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Arbuscular mycorrhizal associations in plant nutrition and health

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Abstract

Plants and arbuscular mycorrhizal fungi have co-evolved over a period of at least 450 million years. This fungal-plant association involves the transfer of carbon to the obligate biotropic fungus, in return for a wide range of beneficial functions. Although this is usually a mutualistic relationship, it can become parasitic to the plant under adverse conditions. Here, the research examining mechanisms by which mycorrhizal associations improve plant fitness is reviewed. Although there is strong evidence that a number of beneficial functions are performed by mycorrhizae, the mechanisms behind these are often not clear. There are numerous factors which influence these mechanisms and their outcomes, one or more of which can be affecting the association simultaneously. The knowledge we have on arbusular mycorrhizal associations with plants could be applied to various land management practices in order to improve soil degradation brought about by anthropogenic activities. These include erosion, drought, nutrient stress and salinization, and are often a result of poor land management. In order to use mycorrhizal fungi as a biomanagement tool, more research is required, particularly in mature field communities over long timescales. There is a need to invest in the development of sustainable agroecological management methods and to design future policy and legislation that encourages large organizations to incorporate more sustainable practices whilst protecting small-scale farmers.

Keywords: Arbuscular, Mycorrhizal, Fungi, Agroecology, Agriculture, Plant nutrition

Review Methodology: The following databases were searched for research articles and review papers: ISI Web of Knowledge, Google Scholar and CAB Abstracts. Topic-specific search terms were used in searches. References cited in the articles obtained by this method were used to check for additional relevant material.

Introduction

One gram of agricultural soil can contain millions of beneficial microorganisms, which improve soil fertility, including bacteria, algae and fungi [1]. In 1981, Jenkinson and Ladd [1] made a conservative estimate that all soil microorganisms constitute a biomass of 500 kg of C per hectare. A more recent study [2] found that fungi account for a fresh biomass of 4000 kg per hectare of temperate pasture soil – greater than bacteria and algae combined. Not only are fungi abundant in the soil – they are also hugely diverse. The vast diversity of soil fungi has interested researchers since Fries [3] suggested in 1825 that fungi may be as speciose as insects, thereby suggesting a figure of over 140 000 species. A generally accepted estimate of 1.5 million species was made by Hawksworth [4], although other studies have suggested that this may be a vast underestimate, with values of up to 9.9 million being given [5].

Fungi established a symbiotic relationship with the root organs in plants of nearly all terrestrial plant ecosystems worldwide [6, 7], and involve up to 80% of all plant families and approximately 150 fungal species [8]. Of the six groups of mycorrhizal fungi – arbuscular, arbutoid, ecto, ericoid, monoptropoid and orchid [6, 9] – arbusuclar mycorrhizal fungi (AMF)–plant interactions are the most common [7, 10, 11] and these are the most prevalent soil microorganisms in natural and agricultural soils [12]. This interaction is thought to date back at least 450 million years, over which time AMF have become obligate biotrophs as they have lost the ability to capture carbon without associating with a plant host [10, 11, 13, 14].

In order to form associations between the soil and the internal structure of the host species, AMF use hyphae – branching threadlike filaments, which make up the mycelium – to proliferate throughout the upper soil horizons and link plants [15–17]. During symbiotic association with a host plant, nutrients are exchanged from fungus to plant in branched, tree-like dichotomous structures formed within plant root cortex cells, called arbuscules [15, 17–20]. These structures transfer nutrients in exchange for carbon through a bidirectional mutualism [10, 21–23], where 5–10% of the host carbon is extracted by AMF [24], thus providing a benefit of host association for the fungus [16]. In return AMF can provide numerous beneficial functions for the host, some examples of which being increased nutrient acquisition [21, 25], improved water relations [26–29], protection from pathogens [30] and sequestration of heavy meals [31, 32], amongst many others. However, it is unclear what factors determine either the relative importance of each function to the plant or which of the aforementioned functions AMF is able to provide in any given situation [33, 34].

