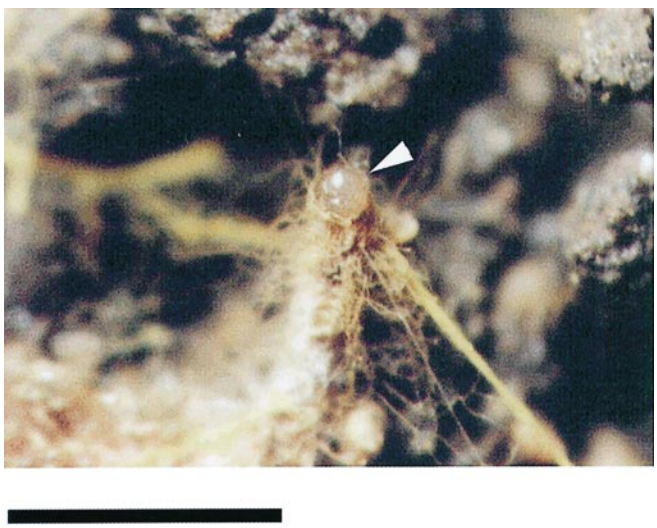

Fig. 7 Sometimes the root tip (*arrow*) emerged from the mantle of *Pisolithus tinctorius* mycorrhiza; *bar* 1 mm

Fig. 8 (**a**) Photographs of composite mycorrhiza. *Single arrow* indicates the Tanashi 01 mycorrhiza, and *double arrow* indicates the *Pisolithus tinctorius* mycorrhiza. (**b**) With the development of Tanashi 01 mycorrhiza (*single arrow*), the original mantle of *Pisolithus tinctorius* (*double arrow*) became dark brown and gradually disappeared; *bar* 1 mm

Pisolithus tinctorius, resulting in a composite mycorrhiza. Some mycorrhizae on *Pinus densiflora* formed by *Pisolithus tinctorius* seemed to be gradually covered by Tanashi 01 hyphae. There are few reports about composite mycorrhizal formation. Agerer (1990) reported that a member of the Gomphidiaceae grows in mycorrhizal sheaths formed by *Rhizopogon* and *Suillus* spp. from which its hyphae penetrate the cortical cells of *Pinus* spp. Similarly, Brand (1992) found that hyphae of an ascomycete, *Leucoscypha leucotricha* colonize *Lactarius subdulcis-Fagus sylvatica* mycorrhizae and intermix with *L. subdulcis* in the mantle. The Pt-T1 com-

