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Bibliographic review

Arbuscular mycorrhizal fungi and their role in agroecosystems

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ABSTRACT

Agroecosystems are ecosystems subjected by humans to continuous modifications of their components. The relationship between biodiversity and the functioning of these ecosystems is very complex and the positive effects depend mainly on the interactions between biotic components or between biotic and abiotic components. Soil microorganisms are essential for the functioning of terrestrial ecosystems, and the relevance of soil microbial diversity for the functioning of agriculture and natural ecosystems has been identified as one of the major areas of research in current science. Within this group of microorganisms, arbuscular mycorrhizal fungi (AMF) represent one of the oldest and most widespread forms of symbiosis. The most recent research on AMF has broadened the context in which mycorrhizal symbiosis is viewed, placing great emphasis on its effects on plant communities and the ecosystem in general and, as a consequence of the multiple functions that AMF fulfill in the ecosystem, the number of ecological studies related to them has increased considerably in recent years. The aim of this work was to review the role of mycorrhizal relationships in their habitat.

Key words: ecosystems, symbiosis, biological diversity

INTRODUCTION

Agricultural systems are dynamic ecosystems commonly managed to achieve high yields and the highest possible crop yields. They are influenced by anthropogenic factors, such as fertilizer and pesticide application, intensive tillage and monoculture. These activities have an impact on soil microorganisms, which represent an essential component of the functioning and sustainability of agroecosystems (1).

Microorganisms constitute the invisible majority of life in soils, but despite their abundance, their impact on the functioning of agroecosystems remains poorly understood. They play a fundamental role in ecosystems and influence a number of important processes, including cycling of elements such as carbon, phosphorus, and nitrogen, increasing crop productivity, and improving soil physical properties [1,2].

An important group of soil microorganisms is the arbuscular mycorrhizal fungi (AMF). AMF are often described as an extension of plant roots that grow out of plants into the soil, delivering nutrients to their host in exchange for carbon. This approach, based on carbon economics, is often the dominant paradigm defining the association between plants and AMF. However, AMF can also have effects not directly related to nutrition, some of which may even be as important as nutrition itself, contributing to increased plant productivity and influencing community and ecosystem dynamics.

Incorporating these non-nutritional effects into the understanding of AMF allows a more precise determination of the conditions under which they can more efficiently favor plants and, therefore, agriculture [3].

Agroecosystems

Agroecosystems are ecosystems subjected by man to continuous modifications of their biotic and abiotic components, with the objective of producing food and fiber. They differ from natural ecosystems in four fundamental characteristics [4]:

- Simplification, farmers prefer some plant species eliminating other plants and animals.
- The consumption of energy used by humans in the form of machinery, fertilizers, pesticides, seed selection and other processes.
- The biomass that is removed during harvesting turns the ecosystem into an open system that depends on external processes to reintroduce appropriate fertilizing substances to sustain the growth and development of new biomass. Natural ecosystems are self-fertilizing with the remains of local organisms.
- The introduction of substances that, depending on their dose or handling, can become pollutants, which, in the case of intensive agriculture, are fertilizers, pesticides and other non-biodegradable chemicals that accumulate in the ecosystem with consequent damage.

Cropping systems are continuously adapting to meet the needs of farmers in a changing socioeconomic context [5]. Some agriculture is developed to increase productivity to meet the ever-increasing demand for food and fiber, which has led to an oversimplification of crop diversity, an increasing reliance on chemical use, and a decrease in the use of beneficial biotic interactions [6,7].

There is growing evidence to suggest that fragmentation of natural habitats, coupled with changes in land use and high levels of agrochemicals, are major causes of the rapid decline in biodiversity in many agricultural settings [8-11], with the potential threat of affecting many ecological services such as pollination and pest control.

The relationship between biodiversity and agroecosystem functioning is very complex. Positive effects depend mainly on interactions between biotic components or between biotic and abiotic components. All these interactions are of great interest to agriculture because of the services they provide to agroecosystems. These range from non-chemical control of pests and diseases to improved conditions for crop development resulting from changes in nutrient availability and soil structure. One biotic component that plays a major role in these benefits is microorganisms.