Although there is evidence for some host or AMF specificity in AMF–plant relationships, this is not always the case [22, 35–39]. Despite such associations usually being mutualistic (beneficial to both), there is evidence that it can be commensalistic (neither favourable nor detrimental to the two individuals), ammenalistic (one species is inhibited whilst the other is not affected) or even parasitic (advantageous to one individual while having a negative effect on the other [39, 40]. For example, Campos-Soriano [41] found that AMF may have evolved the capacity to evade plant defence mechanisms under conditions where plants are not benefiting from an association, whilst keeping the same functionality.

The mechanisms behind the potentially beneficial functions of AMF–-plant associations for plant health and nutrition are discussed below. The degree to which the current literature provides a comprehensive understanding of these processes and the factors which affect them is reviewed. Moreover, the importance of each function in terms of land management is debated. Finally, the implications of these findings with respect to future research and land management are argued.

The Common Mycelial Network and Implications for Plant Community Structure

Biodiversity insures ecosystems against declines in productivity by retaining or increasing species diversity – the greater the variety within a community, the more chance there is that the community will continue to function even if some species can no longer survive in the environment [42]. Species diversity can provide important genetic resources, particularly in environments, which exhibit high genetic diversity, such as semi-natural grasslands [43, 44].

Plant community structure can affect diversity of AMF communities [45, 46]. However, mycorrhizal fungi can also alter plant competition and therefore community structure through a 'common mycelial network' of hyphae linking many plants in one community [35, 47–50]. This concept has been described as the 'wood-wide web', where nutrients can flow between parts of the fungi, and potentially between plants [7, 51]. As a result, plant–plant competition for nutrients may be mediated, at least to a degree, through improved nutrient transfer via the common mycelial network [52–55]. Therefore, microbial soil communities have been described as a driver of plant community dynamics [10], where it is a key mechanism for linking biodiversity and ecosystem functioning and may increase plant biodiversity [56, 57]. However, the degree to which a CMN is beneficial to a host plant is species-dependant [45, 48, 55], and this network may allow for 'cheater' species to obtain benefits of the common mycelial network without investing significant amounts of carbon [54, 58].

Soil Erosion

Land degradation is recognized as one of the most important global environmental issues, particularly in arid and semi-arid regions. This degradation is a result of numerous climatic and anthropogenic factors, including erosion, drought, nutrient stress and salinization, and often as a result of poor land management [15, 59, 60]. The loss of agricultural productivity due to soil erosion costs the UK €9.99 million annually alone [61]. The network of mycorrhizal hyphae can improve soil stability by binding it through 'sticky' secretions of glomalin, a proteinaceous substance [62–64], creating an entanglement of micro-aggregates, which leads to macroaggregate formation [59]. This creates a macroporous soil structure which allows water and air to penetrate and reduces erosion [65–67]. As a result, AMF are thought to be the most important factor affecting soil aggregation [40, 62] and are crucial for soil conservation [68, 69].

The complex network of hyphae produced by AMF can equate to up to 30 m of hyphae per 1 g of soil [70, 71], making a significant contribution to the total fungal biomass in soil [72]. AMF hyphae act as an extension of the plant's own root structure, taking over the role of plant root hairs and creating a more branched root system [73, 74]. These fungal hyphae positively influence ecosystem services associated with the below-ground structure, functioning and carbon sequestration, where a high below-ground biomass results in higher ecosystem stability [75]. Numerous studies have shown that a greater abundance of plant roots and mycorrhizae results in higher carbon sequestration [71, 76, 77]. This can mitigate negative effects of climate change from CO_2 emissions [78, 79].

However, a greater understanding of the processes underlying C sequestration is required in order to understand its potential on a global scale. Then, long-term effects of AMF on carbon storage can be modelled [80].

