

Succession of mycorrhizae: a matter of tree age or stand age?

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Introduction

There is a considerable amount of published evidence to support the view that a succession of mycorrhizae occurs during the development of first-rotation forest plantations (Dighton and Mason, 1985; Dighton *et al.*, 1986; Haas, 1979; Ricek, 1981). As a consequence, 'early stage' and 'late stage' fungi were distinguished, thus reflecting the observations that initial colonizers of tree roots, such as *Laccaria* and *Hebeloma* species, are followed or replaced 6–10 yr after planting by, *e.g.*, *Lactarius*, *Amanita* and *Russula* species (Mason *et al.*, 1982; Last *et al.*, 1983). In contrast to the ability to form mycorrhizae under axenic conditions, 'late stage' fungi did not infect seedlings in non-sterile soils after afforestation of farmland and in soil cores with fungal inoculum (Mason *et al.*, 1983; Deacon *et al.*, 1983).

The physiological status of trees of different ages as well as changes of the substrate and nutrient resources during stand development are considered to be the most relevant factors to explain the temporal and spatial succession phenomena

(Dighton and Mason, 1985). However, tree age and substrate change simultaneously after planting, and it is difficult to decide which factor may be more important. Studies in established stands with nearly constant soil conditions and naturally regenerated trees should provide information to answer this question.

Materials and Methods

Samples of mycorrhizae were taken from 2 stands of *Picea abies* (L.) Karst. in the Black Forest near Freudenstadt. Stand and site descriptions have already been given by Blasius *et al.* (1985).

About 150 1 yr old seedlings and about 100 8–10 yr old trees were removed entirely from the soil and stored at 4°C. Mycorrhizae were dissected from the soil in running water and were washed further in distilled water.

Mycorrhizal types were selected and photographed under a stereoscopic dissecting microscope. Afterwards, they were fixed in glutaraldehyde with cacodylate buffer. Embedding was carried out with ERL (Spurr, 1969) after post-fixation with osmium tetroxide and en bloc staining with uranyl acetate. Serial longitudinal and even transverse semi-thin sections (0.5 μm) for light microscopy were cut with

Table I. Characterization of the mycorrhizae.

Macroscopic features	
color	a: color of the mycelium b: developmental stage of the root and related degree of tannin-storage
morphology	<i>e.g.</i> , ± slim; ± club-like swollen; elongated to sinuate (<i>e.g.</i> , ± typical for <i>Cortinarius</i> species)
surface	<i>e.g.</i> , ± smooth; ± wadding-like, caused by large numbers of single hyphae; rhizomorphs present
degree of ramification	± regular ramification; ± cluster-like concentration of mycorrhizal tips; 'Knollenmykorrhiza' (mainly occurring in <i>Pinus</i> species)
Light microscopy	
emanating hyphae	presence of clamp connections cell wall characteristics like crystals, protuberances and incorporated structures lactifers
rhizomorphs	dimensions structure: <i>e.g.</i> , presence of central elements with enlarged diameter
hyphal mantle	thickness (± variable) architecture: analysis by transverse, radial and mainly tangential sections a: 'synenchyma' = 'pseudoparenchyma' (<i>e.g.</i> , polygonal; epidermoid or puzzle-like) b: 'prosenchyma' and c: intermediate patterns matrices: dimension and structure cystidia: shape, dimension, septation lactifers
Hartig-net	structure [± uniform (Blasius <i>et al.</i> , 1986)] diameter of hyphae } ± dependent upon the age number of layers }
Ultrastructure	
porus-type	
cell wall characteristics	
matrices	
amount of nuclei (even LM-staining methods)	

glass knives and stained with new fuchsin–crystal violet. For electron microscopy ultra-thin sections (80–100 nm) were cut with a diamond knife and stained with lead citrate.

Fresh material of each type was investigated in order to detect alterations of structural features during the fixation process.

The distribution of the mycorrhizal types in relation to tree age was tested. A statistical quantification was not carried out because of methodological difficulties.

Results

Characterization of the mycorrhizae

17 mycorrhizal types (3 ascomycetes and 14 basidiomycetes) were distinguished by the features given in the above, annotated checklist (Table I).

Distribution of the types in relation to tree age

On both stands, all types were detected on seedlings as well as on 8–10 yr old trees. One *Lactarius*-type was very abundant on seedlings and was recognized by the presence of lactifers in the mantle. Furthermore, *Russula ochroleuca* (Pers.) Fr. (Agerer, 1986) was found to form mycorrhizae with seedlings.

Discussion and Conclusion

The investigations revealed, that no differences in the occurrence of mycorrhizal types in relation to tree age were apparent. The distribution should be different if succession depends upon the tree age. Typical 'late stage' fungi, like *Lactarius* and *Russula* species, seem to be able to form mycorrhizae with seedlings in established ecosystems. This observation is concordant with findings of Thomas *et al.* (1983) who detected *Lactarius rufus* (Scop.) Fr. and *R. ochroleuca* on naturally regenerating seedlings of *Picea sitchensis* (Bog.) Carr. These observations confirm the view that succession of mycorrhizae after afforestation of farmland is mainly caused by changes of the substrate and nutrient resources. Dighton and Mason (1985) discussed the changes from r- to K-strategies during stand development as a complex of factors which reflect the adaptation of different species to varying environmental conditions.

However, the interpretation is complicated by the fact that mycorrhizal fungi likely are in contact with both mature trees and seedlings of stands with natural regeneration. Intra- and interspecific transfer of carbon and nutrients between hosts has been proven (*e.g.*, Read *et al.*, 1985;

Woods and Brock, 1964). By this, the carbon demand of late stage fungi which form mycorrhizae with seedlings may be satisfied by older trees. Fleming (1984) discussed the possible role of mature trees as a food base for 'late stage' fungi which colonize seedlings.

Studies on the succession of mycorrhizae after afforestation of areas which were recently deforested should provide further information about the physiological role of substrate or tree age in relation to succession phenomena. Ricek (1981) found differences in the succession of fruit bodies after afforestation of meadows and clear cut forest stands. Fungal species, which appeared late in the succession chain after afforestation of meadows, were observed to be early mycorrhizae formers when afforesting previous forest soils. The author concludes that these species, representing 'late stage' fungi, may have persisted saprophytically and were able to infect seedlings after planting.

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