Plant Soil
https://doi.org/10.1007/s11104-023-06045-z

MARSCHNER REVIEW

Arbuscular mycorrhiza: advances and retreats in our understanding of the ecological functioning of the mother of all root symbioses

Thomas W. Kuyper · Jan Jansa

Received: 14 November 2022 / Accepted: 20 April 2023

Abstract

Background Arbuscular mycorrhizal (AM) symbiosis has been referred to as the mother of all plant root symbioses as it predated the evolution of plant roots. The AM research is a multidisciplinary field at the intersection of soil science, mycology, and botany. However, in recent decades the nature and properties of soils, in which the AM symbiosis develops and functions, have received less attention than desired.

Scope In this review we discuss a number of recent developments in AM research. We particularly cover the role of AM symbiosis in acquisition of phosphorus, nitrogen, heavy metals and metalloids, as well as water by plants from soil; mycorrhizal effects on plant nutritional stoichiometry and on the carbon cycle; the hyphosphere microbiome; so-called facultative mycorrhizal plants; explanations for lack of mycorrhizal benefit; common mycorrhizal networks; and arbuscular and ectomycorrhizal ecosystems.

Conclusion We reflect on what has previously been described as mycorrhizal 'dogmas'. We conclude that these are in fact generalisations on the AM symbiosis that are well supported by multiple studies, while admitting that there potentially is a geographical bias in mycorrhizal research that developed in temperate and boreal regions, and that research in other ecosystems might uncover a greater diversity of viable mycorrhizal and non-mycorrhizal strategies than currently acknowledged. We also note an increasing tendency to overinterpret data, which may lead to stagnation of some research fields due to lack of experiments designed to test the mechanistic basis of processes rather than cumulating descriptive studies and correlative evidences.

Keywords Common mycorrhizal networks · Facultative mycorrhizal plants · Hyphosphere microbiome · Nutrient and carbon transport · Plant growth and fitness · Water

Abbreviations

ABA	Abscisic acid
AM	Arbuscular mycorrhiza(l)
C	Carbon
CEC	Cation exchange capacity
CMN	Common mycorrhizal network
DSE	Dark septate endophyte(s)

Responsible Editor: Ismail Cakmak.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-023-06045-z.

T. W. Kuyper (✉)
Soil Biology Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, the Netherlands
e-mail: thom.kuyper@wur.nl

J. Jansa
Laboratory of Fungal Biology, Institute of Microbiology, Czech Academy of Sciences, Vídeňská 1083, 14220 Praha 4, Czechia
e-mail: jansa@biomed.cas.cz

Published online: 02 May 2023

EcM	Ectomycorrhiza(l)
GRSP	Glomalin-related soil proteins
N	Nitrogen
NM	Non-mycorrhizal
P	Phosphorus
PSF	Plant-soil feedback
SOM	Soil organic matter

Introduction

The arbuscular mycorrhizal (AM) symbiosis between specific groups of fungi belonging to Glomeromycotina and a number of species of the genus *Planticonsortium* [earlier known as fine root endophyte or *Glomus tenue* (Greenall) I.R. Hall] belonging to Mucoromycotina, (Sinanaj et al. 2021) and plant roots (or rhizoids), has been described as the mother of all root endosymbiosis (Parniske 2008). The AM symbiosis is very ancient, dating back around 450 million years, and predates by approximately 50–100 million years the evolution of 'true' roots as specialised plant organs with a gravitropic growth response, protective root cap, and root hairs (Kenrick and Strullu-Derrien 2014). Plant roots therefore evolved within the constraints imposed by a mycorrhizal (especially the AM) fungal world. The complete breakdown of this mutualism has occurred only infrequently, under situations where either other root symbioses replaced the AM symbiosis or where plants evolved specific morphological and / or physiological features (Lambers et al. 2008; Werner et al. 2018). Even in situations where there is a reduction in plant performance in the mycorrhizal condition, because of nitrogen (N) immobilisation in the mycelium or because the mycorrhizal strategy is less effective than the root-based mechanisms in desorbing strongly bound phosphorus (P) or other limiting resources in soil, or because of high fungal carbon (C) demand, have most plants retained the AM symbiosis, inviting questions about the ecological relevance of this interaction. (Lambers et al. 2008; Werner et al. 2018).

The field of AM research continues to flourish with exciting discoveries still being made. It is therefore impossible to do full justice to these developments in the framework of this Marschner review. We also plead guilty to suggestions that we lack the expertise to critically evaluate certain parts of the current literature. We have therefore decided to be selective and focus on issues that have a strong connection with the functioning of AM symbioses under field conditions; therefore many of the included studies are more explicit on soils than studies with a stronger focus on the molecular biology of the mycorrhizal fungus and / or mycorrhizal plant, mechanisms of molecular cross-talk, and molecular mechanisms and their regulation of nutrient and C transport between both organisms. It is our conviction that insufficient attention to the nature and properties of the soils (Fig. 1), in which experiments have been executed, constrains our ability to generalise beyond such experiments towards ecological realism (Read 2002). If such papers with insufficient attention to soil properties are subsequently included in meta-analyses, we may eventually run into a risk of unwarranted generalisations.

