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MARSCHNER REVIEW

The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: role in carbon cycling

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Abstract There is growing evidence of the importance of extramatrical mycelium (EMM) of mycorrhizal fungi in carbon (C) cycling in ecosystems. However, our understanding has until recently been mainly based on laboratory experiments, and

knowledge of such basic parameters as variations in mycelial production, standing biomass and turnover as well as the regulatory mechanisms behind such variations in forest soils is limited. Presently, the production of EMM by ectomycorrhizal (EM) fungi has been

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estimated at ~140 different forest sites to be up to several hundreds of kg per ha per year, but the published data are biased towards *Picea abies* in Scandinavia. Little is known about the standing biomass and turnover of EMM in other systems, and its influence on the C stored or lost from soils. Here, focussing on ectomycorrhizas, we discuss the factors that regulate the production and turnover of EMM and its role in soil C dynamics, identifying important gaps in this knowledge. C availability seems to be the key factor determining EMM production and possibly its standing biomass in forests but direct effects of mineral nutrient availability on the EMM can be important. There is great uncertainty about the rate of turnover of EMM. There is increasing evidence that residues of EM fungi play a major role in the formation of stable N and C in SOM, which highlights the need to include mycorrhizal effects in models of global soil C stores.

Keywords Decomposition · Exploration type · Extramatrical mycelium · In-growth bag · Minirhizotron · Soil organic matter · Rhizomorphs · Turnover rates

Introduction

In forests, the total below-ground flux of carbon (C) represents between 25 and 63 % of gross primary production (Litton et al. 2007) and has a large influence on the physical, chemical and biological properties of the soil. While the flux of C into and out of the soil is relatively easy to estimate, little is known about the processes behind these fluxes. The production and turnover of the extramatrical mycelium (EMM) of mycorrhizal fungi is one of the least understood of these processes, which is an obstacle in modelling ecosystem C dynamics (Chapin et al. 2009; Meyer et al. 2010). In boreal and temperate forests, which is the main focus of the review, the EMM is mainly produced by ectomycorrhizal (EM) fungi associated with trees, but the amount of mycelium produced by arbuscular mycorrhizal (AM) fungi associated with herbs and some tree species can be large especially at high soil pH (Nilsson et al. 2005). The contribution of ericoid mycorrhizas to the soil mycelium remains largely unknown (Read and Perez-Moreno 2003). The EMM plays key roles in ecological processes such

as plant nutrient uptake (Harley 1989), the nitrogen (N) cycling (Hodge and Fitter 2010), mineral weathering (Landeweert et al. 2001) and survival and establishment of seedlings (Smith and Read 2008) and in plant community composition (van der Heijden et al. 1998).

The EMM of mycorrhizal fungi likely has an important role in C cycling in ecosystems. Firstly, C flux through the EMM is probably large, secondly, it may be important for formation of soil organic matter (SOM) and thirdly, it may directly or indirectly affect decomposition of SOM. In this paper we discuss the factors that regulate the production, standing biomass and turnover of EMM, which are crucial parameters needed to assess the overall role of EMM in C cycling. The numbers of papers that present estimates of EMM production are increasing rapidly and we are for the first time putting all these data together to estimate typical mean values for different forest types. We give some attention to the importance of EMM for the formation of recalcitrant forms of C, its indirect and direct effects on decomposition of SOM and its contribution to fluxes of CO₂ in soil respiration. The interested reader may find additional information about the importance of the EMM in recent reviews of soil organic matter decomposition (Talbot et al. 2008), below ground litter quality (Langley and Hungate 2003), mineral weathering (van Schöll et al. 2008; Rosling 2009), soil aggregation (Rillig and Mummey 2006), mycelial networks (Simard 2009), C cycling (Jones et al. 2009; Cairney 2012), N cycling (Wu 2011), phosphorus (P) uptake (Cairney 2011) and broader ecological scopes (Read and Perez-Moreno 2003; Finlay 2008; Leake et al. 2004; Allen 2007; Courty et al. 2010; Hodge et al. 2010). In this review we focus on EM symbioses, these being the most important mycorrhizal type on trees in temperate and boreal forests (Read and Perez-Moreno 2003), but we make some comparisons with AM fungi. Much of the knowledge we have concerning the EMM is based on laboratory microcosm and pot studies, although an increasing number of studies are performed in situ, facilitated by techniques such as mycelium in-growth bags, chemical, molecular or isotopic markers and large scale manipulations such as trenching and girdling experiments (Nylund and Wallander 1992; Ekblad and Näsholm 1996; Ekblad et al. 1998; Wallander et al. 2001; Dickie et al. 2002; Johnson et al. 2002; Leake et al. 2006; Högberg et al. 2010;

Heinemeyer et al. 2007, 2011 and see Wallander et al. 2013 for a discussion of advantages and disadvantages of these methods).

Assessing mycelial growth: which structures to look at and where?

Morphological heterogeneity: fine hyphae and rhizomorphs

Understanding the importance of the EMM of EM fungi in C cycling requires accurate predictions of mycelial growth. Detailed studies of soil microcosms in laboratory conditions show wide variation in growth rates and morphology between mycorrhizal mycelial systems of EM fungi (e.g. Duddridge et al. 1980; Finlay and Read 1986; Bending and Read 1995; Donnelly et al. 2004; Rosling et al. 2004). In many EM fungi, hyphae progressively aggregate behind the growing front to form rhizomorphs that are typically hydrophobic and long-lived (e.g. Unestam 1991; Unestam and Sun 1995; Agerer 2001). All mycelium types explore the soil via fine hydrophilic hyphae, often with substrate particles adhering to the surface, so-called ‘substrate adhesion hyphae’ or ‘exploiting hyphae’. Few quantitative data on the relative proportion of rhizomorphs versus single hyphae of a mycelium are available. In a laboratory study of *Pisolithus tinctorius* in symbiosis with *Pinus taeda* seedlings, the rhizomorphs contributed to only 7 % of the length of the mycelium but their dry matter was twice that of the diffuse mycelium (Rousseau et al. 1994). The rhizomorph proportion of the EMM probably has a large impact on its standing biomass and turnover rate (see section on EMM standing biomass and turnover below). Rhizomorphs may be a more energetically efficient means of supporting an increasingly extended mycelium over large areas (Donnelly et al. 2004).

Exploration types

Based on the amounts of emanating hyphae and the presence and differentiation of rhizomorphs, Agerer (2001) defined five main exploration types, ranging from contact exploration types with smooth mycorrhizal tips having only a few short emanating hyphae, via short and medium exploration types to long distance exploration types with highly differentiated rhizomorphs.

Exploration types have been differentiated based on about 400 different morphotypes of ectomycorrhizas (www.deemy.de; Agerer and Rambold 2004–2011), representing about 5 % of known fungi that can form EM (Taylor and Alexander 2005). From this limited database, it appears that in many genera all known species produce only one exploration type, e.g. species in most of the investigated genera of the Boletales belong to the long-distance exploration type that has hydrophobic rhizomorphs, while in other genera, e.g. *Russula* and *Lactarius*, the exploration type varies between different species and can range from contact, to medium distance or even long distance exploration types (Agerer 2001; Kraigher et al. 2008; Hobbie and Agerer 2010). An EM community’s species composition is made up of a range of exploration types, suggesting a degree of separation of function between them.

Where do EMM develop (organic vs mineral soil)?

The spatial heterogeneity in EMM production and standing biomass is high and laboratory soil microcosm experiments have shown that local ‘hot-spots’ of various inorganic and organic materials stimulate the growth of EM mycelium (e.g. Finlay and Read 1986; Unestam 1991; Bending and Read 1995; Perez-Moreno and Read 2000; Jentschke et al. 2001; Rosling et al. 2004). Field demonstration of such effects comes from the observation of the stimulation of mycelial in-growth into bags spiked with inorganic P sources (Hagerberg et al. 2003; Nilsson and Wallander 2003; Potila et al. 2009) or wood ash (Hagerberg and Wallander 2002) placed in conifer forest soils, and from the formation of hyphal mats in some forests (Cromack et al. 1979; Unestam 1991; Ingham et al. 1991). The higher accumulation of hyphal biomass in these patches is supported by studies of ^{14}C allocation (Finlay and Read 1986; Bending and Read 1995; Leake et al. 2001; Rosling et al. 2004).

Although EM fungi can proliferate into leaf litter in laboratory microcosms (Unestam 1991), the few studies from the field suggest that they do not grow on or utilize young litter material in the forest floor (Treseder et al. 2006; Lindahl et al. 2007). In one of the few studies carried out in forests, new litter was dominated by saprotrophs while EM fungi dominated in old litter, the underlying mor layer and in mineral soil (Lindahl et al. 2007), suggesting that saprotrophs are more competitive in the litter layer. There might be

a niche differentiation not only between EM fungi and saprotrophs but also between exploration types, species and genotypes of mycorrhizal fungi. In support of this, the EM community structure was shown to differ between soil layers estimated both as mycorrhizal root tips (Dickie et al. 2002; Landeweert et al. 2003; Rosling et al. 2003; Tedersoo et al. 2003; Genney et al. 2006; Lindahl et al. 2007) and the EMM (Landeweert et al. 2003). Based on analyses of mycorrhizal root tips, half of the fungal taxa were restricted to the mineral soil in a podzol of a 60–80 year old *Picea abies* forest (Rosling et al. 2003).

