Mycorrhiza (2005) 15: 571–579
DOI 10.1007/s00572-005-0364-3

ORIGINAL PAPER

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The mycorrhizal community in a forest chronosequence of Sitka spruce [*Picea sitchensis* (Bong.) Carr.] in Northern England

Received: 29 April 2004 / Accepted: 1 April 2005 / Published online: 10 June 2005

Abstract Demography and fungal diversity of the below-ground ectomycorrhizal community in a chronosequence of Sitka spruce [*Picea sitchensis* (Bong.) Carr.] in Northumberland, Northern England, were analysed; mycorrhizal root samples were taken from 6-, 12-, 30- and 40-year-old stands, and fungal fruiting bodies were collected in autumn to complement the survey. Naturally germinated seedlings less than 1 year of age (taken from the 30-year-old stand) were also examined. A total of 118,000 mycorrhizal root tips were extracted from 40 soil cores (ten per age class) and from the complete root systems of 25 seedlings and separated into active and senescent root tips according to their morphology and anatomy. Active tips were distinguished according to their mycobionts which were characterised and identified microscopically. Although almost 100% of all fine roots were mycorrhizal, EM fungal diversity throughout the chronosequence was low, consisting of a total of 16 species of which three were only found as fruiting bodies. Of the six mycobionts found most regularly below ground, *Tylospora fibrillosa* was the most common, colonising about 70% of all root tips and more than 90% of those of seedlings and young trees. Root density and mycorrhizal diversity increased, but percentage of vital root tips decreased with increasing tree age, levelling off in the 30- and 40-year-old stand. Among the five subdominant fungal species, *Dermocybe crocea* was found to have its peak of distribution in the 12-year-old stand and *Russula emetica*, *Lactarius rufus*, *Hymenoscyphus ericae* agg. and the unidentified *Piceirhiza sulfoincrustata* in the 30- and 40-year-old stands. The possible correlations between the mycorrhizal community structure and biotic and abiotic factors are discussed.

Keywords Ectomycorrhizal community · Diversity · Demography · Chronosequence · Sitka spruce

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Introduction

It is now widely recognised that mycorrhizal fungi play a key role in determining the patterns both of nutrient flow to the plant (Smith and Read 1997) and carbon flow to the soil (Högberg et al. 2001) in boreal forests. Dense mycelial mantles cover the tips of almost all ectomycorrhizal fine roots in these systems, and the diversity of fungal species involved in the symbiosis is known to be high both at global (Molina et al. 1992) and local (Dahlberg 2002; Taylor et al. 2000) scales. Because they occupy a crucial position at the interface between plant and soil, it is important to gain some understanding of the dynamics both of the populations of these fungi and of the fine roots which they colonise. There is a particular need for knowledge of temporal changes in population structure (Dahlberg 2001). Ecologists are already aware that fine roots show high rates of turnover in forest ecosystems (Pregitzer 2002), but in general, these studies show little awareness that the structures which they are describing are symbiotic or that changes in the mycobiont population may be of importance for stand development.

Previous estimates of the longevity of individual mycorrhizal roots based upon analyses of seedlings grown in microcosms (Downes et al. 1992) or observations in field rhizotrons (Sittig 1998) have confirmed their essentially short life span. That there may be changes in populations of mycorrhizal fungi over time has also been recognised, but the majority of studies of fungal succession have been based upon records of the occurrence, above ground, of macromycete fruit bodies (Dighton and Mason 1985; Dighton et al. 1986; Smith et al. 2002; Norvell and Exeter

2004). Recently, an increasing awareness of the importance of cryptically fruiting or anamorphic taxa as major components of the mycorrhizal community (Baxter et al. 1999; Dahlberg 2001; Kernaghan and Harper 2001; Taylor and Alexander 1990), combined with a recognition that relationships between the occurrence of fruiting bodies and the representation of these fungi in the fine root community were poor (Dahlberg 2002; Gardes and Bruns 1996), has made it clear that direct analysis of the mycoflora of fine roots provides the only basis for understanding mycorrhizal population dynamics.

Incisive analysis of temporal changes of mycorrhizal root communities in natural ecosystems is difficult because the plants supporting the fungal symbionts are normally mixed in terms of both age and species composition (Jumpponen et al. 2002; Kernaghan and Harper 2001). One solution to this problem is to sample populations of a single tree species established over a known chronosequence. Visser (1995) used this approach to determine changes of mycorrhizal root demography in stands of *Pinus banksiana* which were at various stages of natural regeneration after fire.

Even greater precision in terms of both chronology and environmental circumstance can be obtained using plantations of monocultures in which all trees in any cohort were established synchronously and where all cohorts occur within a short distance of one another on the same soil type. Such stands were used in the present study in which the demography of ectomycorrhizal fine root populations was examined in pure stands of Sitka spruce (*Picea sitchensis* Bong.: Carr.) established over a chronosequence on a single soil type in the UK.