We (as authors) are also biased in preferring mechanistic studies. There have been many powerful descriptive studies on AM fungi and their host plants published throughout the years, including those targeting their community ecology. Yet, especially with the increasing possibilities generated by widely accessible metabarcoding approaches, we admit to have been inspired by Harper (1982). In that paper with the short title "After description", Harper reflected on what he saw as dangers in contemporary thinking and writing by ecologists. He was critical about generalisations from descriptions into hypotheses whereby confirmation of a particular hypothesis was considered sufficient and adequate, without necessarily accounting for competing hypotheses that might generate the same prediction under the chosen set of experimental conditions. There are still frequent examples in the mycorrhizal literature where consistency between prediction and outcome is considered sufficient support for a certain hypothesis (Karst et al. 2023). And when (unspecified) context is included in explanatory frameworks to explain a diversity of outcomes, we run into the risk of being able to explain everything, which ultimately is not too different from a theory explaining nothing. Harper was additionally critical about the loose use of language and selected as one of the problematical terms the word "stress", where he noted that the term was usually redundant, as "water stress" is not different from "drought" (or "flooding", depending on the experimental conditions) and "salinity stress" can be well referred to as "salinity". The term "stress" will therefore only appear in the list of references in this paper.

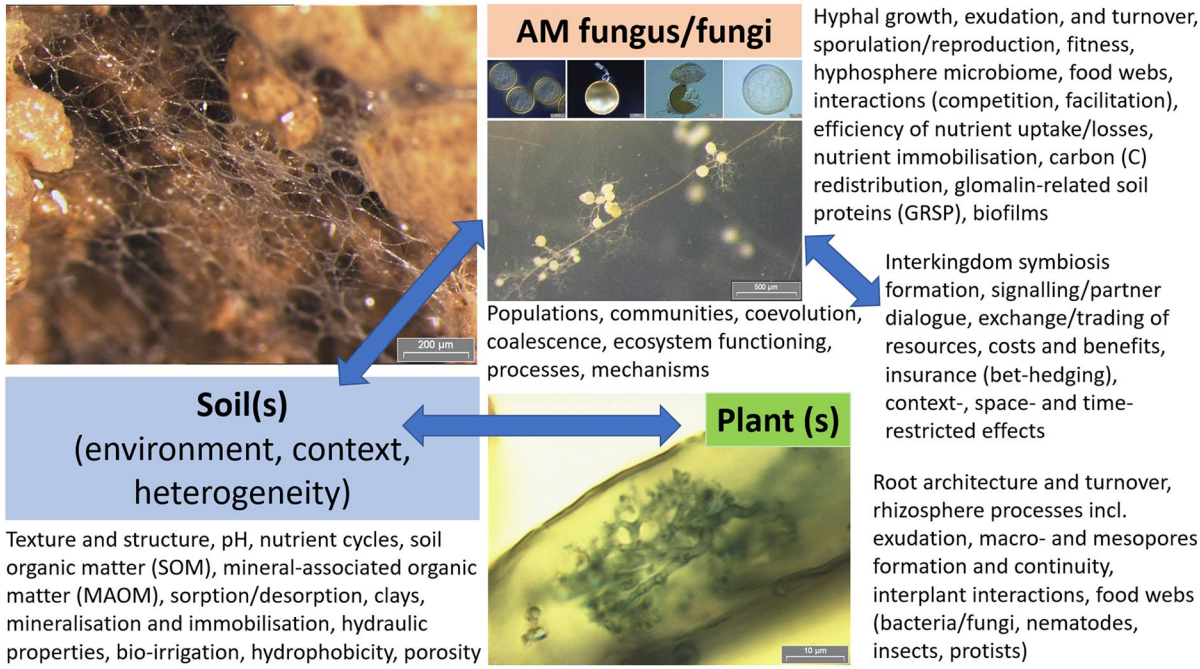

Fig. 1 Arbuscular mycorrhizal (AM) symbiosis in its ecological context – soil as inevitable but often neglected system component

For space reasons, we decided that we would not accommodate applied aspects of AM symbioses, both in agriculture and forestry. Applied mycorrhizal research requires its own critical review, but within the framework of this already lengthy paper we preferred not to squeeze in some additional elements but rather to go for a dedicated review on these aspects in the future.

Arbuscular mycorrhiza and phosphorus acquisition

The textbook mechanism [or as Albornoz et al. (2021) referred to it, one of the current 'dogmas'] for the functioning of the AM symbiosis is through spatial extension of the depletion zone and through that the acquisition of plant nutrients that are beyond reach of roots and strongly buffered in soil through sorption reactions. Phosphorus is generally considered the main element whose acquisition from soil to plant is increased as a consequence of the establishment of the AM symbiosis. In cases where plant productivity is limited by P availability, the mycorrhizal benefits should translate into increased plant biomass and / or increased P mass fractions, and ultimately higher fitness (which is, however, only very infrequently measured in mycorrhizal research) than that of plants that do not form the AM symbiosis. A large fraction of soil P is unavailable to plants due to sorption to mineral soil component such as iron (hydr-) oxides and clay edges, which are positively charged in a pH-dependent manner, contrary to clay surfaces, which are negatively charged in a pH-independent manner (Gérard 2016). We agree with Barrow (2021) that the nature of soil P needs to be interpreted in terms of variable sorption reactions, and that the emphasis on insoluble calcium, iron and aluminium phosphates is unjustified. While there is a continuum of the strengths of interactions between the various forms of P and mineral surfaces, P fractionation schemes have been proposed to understand the rate at which less-available forms of P might desorb through mechanisms that mimic ways in which plants, fungi, and bacteria actively promote the desorption, and hence might enter the pool of (bio)available P. A large part of soil P is in organic forms, and among those myo-inositol hexaphosphate, commonly known as phytate, is usually the most abundant P form. Organic P forms vary widely in molecular size (McLaren

et al. 2020; Reusser et al. 2022) and in the strength with which they are bound to mineral surfaces. This organic-P pool is similarly as the inorganic-P pool subjected to fractionation schemes in order to characterise its physico-chemical properties and reactivity. The role of the AM symbiosis in acquiring P from organic sources through mineralisation of phytate, nucleic acids, and other P-containing biomolecules by enzymes like phytases and phosphomono- and di-esterases has therefore been a major topic in mycorrhizal research in recent years. However, addressing that question can be complicated for various reasons.