Estimation of mycelial growth rates and production in forest ecosystem

Measurement of hyphal length and growth rates using microcosms (in the lab) or minirhizotrons (in the field)

Growth rates of EM hyphae in laboratory microcosm are typically 2–4 mm day⁻¹ (Read 1992), with maximal rates of up to 8 mm day⁻¹ (Donnelly et al. 2004). Similar growth rates were recorded in an outdoor experiment using 2 m tall mesocosms filled with peat. In this work, a maximum growth rate of 2 mm day⁻¹ for *Laccaria proxima*, which does not form rhizomorphs, and of 3 mm day⁻¹ for *Thelephora terrestris*, which forms rhizomorphs, was recorded in July (Coutts and Nicholl 1990). An indirect way to estimate the mycelial growth rate in the field may be to measure the size of genet formed by mycorrhizal fungi on trees planted on areas that have not been covered by plants previously, e.g. large sand pits. A genet size of up to 5 m was found for *Suillus bovinus* (long distance exploration type) in a sand pit with 20-years-old *Pinus sylvestris* (Dahlberg and Stenlid 1994). This would imply a genet growth rate of 25 cm yr⁻¹ over the 20 years, equivalent to an increase of the genet radius of 0.7 mm day⁻¹ over the growing season, assuming that the mycelium growth period is similar to that of the vegetation, which is about 180 days at this site. This rate, which is somewhat lower than the rates recorded in microcosms, is without doubt lower in some periods of the season and significantly higher in others (see further on seasonal variations below).

Some rhizomorph-forming fungi produce dense mycelial mats, in which the rhizomorphs can represent

30–50 % of soil dry matter (Ingham et al. 1991). The hyphal length varies greatly from 2 – 600 km g⁻¹ soil in the mats to only 0.3–0.8 km g⁻¹ in nearby non-mat soil (Ingham et al. 1991), although some mycelial necromass might also have been included in this standing biomass measurement. The mycelial length varies not only spatially but also seasonally; the total mycelial length varied seasonally from 100 to 800 m g⁻¹ soil in the organic mor layer and from 50 and 150 m g⁻¹ in the upper 10 cm of the mineral soil of a boreal *Pinus sylvestris* forest (Söderström 1979).

Minirhizotrons have been used in a few studies of rhizomorph growth (Treseder et al. 2005; Vargas and Allen 2008; Pritchard et al. 2008). However, growth in such studies is recorded as rhizomorph length per photographed frame area, making comparisons with the measurements of expansion of the mycelial front difficult. Nevertheless, yearly growth rates of 0.1–0.6 mm per frame were recorded in a *Pinus taeda* forest, suggesting growth rates of <1 cm m⁻² of frame surface day⁻¹, while in a mixed conifer/oak forest, maximum rates of 100 cm m⁻² of frame surface day⁻¹ were observed (Vargas and Allen 2008), suggesting that the importance of rhizomorph forming fungi can differ very much between different forest sites.

The use of in-growth bags, a method that targets ECM (compared to saprotrophs) and enables us to estimate the production of EMM

One difficulty when making measurements of EMM production in the field is to separate the mycorrhizal mycelium from that of saprotrophs. This step has been facilitated by the use of mycelial in-growth bags (Wallander et al. 2001) or in-growth cores (Godbold et al. 2006; Hendricks et al. 2006). The bags, usually filled with sand, are made of nylon with a typical mesh size of 50 µm allowing the ingrowth of hyphae but not of roots. Saprotrophs can grow into these bags but the fungal biomass within them seems to be dominated by mycorrhizal fungi as judged from trenched controls as well as DNA analyses (Wallander et al. 2001; Kjäller 2006). Using this technique EMM production rates have been estimated at ~140 different forest sites (Table 1). The majority of these sites (107) are located in Sweden, and *Picea abies* is the dominating tree species. Data have also been reported from Denmark (15 sites), Finland (13 sites), North America (2 sites) and France (1 site). These studies indicate an average

production rate in the upper 10 cm of a forest soil of 160 kg dry matter ha⁻¹ year⁻¹ (Table 1). However, this rate varies tremendously between sites, e.g. from 20 kg ha⁻¹ over 12 months in some *Quercus robur* sites in southern Sweden (Nilsson et al. 2007) to 980 kg dry matter ha⁻¹ over 4 months in a *Pinus taeda* plantation at low elevation in North Carolina (Parrent and Vilgalys 2007). It can also vary greatly from year to year at the same site, e.g. in a *P. abies* plantation on a peat soil south west of Sweden, it was close to zero 1 year, but found to be 100 kg dry matter ha⁻¹ the year after (R. G. Björk and A. Ekblad, unpublished). This large variation may derive from the factors regulating EMM production as well as from differences in the various methods used to assess mycelial biomass (ergosterol, phospholipid fatty acids, dry matter etc.; see Wallander et al. (2013)). Although EMM production data exist from a number of sites, there is a strong bias towards Norway spruce (*P. abies*) and southern Scandinavia and data from other areas and other forest types are needed.

Most published data reflect the production of EMM in the upper 10 cm of the soil (which includes the organic layer). However, EMM production can also be high in deeper soil layers as shown in the few studies which report values from more than one soil depth (Table 1). Thus, of the 590 kg ha⁻¹ year⁻¹ of EMM biomass produced down to 30 cm depth in a *Picea abies* forest, half was found in the upper 10 cm and half in the 10–30 cm depth (Wallander et al. 2004), a distribution pattern similar to that of fine roots in this forest (Thelin et al. 2002). Other studies have also shown that the distribution of EMM generally follows that of tree fine roots (Korkama et al. 2007; Pritchard et al. 2008).

The production rates estimated by in-growth bags can be compared to the very few estimates of C allocation to EMM in forests. Recently, Hobbie (2006) surveyed the C allocation patterns of EM plants in 14 culture (laboratory) studies and five field studies. Using the data in Hobbie (2006), we estimate that on average 4.7 % of total NPP (9 % of below ground NPP) in the culture studies and 7.2 % of total NPP (13 % of below ground NPP) in the field studies was allocated to the EMM. If we combine these values together with NPP estimates ranging from 333 to 590 g C m⁻² year⁻¹ in three 40-year-old Swedish *P. abies* forests (Berggren Kleja et al. 2008), we estimate a NPP of the EMM of 16–42 g C m⁻² year⁻¹ or 350–940 kg dry matter ha⁻¹ year⁻¹ (assuming a C content of 45 % of dry matter). These numbers,

which estimate the mycelium production in the whole soil profile, are comparable with the estimates of EMM production in *P. abies* forest soils using ingrowth bags. From the data available in Table 1 we estimate an EMM production in the upper 10 cm of soil in a 40-year-old Swedish *P. abies* forests to be around 200 kg dry matter ha⁻¹ year⁻¹ and for the whole soil profile this value should probably be at least doubled.

Factors regulating the carbon supply for EMM production in forest soils

The EMM is fuelled by C from the host and any factors regulating C availability from the host-plant such as global change, weather conditions, forestry management and plant properties as well as intrinsic properties of fungal C use can potentially cause large variations in EMM production of EM fungi (Fig. 1) that will further sustain differences between sites, seasons and years.

Seasonal effects and forest aging

Seasonal variations in EMM production may be driven by abiotic variables notably light, temperature and moisture but also by phenological phenomenon, both in the hosts and symbionts (for moisture effects see further down).

The growth of EM fungi is mainly dependent on newly produced photosynthates (Söderström and Read 1987; Högberg et al. 2001; Johnson et al. 2002; Högberg et al. 2010; Steinman et al. 2004). The major growth of EMM is therefore expected to occur when below-ground allocation of carbohydrates is relatively large, shortly after fine root production has peaked. In a cool temperate climate this is late summer to early autumn (July–October), while in a temperate planted spruce-beech forest in Bavaria the peak in beech fine root production was in June (Grebenc and Kraigher 2007). Indeed, in a northern boreal *Pinus sylvestris* forest, below-ground C allocation in late August can be 5 times that in mid June (Högberg et al. 2010). While in a temperate forest in France, the below-ground ¹³C allocation after pulse labelling of beech trees was much higher in July than in May and late August (Epron et al. 2011). The few published studies on temporal variations in the production of EMM of EM fungi fit with this view (Lussenhop and Fogel 1999; Wallander et al. 2001; Nilsson et al. 2007). In

Table 1 The production of extramatrical mycelia (EMM) of ectomycorrhizal fungi in various forests. Estimations were made based on sand filled mesh bags or cores that were incubated in the soil. Soil was used as a substrate in a few cases (Hendricks et al. 2006 and Sims et al. 2007). Mesh bags were placed in the soil 1) vertically (covering a range of soil depths), 2) horizontally (at a specific depth) or 3) in the interface between organic and mineral layer. Fungal biomass produced in the mesh bags have been estimated by 1) loss of ignition (LOI), 2) elemental carbon analysis of extracted mycelium (EA), 3) dry matter of harvested mycelium (Dry matter), 4) ergosterol content (Ergo) or 5) phospholipid fatty acid 18:2 ω 6,9 (PLFA). Incubation time varies between sites, but usually a complete growth season is covered in the measurements. For comparisons between sites and tree species, the amount of EMM produced per hectare in the top 10 cm of the soils has been calculated. The average EMM production per site using all 137 sites in the table was 170 kg EMM per hectare. If different methods were used to estimate biomass in one site, the average value was used. The following conversion factors were used: 3 μ g ergosterol mg^{-1} fungal biomass; 2 nmol PLFA 18:2 ω 6,9 per mg^{-1} fungal biomass (Wallander et al. 2001). To convert the biomass values found per gram sand to kg ha^{-1} we used the density of sand (1.56 g cm^{-3}) to calculate the EMM biomass per cm^3