Microorganisms in agroecosystems

Soil microorganisms are essential for the functioning of terrestrial ecosystems and catalyze unique and indispensable transformations in the biogeochemical cycles of the planet (12,13). The relevance of soil microbial diversity to the functioning of agriculture and natural ecosystems remains poorly understood (14,15). Unraveling what soil microorganisms do has been identified as an important area of research in current biological and agricultural sciences.

Soil microorganisms have a major impact on plant productivity. Within this, two fundamental mechanisms can be distinguished: a direct effect on plants via root-associated microorganisms, whether these associations are pathogenic or mutualistic, and an indirect effect through the action of free-living microorganisms that affect nutrient supply rates and the partitioning of these resources (10,14).

The main goal in ecological studies of agroecosystems is to understand the factors that determine the composition and diversity of plant communities. Factors such as soil fertility, geographical position and climate are known to influence plant species richness. There is now growing evidence that soil microorganisms, especially those living in symbiosis with plants, also contribute to plant diversity.

The biological property of soil that receives the most attention is related to the relative abundance of bacteria and fungi in the ecosystem. Bacteria and fungi generally have very different functions, and ecosystems are often characterized by fungal or bacterial dominance in the microbial community or a combination of both (16).

Not much is known about the functional importance of this bacterial or fungal dominance for plant community dynamics; the most widespread idea is that in ecosystems where the nutrient chain is bacterially dominant, nutrient mineralization rates and nutrient availability to plants are enhanced, whereas in areas with fungal dominance, nutrient cycling is slower and highly conservative (16).

Soil microorganisms also regulate plant productivity through a variety of mechanisms. Positive effects are more common in nutrient-poor ecosystems, where they increase the supply of limiting nutrients such as N and P. In these cases up to 90 % of P and N is provided by AMF and nitrogen-fixing bacteria, highlighting the importance of these in regulating plant productivity. It can also find negative effects of microorganisms on plant productivity when they act as pathogens, compete with plants for nutrients, or transform nutrients into forms inaccessible to plants [17].

Several groups of soil microorganisms also regulate plant diversity by changing competitive interactions or promoting the development of specific plant functional groups. Of particular importance are the symbiont microorganisms that associate with more than 200,000 plant species, which are completely dependent on them for their development and survival [2,3].

For a better understanding of how microbiota influence plant diversity and productivity, several crucial points need to be elucidated, mainly understanding how changes in microbial diversity and composition influence plant productivity and plant community dynamics is a major present and future challenge.

Arbuscular Mycorrhizal Fungi

It is widely accepted that the establishment of plant life on land coincided with the establishment and profound evolutionary influence of a mutually beneficial symbiosis between early land plants and a certain class of fungi [18-23].

Most of today's land plants live in symbiosis with fungi that occupy their roots. This symbiosis is known as mycorrhiza, which comes from the Greek mico=fungus and rhiza=root. There are four main types of mycorrhizae [20], but the predominant type is arbuscular mycorrhizae, which are associated with at least 72 % of angiosperms, some bryophytes, most ferns, as well as gymnosperms except for pinaceae [24,25].

Evolution of AMFs

Arbuscular mycorrhizae are one of the oldest and most widespread forms of symbiosis. Paleobotanical and molecular data suggest that the first associations between terrestrial plants and a glomonoid fungus occurred more than 460 million years ago [26], 300 to 400 million years before the appearance of root nodules resulting from symbiosis with nitrogen-fixing bacteria.

Current research on the evolutionary history of AMF and mycorrhizal symbiosis with plants is largely focused on genetic and molecular data [27]. The fossil record [28], however, has made a major contribution to our understanding of the distribution of mycorrhizal symbiosis in past ecosystems [29-37].

Over 410 million years ago, in the Devonian period, Aberdeenshire originated in northeastern Scotland, a complex and well-developed continental ecosystem, which was petrified through inundation with silica-rich water from hot springs [38] and occupies a prominent place in this context.

This fossil is evidence for the presence of hyphae, arbuscules, and spores very similar to present-day AMF in the early terrestrial plant Aglaophyton majus [31,39,40].