A first issue is whether the mineralisation of organic P is limited by the availability of organic P in the soil solution or by the production of the relevant enzymes. Tinker and Nye (2000) have indicated that the rate-limiting step for hydrolysis of organic P is the quantity of organic P in the soil solution and not the availability or activity of the enzymes. Recent research (Jarosch et al. 2019) confirmed that conclusion for phosphate mono-esters but not for phosphate di-esters. Surprisingly, the authors also suggested that phytate mineralisation might be (co-)limited by enzyme availability next to stabilisation of the phytate on mineral surfaces. Despite the fact that the major organic-P pools are strongly sorbed to mineral surfaces, many experiments have been designed under the assumption that enzyme activity is the rate-limiting step. Such experiments involved the use of artificial "soils" that consisted for the largest part of chemically inert quartz (Cao et al. 2015). Experiments with mycorrhizal-root organ cultures in Petri dishes to which phytate is added suffer from similar problems. The importance of organic-P desorption as prerequisite for enhanced P acquisition from phytate was shown by George et al. (2005) who transformed *Trifolium subterraneum* L. with a fungal phytase gene and observed that plants that expressed the gene did not show an improved P nutrition in moist soils. In a subsequent study Giles et al. (2017) transformed roots of *Nicotiana tabacum* L. with both a fungal phytase gene and a citrate transporter and observed that only plants that expressed both genes were able to increase their P acquisition.

A second issue is whether the phytases and other phosphatases are produced by the AM fungi [considering that sequencing has failed to demonstrate presence of genes for those enzymes in AM fungal genomes so far (Tisserant et al. 2013)] or by hyphosphere bacteria or other microbes, an issue that we discuss in the section dedicated to the hyphosphere microbiome.

A third issue is whether AM fungi have the ability to directly take up organic P from the soil solution (a form of organic fungal or plant nutrition) or whether organic P needs to become fully mineralised into inorganic orthophosphate before it can be taken up. Demonstration of direct uptake of organic P needs dual labelling, whereby both the P and C in the molecules is labelled, and where the ratio of labelled P and C then allows quantification of direct uptake of organic P to the fungus. Dual labelling of phytate has not yet been described. However, as labelling of phytate with ^{32}P has been achieved (Whitfield et al. 2018), further developments may allow testing whether organic P can be directly taken up by AM fungi or whether all organic P first needs to be mineralised as conventional wisdom currently notes. If AM fungi are unable to directly acquire organic P, all P must pass through the orthophosphate funnel [see Figure 1 in Li et al. (2022a)]. This means that complementarity for accessing different organic P pools as hypothesised by Turner (2008) is implausible.

Finally, experiments with added organic P, for instance through addition of phytate salts, have not taken competitive sorption and desorption reactions into account (Ognalaga et al. 1994). Addition of phytate might desorb inorganic P from mineral surfaces and this might result in enhanced P uptake by the mycorrhizal plant but with erroneous attribution to enhanced phytate mineralisation by the AM fungi or by bacteria in the hyphosphere microbiome. Model calculations for an experiment by Wang (2016), where 200 mg phytate P kg^{-1} soil was added, indicated that the amendment increased soil solution orthophosphate concentration almost threefold and this change in mineral-P availability might have contributed to enhanced plant performance after phytate addition. However, in this study there was no direct measurement of P availability and because plants in the non-mycorrhizal (NM) condition (see Box 1) did not respond to this phytate addition, any conclusions about importance of competitive sorption / desorption must remain speculative. It is important that studies on AM fungi and organic P (and especially phytate) determine or calculate the effect of organic-P addition on mineral-P availability in soils.

Box 1 Terminology issues relevant to description of genetic capacity and establishment of arbuscular mycorrhizal (AM) symbiosis in various plants under variety of environmental conditions

Facultative AM plant – ambiguous term used to describe both plant species that usually form AM symbiosis but where there are records of the absence of AM fungi in roots and for plants that are considered non-mycorrhizal but where there are records of the occurrence of AM fungal structures (hyphae, sometimes resting spores or DNA sequences) in roots, often considered a proof of a functional symbiosis. Often, statements of facultative AM plants are made without particular attention whether the environmental conditions are conducive or not for establishment/development of the symbiosis

Mycoheterotrophy – a mode of (plant) nutrition based on "eating" mycorrhizal fungi, i.e., showing a net C and energy flow from fungus to plant

Mycorrhizal (plant) – genetically made up (capable) to establish functional mycorrhizal symbiosis

Mycorrhizal condition – situation conducive for developing AM symbiosis. It assumes the presence of (colonization-susceptible) mycorrhizal plant, living AM inoculum and conducive conditions (light, water, nutrient availability). Mycorrhizal plants will establish mycorrhizal symbiosis (and referred to as "AM plants" thereafter). In the case of mycorrhizal plants, the mycorrhizal condition is rather the "control" and the non-mycorrhizal condition the treatment. For non-mycorrhizal plants, the non-mycorrhizal condition constitutes the "control" and the mycorrhizal condition the treatment

Mycotrophy – sometimes referring to mycoheterotrophy (see above) or more often to the capacity of establishing functional mycorrhiza. Sometimes also used as a synonym to mycorrhizal dependency or responsiveness [which themselves are not mutually exclusive terms, see Janos (2007)]. Ambiguous term and not used in our paper

Non-mycorrhizal (plant) – genetically incapable to establish functional mycorrhiza involving active and bidirectional exchange of resources (due to dysfunctional symbiotic dialogue or loss of symbiotic genes)

Non-mycorrhizal condition – situation not conducive for developing AM symbiosis, even if mycorrhizal plant present. Usually due to absence of living AM inoculum, hypoxia/anoxia, overfertilization, cold, drought, pollution. The term is used to describe conditions where a comparison is made between plants in the mycorrhizal condition (actually the "control") and non-mycorrhizal condition (incorrectly often referred to as the "non-mycorrhizal control")

