transcripts in ergosterol biosynthesis in *B. cinerea* successfully decreased conidial germination, mycelial growth and pathogenicity of *B. cinerea* on various fruits. Given that *B. cinerea* delivers trans-species small RNAs to suppress host gene expression, *B. cinerea* strains carrying long-terminal repeat retrotransposons are more aggressive, suggesting that efforts targeting the repeat-induced point mutation machinery to mutate these retrotransposons may result in *B. cinerea* strains with impaired pathogenicity. However, these potential new approaches still require further development and testing.

Where can I find out more?

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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Quick guide

Arbuscular mycorrhizal fungi as biofertilisers

Alessandra Salvioli di Fossalunga and Paola Bonfante*

What are arbuscular mycorrhizal fungi and why are they so important for plants? Do you know that fungi represent the group with the third largest biomass, after plants and bacteria? Notwithstanding, most of them are invisible microbes, they are present in all environments and play crucial roles in our planet, among which is the interaction with plants. In this last area, arbuscular mycorrhizal fungi (AMF) are the lead actors: while a part of their hyphae proliferates in the soil taking up minerals, a conspicuous part of their body lives associated with the roots of around 70% of land plants. The resulting interaction is the fruit of a long evolutionary history dating back to 450 MYA when the first plants emerged from waters and immediately allied with their symbiotic partners. While the plant supports the fungus with organic carbon, the fungus improves the plant's mineral nutrition by releasing minerals essential for the plant's diet, such as phosphorus and nitrogen. AMF depend on the host to live, and are thus defined as obligate symbionts.

Do AMF really provide plants with nutrients like a chemical fertiliser? More than 25 years of research with genetic, molecular and cellular tools have demonstrated that the fungus takes up phosphate from the soil thanks to inorganic phosphate (Pi) transporters, moves the mineral towards the arbuscules, and then releases it at the interface zone between the fungus and the plant cell. The phosphate is actively taken up by the plant cell thanks to its specific Pi transporters. As a consequence, P amount is often higher in mycorrhizal plants versus non-mycorrhizal ones, often having the effect of growth stimulation. The whole process is, however, under a plant regulatory network centered on components of the so-called phosphorus starvation response. In phosphorus-deficient conditions, the activation of Pi starvation genes leads to a gene cascade leading to successful fungal colonization, while under phosphorus-sufficient conditions the Pi sensors turn off the phosphorus starvation response. In conclusion, at higher phosphorus values fungal colonization is inhibited. These results indicate that in agroecosystems where crops are subjected to intense fertilisation, the nutritional benefits of the symbiosis might be jeopardised.

Are AMF good allies of farmers? In recent years, the application of AMF-based biostimulants in the field has become an established practice, increasingly adopted in sustainable agriculture (Figure 1). However, and not surprisingly, assessing the effect of AMF inoculation on crops is not easy. Overall crop productivity is due to an interplay of factors that include the environment, climate, plant genotype, soil type and, last but not least, agricultural practices. A neutral or even negative effect has been sometimes reported upon AMF inoculation — more often, the expected effect on yield and mineral nutrition has not been observed.

Despite these inconsistencies, the bulk of data coming from recent studies at the field scale has clearly shown promising results, and mycorrhizal inocula have allowed a significant reduction of chemical fertilization on crops such as maize, sorghum and hemp. Noteworthy, the positive effects of AMF extend far beyond nutrition to encompass stress tolerance, resistance to pests and increased nutraceutical value of the crops. That is why AMF can be acknowledged as loyal helpers of next-generation farmers, representing an ecologically and economically valuable strategy to reduce the use of agrochemicals and their impact on the environment.

What are the main challenges for the use of AMF as biofertilizers? The global biofertilizers market has witnessed a remarkable surge, and it is expected to further increase by 12.8% in the next ten years. Despite AMF-based inocula taking ever more space in this market, several challenges still wait to be addressed toward a full mastering of their use.

The first issue deals with the quality of the marketed AMF inocula. Owing to

Figure 1. In-field mycorrhizal inoculation.
Propagules of arbuscular mycorrhizal fungi — in the form of spores or colonized root fragments — can be inoculated in crop fields during sowing or early plant development. The inoculum may be supplemented with exogenous Myc-factors (e.g., short-chain chito-oligosaccharides) to promote symbiosis establishment (Volpe *et al.* (2020) Carb. Polym. *229*, 115505). Image courtesy of Andrea Genre.

their complex biology, AMF are more difficult to formulate into an effective biostimulant than, for example, any nitrogen-fixing rhizobacterium. In a recent trial, 80% of the tested AMF-based biostimulants failed to establish the mycorrhiza with host plants. For this reason, a management framework has been proposed that includes the recommendation of standardised tests to ensure the quality of the products released on the market.

Furthermore, the effective application of AMF-based biofertilizers needs to be harmonised with the overall field management practices. To this purpose, the current scientific knowledge indicates that reducing soil disturbance (such as tillage) and periods without roots in the field with the use of cover crops are winning strategies to maximise the benefits of AMF inoculation.

Where can I find out more?

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DECLARATION OF INTERESTS

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Quick guide

Mycoheterotrophy

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What is mycoheterotrophy?

Mycoheterotrophy is the ability of a plant to take up carbon from root-associated fungi. This lifestyle is best known from rare non-green plant species. Historically, botanists often assumed that these leafless plants obtained carbon directly from soil organic matter, hence they were incorrectly described as 'saprophytes'. Yet, early investigators of these 'fully mycoheterotrophic' plants had already demonstrated that fungal filaments were closely associated with their roots, leading to our current understanding that these plants rely completely on fungi for carbon. As there is no apparent benefit for the fungi, mycoheterotrophic plants may be considered to be parasites of their hosts, the fungi. But whether mycoheterotrophs truly have a negative effect on their fungal hosts remains to be shown. Apart from emblematic non-green plants, many mycoheterotrophic plants live a hidden life — in the past decades it has been discovered that some green-leaved plants also gain carbon from root-associated fungi in addition to performing photosynthesis. These plants are 'partial mycoheterotrophs' or 'mixotrophs', as they combine autotrophy with mycoheterotrophy simultaneously. In some plant species, such as the orchid *Ophris insectifera*, the fungi provide only a small fraction of the plant's carbon requirements, while other species like *Corallorhiza trifida* consist almost completely of fungal carbon (Figure 1). Within a partially mycoheterotrophic species, the level of mycoheterotrophy can be somewhat variable and depends on the local conditions. This suggests that there is a dynamic continuum of possible combinations between autotrophy and mycoheterotrophy. The position of a plant along this continuum depends not only on species-specific traits and local environmental conditions, but also on the plant's developmental stage; some