Materials and methods

Study site

The plantations are located in Harwood Forest, Northumberland, UK (center of geographical position: 55°14′N, 2°01′W, National Grid Reference NY 990929). The forest covers an area of ca. 500 ha consisting mainly of pure stands of *P. sitchensis* but with some stands of *Pinus contorta*. The trees were established from around 1950 after ploughing of treeless moorland which consisted mainly of grass (*Molinia caerulea*) with some heather (*Calluna vulgaris*). The soil is recognised by the national soil survey as being a stagnohumic gley, and it is known to suffer from impeded drainage.

Sampling took place during the growing seasons of 2000 and 2001 in pure stands of spruce which were 6, 12, 30 and 40 years old. In 2001, an additional sampling of recently germinated seedlings was carried out in an area under the 30-year-old stand where natural regeneration was occurring.

Sampling and root classification procedures

A cylindrical corer of 45-mm diameter was used to extract soil cores to a standard depth of 120 mm, giving an approximate volume of 200 ml per core. This core depth was sufficient to sample almost the entire population of mycorrhizal roots which, in this soil type, are known to be restricted by anoxia to superficial layers of the soil (Armstrong et al. 1975). Ten cores were extracted per age class, five in early and five in late growing season to minimize effects of seasonal variation in species composition. Cores were secured by wrapping in paper before being sealed into individual zip-lock bags for transport to the laboratory, where they were stored in a refrigerator at 4°C prior to being processed. At the end of the second growing season, 25 recently germinated spruce seedlings (<1 year old) were randomly extracted from the 30-year-old site with their complete root system. Their roots were processed the same way as those from the soil cores.

During the autumn sampling, fruiting bodies of potential mycobionts were also collected and identified.

In the laboratory, all mycorrhizal roots were extracted from each core and processed in a sequential manner. The

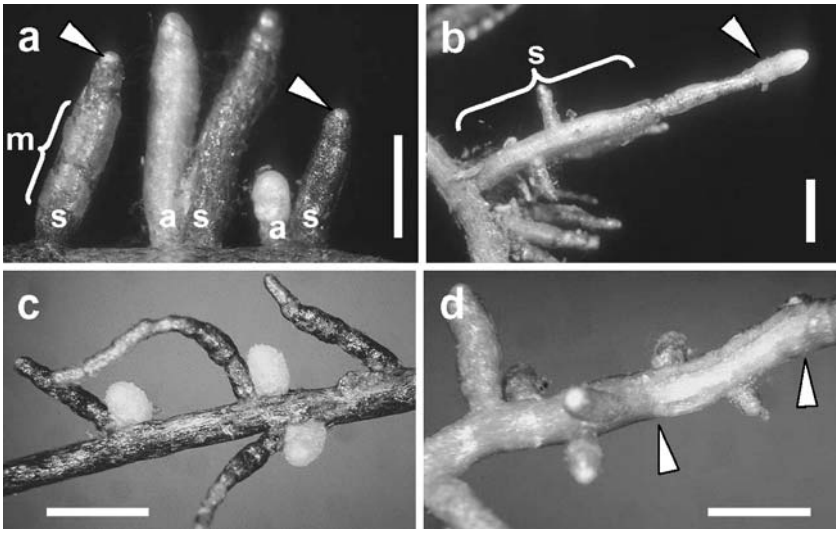

Fig. 1 Phenology of senescent *Picea sitchensis* ectomycorrhizae from Harwood spruce chronosequence. **a** *Tylospora fibrillosa*, active (*a*) and senescent (*s*) tips, the latter with decomposing mantle (*m*) but still with vital apex (*arrowheads*). **b** Senescent mycorrhiza (*s*) with freshly growing tip of *T. fibrillosa* (*arrowhead*). **c** Newly forming mycorrhizae of *Russula emetica* at bases of senescent root tips. **d** Senescent mycorrhizal system, some lateral tips with whitish apex, longitudinal section of main axis between *arrowheads* showing vital looking central cylinder; bar for all figures = 1 mm

larger root clusters were first isolated and individually cleaned in a water-filled tray under a Leica M 10 dissecting microscope with a Schott KL 1500 halogen fibre optic light source. Remaining material was collected in a 0.5-mm sieve which retained smaller clusters and single mycorrhizal tips. These were decanted individually into smaller volumes of water in Petri dishes using the same microscopic procedure.

At this stage, roots of all size categories were classified, on the basis of their appearance under the microscope, into two categories, viz., active or senescent.