The mycorrhiza of *A. majus* is considered the prime example of fossil evidence in the evolutionary history of mycorrhizal systems [41-44]. Even the fossil evidence from Rhynie contributes to the hypothesis that the establishment of plants on land coincided with and was influenced by the evolution of symbiosis between early plants and a certain kind of fungus [18,20,22,23,45-47].

The similarity of fossil structures to present-day AMF need not necessarily be equivalent to the function they had in ancient fossil associations, as the fungal role in these primary ecosystems may have been more varied than it is today or fungi with similar morphology may have had more diverse functionality [20]. Nevertheless, the production of arbuscules in the roots of modern plants is now considered to be a morphological indicator of the establishment of a successful mycorrhizal relationship, and it is likely that a similar view of the symbiotic nature of arbuscules in the fossil record can be accepted.

Importance of AMF in the Soil-Plant system

More recent research on AMF has broadened the context in which mycorrhizal symbiosis is viewed, placing great emphasis on its effects on plant communities and the ecosystem in general. Many authors have highlighted the multifunctional nature of mycorrhizal effects including interaction with bacteria [48,49], carbon cycling [50], effect on the plant community [51], tripartite synthesis with mycoheterotrophs [52,53], and mediation of plant stress response [54].

Insight into the role of mycorrhizal relationships in nature

The greatest achievement, in the first hundred years of mycorrhizal symbiosis research, was to understand that it is an almost universal association present in virtually all terrestrial plant communities. However, most studies on the functional characteristics of the mycorrhizal association have had a reductionist approach and the role of this symbiosis in the dynamics of terrestrial plant communities has often been overlooked.

Weathering and solubilization of minerals

Although it is well accepted that mycorrhizae participate in the acquisition of nutrients found in soil solution, there is growing interest in the idea that mycorrhizal mycelium either by itself or in association with bacteria or other fungi can release nutrients from mineral particles or rock surfaces through weathering [55-57].

Mobilization of nutrients from organic substrates

In addition to enhancing plant acquisition of mineral nutrients, many AMF can play a significant role in mobilizing nutrients from organic substrates. The most significant effect for plants is the mobilization of nutrients such as nitrogen and phosphorus that would otherwise not be available to roots. Nitrogen and phosphorus sequestration by AMF from a wide range of organic substrates such as pollen (58), dead nematodes (59), springtails (60) and saprotrophic mycelia (61) has been documented.

Carbon flux

The flow of energy-rich carbon compounds from plant roots to edaphic microbiota constitutes the main process of carbon supply to soils, with AMF having a preponderant role in this process by flowing significant amounts of carbon through the mycorrhizal mycelium to different components of the soil ecosystem (62).

Bioremediation

Mycorrhizal fungi have a variety of effects that contribute to the amelioration of different types of stresses experienced by plants, including metal toxicity, oxidative stress, water stress, and effects of soil acidification.

Plant diversity and productivity of reconstructed grassland communities have been shown to depend on the presence of a rich assemblage of AMF species (51). Increased fungal diversity results in higher plant species diversity and productivity, suggesting that changes in belowground diversity of mycorrhizal symbionts may generate changes in soil diversity and productivity. The mechanism behind this is likely to be the differential effects of specific plant and fungal combinations on the growth of different plant species. This is consistent with the idea emerging from many molecular studies that the degree of mycorrhizal specificity may be greater than previously assumed. If the addition of new fungal species leads to an increase in the survival and vigor of more plant species that respond to mycorrhizal colonization, then there may be a positive feedback effect on mycorrhizal fungi, leading to more efficient resource utilization and increasing overall productivity. These effects suggest that plant diversity and productivity are more responsive to AMF identity than to AMF diversity (25,50).

Soil characteristics govern rigen mycorrhizal communities

As a consequence of the multiple functions of AMF in the ecosystem, the number of ecological studies related to them has increased considerably in recent years. These studies take into consideration mycorrhizal communities associated with different host plants in different ecosystems, however, studies comparing the occurrence of mycorrhizal species and communities in different soil types are scarce and focus mainly on cultivated soils and different land uses.

Soil types have been reported as a determining factor in the composition of mycorrhizal communities being particularly relevant in stressed environments such as saline soils, soils contaminated with heavy metals, and thermal soils (1,3,13,14).