Forest type	Sites (located in Sweden, otherwise country indicated)	Age (years)	Soil type	Soil depth (cm)	Incub. time (months)	Method used for analysis of EMM biomass (concentr. g^{-1} sand)	EMM production in the upper 10 cm (kg ha^{-1} per growing season)	Reference
Boreal forests								
<i>Picea abies</i>	Betselse	~130	Haplic podsol	Interface	4	PLFA (0.1 nmol)	80	Nilsson et al. 2005
<i>P. abies</i>	Flakastugan	~120	podsol	Interface	4	PLFA (0.2 nmol)	160	Nilsson et al. 2005
<i>P. abies</i>	Kryddgrovan	~120	podsol	Interface	4	PLFA (0.1 nmol)	80	Nilsson et al. 2005
<i>P. abies</i>	Värjisaån	~125	podsol	Interface	4	PLFA (0.25 nmol)	200	Nilsson et al. 2005
<i>P. abies</i>	Flakaliden	35	Podsol	Interface	12	PLFA Ergo	170 150	Leppälampi et al. unpublished
<i>Pinus sylvestris</i>	Värjisaån	~125	podsol	Interface	4	PLFA (0.35 nmol)	280	Nilsson et al. 2005
<i>P. sylvestris</i>	Betselse	~130	Haplic podsol	Interface	4	PLFA (0.12 nmol)	100	Nilsson et al. 2005
Average		~125					151 \pm 28	
Boreonemoral forests								
<i>P. abies</i>	Grängshammar	19	Podsol	Interface	12 (mean 3 y)	Ergo (0.3 μ g)	380	Wallander et al. 2011
<i>P. abies</i>	Hällefors	16	Podsol	Interface	12 (mean 3 y)	Ergo (0.35 μ g)	440	Wallander et al. 2011
<i>P. abies</i>	(62°10'N, 27°16'E) Finland	10	podsol	0-10 cm	4	LOI (0.025–0.15 mg) PLFA (0.1–0.34 nmol)	40–230 80–270	Korkkama et al. 2007
<i>P. abies</i>	Släne	55	Podsol	Interface	8	PLFA (0.12 nmol)	114	Wallander and Thelin 2008
<i>P. abies</i>	Torpa	65	Podsol	Interface	8	PLFA (0.20 nmol)	190	Wallander and Thelin 2008
<i>P. abies</i>	Vrå 72	60	Podsol	Interface	8	PLFA (0.13 nmol)	124	Wallander and Thelin 2008
<i>P. abies</i>	Vrå 180	60	Podsol	Interface	8	PLFA (0.12 nmol)	114	Wallander and Thelin 2008

Table 1 (continued)

Forest type	Sites (located in Sweden, otherwise country indicated)	Age (years)	Soil type	Soil depth (cm)	Incub. time (months)	Method used for analysis of EMM biomass (concentr. g ⁻¹ sand)	EMM production in the upper 10 cm (kg ha ⁻¹ per growing season)	Reference
<i>P. abies</i>	Ebbegårde	16	Podsol	Interface	12 (mean 3 y)	Ergo (0.4 µg)	500	Wallander et al. 2011
<i>P. abies</i>	Toftaholm	16	Podsol	Interface	12 (mean 3 y)	Ergo (0.25 µg)	310	Wallander et al. 2011 unpublished
<i>P. abies</i>	Tönnersjöheden (56°41'N, 4°57'E)	37	Podsol	Interface	13	PLFA (0.4 nmol)	320	Hagerberg and Wallander 2002
<i>P. abies</i>	Tönnersjöheden (5 sites)	5–10	Podsol	Interface	12	Ergo (0.10 µg)	130	Wallander et al. 2010
<i>P. abies</i>	Tönnersjöheden (5 sites)	10–20	Podsol	Interface	12	Ergo (0.21 µg)	270	Wallander et al. 2010
<i>P. abies</i>	Tönnersjöheden (5 sites)	20–30	Podsol	Interface	12	Ergo (0.1 µg)	130	Wallander et al. 2010
<i>P. abies</i>	Tönnersjöheden (5 sites)	30–40	Podsol	Interface	12	Ergo (0.17 µg)	220	Wallander et al. 2010
<i>P. abies</i>	Tönnersjöheden (5 sites)	40–50	Podsol	Interface	12	Ergo (0.05 µg)	65	Wallander et al. 2010
<i>P. abies</i>	Tönnersjöheden (5 sites)	50–90	Podsol	Interface	12	Ergo (0.11 µg)	140	Wallander et al. 2010
<i>P. abies</i>	Tönnersjöheden (5 sites)	90–130	Podsol	Interface	12	Ergo (0.07 µg)	90	Wallander et al. 2010
<i>P. abies</i>	Brevens bruk	68	Sandy	0–10 10–20	12	EA (138 µg) EA (31 µg)	215	Boström et al. 2007
<i>P. sylvestris</i>	Liesineva Finland (12 sites)	80	Peat	Interface	4	PLFA (0.2 nmol) PLFA (0.2 nmol)	160 160	Potila et al. 2009
Average		~50			4 16 4 16	Ergo (0.15 µg) Ergo (0.35 µg)	190 440	
Nemoral forests							188±12	
<i>P. abies</i>	Skogaby (56°33'N, 13°13'E)	45	Haplic podsol	5, 10, 20 cm	12	PLFA (5 cm 0.12 nmol) PLFA (10 cm 0.15 nmol) PLFA (20 cm 0.15 nmol)	100	Majdi et al. 2008
<i>P. abies</i>	Björstorp	60	Podsol	Interface	13		182	Hagerberg et al. 2003

Table 1 (continued)

Forest type	Sites (located in Sweden, otherwise country indicated)	Age (years)	Soil type	Soil depth (cm)	Incub. time (months)	Method used for analysis of EMM biomass (concentr. g ⁻¹ sand)	EMM production in the upper 10 cm (kg ha ⁻¹ per growing season)	Reference
<i>P. abies</i>	<i>Dyneboda</i>	65	Podsol	Interface	13	LOI (0.18 mg), Ergo (0.14 µg)	182	Hagerberg et al. 2003
<i>P. abies</i>	<i>Ignaberga</i>	50	Podsol	Interface	13	Ergo (0.14 µg)	156	Hagerberg et al. 2003
<i>P. abies</i>	<i>Västra Torup</i>	55	Podsol	Interface	13	LOI (0.19 mg), Ergo (0.18 µg)	390	Hagerberg et al. 2003
<i>P. abies</i>	Jämsjö (56°53'N, 15°16,5'E) (4 sites)	60	Dystric cambisol	5, 10, 20 cm	12	LOI (0.04 mg), Ergo (0.3 µg)	300	Wallander et al. 2004
<i>P. abies</i>	Thyregod, W Denmark	25	Inceptisol (FAO)	0–8 cm	8	LOI (10 cm 0.12 mg), LOI (20 cm 0.07 mg)	54	Kjøller et al. Unpublished
<i>P. abies</i>	Klosterhede, NW Denmark	91	Haplic podsol	0–8 cm	12	Dry matter	47	Kjøller et al. Unpublished
<i>P. abies</i>	19 sites in Scania 14 sites in Denmark along a C/N ratio gradient	18–85	Acidic pH (KCl): 2.7–4.9	5 cm	6	PLFA (0.12–0.72 nmol)	40–240	Nilsson et al. 2012
<i>P. abies/Quercus robur</i>	Jämsjö (56°53'N, 15°16,5'E) (4 sites)	40–80	Dystric cambisol	0–30 cm	12	LOI (5 cm 0.19 mg), LOI (10 cm 0.05 mg)	300	Wallander et al. 2004
<i>P. sylvestris</i>	Silvåkra	~30	Sandy	Interface	12	LOI (20 cm 0.04 mg), PLFA (0.4 nmol)	320	Wallander et al. 2001
<i>Q. robur</i>	Halland (5 sites)	> 80		5 cm	12	Ergo (0.23 µg)	390	Nilsson et al. 2007
<i>Q. robur</i>	Småland (6 sites)	> 80		5 cm	12	PLFA (0.03 nmol)	20	Nilsson et al. 2007
<i>Q. robur</i>	Skåne (4 sites)	> 80		5 cm	12	PLFA (0.15 nmol)	120	Nilsson et al. 2007
<i>Q. robur</i>	Öland (4 sites)	> 80		5 cm	12	PLFA (0.14 nmol)	110	Nilsson et al. 2007
<i>P. pinaster</i>	The Landes Forest France (44°42'N, 0°46'W)	13	Podsol	0–10	12	PLFA (0.06 nmol), LOI	50	Nilsson et al. 2007
Average		~60					60	Bakker et al. 2009
Warm temperate							138±9	
<i>Pinus. palustris</i>	Georgia USA	21		0–30 cm	2	Ergo (0.05 µg -sand)	65 (2 month)	Hendricks et al. 2006

Table 1 (continued)

Forest type	Sites (located in Sweden, otherwise country indicated)	Age (years)	Soil type	Soil depth (cm)	Incub. time (months)	Method used for analysis of EMM biomass (concentr. g ⁻¹ sand)	EMM production in the upper 10 cm (kg ha ⁻¹ per growing season)	Reference
<i>P. palustris</i>	Georgia USA	22	Loamy Arenicpaleudult	0–30 cm	12	Ergo (0.2 µg - soil)	260 (2 month)	Sims et al. 2007
<i>Pinus taeda</i>	Duke forest NC USA	20	Loamy Arenicpaleudult Clay loam	Interface	4	PLFA (1.25 nmol)	1,000	Parrent and Vilgalys 2007
Average		~20					611	
Total average of all sites							160±7	

a detailed phenological study in a *Pinus strobus* forest in northern, Lower Michigan the EMM growth of *Cenococcum geophilum* peaked in mid July, three weeks after the peak in fine root growth (Lussenhop and Fogel 1999). In contrast, in a warm temperate *Pinus palustris* plantation, EMM production was high all year around (Sims et al. 2007). Even in a cooler temperate forest, the EMM can grow at a low rate during winter months if air temperatures remain above zero (Coultts and Nicholl 1990). *Thelephora terrestris*, producing rhizomorph, grew at a rate of 0.4 mm day⁻¹ in winter, while *Laccaria proxima*, that produced only diffuse mycelium, grew from June to October and the mycelium disappeared after this (Coultts and Nicholl 1990), suggesting that differences in phenology among the symbionts can be of importance.