Smith et al. (2003) showed that AM plants in the mycorrhizal condition can acquire all their P through the fungal hyphae even when there is no additional P uptake compared with the plants in the NM condition. The mycorrhizal uptake pathway, where the nutrient is taken up from the soil solution mainly or exclusively through the fungal transporters, can downregulate or even fully suppress the plant root (also called the direct) pathway, where the uptake from the soil solution is through the plant transporters located in the rhizodermis and root hairs. However, the mechanism underlying this downregulation has not been elucidated. One hypothesis is that downregulation of plant transporters that are implicated in the direct pathway of P acquisition, is a direct consequence of the spatial geometry of the mycelium, including hyphal branching angle and frequency, and hyphal extension away from the root surface (Thonar et al. 2011). If uptake by AM fungi reduces the P concentration at the root surface below levels of plant C_{min} (i.e., the minimum P concentration at the root or hyphal surface where nutrient efflux is smaller than nutrient influx resulting in net uptake), then downregulation of the plant transporters would be adaptive as they would not contribute to plant nutrition. Differences in spatial geometry of the mycelium might furthermore explain why there are differences between different AM fungal species (if they differ in C_{min} or hyphal architecture) and different plant species in the extent to which the AM hyphal pathway dominates P uptake (Smith et al. 2004). That study showed a larger contribution of the AM hyphal pathway in plants colonized by *Rhizophagus intraradices* (N.C. Schenck & G.S. Sm.) C. Walker & Schüßler than in *Funneliformis caledonius* (T.H. Nicolson & Gerd.) C. Walker & Schüßler, and a larger dependency on that hyphal pathway in flax (*Linum usitatissimum* L.) or tomato (*Solanum lycopersicum* L.) than in medic (*Medicago truncatula* Gaertn.). The observation that the mycorrhizal pathway is more important for plant P nutrition than for plant N nutrition (Smith and Smith 2011) would also be consistent with this mechanism of hyphal architecture as the driving force, as the diffusion coefficient of P (orthophosphate) is much lower than that of N (ammonium, nitrate).

However, there are also studies that would contradict this (adaptive) mechanism as a consequence of hyphal architecture. Low concentrations of P would normally result in upregulation of plant P transporters, conditions under which AM fungi do not necessarily increase P uptake and plants are still P-starved, which casts doubts on this adaptive explanation (Bulgarelli et al. 2020).

In cases where P is limiting plant biomass production, AM plants would usually both increase P uptake and subsequently plant biomass. In several cases it has been noted that mycorrhizal plants both had higher biomass and higher P mass fractions (i.e., concentrations), resulting in a multiplicative effect on plant P content. Such multiplicative effects of biomass and P mass fraction are more common in plants that strongly respond to the mycorrhizal symbiosis than in plants that are less responsive, as shown by van der Heijden (2003). This effect has the counterintuitive consequence that the AM symbiosis both *increases* nutrient acquisition efficiency and *reduces* plant nutrient use efficiency, a parameter that expresses the amount of biomass produced per unit nutrient, the inverse of the mass fraction. Enhanced nutrient mass fractions have often been referred to as a consequence of luxury uptake or luxury consumption, but these concepts actually are only descriptive terms without explanatory power with respect to the physiological state of the plants. Possible explanations might be temporary storage of luxury goods that in later stages of plant growth can still be used to increase plant fitness by allowing higher seed production (Koide 1991), a strategy to prevent uptake by potential competitors that would be able to translate enhanced uptake into enhanced biomass and hence to gain competitive advantage, e.g., by outshading their neighbours, or the fact that plants in the mycorrhizal and NM condition are limited by different factors, e.g., plants being P-limited in the NM condition, and N-limited in the mycorrhizal condition (see below; Cardoso et al. 2004). Luxury uptake by (AM) plants (Riley et al. 2019) and luxury uptake of nutrients by AM fungi (Zhang et al. 2022) have received relatively little attention. However, because luxury uptake in plants in the mycorrhizal condition is usually more evident for P than for N, this process has stoichiometric consequences that have been little explored so far (see below).

Quantum dots, fluorescent nanoparticles that (upon excitation) emit light of different colours depending on their size, have been used in mycorrhizal research (Whiteside et al. 2009) to track uptake of organic N and mineral P (Whiteside et al. 2012). The relevance of the use of quantum dots has been questioned, and two issues have been specifically regarded as potentially problematic:

- Toxicity of quantum dots. Early studies of quantum dots used cadmium-containing nanoparticles (Whiteside et al. 2012, 2009) and concerns over toxicity have been raised (Raven 2022). Recent developments have allowed the use of quantum dots that do not contain cadmium, which should address that concern (Färkkilä et al. 2021).
- Mechanisms for quantum dot uptake. Quantum dots range in size from 2 to 20 nm (Whiteside et al. 2012, 2009) and the apatite crystals used by Van't Padje et al. (2021a), and Whiteside et al. (2019) were even around 200 nm, whereas the ionic radius of orthophosphate anions is around 0.1–0.2 nm, and that of glycine around 0.5 nm, so (almost) one to even three orders of magnitude smaller. It has been suggested that quantum dots are taken up through endocytosis, and while endocytosis has been described for fungi (Read and Kalkman 2003), to the best of our knowledge endocytosis has not been confirmed for AM fungi. There are no studies that have reported fungal and plant transporter expression after the application of quantum dots. However, it is plausible that such an assessment of transporter expression may be misleading. Van't Padje et al. (2021b) suggested possible apatite dissolution and orthophosphate formation before uptake. In that case, we cannot exclude the possibility that the orthophosphate after dissolution was not quantum-dotted and that the canonical transporter-mediated uptake took place. Currently we consider quantum dots a nice method for visualisation, but not yet a fully relevant tracer for 'normal' nutrient uptake and transport in the AM symbiosis [see also Raven (2022)].