If soil type determines AMF species composition and richness, it would be essential to know the determining factor that influences mycorrhizal communities and whether it is a single parameter or a group of physical, chemical and biological properties that are responsible for this influence.

It has been found that different AMF populations in agricultural fields colonized the same host depending on soil phosphorus concentrations [(63)], establishing that soil pH has a strong effect on mycorrhizal communities in agroecosystems [(64)]. However, these studies only consider a limited number of soil properties.

More recent approaches suggest that the effects of soil type on AMF populations cannot be attributed to a single edaphic characteristic, finding that the influence of parameters such as organic matter, soil texture, elements such as zinc and magnesium, among others, play a significant role in the composition of the mycorrhizal community in agroecosystems [(65-67)].

Biotic interactions of AMF in the ecosystem

In addition to increasing host plant uptake area, symbiotic fungal hyphae provide increased surface area for interactions with other microorganisms and provide an important pathway for the translocation of energy-rich plant assimilates (photosynthetic products) to the soil. Interactions can be synergistic, competitive, or antagonistic and may be of importance in areas such as sustainable agriculture [(48)], biological control, or bioremediation.

The extent to which interactions between mycorrhizal mycelia and other microorganisms influence different organic or mineral substrates is still unclear and more experiments are needed to distinguish between the activity of mycorrhizal hyphae and the activities of other organisms. Artursson's experiments show that inoculation with an AMF modified the active bacterial communities associated with mycorrhizal clover and wheat roots [(68)], suggesting that mycorrhizal fungi may influence bacterial community structure.

Detailed studies using *in vitro* systems show that AMF exudates have the potential to influence the vitality and community structure of mycorrhizal bacteria [(69)] and this type of effect may be significant in relation to biological control of plant pathogens.

Approaches based on stable isotope probing, RNA analysis, and metagenomics [(70)] indicate that there are many hitherto unidentified root symbionts and that bacteria and AMF occupying roots show differential activity in C consumption, with some being greater consumers than others. Some experiments suggest that AMF may influence bacterial assemblages in roots, but that the effect is not reciprocal [(71)]. AMF fungal mycelia clearly play an important role in microbial processes that influence ecosystem functioning, but there is still much to learn about the detailed interactions of root-inhabiting microbes and how they are regulated.

To understand the functioning of mycorrhizal fungi in ecosystems it is necessary to take into account all possible biotic interactions occurring in the soil. While a number of these interactions have been shown to be crucial, some such as parasitism have been more neglected in their ecology and deserve greater attention.

Role of resident and introduced AMF in ecosystems

Understanding the potentially large consequences of the globalization of species distributions has become a major focus of ecological studies over the past few decades. This globalization of biota has resulted in ecological degradation [72], biodiversity losses, and increased biotic homogenization [73].

However, there have also been enormous economic benefits associated with the intentional movement of species. For example, virtually all agricultural production is a product of species in non-native habitats. Although not often discussed in the current ecological literature on invasive species, the social benefits and economic gains as a consequence of the movement of biota in an effort to support human societies are considerable.

In this context, the rate and volume of intentional movement of introduced mycorrhizal fungi is increasing as a consequence of the proposed harnessing of beneficial soil organisms for improved agriculture [74], horticulture [75], habitat restoration [76], bioremediation [77], and forestry [78,79].

The intentional movement of mycorrhizal fungal species is growing, but the concomitant potential for negative ecological consequences of mycorrhizal fungal invasions is poorly understood. As far as is known, there are no documented cases where intentional movement of mycorrhizal fungi has directly led to a persistent invasive species problem. However, it is difficult to determine whether this lack of knowledge is because the problems do not exist or because they are not detected.

There is a need to consider the possibility of both overt and subtle undesirable effects of mycorrhizal fungal movement. Undesirable consequences of inoculation, when they occur, are likely to go undetected because large-scale monitoring of inoculation consequences is rarely conducted.

Mycorrhizal fungi are generally considered mutualistic; consequently, there has been little concern about the possible negative consequences of their introduction. However, there is evidence that mycorrhizal function may vary [80-82].