AMF can be significantly reduced – or lost altogether – under conditions of land degradation. This could be through changes in vegetation composition (due to deforestation, agriculture or revegetation) or through agricultural practices such as tillage reducing the inoculum potential [45, 46, 81, 82]. The abundance and diversity of AMF propagules will decrease over time in degraded soils, where plant hosts rely on being colonized by AMF with long-surviving spores [83]. However, the AMF abundance and diversity can be rapidly restored in these soils through transplanting seedlings already colonized by AMF and managed revegetation [60]. The recovery of these AMF communities in highly degraded or desertified ecosystems is essential to successful restoration.

Nutrient Cycling

As a global ecosystem service, the benefits associated with nutrient cycling were valued at US$2.3 trillion in 1997 [84], although a revised version of this study suggests that this may be a gross underestimation [85]. Agricultural management practices often include significant additions of fertilizers, herbicides and pesticides, which have been shown to reduce mycorrhizal functioning [86–92]. Although studies estimating phosphate reserves vary widely [93] the some estimates suggest that our global phosphate resources could be exhausted within the next 100 years [94]. A review by Berruti *et al.* [95] found that AMF could be used as a biomanagement tool, where crops inoculated with AMF required 80% less phosphate fertilizer to produce the same yield. Tawaraya *et al.* [96] also found that the use of AMF combined with lower phosphate application was significantly cheaper per hectare than traditional phosphate fertilizer applications, and therefore is an economically viable option.

The majority of research investigating mycorrhizal fungi has focused on their ability to improve nutrient uptake, particularly of phosphorus [21]. This is because the enhanced availability of nutrients, chiefly phosphorus and nitrogen, is considered the most important function provided by mycorrhizal fungi [10]. Plants rely on AMF for the capture and transfer of soil nutrients through processes of weathering, dissolution and cycling of mineral nutrients and from mobilization of nutrients from organic substances [97]. Up to 90% of plant P and 20% of plant N can be provided by AMF [98]. However, if the soil-N or soil-P availability rises, plants will allocate less carbon to mycorrhizae as they are less reliant on the fungi for their nutrient acquisition, and mycorrhizal abundance will decline [10, 99].

Phosphorus is a major macronutrient required by plants for numerous processes related to plant growth, seed formation and fruit, vegetable and grain quality [100]. Plant-soluble forms of phosphorus, such as phosphate, are very limited in soil [10, 101], making phosphorus availability the most limiting factor for crop yield in 30–40% of arable soils [102, 103]. The inorganic phosphate that is available is rapidly absorbed by plant roots, resulting in a ‘phosphorus depletion zone’ surrounding the root. AMF can bypass this zone by proliferating in soil which plant roots are unable to reach – a mechanism, which is particularly important in P-limited soils [10, 16, 98, 104]. Conversely, in conditions where plants are not phosphorus-stressed, colonization and growth of mycorrhizal fungi decreases as the AMF association becomes less beneficial to the plant [105].

Nitrogen is an essential component in chlorophyll and plant proteins and is required for cell division [100]. AMF transfer a significant proportion of N to the plant [106, 107], and have been shown to increase plant utilization of nitrogen [10, 108]. As with phosphorus, mycorrhizae can proliferate decomposing patches of organic matter which plant roots are unable to reach and transfer inorganic N to plant roots via the mycelium in exchange for carbon [10, 109]. Although AMF association mainly involves transfer of ammonium, AMF can also assimilate nitrate and amino acids to the plant [110, 111].

Salinization

It has been estimated that between 45 and 77 million hectares of agricultural land are affected by salinity or sodicity stress globally [112, 113] and salinization of arable land is expected to lead to up to 30% land loss within the next 25 years and 50% by 2050 [114–117]. In saline or sodic soils, poor drainage results in the accumulation of salt on the soil surface, negatively affecting plant growth. Increased concentrations of sodium and chlorine and a reduction in potassium, calcium, phosphate and nitrate result in water and nutritional stress [118].