Arbuscular mycorrhiza and nitrogen acquisition

The role of the AM symbiosis in N acquisition by plants has been recently reviewed by Corrêa et al. (2015), Hodge and Storer (2015), Jansa et al. (2019), and Xie et al. (2022) and not much needs to be added here. The increasing interest in using organic soil amendments in our transformation towards more sustainable, circular agriculture has focused the attention to the question to what extent AM fungi can directly (that is, without previous mineralisation by saprotrophic organisms) acquire N from organic sources, especially amino acids, oligopeptides, and amino

sugars. Dual labelling of such compounds with ^{13}C and ^{15}N and determining the ratio of both isotopes inside plant tissue is required to address this issue. Extracellular proteolysis or chitinolysis by AM fungi is, contrary to ectomycorrhizal (EcM) fungi, not known, and therefore the role of the AM symbiosis in acquisition of N directly from organic sources is probably limited. N uptake in organic forms has been demonstrated for five (likely AM) Poaceae through dual labelling (Weigelt et al. 2005), but this ability was absent in (likely AM) seedlings in a tropical forest (Andersen et al. 2017). It might be speculated that the quantitatively minor role of AM fungi in organic-N acquisition from amino acids and simple peptides is due to substrate limitation, as N mineralisation rate in these environments usually is high. However, the studies referred to above did not specifically test for any AM effect and for that reason tests are still needed where direct acquisition of N from organic sources is compared between plants of the same species under the mycorrhizal and NM condition. Testing organic-N acquisition by (constitutively) AM plants and non-mycorrhizal plants is needed as well.

A more complex, N-containing organic compound is chitin, which is present in fungal hyphae and in arthropod exoskeletons. Through isotopic labelling with ^{15}N it was demonstrated that a large portion of the N contained in insoluble chitin was taken up by AM fungi and transferred to plants (Bukovská et al. 2018, 2021; Rozmoš et al. 2022); however, in the absence of dual labelling it was not clear in what form(s) the N was taken up. While AM fungi possess transporters for the chitin monomer N-acetylglucosamine, they seem to be expressed intraradically, possibly as a means of recycling N within root cells, and hence not to be involved in direct acquisition of N from chitin or its degradation products. Degradation of chitin (incl. deamination) is thus most likely due to saprotrophic organisms in soil or possibly bacteria that are part of the hyphosphere microbiome (see section on hyphosphere microbiome). Indirect evidence for decoupling C and N fluxes (hence mineralisation of N before uptake) upon degradation of chitin in the AM hyphosphere was the fact that most C (approx. 80%) was quickly lost whereas much more N (40–60%) was retained in the system after a few weeks incubation (Bukovská et al. 2021).

The AM symbiosis is also implicated in reducing N losses, a topic recently reviewed by Okiobe et al. (2022). Besides AM-mediated uptake of N to mycorrhizal plants (see above), AM fungi may also indirectly reduce N losses by increasing uptake of other nutrients that results in larger plants with higher N content, through N immobilisation in the mycelium (see below), and by selecting for specific bacteria of the hyphosphere microbiome that reduce nitrification or promote complete denitrification and hence reduce the flux of N_2O, a major greenhouse gas in agriculture (see section on hyphosphere microbiome).

Hodge and Storer (2015) alluded to the possibility of competition between plants and AM fungi for N. The model of Landis and Fraser (2008), intended to describe variation in mycorrhizal responsiveness and based on the assumption that there was not a close coupling between P and C transfers (see Why do so many plants seem not to benefit from the arbuscular mycorrhizal symbiosis?) is equally based on competition for N between plant and the symbiotic fungus. The mycelium of AM fungi might apparently have much higher N mass fraction than leaf (and especially root) tissues. Hodge and Fitter (2010) reported N mass fractions of 30–50 mg g^{-1} for the fungal mycelium and < 10 mg g^{-1} for the plant. One implication of this differential N mass fraction might be that root N is to a considerable extent fungal N rather than plant N, especially in cases where mycorrhizal colonisation is high. However, other research carried out *in vitro* contradicted those results. A study by Rozmoš et al. (2022) indicated significantly higher N mass fractions in roots of AM plants compared with roots of plants in the NM condition; however, N mass fractions of the extraradical AM fungal hyphae were significantly lower than those of mycorrhizal roots. These data therefore might imply luxury N uptake in mycorrhizal plants (as reported above for P) or differences in N mass fractions between intraradical and extraradical mycelium. As there are only very few data on N allocation towards the fungal mycelium and plant roots, further research in this direction is recommended.

Nitrogen immobilisation in the AM fungal mycelium might result in reduced plant performance and this has been noted previously (Grman and Robinson 2013; Ingraffia et al. 2021; Püschel et al. 2016; Riley et al. 2019; Treseder and Allen 2002). This mechanism has been first noted for EcM fungi (Franklin et al. 2014) and has been referred to as the 'mycorrhizal trap' (Kuyper and Kiers 2014). In many cases, full nutrient budgets are lacking to quantify the N

contents of the fungal mycelium and that of the mycorrhizal plants. Such balances are, however, needed to properly evaluate cases of lower N content of plants in the mycorrhizal than in the NM condition.