The introduction of AMF may have a direct impact on resident mycorrhizal communities and an indirect impact on resident plant community composition. The direct impact of the introduction of these fungi on resident fungal communities must be carefully studied because there is evidence that once introduced they are highly persistent in their new environments [80].

Even if care is taken to introduce only existing species into ecosystems the problem may continue as new ecotypes may outcompete the residents and spread beyond the site of introduction, and may interact differently with resident hosts, soil communities, and abiotic conditions.

Different species of mycorrhizal fungi vary widely in their responses to the environment and in the benefits they provide to host plants. In addition, hybridization or introgression between introduced and resident populations of plants and animals has been shown to have significant negative consequences for resident populations, including extinction, especially when these populations are small or rare (83).

Understanding how introduced AMF coexist with the resident mycorrhizal community and whether they actually lead to changes in agricultural yields is the key to successful application of AMF in agriculture. There are four areas where ecologists could contribute significantly to more effective use of AMF (84):

- Understanding the survivability and colonization of introduced AMF in the presence of an existing mycorrhizal community.
- Understanding the AMF adaptability to environmental conditions that the fungus has not previously experienced.
- The importance of genetic variation within AMF and how it affects plant growth.
- The need to identify whether the effect of AMF introduction on crop yield is direct or indirect, through changes in the resident mycorrhizal community.

Adaptation

To be effective, the fungus has to adapt to a particular soil type or crop. In fact, since high nutrient levels can reduce mycorrhizal colonization, it may be more difficult for AMF to establish in more nutrient-rich soils. However, some AMF species appear to have an extremely large geographic range, suggesting a lack of specialization to certain environments such as *Funneliformis mosseae* and *Rhizophagus irregularis* (85). In fact, some field studies successfully used *in vitro* cultures of *R. irregularis* from arid soils of Spain in extremely nutrient-poor tropical acidic soils and with a plant (cassava) that the fungus had not previously experienced (86).

Colonization and competition

AMF differ in the rates at which they colonize plant roots, as well as their abilities to compete with other mycorrhizal fungi once they are inside the roots. For example, it has been shown that isolates of *Glomaceae* tend to colonize roots significantly faster compared with isolates of *Acaulosporaceae* and *Gigasporaceae*, some of which took up to 5 weeks longer than species of the Glomaceae family (87).

Studies of interactions between resident and introduced AMF species show that competitive results also vary with fungal taxa [(88)].

Although competitive outcomes may sometimes depend on initial relative inoculum densities, some mycorrhizal fungal taxa are clearly more competitive than other species. The presence of one fungus in a root system may alter the ability of another to colonize roots, but this may depend on the stage in the fungal life cycle.

Ecological impact of introducing non-resident AMF

An obvious question is whether the introduction of a nonresident AMF significantly alters the diversity or composition of the existing mycorrhizal community. Several studies that have used metagenomic techniques provide the first picture of mycorrhizal diversity in communities [(86)]. A major challenge is the ecological interpretation of any changes in the resident mycorrhizal community. Although a decrease in AMF diversity is likely to be considered a negative environmental impact, it is not yet clearly understood which aspects of mycorrhizal diversity (richness, evenness) favor crop growth.

Persistence and invasiveness of introduced AMF

Mycorrhizal inoculants are difficult to locate in field experiments. Therefore, in practice, it has been difficult to measure the persistence or invasiveness of an introduced AMF. Another practical problem is that the same fungal species may already be present in the resident mycorrhizal community, which means that a large number of molecular markers used to track the fungus may already exist at the field site [(59,63,80)].

CONCLUSIONS

The introduction of an allochthonous AMF is a biotic disturbance that could alter the structure of the resident mycorrhizal community. However, there is no information on whether mycorrhizal inoculation resulting in improved crop yield is actually due to a direct effect of the fungus, used as inoculum, on the plant or indirectly, through a change in the resident mycorrhizal community. Therefore, it is pertinent to understand the mechanisms governing the community composition of AMF in response to the application of a mycorrhizal inoculum. This is a key ecological issue that requires careful consideration for an ecologically sustainable use of AMF. In addition, variable effects on mycorrhizal crop yields using the same inoculum in different agroecosystems could be determined by its indirect effect on local mycorrhizal communities, which could differ in these locations.

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