Water repellency, mat formation, and leaf-stimulated growth of some ectomycorrhizal fungi

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Summary. Ectomycorrhizal short roots, mycelia, rhizomorphs and mats from conifer soil were examined in relation to their hydrophobic properties. In some cases connected fruit bodies were included in the study. Mycorrhizal soils gathered from the forest and/or colonized in a laboratory rhizoscope were studied, as were mycelia in pure culture. Most forest-derived species were hydrophobic. The drought-resistant *Cenococcum geophilum* and the more ruderal and moisture-dependent *Thelephora terrestris* were both strongly hydrophilic. The hydrophobic mycelium seemed solely responsible for the water repellence properties, and adjacent soil and plant debris remained unaffected and hydrophilic. In hydrophobic fungi, mat formation was induced in the rhizoscope by hyphal contact with alder litter leaves. This stimulating effect was not found when the leaves were covered by water or when fresh, green alder leaves were used. *Thelephora terrestris* did not form such mats in vitro and spread sparsely in air pockets as well as in the adjacent water film. The possibility is discussed that many mycorrhizal fungi in the forest may partly control their soil environment via aeration created by their hydrophobia.

Key words: Mycorrhizal soil – Mats – Mycelia – Hydrophobia – Stimulation

Introduction

Ectomycorrhizal development and hyphal extension in the root environment is certainly influenced by soil composition and structure (Alvarez et al. 1979; Danielson and Visser 1989; Feil et al. 1988; Mikola and Laiho 1962; Parke et al. 1983; Stenström 1990). A reverse influence, i.e. a more or less direct impact by mycorrhizal mycelium on the soil, has also been suggested (Cromack et al. 1979; Tan et al. 1978). The latter effect might be of great importance in the forest, particularly in aged and stable stands that have a persistent and diverse mycorrhizal flora in some kind of dynamic balance

with the tree stand (Dahlberg and Stenström 1991; Perry et al. 1987).

Mat formation in mycorrhizal fungi has long been recognized (Cromack et al. 1988 and references therein; Meyer 1963), but little is known about the mat properties that may affect the environment. Cromack et al. (1979, 1988), however, examined the fauna and soil respiration of such mats and studied their chemical composition.

Cromack et al. (personal communication) have pointed out that soils extensively colonized by the three mat-forming mycorrhizal species, *Hysterangium setchellii*, *Gautieria monticola*, and *Rhizopogon* sp., all of which are associated with Douglas fir, *Pseudotsuga menziesii*, varied in their appearance even on the same site. *G. monticola* soil tended to appear drier than that of the other two, and all looked considerably drier than the adjacent non-mat-soil. However, overall soil moisture, including the mat mycelium, was not considerably different between mat soil and non-mat soil (Cromack et al. 1988). Thus, the fungus seems to interact with the nearest soil, at least in areas of heavy colonization.

I compared mats and mycelia of a few mycorrhizal conifer soils as well as some mycorrhizae in vitro under non-sterile, rhizoscopic conditions in the laboratory.

Materials and methods

A mycorrhizal mat is defined in the present paper as a limited and rather homogenous mycelium of densely interwoven rhizomorphs, strands or hyphae, all belonging to the same species, perhaps the same clone, since clones probably do not mix (Dahlberg and Stenlid 1990) and apparently excluding most other mycorrhizal fungi. The mat has a clearly visible border with the surrounding soil, be it mycorrhizal or not.

Water repellency

The mats of the false truffles *H. setchellii*, *G. monticola* and *Rhizopogon* sp. selected for examination were collected in July and August 1989 in a 50- to 75-year-old Douglas fir stand, 30 km south-