Arbuscular mycorrhiza and heavy metals and metalloids

Heavy metals have usually been defined as metals with a density above a certain threshold, e.g., 5 g cm^{-3}. However, such a definition is hardly useful from a biological perspective as soil biota, including plant roots, cannot assess that density. A more useful classification of metals would be a classification based on binding preferences (Nieboer and Richardson 1980) that results in class A (oxygen-seeking, for instance K^+, Ca^{2+} and Al^{3+}), class B (nitrogen- and sulphur-seeking, for instance Hg^{2+}) and borderline metals (to which Cu^{2+}, Zn^{2+}, Ni^{2+}, Cd^{2+} and Pb^{2+} belong). However, the usefulness of this classification seems still limited from a biological perspective, as the classification is not correlated with toxicity. Toxicity classifications [or reference as a potentially toxic metal (Pourret and Bollinger 2018)] are equally not without problems as toxicity depends on the actual concentration of free ions in the soil solution. Some of these metals are also essential for cellular metabolism (e.g., Cu, Zn, Ni) and biota possess specific transporters to take up these metals, whereas other metals (e.g., Cd) are non-essential and are taken up by transporters for the essential metals or other molecules. Reference to trace metals [an alternative also proposed by Pourret and Bollinger (2018)] may seem counterintuitive in case of soils where, either due to natural causes or to human pollution, these metals occur in higher than trace concentrations. So while we recognise the problematic nature of the term "heavy metal", we have decided to maintain it because of the current lack of suitable alternatives.

AM fungi have been implicated in both enhancing the plant mass fraction of heavy metals, especially the essential metals when they are present in limiting amounts, and in reducing these mass fractions when they are present in excess. While this dual effect may seem paradoxical at first sight, it is likely that there are common underlying mechanisms. Ferrol et al. (2016) referred to this mechanism as heavy-metal homeostasis. However, the boundaries of these mass fractions can be rather variable, varying sometimes more than one or two orders of magnitude between minimum and maximum mass fractions. Most heavy metals (Cd, Cu, Zn, etc.) occur in cationic form and can strongly sorb to negatively charged reactive surfaces in soil such as clay, whose negative charge is pH-independent, and soil organic matter (SOM), whose charge is pH-dependent, as a consequence of which heavy-metal availability increases at lower pH. Because of adsorption to these reactive surfaces, uptake of the metals is diffusion-limited and by extending the depletion zone formed around the roots AM fungi can enhance plant acquisition of the metals. The involvement of the direct and mycorrhizal uptake pathways (for mechanisms related to both pathways, see section on P acquisition above) is apparently plant-species dependent. Coccina et al. (2019) reported a higher fractional contribution of the mycorrhizal pathway in soils with a higher Zn content for bread wheat (*Triticum aestivum* L.) but a higher fractional contribution of the mycorrhizal pathway in soils with a lower Zn content for barley (*Hordeum vulgare* L.). An earlier study by Watts-Williams et al. (2015) also reported a higher fractional contribution of the mycorrhizal pathway in soils with a lower Zn content for tomato.

Various mechanisms prevent accumulation of heavy metals, when they are present in high or excess amounts, in the plant: (1) The fungal mycelium has a high cation exchange capacity (CEC) and hence a high binding capacity for heavy metals (Joner et al. 2000) and this mechanism could therefore restrict entry of these heavy-metals in the fungus and also in the plant; (2) After the heavy metals are taken up, AM fungi could sequester those heavy metals in fungal tissues, (3) AM fungi increase extrusion of heavy metals; (4) Because AM fungi also acquire other limiting nutrients, plants in the mycorrhizal condition are usually larger than plants in the NM condition and as a consequence dilution of heavy-metal mass fractions in plant tissues occur. At first sight, these mechanisms may seem at odds with enhanced uptake of these metals under limiting conditions. A possible explanation could be that the contribution of the mycorrhizal pathway to Zn uptake is fairly low (less than 20–30% in the studies referred to above) compared with the direct pathway, suggesting a major role for fungal processes that take place before the Zn is exchanged for C inside roots. Besides, specific

AM fungal genotypes have been reported that convey greater tolerance to heavy metals to plants than AM fungi from non-polluted environments (Doubková et al. 2012; Weissenhorn et al. 1993) – see below for more details.

Because the uptake of both Zn and P are highly correlated (Jansa et al. 2003), the mycorrhizal contribution to Zn mass fractions in plants also depends on the P availability of the experimental soil, but these soil data have not always been provided. Increased P fertilisation reduces mycorrhizal colonisation and hence plant Zn mass fractions (Zhang et al. 2021). However, increased P fertilisation equally resulted in reduced mycorrhizal colonisation but increased plant Cd mass fractions (Cakmak et al. 2023). Together these results suggest a higher selectivity of AM fungal transporters for Zn compared with Cd than that of plant transporters, a situation comparable to the higher selectivity for P compared with As for AM fungal transporters than for plant transporters (see below). The physiological processes underlying the mentioned phenomena and element interactions demand further study.

Unexpected benefits from the AM symbiosis may be gauged from observations that plants from families that are normally considered non-mycorrhizal do form functional AM symbiosis under heavy-metal pollution. Mycorrhizal colonisation of Brassicaceae (Regvar et al. 2003; Vogel-Mikuš et al. 2005) on heavy-metal polluted sites in Europe, of *Hakea verrucosa* F. Muell. (Proteaceae) on ultramafic soils in western Australia (Boulet and Lambers 2005), and of *Costularia comosa* (C.B. Clarke) Kük. (Cyperaceae) on ultramafic soils in New Caledonia (Lagrange et al. 2013) have received attention. Albornoz et al. (2021) listed further examples of mycorrhizal Caryophyllaceae and Brassicaceae on serpentine soils. The alternative strategy of these plants to mobilise and subsequently acquire immobile nutrients through exudation of carboxylates likely increases the risk that too much heavy metals enter the plant.