Roots were placed in the active category according to criteria used by Cairney and Alexander (1992a,b) and Downes et al. (1992). The diagnostic features of active roots were as follows: the presence of a well-developed fungal mantle showing mycobiont-specific colouration and borne on a fully turgescent root containing white cortical tissues. Roots in this category would also normally have

Table 1 Diversity and distribution of ectomycorrhizal fungi at Harwood chronosequence

fungus/ mycorrhiza	% active EM tips in total (40 samples)	% samples including EM	tree age class (years)				
			<1	6	12	30	40
Tylospora fibrillosa (1.4 as *"Piceirhiza guttata"*: 3: 7 as ITE.6)	70.2 (± 26.0)	100.0	▨	▨	▨	▨	▨
Lactarius rufus (Scop.: Fr.) Fr. (5; 7; 8; 9)	8.3 (± 10.6)	51.4	▨		▨ **	▨ **	▨ **
"*Piceirhiza sulfo-incrustata*" (not identified)	8.7 (± 11.2)	24.3			▨	▨	▨
Russula emetica (Schaeff.: Fr.) Gray (1 as *R. mairei*; 5; 8; 9)	4.7 (± 4.0)	24.3		▨ *	▨ **	▨ ***	▨ ***
Hymenoscyphus ericae agg. (1, 4 as *"Piceirhiza bicolorata"*; 7 as ITE.3; 10)	3.2 (± 4.3)	32.4		▨	▨	▨	▨
Dermocybe crocea (Schaeff.) Gray (1; 2; 9)	0.7 (± 1.1)	21.6		▨ *	▨ **	▨ *	▨
Thelephora terrestris (1)	3.1 (± 5.3)	8.1		▨		▨	▨
ascomycetous (humarioid, 7)	2.6 (± 4.1)	5.4				▨	▨
"*Piceirhiza atro-hirsuta*" (tomentelloid, not identified)	2.1 (± 3.6)	5.4			▨		
Laccaria laccata (Scop.: Fr.) Berk.& Br. (7; 9)	0.9 (± 1.5)	8.1		*			▨
Paxillus involutus (1; 4)	0.5 (± 0.8)	5.4			▨	▨	
Russula ochroleuca (Pers.) Fr. (1; 8; 9)	< 0.1 (± 0.1)	2.7				▨ **	▨ **
Hygrophorus olivaceoalbus ("*Piceirhiza gelatinosa*", 1; 4; 6)	< 0.1 (± 0.1)	2.7					▨
Inocybe boltonii Heim (9)	–	–			*		
Lactarius deterrimus Gröger (8; 9)	–	–					*
Lactarius turpis (Weinm.) Fr. (8; 9)	–	–				*	
Total fungal species/ mycorrhizal types			**2**	**6**	**9**	**11**	**12**

Symbols: shaded cells, ectomycorrhiza present; asterisks, fruiting bodies present (* one to five fruiting bodies; ** six to 20 fruiting bodies; *** more than 20 fruiting bodies); numbers in parenthesis in first column indicate references for species/morphotype names and descriptions: *1* Agerer (1987–2002), *2* Brandrud et al. (1989–1998), *3* Eberhardt et al. (1999), *4* Gronbach (1988), *5* Hansen and Knudsen (1992), *6* Haug (2002), *7* Ingleby et al. (1990), *8* Krieglsteiner (2000), *9* Moser (1983), *10* Vrålstad et al. (2000). According to fungal nomenclature, only the names of those species whose fruiting bodies were found include the authority

intact adhering mycelial elements. Also following the criteria of the above studies, roots were classified as being senescent when their fungal mantles had become wrinkled or detached from the root, when their colour had changed to dark brown or black and the root cortex had become brown (Fig. 1). At this stage, the tissues of the stele could still be white and apparently intact (Fig. 1d). New growth could often be resumed from the tip of roots placed in this category (Fig. 1a, b, d) providing evidence that, in some cases at least, their apical meristems retained viability. A final stage, designated dead or decomposing, was distinguished but not quantified. In this, all the tissues of the root were dark brown or blackish, fragile, soft and more or less structureless.

Roots in the active category were separated on the basis of their colour, morphology and anatomy into mycorrhizal types following the procedures of Agerer (1987–2002) and Agerer (1991). Using this approach, they could be ascribed to known fungal species or mycorrhizal types by comparison with reference descriptions (Table 1). Voucher specimens of mantle preparations and whole mycorrhizae were prepared and archived.

Numbers of both active and senescent root tips were quantified using a hand counter. The identities of fungal fruit bodies were determined using standard keys and descriptions, and the frequency of their occurrence through the chronosequence was recorded.

Statistics

Statistical analysis was carried out using SPSS 10.1. The effect of tree age upon percentage of active and senescent root tips and upon the number of total root tips per area was tested. Differences between single tree age classes were analysed using the Games–Howell post hoc test. Statistics for tree-age-dependent distributional differences between and within fungal species were not tested due to the irregular abundance, especially of the less frequent species.