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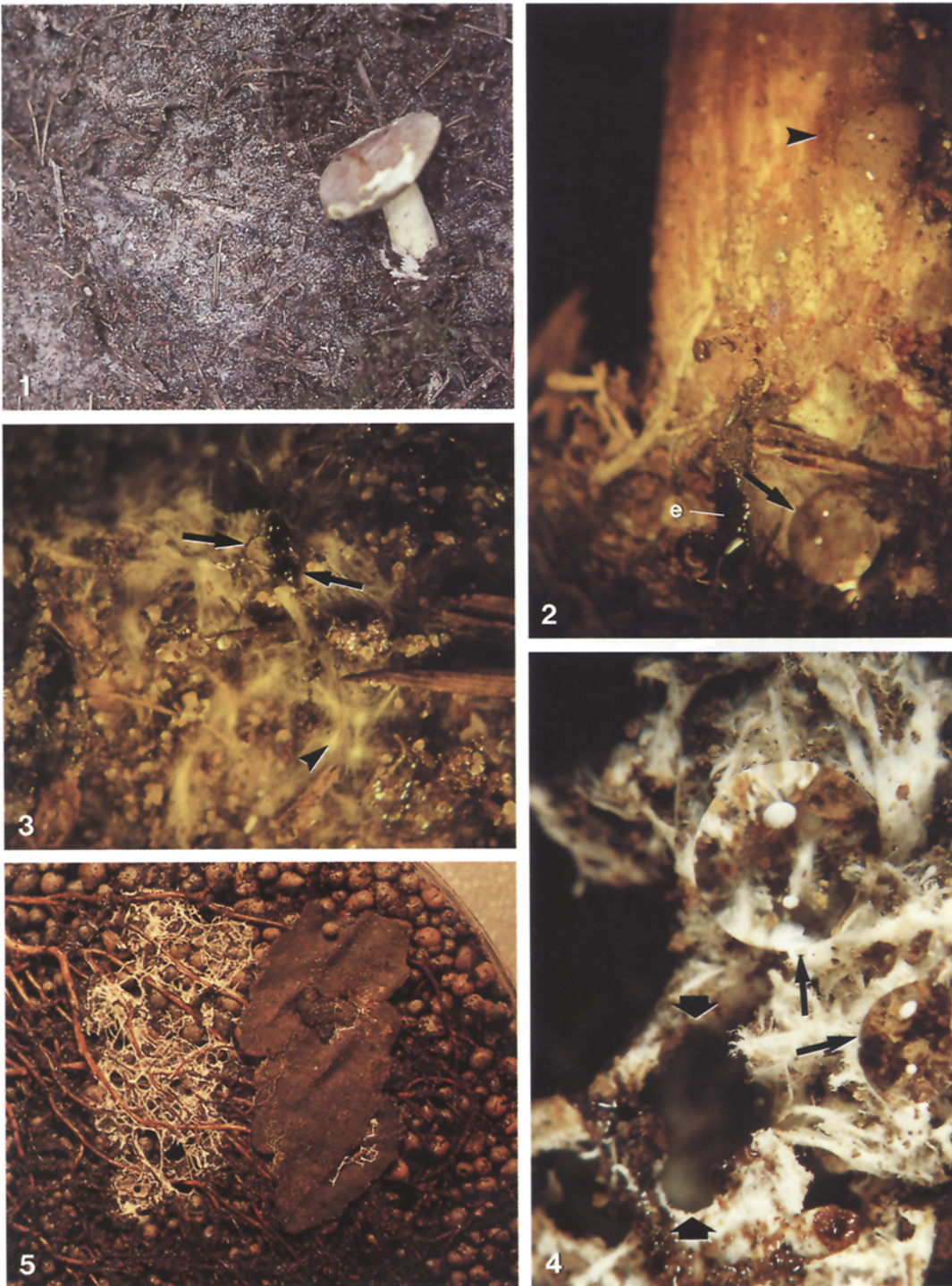
Fig. 1. Mat (white) in the thin raw-humus layer below the litter (removed) on top of the sand, and a fruit body of *Suillus tomentosus* mycorrhizal with *Pinus contorta* on a sand dune, Oregon coast. ×0.2

Fig. 2. *Suillus tomentosus* stipe base. On the mycelium of the base tip a drop of water (*arrow*) remained intact for hours, while on a stipe surface it was absorbed after 1 h (*arrowhead*). A wetted sclerotium of the hydrophilic *Cenococcum geophilum* is also seen (*e*). Approximately ×2

Fig. 3. *Pinus contorta/Suillus tomentosus* mycorrhizae (*arrowhead*) and mat reject water drops (not shown) while the *P. contorta/Cenococcum geophilum* hyphae and mycorrhizal mantel (between

arrows) quickly absorb water. The hypha of *C. geophilum* acted like a wick when in contact with water, slowly translocating water (light reflecting) to the whole mycorrhizal root tip. Approximately ×3

Fig. 4. *Hysterangium setchellii* mat. Water droplets (*stemmed arrows*) rejected by the rhizomorphs and hyphae but not by embedded soil particles (between *course arrows*). Approximately ×3.5

Fig. 5. Douglas fir root system with *Rhizopogon vinicolor* mycorrhiza in a rhizoscope. Red alder leaf section stimulates mat formation in the root substrate, which is evident upon moving the leaf piece to the side. ×1.1

west of Corvallis, Oregon, which had been used earlier for other studies of mycorrhizal mats (Cromack et al. 1988). Mats of other species and from other sites near Corvallis were also collected (e.g. Fig. 1). The mat soil was cut out in discs and fitted in standard 15-cm, plastic petri dishes with minimal disruption to the mat in the disc. The dishes were brought into the laboratory and examined immediately under a stereo-microscope. Small droplets of deionized water (0.01 μl or less) were placed on about 40 microsites per plate – on the mycelium, rhizomorphs, and mycorrhizal sheaths of roots etc. – and were left for at least 2 h at about 20° C and inspected periodically under the microscope to follow the absorption of each droplet. Between these inspections the dishes were kept covered with lids.

The hydrophobia of a fungal or other structure could *not* be determined with the naked eye by simply applying water to the top of a mat or fungus-soil mixture. There are many pitfalls. Since soil particles are always hydrophilic, the droplet must be placed solely in contact with the rhizomorphs, hyphae or other fungal structures without contact to any other particle or surface. Thus, a very thin mycorrhizal mantle of an otherwise hydrophobic fungus may allow the added water to pass by means of capillary forces through minute holes in the fungal sheath (as through a fine net of hydrophobic nylon) to the hydrophilic root surface, which lies only microns away from the water droplet. On the other hand, extremely airy hydrophilic material, such as dry sphagnum peat, may appear water repellent upon inspection with the naked eye. In a dissecting microscope, however, water can be seen (by means of light reflection) to be slowly wicked from one sphagnum leaf to another via contact points only microns wide.