Although extreme saline or sodic soils have been found to delay spore abundance reduce colonization rate and decrease effectiveness of some mycorrhizal associations with plants [119–121], many AMF species are found naturally in saline soils [122]. A recent meta-analysis of studies analysing the effects of mycorrhizal fungi on salt-stressed plants found an overwhelmingly positive response of salt-stressed plants to AMF inoculation [123]. Total yield, flower count, tiller count, leaf area, root fresh weight, shoot length, fruit fresh weight, leaf weight, leaf count, total dry weight, leaf dry weight, shoot fresh weight, biomass yield, fruit count, plant height, root length, grain yield, stem diameter, fruit dry weight, shoot dry weight, root dry weight, stem weight, grain count, total seed weight and root:shoot ratio were all significantly higher for AMF-inoculated plants. Only two variables – shoot:root ratio and shoot growth – showed a significant negative effect.

Numerous mechanisms have been proposed to explain how AMF alleviate salt stress, and many of these mechanisms may occur simultaneously to improve plant tolerance in saline conditions. AMF can enhance nutrient uptake [124–126] and improve rhizospheric and soil conditions [127]. They can reduce production of plant hormones that slow growth, such as ABA [128], accumulate compatible solutes [129] and produce higher levels of antioxidant enzymes [117, 130]. AMF can increase plant chlorophyll concentration [117, 131–133], increase photosynthetic activity [117, 125, 134] and improve water use efficiency and osmotic adjustment at low water potential [117, 131, 135, 136]. Additionally, changes at the cell level, in membranes and cell wall elasticity, have been recorded [137, 138].

Water Relations

Salinity, drought and increasing temperatures are interlinked as these factors all affect the osmostic component of the plant [139, 140]. They are also the most common abiotic stresses affecting crop plants [29, 141]. Humans intercept approximately 60% of water run-off following precipitation, and use 80% of this for agriculture [142]. There has been recent attention on the potential role of AMF to reverse soil degradation in arid and semi-arid areas through improvement of soil quality and subsequent revegetation of land [59, 143, 144].

One of the main processes by which AMF improve water relations under drought conditions is through the secretion of glomalin, a glycoprotein, which can stabilize soil aggregates and therefore increase water retention [63, 145, 146]. However, mycorrhizal fungi are also able to improve water relations directly through transporting water to the plant via fungal hyphae in areas of soil inaccessible to plant roots [97, 147] subsequently improving stomatal control and reducing transpiration rates [135, 147, 148]. The extensive nature of the hyphal network not only leads to greater proliferation into previously inaccessible patches of soil, but also results in a larger surface area for absorption of water (and nutrients) and greater longevity of absorption [149–151]. There is evidence that mycorrhizal hyphae promote plant root development, which leads to improve water uptake [28, 152]. AMF can stimulate the expression of aquaporins – proteinic channels, which facilitate passive water flow and are responsible for cytosolic osmoregulation and water transport [29, 141, 148, 153]. AMF have been shown to increase plant root hydraulic conductivity and to improve water use efficiency via increased nutrient uptake, resulting in more drought-resistant plants [28, 29, 154–157].

Protection Against Soil and Above-ground Organisms

In the USA, the annual cost to agriculture due to nonindigenous species of plants, animals and microbes was in excess of US$138 billion annually [158]. Soil-borne pathogens such as nematodes and pathogenic fungi cause significant damage to plants with a high economic importance, such as agricultural crops [158–161]. In order to reduce the negative effects of plant–pathogen interactions, plants exhibit numerous defence responses, which are brought about by their association with a fungal partner. Cell wall thickening occurs when the plant increases synthesis of chitinases and glucanases [162, 163] and the plant can produce a biochemical response, which can alter root structure and exudate composition [164, 165]. Direct competition with root pathogens for colonization sites and altered soil biota may also reduce the negative effects of pathogens on plants [21, 30, 166, 167]. However, recent research has suggested that competition for colonization sites is not the main mechanism by which AMF inhibits soil-borne pathogens [168]. It is likely that there is a cumulative effect from improvement of plant nutrition and from increased resistance through AMF-induced plant defence responses [30], which drives plant pathogen resistance under AMF innoculation.