Several studies have reported heavy-metal tolerant strains of AM fungi, particularly from Zn-polluted soils (Bui and Franken 2018; Kaldorf et al. 1999), but only exceptionally from Cu-polluted soils (Doubková and Sudová 2016). Fungal strains that are heavy-metal tolerant also have larger benefits to plants under polluted conditions, likely due to efficient mechanisms to deal with excess heavy metals such as binding to the fungal wall (immobilisation), sequestration inside cells, and extrusion of these metals.

The role of the AM symbiosis in heavy-metal remediation has received attention from the applied side (Riaz et al. 2021). Both enhanced phytostabilisation, through the production of glomalin-like compounds, and phytoextraction have been mentioned. The role of glomalin, or rather glomalin-related soil proteins (GRSP), whose production has been hypothesised to be an adaptive response to heavy-metal pollution, is discussed in the section on AM and the C cycle. Phytoextraction, the removal of heavy metals by growing plants that can accumulate large amounts of heavy metals in their shoots, the so-called hyperaccumulators, has been considered an alternative way of dealing with polluted sites. However, hyperaccumulators are often non-mycorrhizal (although some mycorrhizal colonisation has previously been reported in several non-mycorrhizal plants, see above) and the biomass production of such hyperaccumulators is often low. Remediation of heavy metal-polluted sites through phytoextraction by plants that are not hyperaccumulators, may be considered an alternative. However, the general growth-enhancing effect of AM fungi with simultaneous dilution of heavy metals might make the total amounts of heavy metals removed from the soil limited compared with what actually is in the soil.

Somewhat less attention has been devoted to metalloids, especially those that are present in the anionic form, although reviews on the role of AM fungi in dealing with arsenic contamination have previously been published (Mitra et al. 2022). Arsenic is not an essential nutrient, and plants do not possess dedicated transporters for As uptake. Rather As, as arsenate, is taken up via the P transporters, whereas As, as arsenite in the reduced form, is possibly taken up through aquaporins that also function as silicate transporters (Chen et al. 2012). Neidhardt (2021) executed a meta-analysis on the potential alleviation of adverse effects on plants of arsenate by AM fungi. The analysis suggested that, compared with plants in the NM condition, AM plants under mycorrhizal condition had higher mass fractions of P (+28%), lower mass fractions of As (-19%), and hence a much higher P:As ratio (+64%), while also showing larger biomass (+53%). The reduction in As mass fraction was much higher for legumes than for cereals, and the increase in P mass fraction was also higher for the legume

Medicago sativa L. than for the cereals like maize (*Zea mays* L.) and rice (*Oryza sativa* L.), resulting in much higher increases in P:As ratios due to mycorrhization in the legume than the cereals. For sunflower (*Helianthus annuus* L.), no beneficial effect of AM fungi was demonstrated though. Literature seems to suggest at least three different mycorrhizal strategies. These have been described for different plant taxa, so there could also be a phylogenetic signal in how plants deal with excess As. Since only a limited number of plants have been investigated, it is probably premature to generalise about these patterns. Next to plant species differences in arsenate tolerance, there likely is genetic variation within species of AM fungi. Xu et al. (2008) confirmed that at least some strains of AM fungi can be less sensitive to As than plants. The data by Neidhardt (2021) also showed fungal species-specific effects, but it is not clear to what extent these differences are driven by different AM fungus × plant combinations. In general, the AM fungi are sensitive to As, and As-polluted rice field showed a lower species richness of AM fungi than non-polluted fields (Parvin et al. 2019).

For grasses, polymorphisms have been known, where in the same population, even when not exposed to As, plants occur that possess arsenate resistance, which is manifested as suppressed uptake of orthophosphate, while other plants do not possess that resistance. The mechanism is controlled by one gene. This polymorphism has been described for *Holcus lanatus* L. but also for 8 out of 20 further grass species tested (Khan et al. 2013). *Holcus lanatus* plants that possess arsenate resistance exhibit on average larger fractional mycorrhizal root colonisation than plants that lack that resistance gene when growing in non-polluted soils (Wright et al. 2000). These authors hypothesised that the arsenate-resistant phenotype is brought about by a genotype that results in increased accumulation of P in shoots (possibly upon a greater involvement of mycorrhizal P uptake pathway than in the other genotype), and that suppression of the rate of As uptake is a consequence of this high shoot P mass fraction, operating through a feedback mechanism. Because plants with a higher P mass fraction produce more (viable) seeds, these resistant genotypes are more common in the seedling population, and this initial benefit could explain the persistence of the polymorphism. The role of the AM symbiosis in maintaining this polymorphism is, however, still puzzling. A further way of reducing As toxicity, which has been described in rice, is through transformation of inorganic As to organic As compounds, notably dimethyl arsenic acid, a process that is enhanced by AM fungi resulting in lower As toxicity (Li et al. 2016). However, Chen et al. (2013) did not observe methylation of inorganic As in rice, and the difference between both studies has not yet been explained.

A second group of plants exhibit higher P:As ratios in the mycorrhizal condition than in the non-mycorrhizal condition. This higher selectivity allows plants to tolerate As pollution and achieve more biomass in As-polluted soils. The molecular basis of this higher selectivity has not been elucidated as yet. It has been described for *Medicago sativa* (Chen et al. 2007), *Glycine max* (L.) Merr. (Spagnoletti and Lavado 2015), and *Sophora viciifolia* Hance (Wang et al. 2022a). Zhang et al. (2015) additionally reported that methylation of arsenite to form dimethyl arsenic acid occurred only in AM but not in NM plants of *Medicago truncatula*.

A third group, which was not included in the analysis by Neidhardt (2021) consists of As-hyperaccumulating plants. These belong especially to ferns. Several species of ferns, for instance *Pteris vittata* L., are As-hyperaccumulators, taking up large amounts of arsenate, transporting those to aboveground biomass (shoots), reducing the arsenate to arsenite or organic As compounds, and storing the arsenite in the leaves. Such plants have very low P:As ratios in their shoots. Trotta et al. (2006) noted that inoculation of *Pteris vittata* with AM fungi reduced As content in roots but enhanced As translocation to shoots. And because of bioaccumulation of As in aboveground tissue, such ferns can be used for phytoremediation, the cleaning of As-polluted soils through plants (Cantamessa et al. 2020; Zhang and Chen 2021).

