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The significance of mycorrhizas for protective ecosystems

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Summary. On the basis of the reviews presented in this issue, the ecological significance of mycorrhizal symbioses is discussed. Mycorrhizas may have some importance in the acquisition of mineral nutrients during the productive phase of ecosystems in early stages of succession, but their main role is played during the protective phase of ecosystems in the final stages of succession when most resources are incorporated into biomass. In these successional stages, mycorrhizas short-circuit nutrient cycles by directly reacquiring nutrients in organic form from plant (and fungal) litter, and they may reallocate resources between different plant individuals, preventing loss of resources from the entire ecosystem.

Key words. Ecosystem; mycorrhiza; symbiosis.

Introduction: Productive and protective ecosystems

The entire biomass on earth, if it were spread evenly over the planet's surface, would form a thin film of less than 1 mm in thickness[14]. The living organisms forming this biomass render the earth hospitable because they do not occur in an isolated film, but interact with the atmosphere, hydrosphere and lithosphere, generating climate and soil[14]. In this way, the biosphere can be considered to be a web of dynamic interactive structures, powered by solar energy, with their own laws of space and time, of stability and change.

Today, the biosphere is in danger in two senses: directly, through outright destruction and through the monopolization of many areas for 'productive' use with single plant or animal species according to criteria of maximal yield; and indirectly, through the burden of waste transferred for disposal from the destroyed or 'productive' areas to the shrinking 'unproductive' areas, a burden that may overload the protective capacities of these areas[22]. This consideration brings the endangered *protective ecosystems*[22] into focus. Some people may think that such protective ecosystems may be investigated and 'rationalized' with the same approaches that promoted progress in *productive ecosystems.* However, we concur with Odum[22] that protective and productive ecosystems are different and cannot be approached in the same way, as illustrated in the following comparison of their properties.

Productive ecosystems, typical of pioneer stages in secondary successions, are characterized by the rapid transformation of environmental resources (light, carbon dioxide, water, mineral nutrients) into biomass. This includes rapid uptake and assimilation of nutrients from soil. Ruderals are well adapted to the conditions of productive ecosystems, which include high availability of nutrients from the soil as well as a high frequency of disturbance. Most crop plants have been developed by breeding from ruderals, since arable land is subject to the same set of conditions[3], and the principal aim of crop breeding consists in improving the already preadapted strategy of ruderal plants to grow rapidly and to mature quickly on the basis of abundant mineral resources. In contrast, protective ecosystems, typical of the terminal stages of succession leading to the climax, have incorporated most of the available mineral resources into biomass and use the remaining resources (light, carbon dioxide, and water) mainly for maintenance and protection from perturbations[22]. They contain long-living plants which grow slowly, set fruit after a long juvenile period, frequently coexist with a large number of other species, and create, control, and stabilize to a large extent their own microclimate and soil conditions. In these ecosystems, acquisition of mineral nutrients from the soil is of little importance in comparison to the recycling of nutrients within the existing biomass, preferentially in closed cycles with little loss[11]. Hence, productive and protective ecosystems, representative of early and late stages in successions, present rather different constraints for their colonists.

Hitherto, mycorrhizal research has very often been guided by the well-proven approach to crop plants of productive ecosystems, usually focussing on the behavior of an individual plant – preferably a fast-growing seedling – in association with an individual fungus. This approach indicates that mycorrhizal symbiosis contributes to nutrient acquisition from the soil, and culminates in the idea of using mycorrhizal fungi as 'bio-fertilizers'. However, the combination of reviews in this issue brings an additional and different aspect into focus, namely the function of mycorrhizas in interactions between different plants and fungi in species-rich protective ecosystems. In the following, we want to develop the proposition that mycorrhizal symbiosis is of the greatest importance as an integrating network for plants and fungi living in protective ecosystems.

Distribution of mycorrhiza according to habitats and stages of succession

On the basis of paleontological and taxonomical studies, Trappe[28] concludes that the conquest of land was possible only as a common achievement of plants and fungi. In this view, plants which do not form mycorrhizas appear to represent a secondary adaptation to ecosystems in which interaction with the symbiont is no longer profitable, as for example in ecosystems with frequent unpredictable catastrophes. In such ecosystems, mineral resources are abundant but the time for growth is limiting, factors which favor a flora of rapidly changing, short-lived plants called ruderals.

In a successional sequence, the vegetation closes some time after recolonization. Resources become scarce and favor economizing, long-lived plants. The detailed successions depend on the levels of the different resources as well as on biogeographical conditions. Although each succession is in a certain sense unique, certain general trends can be recognized:

1) The ecosystem increasingly comes under biological control, and the niche of each plant is increasingly determined by neighboring plants, leading to an increased niche diversity.

2) The ecosystem develops towards more and more economical usage of the increasingly scarce external resources, and the plants show improved efficiency at the expense of potential capacity, or high performance at low supply and low performance at high supply.