In contrast to the view that maximum EMM production in temperate and boreal forests occurs from late summer to autumn, a detailed study of total mycelium production over 27 months in a *P. sylvestris* forest in mid Sweden, showed two peaks of similar amplitude, one in April-May and one in August-October (Söderström 1979). That study did not distinguish between mycorrhizal and saprotrophic mycelium. Other studies suggest the main EMM growth period to occur in the second half of the growing season (Wallander et al. 2001; Boström et al. 2007; Nilsson et al. 2007) so the spring peak observed by Söderström (1979) may have been dominated by saprotrophs. In a more recent study, spatial separation of EM fungi and saprotrophs, with the saprotrophs dominating in the litter and mycorrhizal fungi dominating in the organic layer and mineral soil, has been suggested (Lindahl et al. 2007). The soil sampling in the latter study was performed in September at the same *P. sylvestris* site studied by Söderström (1979). The question is if this mycorrhizal versus saprotroph dominance is constant or if the two fungal groups have different seasonal dynamics? To answer this question we need further studies on seasonal variations in mycelium production by both saprotrophs and mycorrhizal fungi among EM exploration-types and throughout soil profiles. One problem in such investigations is that the ecological role of a large number of fungal taxa that can be identified by molecular methods in a soil sample is unknown (Lindahl et al. 2007). Increased knowledge in this aspect will therefore increase our ability to draw sound conclusions about temporal or spatial changes in EM/saprotroph ratios or exploration types.

In addition to the yearly effect of season, a multitude of changes take place in an ecosystem over a forest cycle. The most dramatic changes in plant cover, species composition, soil chemistry, hydrology, climate etc. occur directly after tree harvest and then up to canopy closure after which the changes are slower. There are therefore many factors that may directly or indirectly affect EMM production and its standing biomass. Many of these are probably connected to successional changes in species composition above and below ground as well as changes in below ground C allocation, but EMM production has not been studied greatly in this context (Last et al. 1987). Tree growth varies over a rotation period, usually with a peak around canopy closure when nutrient demand also reaches a maximum (Kimmins 2004). This occurs between 25 to 40 years of age in *P. abies* forests in central-southern Sweden (Schmalholz and Hylander 2009). The production of EMM seems to peak around the time when tree growth is highest (Wallander et al. 2010; Kallioikoski et al. 2010).

Effect of elevated atmospheric CO₂

In agreement with the fact that EM fungi rely on C supplied by the host, several studies have shown a stimulation of EMM production under elevated atmospheric CO₂ concentrations (e.g. Godbold et al. 1997; Treseder 2004; Alberton et al. 2005; Fransson et al. 2005; Alberton and Kuyper 2009). However there are exceptions, for example Weigt et al. (2011) found no increase or only a slight increase in EMM length using seedlings of *Picea abies* inoculated with *Piloderma croceum* and exposed to double or ambient CO₂ concentration alone or in combination with addition of ammonium nitrate solution. The effect of elevated CO₂ on EMM production has mostly been studied in laboratory grown seedlings. The few results available from field studies fail to show a CO₂ effect on EMM production (Kasurinen et al. 2005; Godbold et al. 2006; Parrent and Vilgalys 2007). A response shown in many laboratory and some field experiments is that changes in C availability causes an increase in the degree of mycorrhization (Godbold et al. 1997; Garcia et al. 2008). But in forests types, such as Boreal forest where the tree root tips are close to 100 % colonized by EM fungi (Taylor and Alexander 2005), a response to CO₂ is unlikely to be of great significance. More generally the EM-fungal community has been shown to change both in experiments with elevated CO₂ (e.g.; Godbold et al. 1997; Fransson et al. 2001;

Parrent et al. 2006; Parrent and Vilgalys 2007) and in defoliation experiments (Saikkonen et al. 1999; Cullings et al. 2001; Markkola et al. 2004; Saravesi et al. 2008). The change in EM-fungal community has often manifested itself in a shift between morphotypes differing in mantle thickness. A reduction in C availability, by e.g. defoliation, seems to favour smooth mycorrhizal types and disfavour types that produce thick mantles and rhizomorphs (Saikkonen et al. 1999; Cullings et al. 2001; Markkola et al. 2004; Saravesi et al. 2008). So far one laboratory study has reported an increased proportion of mycorrhizas producing thick mantles and abundant rhizomorphs in response to elevated CO₂ (Godbold et al. 1997), and only one of the few field studies showed that rhizomorph production was almost doubled by elevated CO₂ in deeper soil layers in a *Pinus taeda* forest (Pritchard et al. 2008). The production of EMM varies greatly between different exploration types (Weigt et al. 2011) and it seems reasonable to find increased abundance of high C demanding exploration types when C availability is increased by elevated CO₂. Clearly further field studies on the effects of elevated CO₂ on mycelium production are needed.

Effect of soil fertility and potential use of a stoichiometric C:N:P model for understanding fungal C allocation in response to N and P fertilization

Among the factors that can affect the C availability for mycelium production, site fertility – and thus fertilization practices, may strongly regulate belowground C allocation (Fig. 1). Trees allocate proportionally more C to shoots and less to roots at sites with high productivity while at sites of low productivity proportionally more C is allocated belowground to enhance nutrient uptake by roots and EM fungi (Högberg et al. 2003). However, since high fertility also results in high photosynthesis, the total amount of C allocated below ground may sometimes be larger at a more productive site than at a less productive site. Indeed, a positive correlation between EMM biomass and site fertility was found in mixed boreal forests in Finland (Kallioikoski et al. 2010) and fast-growing *P. abies* clones produced more EMM than slow growing clones (Korkama et al. 2007). It was shown that the fast growing clones hosted EM fungi that belong to the types that produce extensive mycelia with rhizomorphs, e.g. *Piloderma*, while the slower growing clones had more fungi that produce less mycelium such as the Ascomycete *Wilcoxina* (Korkama et al. 2007).

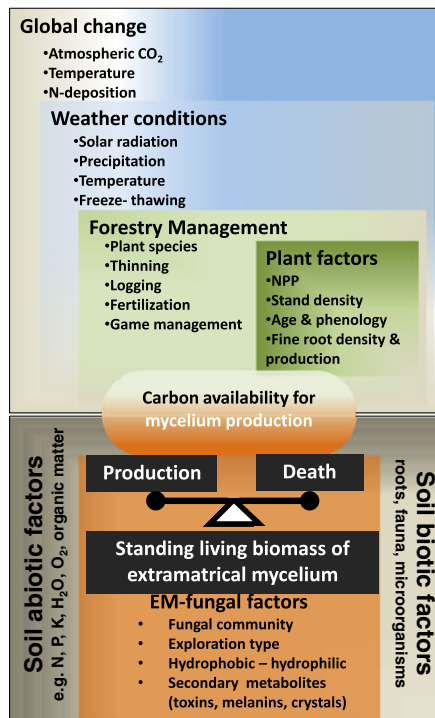


Fig. 1 Overview of the factors that directly or indirectly may affect the production, standing biomass and death of the extramatrical mycelium of ectomycorrhizal fungi

However, when site fertility was increased by high N fertilization of forests, it resulted in reduced production of EMM by the EM fungi (Kårén and Nylund 1997; Nilsson and Wallander 2003; Sims et al. 2007; Högberg et al. 2011), while the effect on mycorrhizal colonization on roots is usually much smaller (Kårén and Nylund 1997; Treseder 2004). This reduction in EMM production may be caused both by a lower standing fine root biomass at high N (Nadelhoffer 2000) as well as that large amount of C is needed to take up and assimilate the excessive N in the fertilized plots (Bidartondo et al. 2001; Ek 1997). This C consumption may result in C limitation of EMM production (Wallander 1995). Under unbalanced nutrient conditions, much of the excess N is transported to the shoot and is stored in the vacuoles in the leaf in the form of amino acids (Näsholm et al. 1997). In laboratory microcosms, a cessation of EMM growth was noted when the mycelial front of certain species reached peat amended with inorganic N (Arnebrant 1994). Different species seems to be more or less sensitive to high inorganic N concentrations and high N fertilization typically causes changes in the species composition of EM fungi making the smooth mycorrhizal types more common (e.g. Kårén and Nylund

1997; Parrent and Vilgalys 2007). Accordingly, Gorissen and Kuyper (2000) applied the terms nitrophilic and nitrophobic species based on their tolerance of inorganic N. *Laccaria bicolor*, a nitrophilic species, retained more N in the fungal biomass while the N sensitive (nitrophobic) *Suillus bovinus* delivered more N to the host plant when studied in a pot experiment (Gorissen and Kuyper 2000). This would imply that nitrophobic species spend more C on N assimilation and amino acid transfer to their host plant while nitrophilic species can tolerate N by spending less C on N assimilation, which would allow them to spend more C on EMM growth under excess N. Difference in C demand and tolerance to specific elements by individual EM species in forest soils may be one explanation for the high diversity usually found in such communities.