Results

A total of 118,000 tips of active or senescent fine roots were obtained from the 40 soil cores and 25 seedlings. Of these, less than 0.5% were non-mycorrhizal in plantation trees. Only the seedlings showed a major proportion of non-mycorrhizal tips (Fig. 2a). The ratio of active to senescent roots decreased progressively with increasing age of the trees; until by 30 and 40 years, only around 15% of roots were in the active category (Fig. 2a). Variance analysis showed that the differences between age classes were highly significant ($p<0.001$), suggesting that the percentage of active and senescent root tips is dependent on tree age. According to the post hoc test, the tree age classes form two statistically distinct groups: one including the 6- and 12-year-old stands and the other represented by the 30- and 40-year-old stands. The absolute numbers of total root tips contained in the 12-cm-deep cores, expressed on an area basis, increased with tree age to a peak of 3.17×10^6 m^{-2} in the 30-year-old site (Fig. 2b); the differences between age classes, according to variance analysis, were also significant ($p<0.01$). The maximum number of active roots expressed on this basis was 0.44×10^6 m^{-2}, this being found in the 12-year-old stand (Fig. 2b).

There was a progressive increase in species richness in the mycobiont population along the chronosequence (Table 1), although at all ages, the numbers of species encountered were low. In total, 16 distinct fungal species were found, three of them only as fruiting bodies (Table 1). Of the 13 mycorrhizal types, six which are depicted in Fig. 3 could be isolated from more than 20% of root samples and were thus regarded as regularly occurring species. Their relative distribution in the different tree age classes can be seen in Fig. 4. The relatively low sample number and the highly variable abundance of each morphotype per sample are expressed in a high standard deviation so that these results may not be truly significant in a statistical sense. However, there is clear evidence that the most frequent and abundant species was *Tylospora fi-*

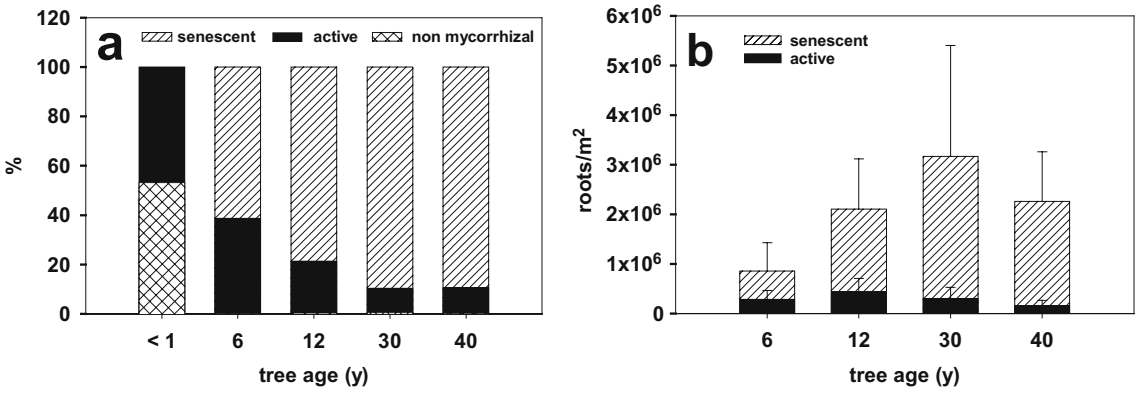

Fig. 2 Demography and distribution of ectomycorrhizae from different tree age classes in Harwood spruce chronosequence. **a** Percentage of active/senescent mycorrhizae and non-mycorrhizal tips on roots from seedlings (<1) and soil cores. **b** Estimated numbers of senescent and active mycorrhizal root tips per square meter, obtained by extrapolating total values from soil cores

