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Arbuscular Mycorrhizal Fungi: how plants managed to colonise land

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Have you ever wondered how life became established on land? and what were the challenges faced by the first plants as they moved from an aquatic environment? Plants, which had been used to getting nutrients, such as N and P, in soluble forms from water and having water around them at all times had to find new ways of accessing both water and nutrients. Then there were the effects of direct exposure to sunlight, which powered photosynthesis, but could also generate damaging free radicals. The surmounting of all these challenges was aided by a partnership between plants and arbuscular mycorrhizal fungi (AMF).

From the beginning of plant life, they have been associated with fungi. We often think of fungi as being harmful and some fungi are but there are also symbiotic relationships, such as mycorrhizas, which occur in almost all plant families. There are two broad categories of mycorrhizal association. In an endo-mycorrhizal association, like AMF, which is geologically older and more ubiquitous, the fungus penetrates the cortical cells of the root and develops highly integrated association. This form of association is found in most herbaceous plant and some trees. In contrast, in the alternative ectomycorrhizal association, the fungus forms a sheath around the outside of the root. This type of association is found in most trees. Different species and types of fungi are involved in these two associations. In both cases the root-associated fungi connect with hyphae which extend out into the soil thus extending the plant's access to soil resources and better connecting the plant with its soil environment (**Figure 1**). The hyphae give a surface for absorption, which is much greater than that of the root surface area alone. This connection between plant and soil was key to plants being able to survive the hostile environment found on land.

Figure 1. Arbuscular Mycorrhizal Fungal Hyphal (the purple fibres) development in the media around a root (the black structure at the top left of the figure). The hyphae provide a large surface for absorption from the growth media and penetrate the root cells establishing arbuscles in the plant tissue for the transfer of absorbed materials.

AMF are a distinct taxonomic group within the fungi. The fungal hyphae have no cross cell walls and contain several nuclei. They do not have a sexual stage and reproduce through asexual spores. Their long association with plants is such that they are no longer capable of independent existence. The association between plants and AMF has existed for around 500 million years i.e. from the Ordovician period. The success of this mycorrhizal association is such that currently almost 80% of plant species, from mosses and ferns to apple trees, have an AMF partnership. Following initial contact between the plant and fungal partners, the fungus penetrates the wall of a root cortical cell and branches within the cell so as to produce a tree like structure, the arbuscule. This has a fungal membrane on the fungal side and a plant membrane on the plant side of the association. It thus resembles the transfer cells found in other plant tissues such as the phloem where a folding of the membrane provides a large surface for nutrient exchanges. The arbuscule thus allows the fungus to receive photosynthetic assimilates from the plant and the plant to receive mineral nutrients absorbed by the fungus from the soil. It also facilitates the exchange of signal molecules.

Whilst all of the above is functionally important, the mycorrhizal association is more embracing than a mere exchange of simple chemicals. The relationship begins when the fungus approaches a root in the soil - underground communication, a transfer of information, begins. Much of this is molecular and involves the genome expression of both partners. For example, the initial contact between plant and fungus does not initiate rejection, as would be the case with pathogenic fungi. In addition, the partnership results in structural changes and a high degree of physiological, biochemical and molecular integration in both plant and fungus. Arbuscule differentiation and changes to gene transcription within the cells of the root rapidly cause a reorganisation of the contents of the host cell. There are also changes in the activity of the genes such as those coding for proton pump ATPases which move nutrients across membranes and to the plant-fungal interface so as to facilitate movement of assimilates and of RNA and other messengers. Some plant genes involved in nutrient uptake are down regulated because the fungus has taken over responsibility for this activity. The cumulative effect of these changes is a plant which is better tuned to its external environment and better provided with mineral resources and, ultimately, a plant which is better able to cope with the range of physical biological and environmental stresses, which are part of life on land.