In contrast to the negative effect of high doses of N on EMM production, intensive fertilization with a balanced nutrient mix, including all elements needed, resulted in no change in EMM production in two sites but a reduction in a third site (Wallander et al. 2011). This suggests that the balance between the availability of C and N and possibly other nutrients is of importance. Recently, Johnson (2010) recommended a stoichiometric C:N:P perspective to provide the basis for a more predictive understanding of fertilization responses of AM symbioses to N and P fertilization. It was predicted that the function of the AM symbiosis is dependent on the availability of N and P such that the mutualistic benefit is greatest at the combined condition of high N and low P, which would give high photosynthesis rates when the symbiont is efficient in P uptake. Furthermore, the study also predicted the response of plant and fungal morphology to a change in resource availability, e.g. N fertilization can induce P-limitation, which would result in more C allocation to production of roots and AM fungi. Johnson (2010) brings up several field and laboratory experiments supporting these models for AM symbioses. In EM symbioses, localized additions of inorganic N can stimulate the proliferation of mycelium production, at least of some fungi (Jentschke et al. 2001; Clemmensen et al. 2006). However, as pointed out above, large scale N fertilization in temperate and boreal forests is known to result in reduced production of EMM (Kårén and Nylund 1997; Nilsson and Wallander 2003). The reason for this discrepancy between AM and EM systems is unknown but it may be that P availability is not low enough in many temperate and boreal forests to allow N-induced P limitation to develop over the experimental

period. It has been shown that N fertilization can give rise to P limitation of forest production in boreal *P. abies* forests in long-term factorial fertilizer experiments (Tamm 1991), but it remains to be shown what happens to the EMM production in such experiments. Indeed, laboratory experiments on *Pinus sylvestris* seedlings with EM showed very high EMM production at the combination of high N, low P conditions (Wallander and Nylund 1992; Ekblad et al. 1995). It should be noted that in the paper by Wallander and Nylund (1992), there were similar EMM production responses to the N and P conditions in both the nitrophilic *Laccaria bicolor* as well as in the nitrophobic *Suillus bovinus*. This suggests that a C:N:P perspective may be valid for a nitrophobic as well as a nitrophilic species when studied separately. However, in the soil with many different species competing for a living space on the same tree root system, species differences in the C and N use (see above) could potentially have large impact on the competition between species. Phosphorus fertilization of naturally P-limited soils would be an alternative way of testing the validity of the C:N:P model for EM symbioses. Peat soils are naturally low in P and K and recent results from a long lasting PK-fertilizer experiment on a drained peatland show that the production of EMM, as well as the colonization of roots, was stimulated by low P availability, and the EMM production was also stimulated by low K conditions (Potila et al. 2009). These results also support the applicability of a stoichiometric C:N:P model for EM symbioses. The availability of different forms of N and P, and the ability of different species and genotypes of EM fungi to use them may also be important factors in regulating tree growth and C allocation feedbacks. We identify the need for studies of EMM production in long-term factorial N, P fertilizer experiments in forest ecosystems to further test the C:N:P model for EM symbioses.

Abiotic and biotic factors regulating mycelial growth

Soil moisture

Extramatrix mycelium production can be sensitive to soil moisture, for example it can be reduced by 50 % in a dry year compared to a wet year in a well-drained *P. abies* forest (Majdi et al. 2008). However, it appears that mycelial production, at least of some fungal species, is not as sensitive to drought as sporocarp production, which responds strongly to soil moisture conditions

(Wiklund et al. 1995). Indeed, despite a very dry year with very few fruiting bodies produced, high mycelial in-growth in the upper 6 cm of the soil was found in a *P. taeda* forest (A. Ekblad et al. unpublished). Production of EMM can be extensive in the deeper mineral soil (Wallander et al. 2004; Boström et al. 2007; Majdi et al. 2008) and so potentially a reduced production of mycelium in the surface could be compensated for by an increase in production or a slower turnover rate further down in the soil (Pritchard et al. 2008). The survival and growth of mycelia during drought conditions may be enabled by the passive movement of water from deeper moist soils to dryer surface soils via roots by so called nocturnal hydraulic lift (Caldwell et al. 1998; Querejeta et al. 2003, 2007). Indeed, ¹⁸O tracer experiments indicate that sporocarps of fungal species formed during very dry conditions derived 30–80 % of their water from hydraulically-lifted or deep water (Lilleskov et al. 2009). Recently, an experiment using deuterium labelled water presented strong evidence for hydraulic redistribution of soil water by a common mycorrhizal network from mature trees to seedlings under field conditions (Warren et al. 2008).

Periodically dry habitats seem to be dominated by rhizomorph-forming fungi, many of them hydrophobic (Unestam 1991). Wet conditions may instead be detrimental to rhizomorph-formers since laboratory studies show that mycorrhizal colonization of hydrophobic but not hydrophilic fungi may be hampered by wet conditions (Stenström 1991). In fact, recent mini-rhizotron data show that rhizomorph length was negatively correlated with soil water content in a mixed conifer and oak forest and daily recordings show that the rhizomorphs grew rapidly at very low soil water content, so it was hypothesised that plants invest in C for rhizomorphs in exchange for water during harsh conditions (Vargas and Allen 2008).

Grazing effects

Grazing of above ground plant parts normally consumes a minor part of net primary production in forests and usually has minor effects on the standing plant biomass in such ecosystems (Kimmins 2004). However, grazing is selective and can have significant impact on plant species composition in a community (Pastor and Naiman 1992; Persson et al. 2000) and may therefore indirectly affect species composition of mycorrhizal fungi (Gehring and Whitham 2002), and consequently also

have effects on EMM production. Severe grazing of leaves can result in drastically reduced photosynthesis, reduced C allocation below ground and reduced mycelium production, similar to that of experimental defoliation (see above).

The presence of fungivores as well as of other soil organisms could potentially affect growth, standing biomass and turnover of the EMM in the soil. Laboratory microcosm experiments suggest that the growth of EMM may be reduced, unaffected or stimulated by the presence of grazing invertebrates such as collembola. The direction of this change may be determined by the species composition and population density of the fungivores (Fitter and Sanders 1992; Ek et al. 1994; Setälä 1995; Setälä et al. 1999). However, it is not clear to what extent changes in EMM biomass are a direct effect of animal grazing or the result of other processes acting indirectly on the EMM (Setälä et al. 1999) involving e.g. selective grazing of competing saprotroph fungi, recycling of minerals locked up in senescing tissues or removal of growth inhibitors (Fitter and Sanders 1992). Indeed, soil arthropods significantly affect the rate of N mineralization in forest soils (Persson 1989).

As with grazing above ground, below ground grazing is probably selective. This selection may be directed by the fungal odour (Bengtsson et al. 1988; Bengtsson et al. 1991) together with contents of defence substances (e.g. crystals on the surface and content of repellents) rather than its C and N content (Taylor and Alexander 2005; Böllmann et al. 2010). The vitality of the mycelium may also be important because severed mycelium, and mycelium of *Pisolithus tinctorius* grown on agar was grazed more by the collembolan *Folsomia candida* than mycelium connected to a host plant (Kaneda and Kaneko 2004). Many fungi produce bioactive secondary metabolites that have been shown to be nematocidal (Stadler and Sterner 1998), e.g. many *Lactarius* and *Russula* species produce the biologically inactive precursor stearoylvelutinal that after a wound is rapidly converted to strongly antibiotic and pungent sesquiterpenoids (Stadler and Sterner 1998; Spiteller 2008). The EM fungus *Laccaria bicolor* was even shown to paralyse, probably by a toxin, and then invade and kill the springtail *F. candida* (Klironomos and Hart 2001). The N in the springtail was found to be beneficial for growth of the host plant, which is a demonstration of a dramatic shortcut of the N-cycle. It is unknown if other EM fungi have this striking capacity.

In accordance with optimal foraging theory, animals will feed on the food source yielding the greatest reproductive success (MacArthur and Pianka 1966). Laboratory experiments have shown that soil fauna can graze on EM fungi grown in vitro (e.g. Shaw 1988). In grassland, in situ ^{13}C labelling has unequivocally demonstrated that collembola can significantly affect release of recent assimilate by external arbuscular mycorrhizal mycelium (Johnson et al. 2005). In a field ^{13}C pulse-chase experiment in a young *Pinus sylvestris* forest some Collembola were ^{13}C -labelled within days, which was interpreted as evidence for grazing of active hyphal tips of EMM by these animals (Högberg et al. 2010). However, in this experiment, it cannot be excluded that the ^{13}C label was derived from grazing of algae or lichens on the soil surface, or from grazing of microbes in the rhizosphere, since it is known that many Collembola can feed on several different substrates (Hopkins 1997). In fact, some other recent studies suggest that the EMM of EM fungi is the optimal food for relatively few soil animals in situ. Indeed, tree girdling experiments in Sweden of two *Picea abies* forests and one *P. sylvestris* forest reduced the population of Protura and only one species of oribatid mite, *Oppiella nova*, but the latter was only reduced in the *P. abies* forests not in the *P. sylvestris* forest (Remén et al. 2008; Malmström and Persson 2011). The collembolans were either not affected or stimulated by the girdling (Malmström and Persson 2011). Furthermore, in a windfall area of a *P. abies* forest, very high densities of Protura were found in the vicinity of small *P. abies* plants, while in areas without surviving *P. abies*, the proturan density was low, supporting the view that EM fungi is an important food source for this animal group (Krauss and Funke 1999). In a microcosm experiment, it was found that *O. nova* could grow and increase its population on some EM fungi in symbiosis but not on others, while none of the other common soil animals tested succeeded to reproduce when feeding on EM fungi (Remén et al. 2010). Furthermore, in laboratory microcosm the presence of four different EM fungi grown in symbiosis with *P. sylvestris* had no effect on soil animal populations (Setälä et al. 1999; Setälä 2000). It seems that the importance of EMM as an easily available food source for the detritus soil food web could be smaller than previously believed (Setälä 2000), although more targeted experimental work needs to be undertaken under field conditions. It is

possible that EMM should be considered a large C store in the soil rather than a C source (see further below and Setälä et al. 1999), and that grazing of saprotrophic microorganisms is relatively more important than grazing of EM fungi. If so, this may have major implications for plant-microbe interactions and the cycling of limiting mineral nutrients, such as N and P. For example, the positive effect of bacterial and fungal feeding nematodes on the biomass production of non-mycorrhizal *P. sylvestris* was of equivalent magnitude to the positive effects of formation of mycorrhizas, suggesting that the grazing by the nematodes released N that otherwise was locked into saprotroph biomass (Setälä et al. 1999).