3) In the course of succession, the duration of the life cycles of the plants becomes longer and the importance of their maintenance metabolism increases, leading to a reduction of their relative growth rates.

4) The ecosystem becomes increasingly stabilized in a dynamic equilibrium in which the remaining disturbance is increasingly due to biological factors, in particular to the death of plants and plant parts, which opens the way to new growth and development.

In recent years, the role of mycorrhizas in plant succession has come into focus[4, 25]. The non-mycorrhizal ruderals of the initial stages of succession are initially replaced by facultative mycotrophs and finally by obligate mycotrophs[15]. This succession, which clearly shows the increasing importance of the mycorrhizal symbiosis in the progression from productive to protective ecosystems, is determined to a large extent by the quality and quantity of diaspores of mycorrhizal fungi present in the soil and dispersed by animals like insects and mice but also by the wind[2], and by the build-up of mycorrhizal networks capable of rapidly colonizing any newly germinating plant[24].

It is interesting to realize that in the final stages of succession, different types of mycorrhiza are dominant in different climates. As the final stage of successions changes from grassland to deciduous forest, boreal forest and heath along the gradient from warm-dry to cold-wet climates, the dominant type of mycorrhiza changes from VAM (vesicular-arbuscular mycorrhiza) to ecto- and ericoid mycorrhiza[4, 25]. The fungal partner in the evolutionarily 'older' VAM is more dependent on its host plant than it is in the 'younger' ecto- and ericoid mycorrhizas[18]. On the other hand, the host plant depends more on the fungal partner in ecto- and ericoid mycorrhizas than in VAM, and the mycorrhizal symbiosis is therefore particularly important for the plants in boreal and deciduous forests and heath ecosystems[4].

Morphological and physiological aspects are important in our understanding of the significance of mycorrhizal fungi for the plant. At the morphological level, mycorrhizal fungi improve soil structure, exploit more soil space per biomass than do roots, invade soil compartments unavailable to roots or root hairs, and bridge plants of the same or different species[26]. At the physiological level, mycorrhizal fungi mobilize nutrients unavailable to non-symbiotic roots[4] and may protect the root from toxic metals and pathogens[7, 25]. In addition, the host root changes its physiology in response to the mycorrhizal symbiont because of an altered partitioning of assimilates and minerals and because of hormonal influences[9].

Architecture of mycorrhizas

The architecture of mycorrhizas is of central importance for their function. A large part of each mycorrhiza consists of the soil mycelium. It has been estimated that the majority of the fungal hyphae in soil comes from mycorrhizas[24].

Since many mycorrhizal fungi have a relatively broad host range, the hyphal network of one fungal individual can be attached to several plant species, permitting at least in theory a degree of independence from the life cycle of a single host plant. In addition, hyphae can survive even upon separation from the plant, particularly in dry soil[27]. The soil mycelium of VAM with its associated flora can be decisive for soil structure[20]. It increases the stability of soil aggregates and thereby improves soil aeration and water permeability while reducing erosion. In addition, the soil mycelium increases water availability for the roots since hyphae can invade smaller micropores than root hairs. This also leads to an increase in water desorption under field conditions[12].

Particularly important is the increase in exploited soil volume due to the soil mycelia of mycorrhizas. A simple calculation shows that per unit biomass, hyphae, which have a diameter about 100-fold smaller than fine roots, can produce 100 times more surface and 10 000 times more length in comparison to roots. Assuming an approximately 10-fold higher metabolic cost for hyphae compared to roots, this means that the plant investing in hyphae instead of roots can obtain 10 times more surface and 1000 times more length of absorbing organs. In a model calculation, Fitter[5] assumes equal allocation of assimilates to fungus and root in the VAM of herbaceous plants and finds that the model predicts an approximately 5-times-increased capacity for uptake of mineral nutrients, as compared to a non-mycorrhizal situation where the root gets all assimilates.

Considering the architecture of the whole plant, mycorrhizal symbiosis allows for a reduction in assimilate allocation to the roots, resulting in reduced root biomass and either increased shoot growth or increased storage of assimilates or secondary metabolites. In more general terms, it increases the potential for adaptations in situations of fluctuating nutrient supply. According to Chapin[3], wild plants typical of late succession stages are adapted to a predominant paucity of nutrients and react to a sudden surplus of nutrients primarily with an increase in storage, while ruderals, typical of early succession stages, and also cultivated plants, are adapted to a high level of nutrients and react to fertilization with increased growth.

A particularly interesting aspect is the influence of mycorrhizal symbiosis on root architecture. On the basis of topological considerations, Hetrick[13] describes two types of root architecture, representing two strategies of nutrient acquisition. The exploratory type, characterized by long roots with little branching, is typical for exploration of a large soil volume with low exploitation of nutrients. The adsorptive type, characterized by short, heavily branched roots, is typical for high-intensity exploitation of nutrients in a small soil volume. Hetrick[13] demonstrates that infection of roots with VAM fungi causes a shift to a more exploratory type of root architecture, probably because the fungus takes over the absorptive function.