Biotic reactions among plants and microorganisms below-ground may be equally – if not more – significant than above-ground reactions in determining the outcome of competition between plant species [40, 169–171]. Pineda *et al.* [171] suggested that it is now widely accepted that ‘plant interactions belowground orchestrate a cascade of events that affects the interactions of plants with organisms that live aboveground, and *vice versa*’. Above-ground ecosystems have tended to be considered separate from below-ground ecosystems [172], however there has been recent increased interest in the interaction between soil organisms and above-ground organisms. There is evidence to suggest that fungi may trigger an indirect plant defence response against herbivores, and vice versa [173–176] since plant defence response to insect predation is not limited to the roots and can result in accumulation of anti-feedant compounds in shoots [126, 127] and up-regulation of genes associated with plant defence [177, 178]. However, AMF is not entirely selfless in its mechanisms of protection: removal of above-ground biomass by herbivores can suppress AMF by altering the plant carbon allocation due to preferential allocation of carbon to other plant parts rather than plant roots [179].

The effects of mycorrhizal colonization vary depending on the organism attacking the plant. For example, a meta-analysis of insect herbivores found that chewing insects and leaf miners were not significantly affected by mycorrhizal colonization, whereas mycorrhizae positively affected sucking insects and negatively affected gall-forming insects [180]. Pozo *et al.* [177] suggested that generalist insects are more strongly affected by plant defence responses than specialists, which can evade these mechanisms. When there is a positive outcome, effects have been linked to improved plant palatability, whereas negative effects are associated with reduced palatability or plant defence responses [181]. However, a recent meta-analysis found that studies need to consider the three-way interactions between plants, microbes and insects. For instance, insects may affect the abundance, susceptibility or accessibility of plants to microbial symbionts and the plant–microbe interactions. Similarly, plants may alter insect–microbe interactions through alterations in food quality for herbivore or susceptibility of insects to plant pathogens [174].

As a result of fungi-induced plant protection, Gianinazzi and Gianinazzi-Pearson [182] described mycorrhizal fungi as 'health insurance' for plants. As a result, mycorrhizal fungi could be used as a biocontrol agent to reduce negative effects of soil and above-ground organisms on plants [174, 183–186]. A review of current literature found that mycorrhiza-induced biocontrol was enhanced under conditions of abiotic stress such as drought, nutrient limitation and salinity, therefore mycorrhizal associations may become more important over time as biotic and abiotic stresses on plants are expected to increase [187]. However, their actual use as a biological control agent is still limited as success varies depending on the AMF isolate, pathogen, plant and environmental conditions [188, 189]. More research is required to develop a comprehensive understanding of the potential role of AMF.

Remediation of Heavy-metal Contaminated Soils

In natural conditions, heavy metals are found at low concentrations in rock and soils, posing no significant environmental risk [190]. Many heavy metals are required by plants in small concentrations in order to act as enzyme cofactors or to maintain a functional plant metabolism; however, some heavy metals such as cadmium have no known benefit to plants [191–193]. High concentrations of heavy metals can result in reduced plant growth, changes to mineral concentrations in plant tissues, root browning and altered photosynthesis [194]. Heavy metal contamination of soils has increased due to industrial and agricultural practices such as mining, smelting, industrial effluents, manufacturing and processing of goods, and addition of natural and synthesized fertilizers in agriculture [18].

A number of remediation technologies exist to treat contaminated soils, such as excavation and subsequent land fill, thermal treatment, electro reclamation, soil washing, vitrification, acid leaching, evaporation, ion exchange and solvent extraction [31, 32]. However these methods are expensive and inefficient, and have been found to negatively affect numerous soil properties and destroy the majority of organisms within the soil [31, 32, 195]. Bioremediation is suggested as a viable alternative [196, 197], particularly using phytoremediation by plants through phytostabilization (stabilizing pollutants through immobilization) phytodegradation (plant metabolic processes break down pollutants) and phytoextraction (pollutants hyperaccumulate in plant tissues which are then harvested) [31].