The root system of an 8-week-old Douglas fir seedling was then placed on the same mat surfaces of replicate discs with the shoot sticking out through a hole in the lid. The dish, now a rhizoscope (Unestam and Stenström 1989), was kept vertically in a growth chamber with 16 h light (incandescent plus fluorescent) and at 18–22° C, in order to follow mycorrhization of the seedling from the mat.

Fruit bodies, attached mycelium and mycorrhizal roots (Figs. 1, 2) of ectomycorrhizal fungi were also collected for study, even where no proper mats were evident. Soil or rotting wood with non-fruiting mycelia or rhizomorphs, such as formed by *Piloderma bicolor* and *Cenococcum geophilum*, were also taken from a variety of sites.

Effects of leaves

Mycorrhizal seedlings grown in petri dish rhizoscopes, with brick pellets and sphagnum peat (Unestam and Stenström 1989), were also used for inducing mat formation in the non-sterile in vitro system and for studying the water-repelling properties of mycorrhizal fungi. Roots of 7- to 12-week-old rhizoscope seedlings were inoculated with agar-grown or liquid culture mycelium, or with transplants of rhizoscope mycorrhizal root tips (*Suillus bovinus, S. flavidus* and *Amanita muscaria*, all from our department collection, and *Hebeloma* sp., isolated by C. Y. Li) or spore suspensions (*Rhizopogon vinicolor, R. parksii*, both from the USDA Forest Research Laboratory Corvallis, Ore.). *Thelephora terrestris* that had spontaneously formed mycorrhiza on a *Pinus contorta* root system was also transferred to rhizoscope plants in the form of living mycorrhizae.

In September 1989, fresh red alder (*Alnus rubra*) leaves and the previous year's fallen leaves from the soil surface were sampled near Corvallis. Four to six pieces about 1.0 × 1.5 cm were cut from the leaves and placed on the root-mycorrhiza surface of the rhizoscope; the rhizoscope seedlings were incubated in the growth chamber as described above. Pieces of frozen or autoclaved leaves were also used.

Results

Water repellency

The water-repelling characteristics of different ectomycorrhizal fungi are summarized in Table 1. Most species were hydrophobic. *Thelephora terrestris, Cenococcum geophilum* and an unidentified grey fungus were hydrophilic. *C. geophilum* hyphae even served as wicks, translocating water over distances of 1 cm or more, as seen in rhizoscope soil and natural soil (Fig. 3), as well as in vitro on aseptic hyphae (on agar plates). Thus, hyphae projecting into the air from a sclerotium or colonized root (as in Fig. 3), when contacting a water droplet, slowly conducted the water to wet the root or sclerotium.

The stipe of the fruit body of *Suillus tomentosus* was less hydrophobic than the soil mycelium and strands at the end of the stipe (Fig. 2). After gentle bruising of the stipe by light pressure of a fingertip, it became even more water attracting; this again shows that hydrophobia must be examined very carefully with undisturbed material. The thin mantle of *Cortinarius* s.g. *bulbopodium* did not appear to repel water from the mycorrhizal roots, even if the hyphae in the soil did so (see Materials and methods). Thick mantles always clearly repelled water in hydrophobic fungi.

Soil particles and leaf debris in mats were consistently hydrophilic (Fig. 4) and apparently unaffected in that respect by adjacent, hydrophobic hyphae.

Mat formation stimulated by leaves

In a few days, hyphal growth was stimulated under the fallen-leaf pieces, whether autoclaved, frozen or untreated and placed on the relatively sparse mycorrhizal mycelia of *Suillus bovinus, S. flavidus, Amanita muscaria, Rhizopogon vinicolor, R. parksii* and a hydrophobic *Hebeloma* sp. Within a few weeks, miniature mats of rhizomorphs, strands and hyphae of all these fungi formed under the leaf pieces (Fig. 5). In *Telephora terrestris*, no mats or stimulation were seen. Under green leaf pieces, no mat formation or other stimulation of fungal growth was ever noticed.

During this time, the mat-forming fungi also appeared on the outer leaf surface which faced the lid. When a rhizoscope was watered, a water film was always created by capillary force between the leaf and the lid (Figs. 6, 7). Where air formed an inward bend or pocket in this film, the fungus colonized the leaf-lid interface in the pocket but never invaded the water (Fig. 6). Added water did not invade the mat-covered leaf surface, apparently due to the hydrophobic properties of the hyphae and strands. When the substrate slowly dried between waterings, the water film retracted somewhat, the pocket widened and the pocket mat expanded.