The significance of mycorrhizas for the co-existence of plants in ecosystems has been studied only in the last decade. Francis and Read[6] demonstrated hyphal connections between different plants of the same or of different species which transferred not only water and mineral salts but also assimilates between roots of different plants. Particularly intriguing was the finding that the direction of transfer could be experimentally manipulated: shading of one plant caused an importation of assimilates through hyphal connections from neighboring plants. The significance of such mycorrhizal connections for the coexistence of different plants was studied in 'microcosms' with 20 different species[10]. The species diversity was larger in mycorrhizal microcosms, apparently because subdominant species could grow at the expense of dominant species.

Physiology of mycorrhiza

In addition to morphological adaptations to optimize nutrient acquisition, physiological adaptations are equally important in non-mycorrhizal as well as mycorrhizal roots. In particular, depletion of nutrients by active uptake, mobilization of inorganic nutrients by secretion of ions and chelating agents, and acquisition of organic nutrients by the secretion of enzymes are important. In general, the VAM symbiosis appears barely to affect the physiology of nutrient acquisition[4] except indirectly, by influencing the microflora of the mycorrhizosphere[7], whereas the contribution of ectomycorrhizas and ericoid mycorrhizas in humus-rich soils is important[4,25]. The Ascomycetes and Basidiomycetes involved in the latter forms of mycorrhizas have maintained at least in part the enzymatic equipment characteristic of saprophytes (e.g. glycan hydrolases, proteinases and phosphatases) and thereby compete with free-living saprophytes for organically bound mineral nutrients, promoting the accumulation of nutrient-poor raw humus in the soil. Particularly intriguing is the recent demonstration that these mycorrhizal fungi are able to digest proteins in the soil, to take up the amino acids released and to pass them on to the plant[1]. This means that mycorrhizal symbiosis eliminates the saprophytic mineralization of nitrogen and thereby short-circuits the nitrogen cycle to keep it under control by the symbiotic association.

This short-circuiting of nutrient cycling is particularly important for mature forest trees[17]. The nutrient-absorbing mycorrhizal roots become concentrated in the organic soil horizons, particularly in the raw humus (which consists to a considerable extent of fine roots and hyphae shed by the symbiotic association). This almost forces a division of labor between roots responsible for nutrient acquisition in the surface layers, and roots involved in water uptake and anchoring in the mineral horizons of the soil. In current discussions on forest decline, acid rain has often been cited as the culprit, and liming of forests has been recommended to fight acidification of the upper soil[29]. However, acid conditions are unlikely to harm the nutrient-absorbing mycorrhiza in the organic soil horizons since the fine roots are protected by their fungal mantle, which is known to tolerate and even to favor acid conditions[25], as soon as they start to grow. Damage by acid conditions was only observed in seedlings which formed root tips unprotected for a prolonged time before mycorrhization[8]. On the contrary, acid conditions, to which the fungal partners of the symbiosis contribute, reduce activity of bacterial saprophytes and thereby maintain the closed nutrient cycle. Thus, surface liming does not help the mycorrhizal symbiosis but favors saprophytic mineralization and hence the formation of highly mobile nitrate which may be washed out together with basic cations[16], opening the nutrient cycle. The nitrogen supply by atmospheric pollution, which may exceed the assimilation potential of trees[21], may be a bigger problem for mycorrhizal symbiosis than acid precipitation since mycorrhiza formation can be inhibited in a situation of nitrogen surplus, particularly when the surplus is in the form of nitrate[19]. Most ectomycorrhizal fungi favor ammonium ions over nitrate as a source of mineral nitrogen[23].

Conclusion

As indicated above, the reviews assembled in this issue lead to the conclusion that the main ecological significance of mycorrhizas concerns the protective rather than the productive phase of a plant individual as well as of an ecosystem. This phase of the life cycle is all too often neglected, not only by those carrying out research on mycorrhizas but also by biologists in general. Scientists tend to focus on the early phase of a life cycle, the productive phase of juvenile growth. Comparatively little is known about the protective phase of maturity. The criteria for measuring fitness change during the life cycles of individuals and ecosystems. During the productive phase of young plants, and of early stages in a succession, the relative growth rate may be a useful measure of fitness, and the supply of abiotic resources may be the main factor limiting it. However, the limits to growth shift from the outside to the inside with time. Genetic constraints on shape and structure start to take effect, and the maintenance and cycling of resources already incorporated becomes more important than the acquisition of new ones. At this stage, competition for new resources among individuals in an ecosystem may be replaced by collaboration to maintain the resources acquired, and it is in this almost unexplored domain where the mycorrhizal symbiosis might have its key function.

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