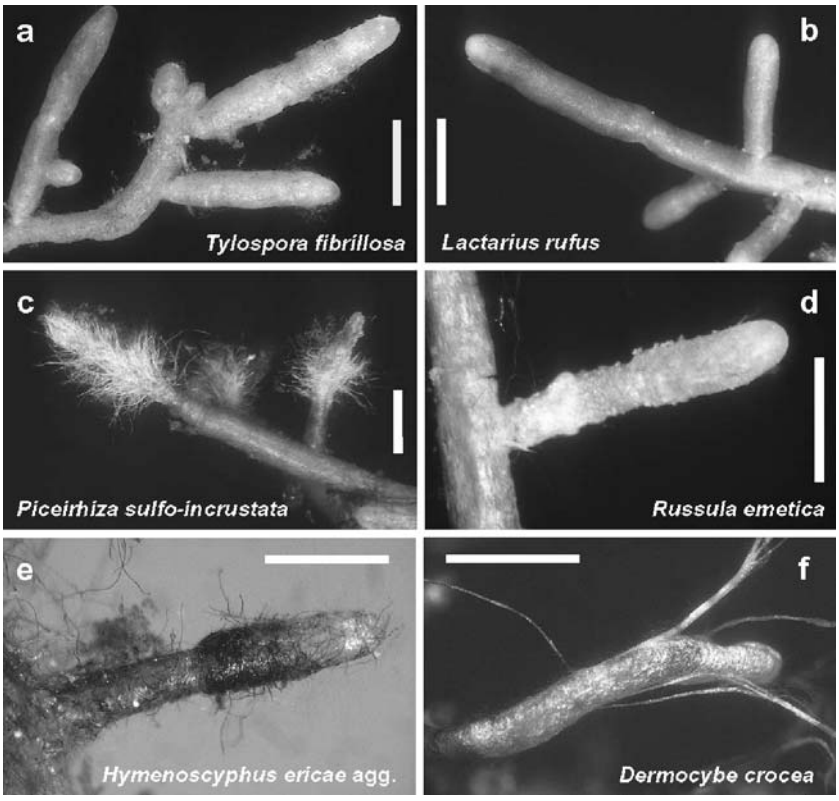

Fig. 3 Most frequent ectomycorrhizal types from Harwood spruce chronosequence (bar=1 mm)

brillosa (Fig. 3a) which could be found in all samples, colonising 70% of active root tips across all age classes and representing more than 90% of ectomycorrhizae in seedlings and 6-year-old trees (Fig. 4a). As the numbers of *T. fibrillosa*-colonised roots declined with age of stand, those of other species increased.

Lactarius rufus (Fig. 3b) was found in about 50% of all samples and in all age classes except the 6-year-old stand; it occurred in the 30-year-old stand in numbers similar to those of *T. fibrillosa* and constitutes the second most prominent species (Fig. 4b). All other mycorrhizae were present in much smaller numbers: *Hymenoscyphus ericae* agg. (Fig. 3e) also showed maximum representation at 30 years (Fig. 4e). Two ectomycorrhizae, the unidentified *Piceirhiza sulfo-incrustata* (see description below and Figs. 3c, 5) and *Russula emetica* (Fig. 3d), showed their largest representation in the population at the 40-year stage (Fig. 4c, d). Roots colonised by *Dermocybe crocea* (Fig. 3f) occurred almost exclusively in the 6- and 12-year-old stands (Fig. 4f).

Description of *P. sulfo-incrustata*

A conspicuous mycorrhizal root type was found regularly in Harwood samples and could be easily recognised by its colour and shape. As it has not been described before and could not be safely assigned to a fungal taxon, it is described here morphologically and anatomically under the provisional name *P. sulfo-incrustata* according to Agerer (1991).

Morphology (Figs. 3c, 5a): Mycorrhizae short, thin and unramified, up to 2 mm long, diameter 0.2–0.4 mm; colour pale sulphurish yellow, occasionally with greenish tints, very young tips sometimes with dark blue-green spots; surface loosely hairy or stringy due to hair-like, up to 1-mm-long hyphal aggregates; rhizomorphs lacking.

Anatomy (Fig. 5b–f): All layers of fungal mantle plectenchymatous, hyphae without clamp connections; mantle surface with numerous emanating hyphae, frequently glued together in bundles of two to five by a thick, gelatinous, semi-transparent extracellular sheath to form hair-like aggregates up to 1 mm in length; cell walls and gelatinous sheath with yellow pigment, typically forming thin, flaky incrustations on sheath surface; hyphal diameter 2–3 μm without sheath, 4–6 μm including sheath, adjacent hyphae often connected by anastomoses which are either open or closed by a septum; outer mantle layer very loosely plectenchymatous without distinctive pattern, hyphae 2–3 μm in diameter, mostly without gelatinous sheath, often ramified or forming open anastomoses, cell walls thin or slightly thickened, yellowish or colourless, septa without clamps; inner mantle layers compactly plectenchymatous, hyphae without gelatinous sheath, other hyphal characteristics like those of outer mantle layer.

Discussion

Belowground monitoring of ectomycorrhizal communities usually consists of two phases: the identification of the fungal taxa, performed on a few tips of each root mor-