Estimation of standing biomass and turnover of EMM

The data discussed above suggest that there is substantial amount of C invested in the production of EMM. However, in order to fully assess its importance in the forest C cycle, data on its standing biomass and turnover are required. In this section we will present the few data available, and briefly discuss the factors that may affect EMM turnover. A large standing biomass can be the result of a high production or a slow turnover or a combination of both.

The standing biomass and turnover of EMM

Laboratory studies show that mycelial fans of EM fungi, consisting of thousands of single hyphae, can develop and disappear in a few weeks (e.g. Finlay and Read 1986; Bending and Read 1995). These studies have led to the general view that EMM turnover is very rapid perhaps occurring once per week during the growing season (Finlay and Söderström 1992; Smith and Read 2008). However, it is unknown if these results of laboratory studies, typically using monocultures of EM fungi living in symbiosis with small seedlings under low light conditions, are directly applicable in the field. For field studies, quite a large number of EMM production estimates have been published (Table 1), but to calculate the turnover rate we need both production and standing biomass estimates. This is problematic due to the difficulty to distinguish mycorrhizal from saprotrophic mycelium. We know of only one study in which estimates of both standing biomass and production of EMM have

been made. Using a soil-incubation technique, it was estimated that EM fungi contributed to approximately half of the standing mycelial biomass in coniferous forests soils in southern Sweden (Bååth et al. 2004). Based on these results, Wallander et al. (2004) calculated total EMM standing biomasses in the upper 70 cm of the soil of 4.8×10^3 kg ha⁻¹ in a *P. abies* forest and 5.8×10^3 kg ha⁻¹ in a mixed *P. abies/Quercus robur* forest. This is an order of magnitude higher than the production rates determined from in-growth bags, suggesting a mean residence time of 10 years (Wallander et al. 2004), or a turnover rate of about 0.1 year⁻¹, which is considerably lower than those of fine roots in boreal and temperate forests which have been estimated to be between 0.4–1.3 year⁻¹ (Gill and Jackson 2000; Finér et al. 2011; Brunner et al. 2012). A mean residence time of the whole mycelium of 10 years is surprisingly high as shown above, and suggests a large contribution of long-lived rhizomorphs (see below) to the standing biomass in these forests. Alternatively, this dichotomy is simply an illustration of the difficulty of estimating EMM standing biomass and production accurately. For example, one problem may be a possible underestimation of EMM production rates with the sand bags (Hendricks et al. 2006) as well as the imprecise conversion factors between fungal biomarkers and biomass. An underestimate of production combined with an overestimate of standing biomass would result in an underestimate of the rate of turnover. A solution to this problem may be to combine sequential harvesting of in-growth bags with a ¹³C₂ pulse labelling of the mycelium via the plant and analyses of ¹³C in structural components of the mycelium such as glucosamine (for further technical discussions, see Wallander et al. 2013).

Rhizomorph longevity

Different parts of the mycelium definitely turn over at different rates and it is likely that single hyphae of many fungi turn over much more rapidly than rhizomorphs. Recent minirhizotron studies show that mean life-span of rhizomorphs can range from 7 to 22 months and some can survive several growing seasons (Treseder et al. 2005; Pritchard et al. 2008; Vargas and Allen 2008). In a *Pinus taeda* forest exposed to elevated CO₂, the average life-span of rhizomorphs was dependent on rhizomorph diameter, soil depth and the CO₂ treatment (Pritchard et al. 2008). The longest average life-span was found for thick, rhizomorphs,

at greater soil depth and under high CO₂-conditions. These findings suggest that the turnover of the complete EMM is probably highly dependent on the relative contribution of rhizomorphs to the standing biomass and possibly their average diameter and soil depth distribution. Knowing that a forest's EM community is typically dominated by a few fungal species, with a large number of other species that are rare (Dahlberg 2001), even a minor shift in species composition may therefore have a profound effect on the standing biomass and turnover of the EMM. It should be noted that most rhizomorphs are hydrophobic, but some fungi, e.g. *Thelephora terrestris*, produce hydrophilic rhizomorphs (Unestam 1991). It is unknown if hydrophobicity affects the turnover rates, but a hydrophobic surface is probably less easily attacked by extracellular enzymes which could result in suppressed microbial degradation rates.

Rhizomorphs can be much more long-lived than roots, as demonstrated in the *P. taeda* forest mentioned above. In this forest, the mean life-span of rhizomorphs was 2 to 9 times longer those of the mycorrhizal tips (Pritchard et al. 2008). This difference has several important ecological implications. For instance, new roots can, at relatively low C and N costs, connect to and take advantage of all the benefits of an established extensive mycelial network. A long life-span is advantageous to the fungus which is more likely to cover a large area of the forest floor. In addition, a large mycelial network will immobilize N, reducing the N leakage from the forest. Indeed, leakage of N after heavy N-fertilization is suggested to be intensified due to the reduction of EMM (Högberg et al. 2011). However, the mean life-span of rhizomorphs is not always longer than that of the root tips, as was shown in a mixed conifer oak forest (Vargas and Allen 2008). Differences in estimates of longevity may reflect the species composition of fungal communities and illustrates the need for further studies comparing the longevity of rhizomorphs and root tips.

Variation in EMM biomass and turnover

Large seasonal and year-to-year variations in standing biomass and turnover are likely due to environmental factors that directly affect the mycelium, such as winter soil freezing, but also indirect effects via the host, such as seasonal changes in C availability or more catastrophic events such as drastic declines in leaf area, and thus reductions in the C supply to the mycorrhizas. Thus, a

summer drought combined with an ice storm in December of the same year resulted in reduced leaf area index and in high rhizomorph mortality, reduced production and standing biomass of mycorrhizas and rhizomorphs the following year (Pritchard et al. 2008). Since the EMM biomass contains a large pool of N, reductions in its standing biomass are likely to cause an increase in easily available N, as indicated by the increased N concentration and increased $\delta^{15}\text{N}$ of dwarf shrubs the year after tree girdling in a boreal forest (Bhupinderpal-Singh et al. 2003).

Changes with soil depth in disturbances such as drying-wetting cycles are likely to result in faster turnover of mycelium in the upper soil horizons, which may at least partly explain the depth differences seen for rhizomorphs. It is not known whether there are also substrate-characteristic differences in turnover rates. Laboratory studies show that the intensive colonization of organic patches with EM mycelium is of short duration and recedes after a few weeks (e.g. Finlay and Read 1986; Bending and Read 1995; Donnelly et al. 2004). In contrast, when mineral material from the E-horizon (60 % sand and 40 % silt) of a podzol was used, the EMM grew vigorously throughout the experiments (14 to 19 weeks; Rosling et al. 2004). However, since different fungi were used in these experiments, we cannot exclude species differences as a possible source of variation rather than substrate effects. On the other hand, a substrate dependent difference in longevity was indicated when the EMM of *Rhizopogon* colonized either small patches with organic materials or acid washed silica sand; the mycelium disintegrated within a few weeks after colonizing the organic patch while it remained vital in the mineral patch throughout the experiment (Wallander and Pallon 2005). We propose that a substrate dependent difference in turnover would be a logical consequence of the different functions that the mycelium may fulfil. Thus, in the mineral soil the main activity of EMM is to take up minerals like P and K, and additionally aid their release by the weathering of primary and secondary minerals. Weathering is a very slow process and therefore the mycelium is more persistent in these environments. In contrast, in the organic horizons, the availability of nutrients varies both temporally and spatially and the strategy is to rapidly colonize short-lived patches of labile organic matter. When the first patch is depleted, the mycelium autolyses and some of the material in the old

mycelium is translocated to other hotspots. However, further studies are needed to test if there are substrate differences in the growth habits of EM fungi. It is also unknown how much of the fine mycelium that is autolysed and reused and how much that is decomposed by other organisms.

The direct effect of grazing by soil microarthropods on EMM production may be small (see above) but indirect effects of fauna on EMM turnover and standing biomass of mycelial materials could still be of importance, e.g. grazing or disturbance caused by activities of mesofauna and larger animals may be of importance but this is unknown. Such faunal effects on EMM turnover may vary between ecosystems, along with differences in faunal and fungal communities. For example, in soils with high activity of earthworms, such as in many broad leaved forests in Europe, the physical disturbance to the mycelium is likely to be large, which would increase the turnover of EMM and reduce its standing biomass. In areas with high density of wild boar the disturbance caused by their rooting can be tremendous (Massei and Genov 2004). Hypogeous sporocarps can contribute significantly to the wild boar diet which can stimulate the production and spread of these sporocarps (Lawrynowicz et al. 2006).