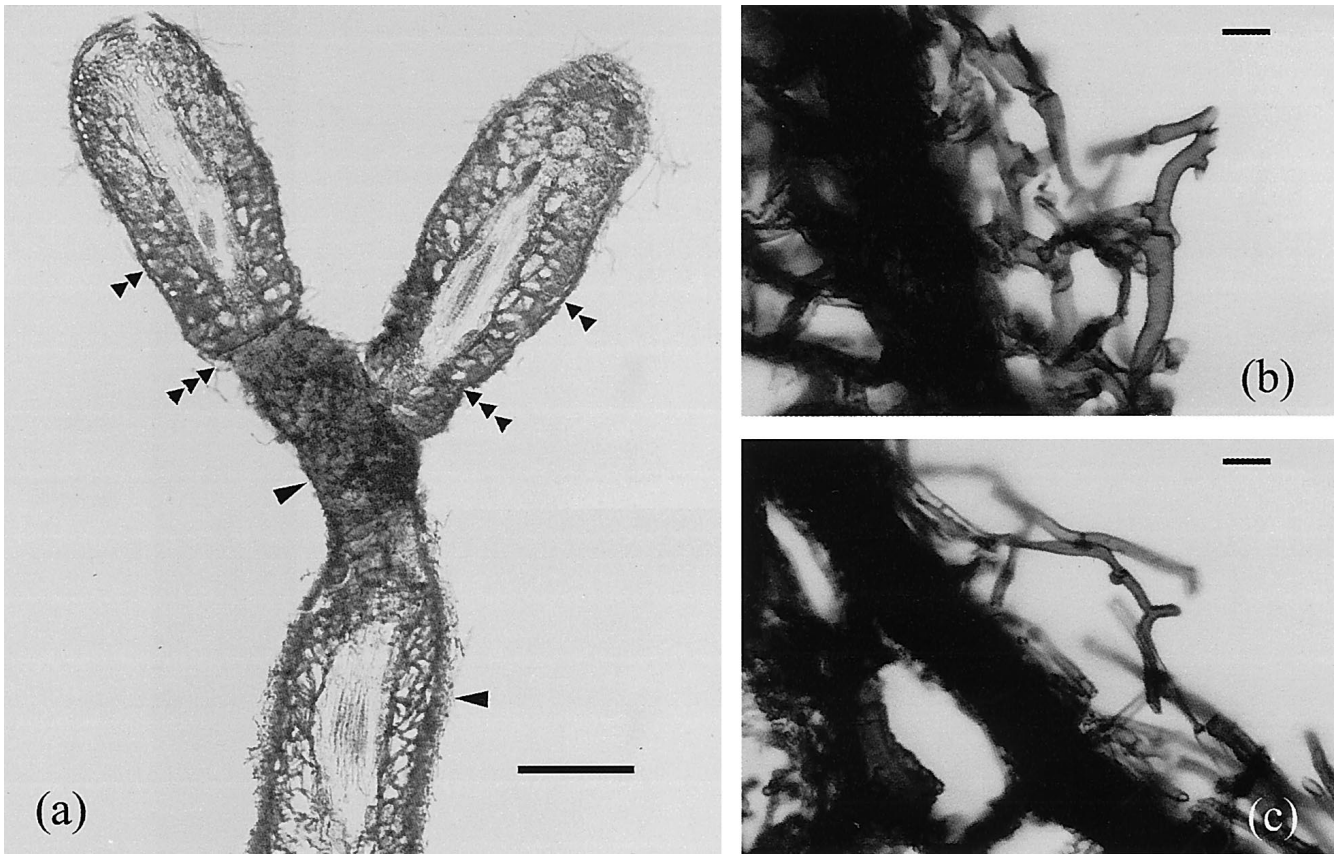

Fig. 9 (**a**) Longitudinal section of Pt-T1 composite mycorrhiza, (**b**) *Pisolithus tinctorius* hyphae in the mantle and (**c**) Tanashi 01 hyphae in the mantle. *Single arrow*, the mantle of *Pisolithus tinctorius* mycorrhiza. *Double arrow*, the mantle of Tanashi 01 mycorrhiza. *Triple arrow*, demarcation between the mantles of *Pisolithus tinctorius* and Tanashi 01; Hyphae in (b) and (c) were stained with toluidine blue 0; *bars* 200 μm (a) and 10 μm (b, c)

posite mycorrhiza in our experiment, however, differed from the above examples. First, the hyphae did not penetrate the cortical cells and, second, the mantle of Tanashi 01 was contiguous with the mantle of *Pisolithus tinctorius* but they were not intermixed. The structure of the composite mycorrhiza observed in our experiment was similar to the co-infected mycorrhiza on slash pine observed by Zak and Marx (1964). Root tips in the mantle of mycorrhizae sometimes grow and protrude from the mantle (Guo and Bi 1989; Egli and Kalin 1990). In the case of *Fagus* spp., the root tip growing out of the mantle was usually reinfected immediately after protrusion by hyphae from the Hartig net or from soil (Guo and Bi 1989). Egli and Kalin (1990) observed that a pathogen also entered the mantle of spruce mycorrhizae through a split and induced subsequent decay of the root tip. In the present study, the root tips seen protruding from the mantle of *Pisolithus tinctorius* may have been infected by Tanashi 01 because the growth of *Pisolithus tinctorius* hyphae around the root tips seemed to be inhibited more than that of Tanashi 01. Since *Pisolithus tinctorius* mycorrhizae which had been mostly covered by Tanashi 01 hyphae were observed in the overlapping region of both species, the Pt-T1 composite mycorrhiza can be considered as an intermediate state in the replacement of *Pisolithus tinctorius* by Tanashi 01.

In conclusion, the present study showed that interactions between mycorrhizal fungi can cause some to become dominant and others secondary. Composite mycorrhizae were initiated by infection by a dominant fungus of root tips which protruded from the mantle of a secondary fungus.

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