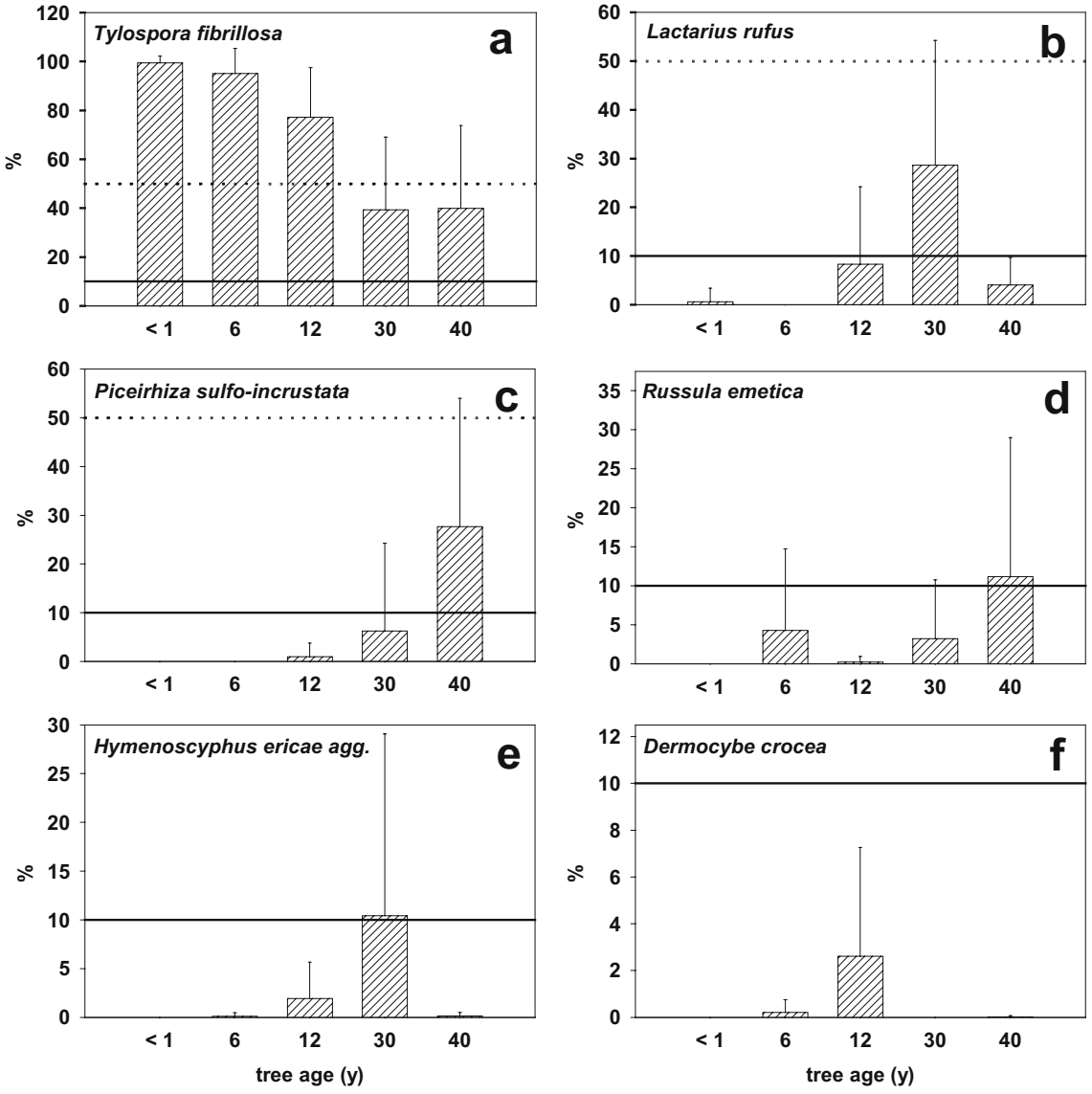

Fig. 4 Relative distribution (%root tips) of the six most frequent fungal colonizers on fine root tips in five tree age classes from Harwood spruce chronosequence

photype, and the subsequent sorting of the bulk mass of root tips into the previously determined taxonomic categories. Whereas the identification of reference specimens can be done either microscopically, by use of molecular tools or ideally by a combination of both methods, the subsequent classification of large numbers of root tips is usually done visually on the morphotype level (Visser 1995; Peter et al. 2001). Morpho-anatomical identification of ectomycorrhizal fungi is cost-efficient but may be of limited accuracy compared to molecular methods, especially at sites with high fungal diversity where similar or identical morphotypes, formed by closely related taxa, may occur in the same samples (Peter et al. 2001). In this study, however, microscopical identification was considered sufficiently accurate due to the overall low fungal diversity observed on both, morphotype and sporocarp levels, the distinctive and characteristical morphology and anatomy, especially of the most frequent morphotypes, which matched exactly the reference descriptions, and because some mycorrhizal species were repeatedly found associated with the corresponding basidiomata (*D. crocea*, *L. rufus*, *R. emetica*).

Two main phenomena characterise the mycorrhizal community of the Harwood Sitka Spruce chronosequence. These are the dominance of *T. fibrillosa* as a colonist of the active root tips, especially in the younger stands, and the high values of the numbers of senescent tips in older stands which seem to be related to increasing tree age.