AMF are abundant even in highly degraded soils [198]. Under heavy metal stress, AMF associations resulted in less uptake of heavy metals in plant tissues, better growth and internal detoxification of metals [199, 200]. However, Audet and Charest [201] suggested that the remediation mechanisms may depend on the heavy metal concentration in the soil. The production of glomalin, fungal polyphosphates, phytochelatins and metallothioneins by AMF could result in chelation of toxins, reducing the plant-available heavy metals [202–204]. Fungal colonization can reduce plant root access to heavy metals due to fungal sheath cover at the root surface [205], and the large biomass of AMF can dilute the heavy metal concentration [206]. Fungi may reduce transport of heavy metals through immobilization and compartmentalization via absorption into hyphal walls, reducing concentrations in above-ground plant tissues or accumulating in hyphal walls in a non-toxic form [206–209]. They have also been found to sequester heavy metals in plant roots, preventing translocation to shoots [210–213]. The ability to immobilize heavy metals in the fungal mycelium is thought to be the main protection mechanism for plants in contaminated soils [208, 214]. Accumulation of contaminants can also occur through fungal structures such as arbuscules, vesicles and vacuoles, minimizing toxicity in the plant itself [191]. Finally, since AMF leads to enhanced plant nutrition and water availability resulting in an increase in plant yield, AMF may indirectly dilute the effects of heavy metals by promoting plant growth [208, 215].

Increased heavy metal contamination has often been shown to cause a decrease in mycorrhizal species diversity [216], spore abundance, colonization rates and growth of the extraradical mycelium [217]. In some cases AMF has been completely eradicated under conditions of heavy metal pollution [218]. However, mycorrhizal communities are generally able to recover from the initial inhibition as immobilization limits toxicity and changes in community structure leads to more tolerant organisms [219]. Effective use of mycorrhizal fungi in bioremediation requires an understanding of the AMF species present in the soil at a given contaminated site, since AMF will vary in their ecological diversity, functional compatibility with phtoremediation plants and sensitivity to heavy metal contamination [31, 200, 220]. Although numerous underlying mechanisms for improved plant tolerance through AMF associations have been suggested, these are still poorly understood and require further research [221].

Plant Yield and Reproductive Structures

A major indicator of plant nutrition and health is yield, particularly for economically important crop and tree species. However, it may be more useful to examine the effects of a stressor on root:shoot ratio, rather than investigating changes in above- and belowground biomass. Resource allocation to roots has been shown to regulate intensity of formation of mycorrhizal structures and carbon availability to the fungus [99, 222–224]. Conversely, it has been suggested that a decrease in mycorrhizal colonization could lead to a reduction in the amount of carbohydrates allocated to roots and a reduction in the size of the common mycelial network [10, 225]. This reduction would lead to a decrease in the root biomass and thus the root: shoot ratio [226, 227]. Studies have found that plant dependence on mycorrhizal fungi may increase as greater root branching causes more resources to be allocated below-ground to roots and hyphae [73, 74].

Although biomass is important for a number of plant species, the effects on reproductive structures, particularly fruits and seeds, can have a significant effect the horticulture industry, which depends on the formation these structures. A reduction in allocation to reproductive structures can negatively affect plant success over multiple years. However, the effects of AMF association on reproductive structures do not always mirror the effects in nutrition and yield [228]. This is because resource allocation may differ for various plant parts, depending on a multitude of factors. For example, removal of above-ground biomass can cause the plant to preferentially allocate carbon away from the roots to other plant parts, resulting in altered carbon allocation to AMF [179]. Conversely, increased growth of plant reproductive structures results in a greater requirement for resources in order to produce sufficient branches, leaves and roots [229]. Mycorrhizal fungi have been shown to affect economically important plants, for example by improving growth of tomato plants and mineral nutrient content of fruits [230].