Thus infection with AMF results in a number of plant genes being either up or down regulated i.e. they are more or less active in the production of genetic messengers, following infection. Plants have to flourish in the presence of potentially harmful microorganisms some of which are other fungi or protozoa. This is another of the challenges of life on land. Genes which are up regulated to produce more RNA in the presence of harmful microorganisms such as pathogenic fungi, are down regulated with AMF, a sign of the integrated nature of the relationship. Gene up regulation in the presence of a pathogen can result in structural changes to the morphology of the plant making it harder to infect, to the production of chemicals toxic to the pathogen or to an increased ability by the plant to flourish in the presence of infection. Infection with AMF thus increases the resistance of some crop plants to infection by significant pathogenic fungi such as *Rhizactonia, Fusarium, Verticillium Phytophthora* and *Pythium*. An example of these effects is shown in **Figure 2**.

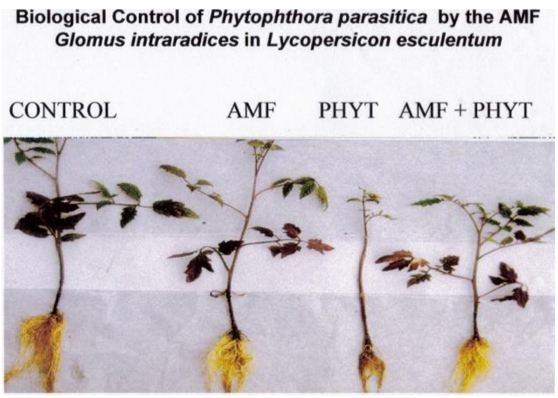

Figure 2. The impact of AMF and Pathogen infection on tomato growth

This shows tomato plants (*Lycopersicum esculentum*) which have been grown in solution culture either with or without (the control) AMF (*Glomus intraradices*) or a fungal pathogen (*Phytophthora parasitica*) or in the presence of both AMF and the parasite. In the presence of AMF growth is similar to that of the control but the shape of the plant is changed. In the presence of only the pathogen the size of the plant is greatly reduced and is likely to die. If both AMF and the pathogen are present then while the size of the plant is reduced, particularly its height, it is withstanding the adverse impact of the infection and is likely to survive and produce fruit.

In addition to all of the above there are also subtle changes to the form of the plant as a result of infection with AMF. For example, infected plants have a more branched root system and a higher number of orders of branching. This impacts on the amount of carbon invested in the root system and in the length of time that roots survive in the soil. This is important in the context of climate change as it results in an increased storage of carbon, originally derived from the atmosphere, in soil organic matter where it can remain for long periods of time.

Root system morphology also impacts the ability of the plant to respond to changes in soil resources such as the changed water and nutrient availability, which happen in periods of drought. Changes in morphology result from AMF influencing plant hormone regulation and cell division within the root system. Providing an adequate supply of water has always been one of the greatest challenges of life on land. AMF impact plant water relations. The diameter of individual hyphae, commonly 1-5 microns, suggests that enhanced water transport to the plant through the fungal hyphae is probably not the major mechanism for water absorption. AMF can, however, act as biosensors. Their hyphal network (**Figure 1**) allows them to sample the soil in areas where plant roots have yet to reach and to indicate potential restrictions to water availability. This allows plants to modify where the root system develops in soil and reduce their water loss by closing their stomata earlier or more completely. This is another aspect of plant regulation under hormonal control and influenced by mycorrhiza.

The need for the plant to supply the fungus with the products of photosynthesis, which might otherwise have been used for plant growth, could be considered a downside of the symbiosis. However, infection by AMF can increase the rate of photosynthesis. This increased activity may also permit the faster turnover of photosynthetic intermediates such as ATP and as a result help reduce damage, which can be caused by the creation of free radicals in the plant cells by the energy contained in sunlight. The plant AMF association is thus wholly integrated and whilst plants can exist without the fungal partner, the uninfected plant is restricted in its performance under stressful conditions and is less responsive to its environment.

AUTHOR PROFILE

Dr David Atkinson began his research career at East Malling Research Station where he studied fruit tree root systems and their associated mycorrhizal fungi. He continued to explore the relationship between crop root systems and mycorrhizas at the Macaulay Institute in Aberdeen, the University of Aberdeen where he was professor, and the Scottish Agricultural College (now SRUC) where he was Deputy Principal. He is currently an ordained minister in the Scottish Episcopal church where, as Convenor of its Church in Society committee, he endeavours to link current science issues such as genome editing to the Christian faith.