Thelephora, being hydrophilic (Table 1), formed sparse strands and hyphae on leaf surfaces but never mats. In contrast to the hydrophobic fungi, its hyphae

Table 1. Mycorrhizal fungi repelling or attracting water droplets placed on mycelium, rhizomorph/strand, mantle, and the connected fruit-body stipe base, or on mycelium (of other strains) grown aseptically in vitro on agar. Droplet remaining intact for less than 15 s (0); for about 2 min (1); remaining after 1 h (2)

Fungus/host	Mycelium/hyphae	Rhizomorph/strand	Mantle	Stipe	Fungus in vitro
Amanita muscaria[a]/Pinus contorta	2	2	2	—	2[b]
A. vaginata/Abies procera[c]	2	2	2	2	—
Cenococcum geophilum/A. procora[c]	0	0[d]	0	—	0[b]
Cortinarius s. gen. bulbopodium/A. procera[c]	2	2	0	2	—
Gautieria monticola/Pseudotsuga menziesii[c]	2	2	2	—	—
Gomphus floccosus/A. procera[c]	1	2	—	2	—
Grayish, mycorrhiza mycelium/A. procera[c]	0	0	0	—	—
Hebeloma sp.[e]/P. contorta[f]	2	2	2	—	2
Hysterangium setchellii/P. menziesii[c,f]	2	2	2	—	—
Lactarius deliciosus/Tsuga heterophylla[c]	2	2	0	2	—
Piloderma bicolor/A. procera[c]	2	2	2	—	2[b]
Rhizopogon vinicolor[e]/P. menziesii[f]	2	2	2	—	—
R. parksii[b]/P. menziesii[c]	2	2	2	—	—
R. sp./P. menziesii[c]	2	2	2	—	—
Russula sp./A. procera[c]	2	2	2	2	—
R. s. gen. emetica/A. procera[c]	2	2	2	2	—
Suillus bovinus[a]/P. contorta[f]	2	2	2	—	2[b]
S. flavidus[a]/P. contorta[f]	2	2	2	—	2[b]
S. tomentosus/P. contorta[g]	2	2	2	1	—
mixed with C. geophilum	0	0[d]	0	—	2[b]
Thelephora terrestris/P. contorta[f]	0	0	0	—	0
Xerocomus (subtomentosus)/A. procera[c]	2	2	—	2	—

[a] Swedish isolate
[b] Three to five isolates tested with each fungus
[c] From the field, Mary's Peak, Ore.
[d] Sclerotia
[e] Oregon isolate
[f] Rhizoscope with seedling
[g] Sand dunes, Oregon coast

penetrated air pockets and water without discrimination (Fig. 7). Hydrophilia was earlier observed in this fungus, *Hebeloma crustuliniforme* and *Laccaria laccata* (Stenström 1991).

About 2 months later, *Thelephora* formed fans on the lid's plastic surface (Fig. 8) regardless of water coverage. Where the fan passed beyond the lid and out of the dish, a dark-brown band formed across the fan (Fig. 8), possibly the result of phenol oxidation in contact with free air. Such fans were also found to sheath the plant stem outside the dish under the humid conditions maintained by a plastic bag placed over the plant and dish. These sheaths around the stems resembled those often seen around conifer seedling stems in the nursery that precede the formation of mature fruit bodies. However, no basidia-bearing hymenia were formed under the rhizoscope conditions. The fans and sheaths were hydrophilic and may be fruit-body initials, but they differed distinctly in structure from the premordia formed by *Laccaria laccata* and other mycorrhizal Agaricales in rhizoscopes (Stenström 1990; Unestam and Stenström 1989).

### Mats from the field, additional results

For comparison, I also studied a number of mycorrhizal mats in the raw-humus surface facing granite bedrocks (Fig. 9) or loose superficial granite moraine stones in a Swedish conifer forest (in the vicinity of Uppsala). These surfaces commonly supported mats, often 1 cm or more thick ("the rock effect"), composed of a large single-species mat or a mosaic of several small mats, each apparently consisting of a single species (Fig. 9). All of the nine mat-forming mycorrhizal species found in conjunction with a typical bed rock were hydrophobic. *Piloderma croceum* was also present (Figs. 9, 10) but seldom formed real mats. Its small, densely woven octopoid "tentacles" were mostly mixed with other mycorrhizal fungi. *C. geophilum*, which never forms mat-like or dense conglomerations outside roots and sclerotia, was nonetheless often present, interspersed within the mats or among *P. croceum* tentacles. Sometimes a sparse *P. croceum* colony covered

Fig. 6. a *Suillus bovinus* mat (rhizoscope) invading an air pocket in the water film on a previous year's fallen red alder leaf. Additional water was prevented from entering the newly occupied pocket by the hydrophobic property of the hyphae and rhizomorphs. The leaf was always hydrophilic. As the water edge slowly retracted over a period of a few days after watering, the hyphae advanced and thus widened the conquered pocket. × 2. **b** Same pocket, × 8. Note density of hyphae in the pocket periphery