Management Implications

Approximately 925 million people globally are suffering from malnutrition [231]. Food security is of particular concern in developing countries, where arid climates and poor land management have led to low yields, nutrient deficiencies, soil toxicity and acidity [232]. In Africa, one of the worst-affected regions, the impacts are substantial: 65% of arable land, 30% of grazing land and 20% of forests are already damaged [233].

Agricultural management must incorporate sustainable practices by respecting natural ecological processes and supporting long-term productivity [234]. Since the first ‘green revolution’, despite an increased interest in the use of mutually beneficial soil microorganisms in agriculture [235], limited attention has been given to the potential contribution of AMF [236]. Although most agricultural crops associate with AMF, intensive management tends to significantly reduce AMF diversity through practices such as monoculture cropping, tillage and fertilizer addition [237–240], although this is not always the case [241].

Fertilizer use is no longer an appropriate management solution to increase nutrient concentrations as this has become more expensive in recent years and some fertilizers are running out [94, 242]. A recent review found that AMF could be used as a biomanagement tool in order to reduce phosphate fertilizer application by up to 80% [95, 96]. Yield has been known to increase when there is a plant–AMF association in stressed environments, such as nutrient deficiency [95], salinity stress [123] and heavy metal pollution [215]. The successful use of plants in soil restoration depends on mycorrhizal associations [200], and it has been demonstrated that a ‘phyto-microbial’ approach to soil restoration is an economically viable option [96].

In addition to revegetation of degraded land, there is an increasing need to also improve the soil quality [243, 244]. The multiple benefits associated with mycorrhizal fungi ultimately bring about improvements in soil quality and agricultural productivity in areas experiencing severe biotic and abiotic stress [245]. Bethlenfalvay and Linderman [246] stated that ‘the role of AMF may be critical if agriculture is to return to the state where luxury levels of farm inputs of fertilizers, pesticides and/or chemicals are decreased to levels that are still economic, yet do not pollute the environment or pose health risks to consumers or handlers’.

In order to incorporate agroecological management practices such as AMF use on a large scale, numerous issues first need to be addressed. Agricultural policy, mainstream trade and land tenure legislation can also no longer punish smallholder farmers, who are the main practitioners of agroecology. Further investment is required to ensure that new approaches to agroecological management are developed, and future policy and legislation should encourage large organizations to incorporate more sustainable practices [247]. These agricultural practices must also be able to strengthen rural communities, improve livelihood of smallholder farmers, and avoid negative social and cultural impacts such as the loss of land tenure and forced migration [248].

Although there have been attempts to develop global policies and legislation on sustainable use of soils, these have not been entirely successful: policies either led to ineffective ‘real-life’ results or were never implemented due to insufficient international support [249]. Currently, farmers may use negligent, short-sighted or exploitative management practices, while policies may be poorly planned, discriminatory or simply ineffective [250]. In order for mankind to use AMF as a sustainable biomanagement tool to improve degraded soils and reduce malnutrition, the degree to which resources are invested in practitioner education and legislation is as important – if not more so – than investment in research.

Further Research

Although there is a significant body of research on many of the benefits of AMF for plant nutrition and health, there are limitations with current research when attempting to extrapolate results to real-life conditions. These issues can be separated into four key points:

(i) Species diversity

Plants are often grown in low-diversity mixtures for use in pot experiments [180, 251], whereas plant communities are associated with numerous interacting AMF species simultaneously in the field, and *vice versa* [38]. Since both plants and AMF can preferentially allocate resources to higher quality partners [50, 99] the outcome of an experiment is likely to be strongly dependant on the plant and mycorrhizal species used. Pot experiments have compared mycorrhizal plants with non-mycorrhizal plants [195], however since ~80% of terrestrial plants are associated with mycorrhizal fungi [8] this is not a true representation of natural conditions. Field-based experiments control AMF in this way by either using fungicide treatment in non-AMF plots, which rarely leads to a true 'non-AMF' treatment, or by comparing natural plots to those where AMF has been added [252]. These variances in experimental setup represent a confounding factor for analysis of treatment differences.