Importance of mycelial C cycle for SOM formation and cycling

The amount of C invested into EMM is large and this important component of the soil biomass may potentially affect the amount of C stored in SOM in several ways. Firstly, residues of the EMM may contribute to the formation of stable SOM (Godbold et al. 2006). Secondly, the activity of the mycorrhizal roots and EMM may indirectly or directly affect the decomposition of organic materials.

Soil organic matter formation

There is increasing evidence that microbial residues play an important role as precursors for stable SOM (Ehleringer et al. 2000; Godbold et al. 2006; Wallander et al. 2011), however which residues are involved remains unclear (Koide and Malcolm 2009). The precursors may both come directly from mycorrhizal tissues (Godbold et al. 2006) or as a result of microbial turnover during the degradation of plant

necromass (Ehleringer et al. 2000). Much of the early evidence for the importance of microbial residues in formation of SOM is based on measurements of changes in isotopic ratios. In forest soils, there is an enrichment of ^{13}C and ^{15}N and a decrease in C/N ratio of the SOM with soil depth, which approaches that in the fungal biomass (Gebauer and Schulze 1991; Högberg et al. 1996; Wallander et al. 2003; Gleixner 2005; Boström et al. 2007). The enrichment of ^{13}C and ^{15}N has been used to suggest increased importance of microbial input to SOM with increasing soil depth. In fact, the $\delta^{15}\text{N}$ signature of SOM in the mineral soil approaches that of EM fungi (Boström et al. 2007), suggesting that EMM is the main precursor of this material. In support of the idea that the EMM may be important in formation of SOM, analyses of the $\delta^{13}\text{C}$ of mycelial and root in-growth cores suggested that EMM was the dominant pathway through which C entered the SOM pool (Godbold et al. 2006), contributing up to 60 % of newly formed SOM. In this work, by using in-growth cores with different mesh sizes the input from the EMM could be distinguished. A greater recalcitrance of fungal substances such as chitin compared to plant residues from cellulose and lignin has been used as an explanation for the apparent accumulation of microbial residues (Gleixner et al. 1999; Gleixner et al. 2002; Godbold et al. 2006). Other potentially important fungal substances include melanin, hydrophobins, and in AM fungi, glomalin (Treseder and Allen 2000). The assumption that fungal cell walls (chitin) may be more resistant to degradation than plant cell walls (cellulose and lignin) is based on comparison of decomposition rates of whole tissues. The decomposition rate of EM root tips in the field in a study by Langley et al. (2006) was 65 % slower than non-mycorrhizal root tips despite having a lower C:N ratio which would, in plant material, be expected to increase the decomposition rate. However, recent data question whether EM roots tips have slower rates of decomposition than non-mycorrhizal root tips (Koide et al. 2011), and the higher recalcitrance of chitin than lignin (Koide and Malcolm 2009). The higher recalcitrance of chitin than other fungal compounds has also been questioned (Fernandez and Koide 2012). Estimates of the rates of decomposition of EMM are few (Wilkinson et al. 2011; Fernandez and Koide 2012). Söderström (1979) showed that only 2–4 % of hyphae isolated from a *P. sylvestris* forest were metabolically active, suggesting that the degradation of

inactive hyphae is slow. However, EM mycelium grown in the laboratory have been shown to decompose within several weeks (Fernandez and Koide 2012), with a relationship between the C:N of the mycelium and rates of decomposition (Koide and Malcolm 2009). But in contrast, Wilkinson et al. (2011) could find no relationship between the efflux of CO₂ of decomposing hyphal material and the C:N ratio of the added necromass. They did, however, find that CO₂ efflux was dependent on the species richness of the necromass added. Clearly our current understanding of decomposition of fungal tissues is poor. A recent analysis (Schmidt et al. 2011) has questioned the importance of both composition and chemical recalcitrance of litter in the formation of SOM. These authors suggest that rather the persistence of organic matter is due to complex interactions with the soil environment such as sorption onto clay minerals and isolation in aggregates. Thus close contact of the fine hyphae of the EMM with soil mineral surfaces could explain the apparent persistence of mycorrhizal inputs in some forest soils but not in all. For example this mechanism is not applicable in most forest soils in Sweden which typically have very low clay content, without aggregate formation in the mineral soil and an organic layer on top.

We suggest that the decomposition of EMM could, in principle, follow three initial pathways: firstly, by autolysis, where by much of the hyphal material may be reused, secondly, through the activity of saprotrophic fungi and bacteria, and thirdly by grazing soil animals (Fig. 2). The relative importance of these mechanisms is unknown. Physical disturbances that disrupt the mycelium contact with the C supply of the host can cause rapid growth of saprotrophic fungi that use the dying mycorrhizal mycelium as a substrate (Lindahl et al. 2010). Such functional shifts in fungal communities, induced by disturbance, may be highly important for the nutrient release from EMM mycelia in boreal forests (Lindahl et al. 2010). The residual materials produced in the above three principal pathways may have different quality. In the first two cases, i.e. internal cycling (autolysis) or saprotrophic microorganisms, the residues are probably N poor and further decomposition may be relatively slow. Grazing, on the other hand, could leave a residue that is fragmented and relatively nutrient rich making further decomposition faster. Not all animals that feed on mycelium are grazers; Protura, one of the few groups

of microarthropods that might be specialized on EM fungi, seem to have adapted to suck on hyphae (Pass and Szucsich 2011). Whether they suck out a minor part of the cytoplasm and leave living hyphae behind, or if they leave dead membranes is unknown. Currently, we can say no more than that microbial precursors appear to be very important in formation of SOM, and that the nature of these precursors and the pathways involved are still inadequately investigated.

Heterotrophic activity

The role of EM fungi in the decomposition of organic matter is currently a subject of much debate. Laboratory experiments have shown that many ericoid and EM fungi can decompose complex organic compounds (Read and Perez-Moreno 2003) and culture studies showed that EM can mineralize cellulose and lignin, but typically only at one tenth the rate of saprotrophic fungi (Trojanowski et al. 1984).

Several recent studies have tried to identify the factors triggering saprotrophy in EM fungi, and to assess its ecological significance (Courty et al. 2007; Cullings et al. 2008; Talbot et al. 2008; Cullings and Courty 2009). They hypothesise that saprotrophic C acquisition by EM fungi may be an alternative strategy: (1) during periods with low photosynthate supply from the host, (2) during periods of high photosynthate supply from the host, but when a supplementary resource for massive mycelial production is required, or (3) during decomposition of dying tree roots (Talbot et al. 2008; Baldrian 2009). However, there is presently little evidence for any of these hypotheses. In one of the few field studies testing the saprotrophic activity of EM fungi, addition of ¹⁴C-labelled litter to an oak forest floor showed that the EM fungi did not utilize the litter C and were totally dependent on host C (Treseder et al. 2006). While generalizations are impossible due to the missing experimental data, the ecological relevance of saprotrophic behaviour of EM fungi should be placed in the context of the large sustained supply of C derived from the autotrophic plant.

While the importance of the saprotrophic capacity of EM fungi to the C cycle is unknown, there is good evidence for their involvement in degrading N and P containing organic compounds. For instance, protease and chitinase production in EM fungi has

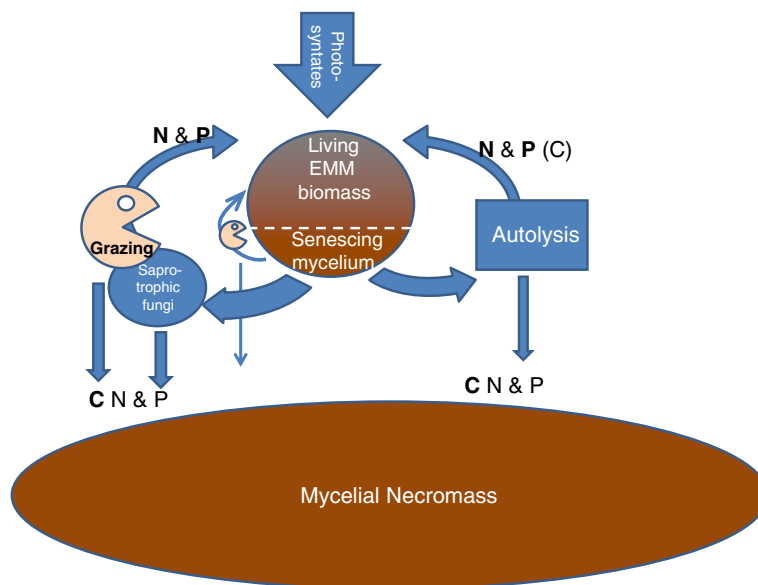


Fig. 2 Simplified scheme showing the different routes for turnover of extramatrical mycelium (EMM). Carbon for growth of the fungal biomass is supplied by plant photosynthates. The fungus is present as living hyphae (living EMM), senescing mycelium and mycelial necromass. The decomposition of the EMM could in principle follow three initial pathways: firstly, by autolysis, where by much of the N and P may be reused, secondly, through the activity of saprotrophic fungi and bacteria, and thirdly by a direct

grazing by soil animals. The relative importance of these pathways is unknown but probably of great importance for the further decomposition of the materials. In this figure the direct grazing of the EMM is smaller than grazing of saprotrophic microorganisms, since this is suggested by recent studies (see section on grazing of mycelium) and the necromass is much larger than the standing biomass

been reported in several species (Hodge et al. 1995; Lindahl and Taylor 2004; Nygren et al. 2007), which will release amino sugars and amino acids from the degradation of chitin or polypeptides. The genome of *L. bicolor* contains >100 putative extracellular proteases and several chitinases and testifies to the ability to use a variety of N-containing compounds (Martin and Selosse 2008) but the ability to use proteins and peptides varies greatly among EM fungi (Abuzinadah and Read 1986). The acquisition of organic P by EM fungi is mediated by the widespread activity of surface-bound phosphatases (Alvarez et al. 2006), although these activities appear to be largely species-dependent (Plassard et al. 2011).

