

Chapter 1

Plant Associated Soil Micro-organisms

Mika Tarkka, Silvia Schrey, and Rüdiger Hampp(✉)

1.1 Micro-organisms of the Rhizosphere

1.1.1 *The Rhizosphere*

Roots constitute important plant organs for water and nutrient uptake. However, they also release a wide range of carbon compounds of low molecular weight. These can amount to between 10% and 20% of total net fixed carbon (Rovira 1991) and form the basis for an environment rich in diversified microbiological populations, the rhizosphere (Hiltner 1904). The rhizosphere has been defined as a narrow zone of soil which is influenced by living roots. Bacteria are an important part of micro-organisms inhabiting this ecological niche. Abundance and turnover of rhizobacteria are regulated by microfaunal grazers such as protozoa. Consequently, beneficial effects of protozoa on plant growth have been related to nutrients released from consumed bacterial biomass. This has been termed ‘microbial loop’ (Bonkowski 2004) and works as follows: organic compounds released from roots stimulate bacterial growth. Bacteria can solubilize nutrients from the mineral soil layer, but will sequester them. Consumption of bacteria by soil protozoa and nematodes will then liberate nutrients, which in due course will become available for plants. Fungi form another important part of the rhizosphere. Most terrestrial plants develop symbiotic structures (mycorrhiza) with soil-borne fungi. In these interactions the fungal partner provides the plant with improved access to water and soil nutrients due to more or less complex hyphal structures, which emanate from the root surface and extend far into the soil. The plant, in return, supplies carbohydrates for fungal growth and maintenance (Hampp and Schaeffer 1998; Smith and Read 1997). Due to leakage and the turnover of mycorrhizal structures, these solutes are

R. Hampp
Botanical Institute, Physiological Ecology of Plants, University of Tübingen,
Auf der Morgenstelle 1, 72076 Tübingen, Germany
e-mail: ruediger.hampp@uni-tuebingen.de

also released into the mycorrhizosphere where they can be accessed by the other micro-organisms. It has been shown that microbial communities within the rhizosphere are distinct from those of non-rhizosphere soil (Curl and Truelove 1986; Whipps and Lynch 1986).

1.1.2 Fungi: Symbionts, Saprotrophs, Pathogens

Plants and soil communities are mainly linked by the provision of photoassimilates by the plant. In addition, plants supply organic matter by litter such as leaves, or by root exudates.

For nutrient recycling and supply to plants, symbiotic and saprotrophic fungi are essential components of the rhizosphere.

1.1.2.1 Arbuscular Mycorrhiza (AM)

With regard to symbiotic root fungus interactions, two major types exist; the arbuscular mycorrhiza (AM) and the ectomycorrhiza (ECM). They differ in morphological features and in the type of fungi. AM are typical for most herbaceous plants, including crop plants and also for the majority of tropical tree species (Janos 1987). In addition, AM constitutes the most ancient form of mycorrhiza documented by fossil findings (Redecker et al. 2000), which can explain its global occurrence.

The fungi involved are obligate biotrophs. They belong to the order of the Glomales (Glomeromycota). Typically, they form extra- and intraradical mycelia, as well as inter- and intracellular hyphae, coiled hyphae, arbuscules, vesicles, auxiliary cells close to or within the cortex of the host root. Most of these structures increase the effective surface area for solute exchange (see also Smith and Read 1997).

Colonization of fine roots by AM fungi starts with the formation of appressoria on the surface of epidermal cells and is then followed by the development of penetration hyphae. After successful epidermal penetration, hyphae invade the apoplast of the root cortex. Typical arbuscules are formed as intracellular terminal structures of trunk hyphae.

Gallaud (1905) described two major structural classes of arbuscular mycorrhizae, which he named *Arum*- and *Paris*-type, after the plants in which they were first described (for review see Smith and Smith 1990). In the *Arum*-type the fungus spreads relatively rapidly in the cortex via intercellular air spaces (Brundrett and Kendrick 1990). Short side-branches of the fungus penetrate the cortical cells and ramify dichotomously to produce characteristic arbuscules. Hyphal coils may be formed, but they are usually not a major component of the intraradical mycelium. In the *Paris*-type, colonization of the roots is characterized by extensive development of intracellular coiled hyphae, which spread directly from cell to cell within the cortex. From these coils arbuscules can be developed, and there is very little, if any, intercellular growth. As a consequence, the growth rate of the infection units within the root is much slower than for the *Arum*-type (Smith and Read 1997).

Investigations of Barrett (1958) indicated that the host, not the endophyte, determines the structural class of AM mycorrhiza. A similar conclusion was drawn by Gerdemann (1965), who showed that the same fungus can form a *Paris*-type mycorrhiza in *Liriodendron sp.* and an *Arum*-type in *Zea mays* plants.

1.1.2.2 Ectomycorrhiza (ECM)

ECM establishes with fine roots of autotrophic trees and shrubs, especially of the families *Betulaceae*, *Pinaceae*, *Fagaceae*, *Salicaceae* and *Dipterocarpaceae* (Read 1991; Smith and Read 1997). The fungal partners belong to the basidiomycetes and ascomycetes. Typically, hyphae form a mantle of varying thickness around the fine roots. From there, hyphae or more specialised hyphal aggregates (rhizomorphs) radiate into the substrate in order to exploit nutrients and water. Mantle hyphae also extend into the apoplast of the root cortex. Here, they form highly branched networks, which establish a large surface area for solute exchange. This structure is called the Hartig net and constitutes the interface for the exchange of photoassimilates, soil water and nutrients between the host plant and its fungal partner.

Communities of ECM trees are dominating in the boreal and temperate plant biomes and are also important in certain tropical rain forest environments (Read 1993). In these diverse plant formations, ECM fungi are best adapted to mobilise the sparse heterogeneous resources in phosphorus and especially in nitrogen from the litter layer. This function is ensured by a high diversity of fungi, which has been estimated between 5000 and 6000 species (Molina et al. 1992). This high biodiversity of ECM fungi corresponds to a broad range of capabilities for the uptake of specific forms of organic and inorganic nitrogen and phosphorus, allowing the development of tree vegetations with low plant species diversity despite the above-mentioned heterogeneity and limitation of nutrient resources (Read 1993).

Due to competition for photoassimilates, mycorrhiza-forming fungi can become protective for their source plant by preventing pathogenic fungi or nematodes from root colonization (Graham 2001). However, some can also become highly parasitic (Jonsson et al. 2001).

1.1.2.3 Saprotrophs

While interactions between wood-decay fungi themselves have been reviewed by Boddy (2000), there is only little information about their interaction with mycorrhiza-forming fungi (Leake et al. 2002). In a forest ecosystem both types of fungi rely on a large supply of organic carbon, either from photosynthesis (symbiotic fungi) or from wood and other litter (saprophytes). Both types of fungi can explore large volumes of soil due to their ability to form hyphal aggregates (rhizomorphs), which allow for long distance solute transport (Finlay and Read 1986a,b; Boddy 1993, 1999). Except for the difference in carbon source, their strategies for nutrient



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