Fig. 7. *Thelephora terrestris* mycorrhiza (*arrow* on short roots, the mantles of which attract water) on *P. contorta* in a rhizoscope. No mat is formed on the added red alder leaf, and hyphae and strands (*arrowheads*) grow freely through the water film band on the leaf surface. × 5
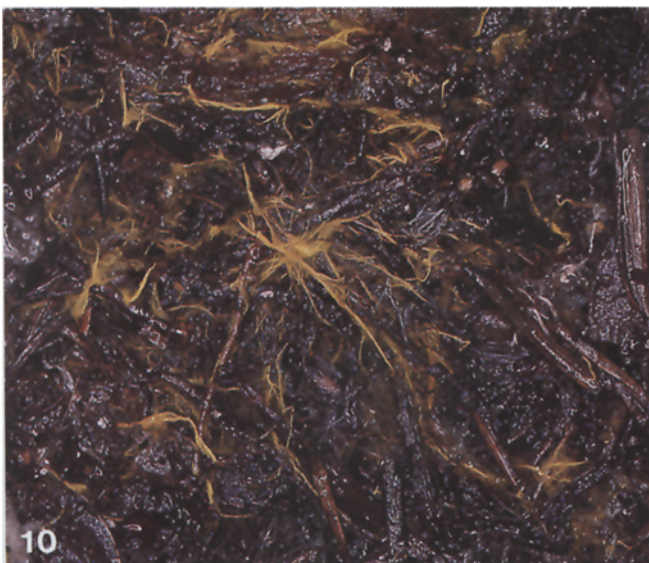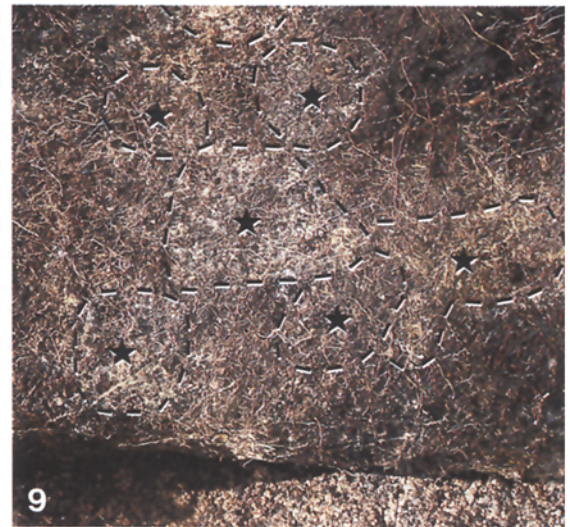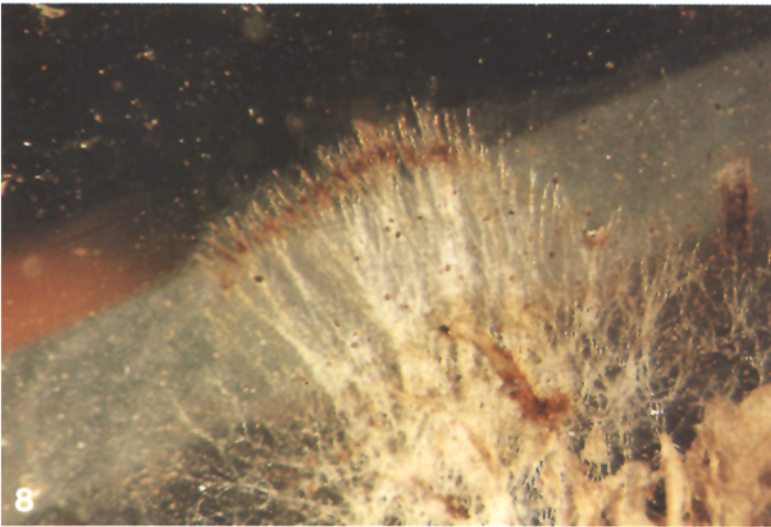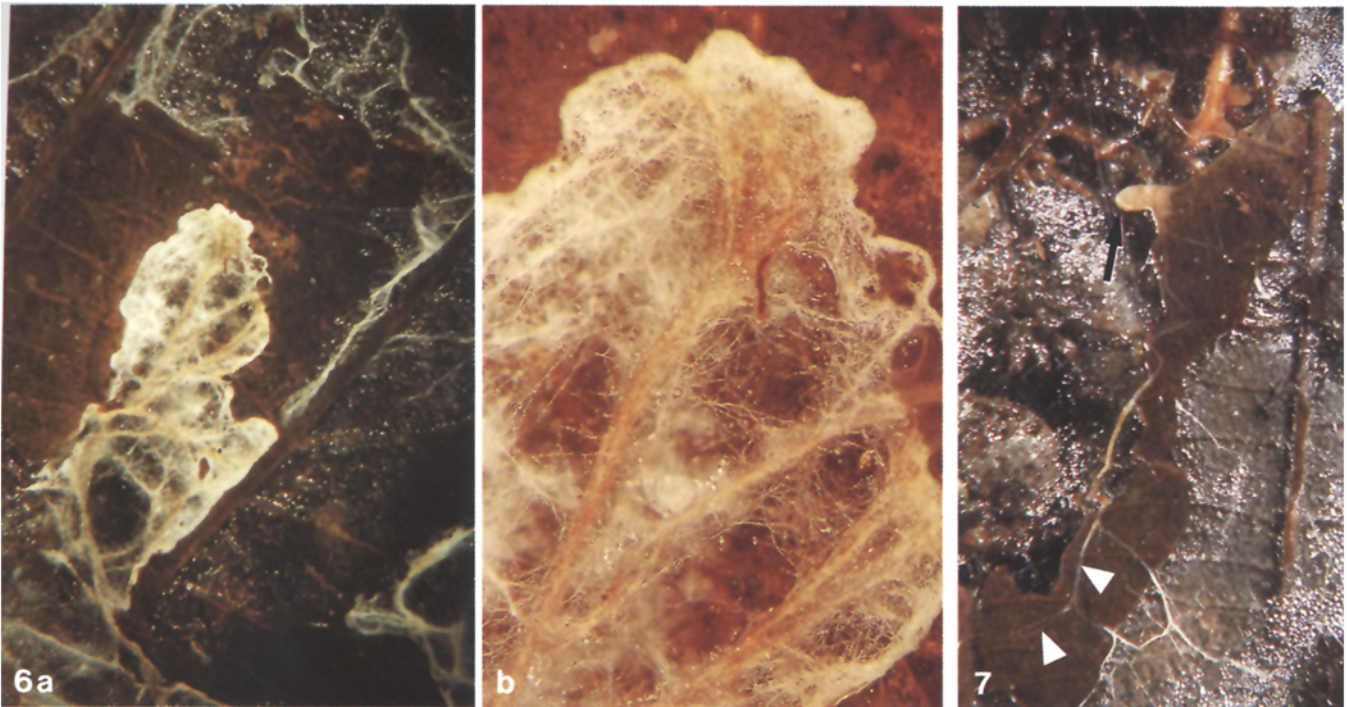
Fig. 8. *Thelephora terrestris* mycorrhiza on a *P. contorta* root system of a rhizoscope. When strands reach the edge of the rhizoscope lid, a fan but not a mat of hyphae and strands forms, producing a brown front in the driest area. Later, a sheet of brown *Thelephora* hyphae sheathed the seedling stem outside the dish (initiation of fruit body). Approximately × 14