Ectomycorrhizal fungi can also affect decomposition indirectly. Litter decomposition is less in plots with mycorrhizal roots than in plots without these roots (Gadgil and Gadgil 1975; Berg and Lindberg 1980). This so called ‘Gadgil effect’ is suggested to be caused by the efficient uptake of N and P by EM fungi reducing the availability of these nutrients for other microorganisms. Such a nutrient limitation may

be strengthened further by the immobilisation of N and P into a large biomass and possibly necromass of EMM (see above). Indeed, molecular methods show that forests dominated by EM trees have low abundance of bacteria (de Boer et al. 2005) and saprotrophic fungi that are primarily found in the surface litter (Lindahl et al. 2007). An alternative explanation of the ‘Gadgil effect’ is that water uptake by mycorrhizal roots and EMM reduce the soil water content causing a water limitation of decomposition (Koide and Wu 2003). The opposite effect, a stimulation of decomposition as a result of water uptake by mycorrhizal roots and EMM was found in soils with high groundwater levels (Jaatinen et al. 2008). The presence of EM hyphae can theoretically increase microbial decomposition of complex organic compounds by priming the co-metabolism of recalcitrant substrates by saprotrophic microorganisms, e.g. by the production of low molecular mass organic acids like oxalate (Kuzakov et al. 2000; Fontaine et al. 2003) or specifically affect (inhibit) the activity of certain groups of decomposers by antibiosis (Tsantrizos et al. 1991; Frey-Klett et al. 2005). Because these indirect and

direct effects of EM fungi on decomposition may act simultaneously, the net effect is difficult to calculate.

Importance for soil CO₂ fluxes and Dissolved Organic Carbon (DOC)

Soil CO₂ and dissolved organic carbon (DOC) efflux are the major pathways for C loss from soils. Partitioning of soil CO₂ efflux into autotrophic respiration (from roots, mycorrhizal fungi and rhizosphere organisms, driven by photosynthates) and heterotrophic respiration from decomposition of SOM is recognized as critical for further improvement of models of ecosystem C budgets (Hughes et al. 2008; Chapin et al. 2009). Among the autotrophic components, mycorrhizal roots often exhibit higher specific respiration rates than non-mycorrhizal roots (Colpaert et al. 1996; De Grandcourt et al. 2004). This has been ascribed to higher construction costs that lead to a higher growth respiration coefficient and cost of nutrient absorption. The maintenance cost per unit biomass is indeed higher for hyphae than for roots (Fitter 1991).

While recent studies have documented the substantial amount of C translocated to the production of EMM, the contribution of the EMM to the soil CO₂ efflux has rarely been studied under field conditions. This has been estimated using in-growth cores partly or wholly covered by fine mesh of different size, allowing or restricting the EMM growth into the core. Thus, it was estimated that the EMM contributed up to 60 % of the autotrophic soil CO₂ efflux and 25 % of the total soil CO₂ efflux in a *Pinus contorta* forest (Heinemeyer et al. 2007). A four-year study in an oak forest, attributed 18 % of the annual soil CO₂ efflux to EMM respiration (Heinemeyer et al. 2011), also showing the large seasonal and annual variability of the EMM contribution that may explain diverging findings; Moyano et al. (2008) reported lower contributions of EMM to the total soil CO₂ efflux (8 % in a spruce forest and only 3 % in a beech forest).

Dissolved organic C in forest soils is a complex mixture; most is humic substances and a small proportion, often <10 %, is compounds such as organic acids, amino acids, sugars and phenols (Kalbitz et al. 2000; Jones et al. 2004). The processes leading to its formation are still poorly understood and the contribution of roots and especially of EMM has only recently been

addressed. The amount of water extractable organic C in the mor layer of a *Pinus sylvestris* forest decreased by 45 % 1 month after tree girdling compared to the control (Högberg and Högberg 2002). This points to a direct link between assimilate transport to roots and soil solution chemistry (Giesler et al. 2007). Similarly, the water extractable organic C was several times higher in mycelial mats than in soils outside mats (Griffiths et al. 1994) and in the mineral soil, oxalate concentration was 40 times higher in mats than in non-mat soil (Kluber et al. 2010), suggesting a large contribution of EMM to DOC production. In a laboratory experiment, the DOC produced by *P. sylvestris* seedlings with EM was 50 % larger than the controls without EM (Johansson et al. 2009).

Both laboratory and field studies confirm the potential of EM to contribute to DOC in forest soil solutions, although there is a need for more detailed investigations which can be extrapolated to field conditions.

Conclusion and future research

Until a decade ago our knowledge about EMM production and its importance in C cycling was mainly based on laboratory experiments. Recent research using in-growth cores and mesh bags has demonstrated that the production of EMM is up to several hundreds of kilograms per ha per year in forests ecosystems, but the production seems to vary greatly between different forests and between years. We conclude that much of the recorded variation in EMM production can be explained by variations in the availability of C and other factors, such as N and P availability, may act mainly indirectly via the plant. Whether a change in EMM production is preceded by a change in the EM community is unknown, but perturbations that decrease the C availability seem to favour contact and smooth exploration types.

The EMM may not be an easily available food source for the decomposer community. Relatively few species of soil animals exhibit feeding preferences towards EM fungi and it is possible that animal grazing of saprotrophs is quantitatively more important than that of EM fungi, but this is an open area of research.

The lack of data on mycelial turnover rates is an obstacle to development of models of forest C cycling.

We suggest that the slowest turnover rates of the total EMM are to be found in forests where long distance types are common in the fungal community. In such forests, both the standing EMM biomass as well as its N and P retention capacity may be large.

The classification of EM taxa into exploration groups based on morphological growth characteristics may be one way to describe the complex EM communities from a functional perspective. However, the ecological role is poorly known for many of the fungal

taxa in a soil sample, and future research aiming at better characterization of these taxa is needed.

We hypothesise that the turnover of EM hyphae is more rapid in organic materials than in the mineral soil, which is motivated by the different functions the mycelium probably has in the two substrates. These two functions might be equally important as indicated from the few studies reporting EMM production rates also in the mineral soil. But this topic needs further studies.

Table 2 Critical questions for future research on the extramatrical mycelium (EMM) of ectomycorrhizal (EM) fungi

Question	Comment
Are there geographical and/or tree species differences in EMM production, standing biomass and turnover?	Much of the current knowledge comes from <i>Picea abies</i> and Scandinavia.
How much of the variation in this respect is explained by variations in the EM community?	There are likely to be large differences between different exploration types but also within a single type.
How much of the variation in this respect is explained by variations in the C:N:P stoichiometry?	Long term factorial fertilizer experiments are needed perhaps combined with defoliation experiments.
Why is not increased C availability, by elevated CO ₂ causing an increase in the occurrence of long distance types?	Perturbations that decrease the C availability for EMM growth seems to make contact and smooth exploration types more competitive than long distance types. Why not the opposite?
Are there soil depth differences in mycelium production, standing biomass and turnover?	Most studies have focussed on the upper organic layer.
Ditto for substrate differences?	We need to test our hypothesis that mycelium turnover is slower in mineral soil than in organic layers. A difference in turnover is motivated by the different possible functions of the EMM in the two substrates.
How large proportion of the production and standing biomass is rhizomorphs?	We know of only one laboratory study. This is very important to know for C-turnover models.
How large are the seasonal and between year variation in production and standing biomass?	We need studies with higher time resolution, one harvest of ingrowth bags per year is not enough.
Is the EM fungal versus saprotroph niche separation as found in a boreal forest (dominance of EM in the organic layer and mineral soil and saprotrophs in the litter) stable or has the two fungal groups different seasonal dynamics?	Only one study at one time of the year so far.
Is this niche separation the rule also in other forest ecosystems?	In many broad leaved forests, the soil mixing by earthworms may make this depth separation of fungal functional groups less clear, but this needs to be studied.
How fast is the decomposition of the mycelium?	There are probably large species differences. Mycelium grown in pure culture may differ significantly from that of a natural mycelium.
How important are soil animals for the turnover of EMM?	The picture we get from the few field studies is that the grazing of EMM may be limited but that conclusion is based on few studies. In many broad leaved forests the disturbance from earthworms may cause the mycelium to turnover more rapidly than in coniferous forests.
How important are mammals for the EMM standing biomass and turnover of EMM?	Selective grazing above as well as below ground may have great importance, e.g. the rooting of wild boar can be important.
Is EMM an important precursor for stable soil organic matter?	There is some evidence supporting this but much more work is needed on this tricky question!
What is the relation between the biomass of EMM, environmental factors and the production of CO ₂ and DOC?	So far, no study has analysed CO ₂ efflux in combination with EMM biomass.

Although the number of papers on EMM in forest soils has increased dramatically over the last decade, there are still very big gaps in our knowledge in most of the topics brought up in this review. As a guide for future research, the most important of these gaps are formulated as questions in Table 2. The EMM of EM fungi has several important roles in ecosystems. In this paper we have focused on its role in the C-cycle. There is increasing evidence that residues of EM fungi play a major role in the formation of stable N and C in SOM, calling for a greater inclusion of EM inputs into models of soil C stores in forests.

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