(ii) Scale of experiment

While small-scale pot experiments are useful when determining specific interactions of mycorrhizal fungi with a number of biotic and abiotic factors, the outcome of these experiments could be very different in more complex systems [34], for example at the community level *in situ*. Pot experiments tend to use juvenile plants; however the benefits of mycorrhizal colonization differs depending on the age of plant hosts, where young hosts may receive stronger positive or negative effects from AMF associations compared with species in mature ecosystems [53, 253]. The issues with trying to replicate field conditions in a pot experiment are not limited to issues with plants. For example, since an insect herbivore is rarely selected due to a known preference for a given plant species and mycorrhizal fungi additions, it may not be an interaction seen under natural conditions [180], therefore studies are increasingly placed in a community context [174].

In field experiments, many factors such as changing precipitation, irradiation, temperature and small scale soil properties can confound results [254]. Although pot experiments allows for numerous factors to be controlled, edge effects such as elevated temperature and obstruction can negatively affect plant growth and alter the behaviour of AMF [255]. Pot size may affect root growth, as a lack of space may lead to roots being very crowded in the soil [255, 256]. Nutrient availability can be limiting in pots, restricting plant growth [255]. The effects of AMF may be underestimated in pot experiments, since colonization can be lower when there is a relatively high root density in a confined pot [252]. One promising approach would be to match fungal species with their environmental conditions, for example by tillage regime, soil type, pH or host diversity [80]. Finally, although individual experiments are useful, there is a need for 'big data' research involving the collation of large quantities fine-scale field data in order to understand global soil quality [257].

(iii) Duration of experiment

The majority of studies on mycorrhizal effects on plants have been conducted over one growing season or less, despite evidence that communities experience phases of vegetation dominance and adapt to environmental changes over timescales significantly longer than this – potentially decades [257–259]. Differences in the duration of the experiment have also been found to lead to variability in response to biotic stressors, such as herbivory [260, 261]. Experiments must consider the temporal variability in abiotic stressors since soil variables such as nutrient concentration [262] and water content [263] vary over time, therefore the duration of the experiment will have a significant impact on the outcome.

(iv) Hierarchies of effects

In order to successfully use AMF to improve degraded soil or increase agricultural productivity, a better understanding of how functional mechanisms differ is necessary [34]. Since numerous variables may interact with one another and affect AMF simultaneously, there is a hierarchy of effects in any given situation depending on the plant stressor(s). Any given variable is controlled by, and controls, a number of factors at any one time, so it would be expected that direct changes in that variable will influence the effects on other variables, and *vice versa* [264]. Studies can show an overall effect on a given variable, but cannot unequivocally reveal the mechanisms, which cause community-level changes [265]. Therefore Koide [266] stated that 'an understanding of ecologically relevant traits that determine environmentally context-dependent interaction hierarchies is the key to elucidating general principles that structure biological communities'.

Conclusion

AMF receive plant carbon in return for numerous benefits to plant nutrition and health under conditions of stress. However the plant–AMF association is not always mutualistic, and can be parasitic under environmental conditions, which are favourable to the plant. These benefits have implications for a wide range of uses of AMF, particularly as part of agroecological management practices, which aim to restore degraded soils, revegetate land and increase plant yield in a sustainable manner. In order to effectively use these management methods, further research is required, which focuses on studies that can be extrapolated to natural conditions in the field. Although scientific knowledge on the use of AMF in agriculture is useful, translating this knowledge into effective policies has largely failed, particularly at the global scale. If agroecological management is to be successful, advancements need to be made both in our scientific knowledge of biotechnological uses mycorrhizal fungi whilst also educating agricultural practitioners and improving agricultural policy. These policies should encourage large-scale farmers to manage soil sustainably, whilst allowing the socio-economic status of small-scale farmers to improve.

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