Multi-author Review

Structure, function and ecology of the mycorrhizal symbiosis

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Introduction

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In the soil, plants come into contact with the environment through a kind of interface, closely surrounding all the active root tips: the so-called 'rhizosphere', with its rich microflora. Some fungi of this microflora are specialized to colonize the plant root and to form with it a symbiotic organ, the so-called 'mycorrhiza'. In the mycorrhizal symbiosis, both root and fungus sacrifice some of their independence and form a unity that controls the metabolism of plant and fungus alike. There are different types of mycorrhiza, distinguished primarily by the morphology of the contact zone between the partners. The high degree of differentiation of this contact zone suggests a long co-evolution of the symbiotic partners. The symbiosis is not carried through the seeds, however, so that it must be re-established in each plant seedling after germination. The specificity of many mycorrhizal fungi is fairly low, so that one hyphal network may connect not only several plants of the same plant species but also many different plant species at a given location.

The mycorrhizal symbiosis is not a rare speciality among plants but is characteristic of most land plants, including many crop plants. Although its existence has been known for over a century, its study is nevertheless still a neglected area of botany, and students of well-established areas like plant physiology and plant ecology too often fail to consider the potential significance of mycorrhizas in their field of study. The present multi-author review attempts to demonstrate the importance of mycorrhizal symbiosis for plants. Its aim is not to provide a synopsis of all research on mycorrhizas, since several excellent monographs and reviews are available[1–5]. Rather, it combines presentations of several current approaches with the aim of putting the functional role of mycorrhizas in ecosystems into perspective.

The starting point is provided by an overview by Dexheimer and Pargney of the variety of mycorrhizal morphologies, focussing on the functional interface between roots and mycorrhizal fungi. Martin and Hilbert review the physiology of early mycorrhizal development and characterize the strong mutual influence of the partners on each other's metabolisms. Gogala discusses the role of plant hormones in the readjustment of plant metabolism in the symbiotic organ. Plassard et al. compare nitrogen assimilation by the partners when living separately and in symbiosis. They are particularly interested in the question of ion balance and pH regulation in the symbiosis, as influenced by ammonium or nitrate assimilation, and in the resulting changes in soil conditions.

The remaining contributions concentrate on the ecological significance of the mycorrhiza, both with respect to nutrient acquisition (autecology) and to biological interactions with other organisms (synecology). With regard to nutrient acquisition, optimization of root architecture is a major strategy to exploit immobile mineral ions like phosphate. Mycorrhizal fungi extend the plant's possibilities for exploring the soil. Fitter presents a cost-benefit model to estimate the optimal intensity of root colonization by mycorrhizal fungi. Hetrick discusses the influence of mycorrhizal symbiosis on root architecture. Another possibility for improving nutrient acquisition is the exploitation of soil resources not immediately available to plants, for example nutrients in organic forms. Dighton reviews the significance of mycorrhizas for the recycling of organic nutrients from plant litter and the relationship between mycorrhizal and saprophytic fungi. The rhizosphere in general has a higher level of biological activity than the remaining soil. The mycorrhizal symbiosis has a dominant influence on the rhizosphere. Garbaye uses the term mycorrhizosphere to stress the importance of the mycorrhiza for the microflora in its immediate surroundings, and discusses the biological interactions among them. Even when the mycorrhizosphere is included, the consideration of single plants in association with mycorrhizal fungi falls short of reality in ecosystems where several different species of plants grow in close association as, for example, in forests or heaths or in other terminal stages of succession. In these ecosystems, many plants of the same or of different species may be connected by a common network of hyphae. Read presents an integrated view of mycorrhizas in ecosystems and considers the possibility that such hyphal networks integrate biological activities in the ecosystem by reallocating nutrients and even assimilates between different plants, shedding new light on the intriguing question of how plants co-exist in communities.

In the concluding chapter, we (Pankow, Boller and Wiemken) attempt an evaluation of the ecological significance of mycorrhizas and propose that their main importance is not in the productive ecosystems in early stages of the succession, although they contribute to nutrient acquisition in these stages, but in protective ecosystems in the final stages of succession, where they keep nutrient cycles closed and prevent loss of resources from the entire ecosystem.

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Comparative anatomy of the host-fungus interface in mycorrhizas

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Summary. There are several types of mycorrhizal symbiosis (ectomycorrhiza, endomycorrhiza, ectendomycorrhiza), and the interfaces between the host-plant and the fungal symbiont have different organizations. The interfaces between the partners are always limited on the one side by the fungal plasmalemma and on the other side by the plasmalemma of the host plant or the perisymbiont membrane derived from it. The cytoplasms of the partners are therefore separated by a mixed apoplast consisting of a fungal wall and a host wall or an apposition layer.
Key words. Ectomycorrhiza; endomycorrhiza; ectendomycorrhiza; interfaces; plasmalemma; matrix; perisymbiont membrane; mixed apoplast.

The confrontation of two organisms in a parasitic or symbiotic association leads to the formation of a contact zone or 'interface' composed of elements derived from both partners, through which most of the interactions and exchanges between the partners take place. Mycorrhizal symbioses, in particular, develop interfaces of widely different organization which are characteristic of the different types of mycorrhiza (ectomycorrhiza, endomycorrhiza, ectendomycorrhiza).

In this article we discuss the different mycorrhizal interfaces, firstly those of vesicular-arbuscular (VA) mycorrhizas, then those of other endomycorrhizas (ericoid mycorrhizas, orchid mycorrhizas, *Terfezia* mycorrhizas) and of ectomycorrhizas, and finally the intracellular structures of *Monotropa* ectendomycorrhizas.

Interfaces of vesicular-arbuscular mycorrhizas

Vesicular-arbuscular mycorrhizas are the most widespread among plant species. The fungi involved are Zygomycetes belonging to the family of Endogonaceae. The fine structure of these mycorrhizas is well known and there are numerous ultrastructural studies, as summarized in recent reviews [9, 30, 54, 89].

The fungus produces a network of intercellular hyphae within the root cortex. From the hyphae of this network, branches penetrate the cell wall and form ramified intracellular structures, the arbuscules (fig. 1). In some host-plants, cells of the superficial layers of the cortex contain coils of large hyphae. Often the hyphae dilate to produce ampoules with thickened walls, the vesicles.

Both partners of the symbiosis may, to a certain extent, modulate mycorrhizal morphology [9, 16, 49, 66, 67]. For example a given endophyte associated with different host-plants may form a mycorrhiza with or without coils, and with or without a network of intercellular hyphae. Components of the host cell wall and in particular phenolic compounds appear to be responsible for this modulation [10].

Interfaces of the intercellular hyphae

In most VA mycorrhizas, the hyphae of the intercellular network are located in the spaces between the cortical cells where they are in close contact with the outer surface of the walls of the cells and sometimes penetrate between two cells by separating the middle lamella. This network presents an organization similar to the one of the ectomycorrhizal Hartig net [67].

In some mycorrhizas (Jeanmaire, personal communication), the outer surface of the walls of the cortical cells is coated with a layer of a dense polysaccharide which prevents any direct contact between the hyphae and the walls. The endophyte cell walls produce notched protuberances which pervade this layer to anchor the hyphae to the wall (fig. 2).