Fig. 9. "The rock effect" in a Swedish *Pinus sylvestris-Picea abies* forest. Mycorrhizal mycelia of several kinds formed small mycorrhizal mats (each centre indicated by a *star*) in the raw humus layer (here folded away from the bed rock) adjacent to the granite rock surface seen at the bottom of the picture. The yellow *Piloderma croceum* is easily identified but does not form proper mats. × 0.2

Fig. 10. *Piloderma croceum* forms hydrophobic tentacles of densely interwoven hyphae but never mats (photo A. Dahlberg). × 0.7

1.0 m² or more. Other bed rocks and loose stones showed the same pattern and no hydrophilic mat formers were observed.

Discussion

One of the features of mats examined in the Douglas fir forest was the dry appearance of the fungus-permeated soil, perhaps more so in that colonized by *Gautieria monticola* than by *Hysterangium setchellii* and *Rhizopogon* sp. Stereo-microscopic observation revealed that water was strongly repelled by hyphae, rhizomorphs or strands of all three fungi (Table 1). In contrast, soil aggregates and mineral crusts, needle debris, miscellaneous humus particles, etc. (cf. Paul and Clark 1988) were all strongly hydrophilic and readily absorbed the added water drops (Fig. 4). So, the hydrophobic property was seen only in the fungus itself and was not "transferred" to the soil particles. Everything else seemed hydrophilic at this soil level. The black ascomycete *Cenococcum geophilum* (sclerotia, mycorrhizae and hyphae) scattered in these mats also attracted and conducted water over considerable distances. In addition, my rhizoscope studies (Fig. 6) and field mat observations suggest that the hydrophobic property of mats or patches tended to make any created air space permanent.

Hydrophobic ectomycorrhizal fungi abound in the conifer forest soils studied (Table 1 and results above). This characteristic may have evolved as an ecological strategy. It might increase the competitive capacity of mycelia adapted to reproduce and live in relatively dry conditions. This property would suppress many bacteria, protozoa and small animals, and attract other microfauna and flora (cf. Cromack et al. 1988) that prefer a drier, well-aerated habitat. These hydrophobic mycorrhizae seem themselves to prefer highly aerated soil, while hydrophilic species such as *T. terrestris, Hebeloma crustuliniforme* and *Laccaria laccata* (this paper and Unestam and Stenström 1989; Stenström 1991) do not have such a clear preference. Cromack et al. (1988) and Caldwell, Griffiths and Cromack (personal communication and abstracts of the 8th North American Congress of Mycorrhizae, 1990) showed that the overall biological activity (respiration, extracellular enzyme activity, biomass) and concentrations of oxalate and siderophores in our mats in Oregon were considerably higher than in the surrounding soil. Despite this enhanced activity the increase in needle decomposition was small (Entry, Rose and Cromack, personal communication and abstracts of the 8th North American Congress of Mycorrhizae, 1990). Thus, in a very active mat, the dense mycelium may accomplish a more or less direct uptake of nutrients from the interwoven litter (cf. Read 1987; Read et al. 1985), thereby shortening the nutrient cycle. Denitrification was lower in these mats than in non-mat soil, possibly due to the described aeration.