Ectomycorrhizal communities of coniferous forests have been previously reported to be dominated only by a few fungal species, even if total EM fungal diversity was high (Dahlberg 2001, 2002; Horton and Bruns 2001). Erland and Taylor (2002) suggest better adaptation to edaphic conditions and a stronger nutritional impact of the dominant fungi on the host tree as main reasons for this phenomenon. Taylor et al. (2000) reported a positive cor-

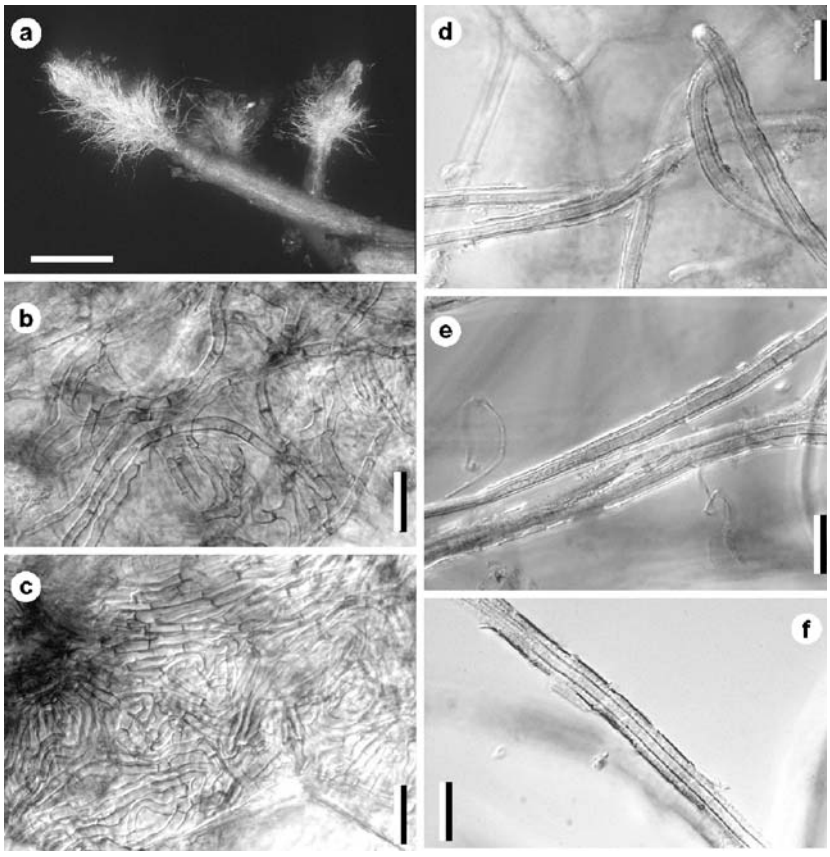

Fig. 5 Morphology and anatomy of *Piceirhiza sulfo-incrustata*. **a** Mycorrhizal tips with numerous, hair-like hyphal bundles (bar=1 mm). **b** Outer mantle layer, loosely plectenchymatous. **c** Inner mantle layer, densely plectenchymatous. **d**–**f** Hyphae of mantle surface with gelatinous, pigment-encrusted sheath. **e** A section of a hair-like hyphal bundle (**b**–**f** with Nomarski DIC, bars=10 μm)

relation between increasing content of mineral N and increasing dominance of *T. fibrillosa* EM on spruce roots with a simultaneous decrease in EM fungal diversity in four different forest soils within a European north–south transect: interestingly, the most N-polluted site showed a very similar community structure as Harwood. Despite a lack of soil data for Harwood, a high concentration of extractable N seems unlikely in this former moorland ecosystem, and the vegetation type also indicates a nutrient-poor substrate. Instead, other factors like exotic, monospecific tree hosts, the extreme substrate conditions (frequently water-logged, anoxic soil) and the relatively frequent and destructive crop rotation approximately every 40 years may strongly reduce the range of potential mycobionts. This would explain both poor total fungal diversity and the conspicuous ubiquity of a single, probably best adapted species, especially on the youngest plants. Apart from an obviously high tolerance of *Tylospora* for wet soil, another reason may be the predominance of this fungus on the nursery plants used as the original planting stock after clear-cutting: Ingleby et al. (1990) describe the mycorrhizal type ITE.6 which is identical with *T. fibrillosa* as frequent on nursery seedlings of Sitka spruce. Alternatively, fungal inoculum might be adapted to survive in the soil or on remaining moribund tree roots of the harvested areas. In support of the latter assumption, Grogan et al. (2000) and Stendell et al. (1999) provided evidence for the survival of ectomycorrhizae on root systems of burnt trees after forest fire. Spreading by spores to the virgin sites from surrounding earlier established plantations seems little likely as we did not find fruiting structures of *T. fibrillosa* during the surveys; also, establishment of mycelia from spores on early succession sites is probably slow (Baar et al. 1999) and would not explain the almost complete prevalence of *Tylospora* even on the youngest trees on recently clear-cut sites.