Microbiological activity among both saprophytes and the symbiont would of course be limited under exceedingly dry or wet circumstances in the mat, but it may be enhanced by aeration and adsorption of enzymes and other organic matter (Griffin 1972) at the "interface" between wet areas and drier parts in the mat created by hydrophobic fungi. The microorganisms and mesofauna in a dry mat, on the other hand, may depend to a great extent on carbon and water supplied in some way by the mycorrhizal strands and hyphae; the primary consumers could be particularly efficient in capturing such leached or deposited carbon. In the rhizoscope, insect larvae often eat hyphae like spaghetti (Stenström and Unestam, unpublished work).

Cromack et al. (1979) and Castellano (personal communication and abstracts of the 8th North American Congress of Mycorrhizae, 1990) found that mats (such as mine) were long-lived, were less than 1 m wide, and commonly had a limited depth of less than 10 cm. Their total coverage could be 25% or more of the forest floor surface in a Douglas fir forest. Since the mat soil may have 3–4 times the microbial biomass of the non-mat soil, probably due primarily to the mat mycelium itself (Cromack et al. 1988; Entry, Rose, and Cromack, personal communication and abstracts of the 8th North American Congress of Mycorrhizae, 1990), mats must exercise substantial control over the root systems in this forest by affecting the rhizosphere's physical, chemical and biological properties, as well as nutrient uptake. None of the mats in Oregon was, in my study, found to be associated with rocks, whereas in Sweden the association was very common. Despite this difference, both types may have the same strategy. The hydrophobic rock mat seems to be formed in association with the interface between the hydrophilic raw humus layer with its hydrophobic mycorrhizal patches and the hydrophilic rock surface. Is one of the mat's primary functions that of improving aeration?

Even after a light rain, the aerated water, reaching a partly exposed rock, seeps along the sloping, hydrophilic granite surface where the dense mat mycelium may reach it and utilize its nutrients (picked up from the air, crown leachate, soil in contact with the rock, etc.). A more sparse and diffuse mycorrhizal mycelium within the soil may not have that advantage, since a light rain might not reach it. However, the question is how the hydrophobic mycelium reaches the water and nutrients.

The mat-forming, false-truffle fungi apparently eliminated most competition by other mycorrhizal fungi, although not all; the hydrophilic *C. geophilum*, for example, survived in the mat environment. *C. geophilum* was also very often scattered among the hydrophobic mats or patches, and together with *P. croceum* in the Swedish forest floor. This unique, hydrophilic ascomycete certainly plays its own ecological role among the hydrophobic strands and hyphae. It has been found to withstand drought (Meyer 1987 and references therein) and could survive in these mats, often desiccated for months during the Oregon summer. Other fungi such as fine root pathogens and saprophytes are also possibly inhibited (cf. Gadgil and Gadgil 1975), allowing the truffle mycelium to control nutrient uptake in the mat.

After rain, the densely growing fungus should be one of the first to absorb the ions appearing from any temporarily wetted particle or stone surface. It remains to be investigated whether the hyphae are able to reach the ions by means other than via the relatively impermeable hydrophobic hyphae of the mat. Are peripheral, "pioneering" hyphae less hydrophobic (as suggested by Fig. 6b), thereby serving as the feeder hyphae of the mat? It is known that hyphal properties may vary during the life cycle in a single fungal mycelium (Pugh and Boddy 1988). The moist leaf or rock would provide a physical interphase suitable for such variation to exist, conducting water (and nutrients) without being "flooded".

The dense part of a mycorrhizal mat, such as the patch supported by a partially deteriorated alder leaf, seems able to expand (Fig. 6) during sufficiently "dry" periods and to maintain its new territory when soil is again wetted. Debris, such as leaves embedded in the soil, may provide a suitable environment for the development of such hydrophobic mats or patches, e.g. by supplying available organic nitrogen, carbon etc. from the debris and its microflora (Read 1987) and by conducting water to the entire patch. In turn, a patch (small or large) will provide aeration for its own "saprophytic" activity (cf. Haselwandter et al. 1990), thereby partially explaining mycorrhizal affinity for the "F-horizon".

The mat may develop (as seen in Fig. 6) from a single locus and expand by its own hydrophobic property (and other competitive capacities) as far as the root can support its activity and constitute a genet or ramnet. Thus, water and litter distribution may contribute to patchiness of genets and ramnets in forest soil (cf. Dahlberg and Stenlid 1991).

Ectomycorrhiza were suggested to be most prevalent in climates with periodic drought (Harley and Smith 1983). The hydrophobic tendency discussed in this paper, the capacity to create air pockets, and the inhibition of hydrophobic ectomycorrhiza when temporarily flooded (Stenström 1990; Unestam and Stenström 1989) indicate an adaptation to a relatively dry environment and may be naturally selected to maintain aerated conditions around the root in the conifer forest even during wet periods. Of course, the lipoid, hydrophobic fungal surface simultaneously protects the fungus (as well as the root) against desiccation during drought periods. I noticed that the mycorrhizal root could withstand a far drier soil environment in the rhizoscopes than the non-mycorrhizal root (hydrophilic). Furthermore, Feil et al. (1988) observed that drought could not completely stop mycorrhizal growth. Mycorrhizal rhizomorphs translocating water (Duddridge et al. 1980; Read et al. 1985) may of course do so more efficiently if the surface is impermeable to water, i.e. hydrophobic.

From a taxonomic and ecological point of view, it may be wise to include the hydrophobicity of a mycorrhizal fungus or fungal community as a part of a complete description.

Note added in proof. The stimulatory effect of red alder leaf litter was also found with *A. glutinosa* litter (N, 3.5% of dry weight), but not with *Quercus robur* (1.4% N) or *Populus tremula* (1.5% N). Consequently, enzymes liberating proteins from tannin complexes, particularly in the alder leaves, may support the growth of the mat-forming forest mycorrhizal species. This activity was actually higher among mat-forming mycorrhizal fungi in Oregon than among non-mat formers (B. Caldwell, personal communication). This can partially explain my results.

References

Alvarez IF, Rowney DL, Cobb FW Jr (1979) Mycorrhizae and growth of white fir seedlings in mineral soil with an without organic layers in a California forest. Can J For Res 9:311–315

Cromack K Jr, Sollins P, Graustein WC, Speidel K, Todd AW, Spycher G, Li CY, Todd RL (1979) Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus *Hysterangium crassum*. Soil Biol Biochem 11:463–468

Cromack K Jr, Fichter BL, Moldenke AM, Entry JA, Ingham ER (1988) Interactions between soil animals and ectomycorrhizal fungal mats. Agric Ecosyst Environ 24:161–168

Dahlberg A, Stenlid J (1990) Population structure and dynamics in *Suillus bovinus* as indicated by spatial distribution of fungal clones. New Phytol 115:487–493

Dahlberg A, Stenström E (1991) Dynamic changes in nursery and indigenous mycorrhizae of outplanted *Pinus sylvestris* seedlings in forest and clear-cut areas. Plant Soil 136:73–86

Danielson RM, Visser S (1989) Effects of forest soil acidification on ectomycorrhizal and vesicular-arbuscular mycorrhizal development. New Phytol 112:41–47

Duddridge JA, Malibari A, Read DJ (1980) Structure and function of mycorrhizal rhizomorphs with special reference to their role in water transport. Nature 287:834–836

Feil W, Kottke I, Oberwinkler F (1988) The effect of drought on mycorrhizal production and very fine root system development of Norway spruce under natural and experimental conditions. Plant Soil 108:221–231

Gadgil RL, Gadgil PD (1975) Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. NZ J For Sci 5:35–41

Griffin DH (1972) Ecology of soil fungi. Chapman & Hall, London

Harley JL, Smith SE (1983) Mycorrhizal symbioses. Academic Press, London New York

Haselwandter K, Bobleter O, Read DJ (1990) Degradation of ^{14}C-labelled lignin and dehydropolymer of coniferyl alcohol by ericoid and ectomycorrhizal fungi. Arch Microbiol 153:352–354

Meyer FH (1963) *Laccaria amethystina* (Bolt. ex Fr.) Berk. et Br., ein zur Mykorrhizabildung an der Buche befähigter Pilz. Ber Dtsch Bot Ges 76:90–96

Meyer FH (1987) Extreme Standorte und Ektomykorrhiza (insbesondere *Cenococcum geophilum*). Angew Bot 61:39–46

Mikola P, Laiho O (1962) Mycorrhizal relations in the raw humus layer of northern spruce forests. Commun Inst For Fenn 55:1–13

Parke JL, Linderman RG, Trappe JM (1983) Effects of forest litter on mycorrhiza development and growth of Douglas fir and western red cedar seedlings. Can J For Res 13:666-671

Paul EA, Clark FE (1988) Soil microbiology and biochemistry. Academic Press, San Diego

Perry DA, Molina R, Amaranthus MP (1987) Mycorrhizae, mycorrhizospheres, and reforestation: current knowledge and research needs. Can J For Res 17:929-940

Pugh GJF, Boddy L (1988) A view of disturbance of life strategies in fungi. Proc R Soc Edinb 94B:3-11

Read DJ (1987) In support of Frank's organic nitrogen theory. Angew Bot 61:25-37

Read DJ, Francis R, Finlay RD (1985) Mycorrhizal mycelia and nutrient cycling in plant communities. In: Fitter AH, Atkinson D, Read DJ, Usher MB (eds) Ecological interactions in soil. Blackwell, Oxford, pp 193-218

Stenström E (1990) Ecology of mycorrhizal Pinus sylvestris seedlings - aspects of colonization and growth. PhD dissertation, Swedish University of Agricultural Sciences, Uppsala

Stenström E (1991) The effects of flooding on the formation of ectomycorrhizae in Pinus sylvestris seedlings. Plant Soil 131:247-250

Tan KH, Sihanonth P, Todd RI (1978) Formation of humic acid like compounds by the ectomycorrhizal fungus, Pisolithus tinctorius. Soil Sci Soc Am J 42:906-908

Unestam T, Stenström E (1989) A method for observing and manipulating roots and root-associated fungi on plants growing in nonsterile substrates. Scand J For Res 4:51-58