Looking at the distribution patterns of the remaining taxa, all identified EM fungal species are typical colonisers of conifers in boreal forests. Reported ecological data for most fungi coincide well with the general conditions at Harwood: *L. rufus* is common on acid soils and *R. emetica* and *D. crocea* on damp or boggy sites (Brandrud et al. 1989–1998; Courtecuisse and Duhem 1995; Krieglsteiner 2000; Moser 1983). However, we observed some specific differences in the distribution of individual species: *L. rufus* and *H. ericae* agg. were most abundant at the 30-year-old stand and *R. emetica* and *P. sulfo-incrustata* at the 40-year-old stand. *H. ericae* agg. has previously been described as *Piceirhiza bicolorata* on *Picea abies* (Gronbach 1988), probably being identical with ITE.3 on *P. sitchensis* (Ingleby et al. 1990), and was subsequently identified by DNA analysis by Vrålstad et al. (2000). It was first known to form mycorrhizal associations with ericaceous plants (Smith and Read 1997), like *C. vulgaris* which is common at Harwood, but is obviously also capable of colonising ectomycorrhizal trees like *Picea* spp. *D. crocea* was regularly found in the 12-year-old stand, whereas the same species was very rare or absent in samples from all other age classes. Whether this is an effect of stand-specific conditions, cannot be explained by our data.

Due to the limited time scale of this study, it was not possible to repeat sampling in identical tree age classes at other sites; therefore, there is no statistical certainty that differences in species richness and frequency between the sampled stands are true effects of tree age and could be observed in other chronosequences as well. However, there is no evidence that other factors like topography, soil quality and climate, which might determine differences in the composition of the fungal community, show major differences between the sampled stands. Also, both sampling campaigns (early summer and autumn) yielded very similar results.

Harvesting by sequential clear-cutting as practised at Harwood obviously represents a catastrophic event for the ecosystem and puts strong selection pressure on the mycorrhizal community (Dahlberg 2001), as the sudden death of all trees annihilates the main carbon source for EM fungi; consequently, a substantial reduction of EM fungal diversity in forest gaps or clear-cuts has been reported (Kranabetter and Wylie 1998). Ectomycorrhizal succession after similar but natural catastrophes like forest fires has been studied by various authors. Visser (1995) found *Suillus brevipes* and *Coltricia perennis* to be the dominant mycorrhizal colonisers of newly established trees in previously burnt stands of Bishop pine, the remaining more than 40 fungal species accounting only for a minor percentage of mycorrhizal root tips. Whereas *C. perennis* was almost absent in old-growth forest, *S. brevipes*—like *T. fibrillosa* in Harwood—could be found throughout the chronosequence.

The morphological and anatomical categories we used to classify active and senescent mycorrhizae of Sitka spruce have previously been correlated with physiological evidence using vital fluorescence staining in a series of studies by Cairney and Alexander (1992a,b) and Downes et al. (1992). Our study of mycorrhizal demography showed relatively few active mycorrhizal root tips, the bulk being in the senescent phase, especially in the mature forest stands. This may be due to a short life span of individual mycorrhizae and a high turnover rate of fine roots. In fact, the above authors observed an average active period of less than 50 days for individual mycorrhizae, whereas the stage of senescence could last more than 150 days. Ullrich et al. (1997), who used five categories of vital fluorescence staining to classify the vitality of mycorrhizal fine roots in two afforested stands of Scots pine (*Pinus sylvestris* L.) on former brown coal pits in East Germany, found a percentage of about 20% of fully vital root tips, very similar to our values of active tips. Also, similar to our findings, in the same study, the younger stand (20-year-old) showed a higher percentage of vital mycorrhizae than the older (32-year-old) stand, which the authors interpret as an effect of different abiotic factors in both stands and as an increase in the average mycorrhizal life span due to progressing soil development.

The percentage of active tips within the mycorrhizal network, sufficient to satisfy the nutrient and carbon compound demands of the participating symbionts, seems to be lower in adult tree cohorts than in young stands, on one hand possibly because the mycelial networks and root systems, which constitute the mycorrhizal web, are fully developed and therefore more efficient in mature forest than in earlier pioneering stages and, on the other hand, requiring less metabolic activity for their formation and regeneration in the climax stage than in earlier, more dynamic growth phases. The possible function—if any—of the many senescent fine roots remains unclear. In case that they still receive nutrients from the tree via the apparently functional central cylinder, their maintenance over a longer period without receiving the full benefits of the mycorrhizal symbiosis probably constitutes a considerable metabolical investment for the phytobiont; on the other hand, the senescent tips may survive some time on previously deposited nutrient reserves. In this context, it would be interesting to analyse seasonal dynamics of mycorrhizal communities when net nutrient allocation to and from fine roots occurs.

Acknowledgements This study was funded by the European project Forest Carbon and Nitrogen Trajectories (FORCAST, 5th Framework) which is part of the CARBOEUROPE project cluster. The authors like to thank David Hollingworth and Glyn Woods, University of Sheffield, for processing and digitalising the photomicrographs.

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