Nanoparticles are of increasing concern for environmental health, and the question has been raised to what extent uptake by AM fungi and subsequent transport to the plant of these nanoparticles results in bioaccumulation, hence higher nanoparticle concentrations in (edible) plant parts, from where they could enter the human food chain. Wang et al. (2022b) summarised the effects of AM fungi on acquisition of nanoparticles by plants. They stated that AM fungi immobilise nanoparticles and thereby reduce the translocation towards and accumulation in plant

shoots. The authors are not specific with respect to the uptake mechanism(s) of these nanoparticles, and while they cite earlier studies that suggest a role for fungal transporters, the studies they referred to did in fact not specify any mechanism, transporter-mediated uptake, endocytosis, or others. The effects on nanoparticles might be specific for different kinds of nanoparticles. Feng et al. (2013) reported toxicity of nanoparticles of iron oxide on mycorrhizal plants, whereas the mycorrhizal symbiosis mitigated the effects of nanoparticles of silver. Our current understanding of the impact of nanoparticles on AM fungi is still in its infancy, and there is lack of knowledge of the specific mechanisms underlying their uptake and transport throughout the soil and towards plants by AM fungi.

Arbuscular mycorrhiza and nutritional stoichiometry of plants

Because of differential effects of AM fungi on the uptake of nutrients with differential mobility and because of differences in stoichiometry between AM fungi and plants, the mycorrhizal symbiosis induces stoichiometric modification in plants. Focus on stoichiometry started with a review by Allen et al. (2003) and then was elaborated by two major papers by Johnson (2010) and Johnson et al. (2015). They explored how the relative abundance of N and P in the soil on the one hand (i.e., the resources that can be supplied by the fungus, especially P) and C on the other hand (i.e., the resource provided by the plant) would determine trade relationships between both partners and how that trade balance would determine relative benefit of the symbiosis for the plant and for the fungus. Their stoichiometric model could provide an ecological explanation for the biogeography of the various mycorrhizal symbioses, with EcM (and ericoid mycorrhizal) ecosystems being dominant under conditions of N-limitation and AM ecosystems under conditions of P-limitation (see section on AM and EcM ecosystems). Their model would also describe conditions under which the symbiosis is less beneficial to (or even results in a negative growth response by) the plant. Such conditions, sometimes called mycorrhizal parasitism, was hypothesised to occur at ample nutrient (of both P and N) supply and C supply by the plant driven by a high fungal C demand. The model was suggested to explain the N paradox (Johnson 2010) where N fertilisation would reduce mycorrhizal benefit at ample P supply but enhance mycorrhizal benefit at low P availability. Thirkell et al. (2016) proposed a solution to the N paradox by demonstrating enhanced N acquisition by plants in the AM condition after addition of an organic patch to the soil that was decomposed by saprotrophic microbes and the N that was simultaneously mineralised and then transferred by AM fungi to the plant. However, their experimental conditions resulted in stronger N limitation for plants in the NM condition than for AM plants, a situation that is likely exceptional in view of the claim by Johnson et al. (2015) that a shift from P limitation to N limitation is an inherent feature of AM symbiosis. Johnson's model did not describe situations of actual competition for N (the mycorrhizal trap) that could result in lower plant performance in the mycorrhizal than in the NM condition. Such conditions are potentially relevant in a world of elevated CO_2, which could explain why, contrary to model predictions, mycorrhizal benefits decline under higher CO_2 supply. This phenomenon is known as mycorrhiza-induced progressive N limitation (Alberton et al. 2007) described both for EcM and AM ecosystems (Terrer et al. 2021) where elevated CO_2 marginally reduced plant N acquisition. Johnson (2010) also noted that mycorrhizal benefit can be predicted from the leaf N:P ratio of plants in the NM condition, with plants with low N:P ratios (indicating N-limitation) showing little or no mycorrhizal growth benefit compared with plants with high N:P ratios (indicating P-limitation). Shifts in nutrient limitation raise general questions about the stoichiometry of plants under the mycorrhizal and NM condition. Enhanced P acquisition could result in lowering of N:P ratios and a shift from P-limitation towards co-limitation by N and P and / or N-limitation. Such shifts are likely important for studies where mycorrhizal plants in the mycorrhizal and NM condition are compared as studies with plants that are limited by different resources might need a larger number of NM controls (i.e., a number of treatments with variable nutrient inputs as controls, rather than a single control treatment) to match the N:P stoichiometry of mycorrhizal plants (Slavíková et al. 2017). Such shifts would also be relevant for our understanding of cases of luxury P-uptake, acquisition of additional P that is

not translated into increased biomass [see section on AM and P acquisition and Janos (2007) for more details].

Other stoichiometric shifts occur in the K^+/Na^+ balance as a beneficial effect of the AM symbiosis under saline conditions (Giri et al. 2007; Klinsukon et al. 2021) due to larger uptake of K^+ and a lower uptake of Na^+; as well as a shift in P:As ratio over a range of As availabilities (Xu et al. 2008).

A potential stoichiometric shift as a consequence of the AM symbiosis establishment could also be the P:Mn ratio, a topic that has hardly been studied experimentally. Non-mycorrhizal plants that grow on P-impoverished soils acquire P through carboxylate exudation, a process that also mobilises Mn. Such plants have therefore elevated leaf Mn mass fractions (Lambers et al. 2015; Lambers et al. 2021). As the environment where this strategy is ecologically superior is characterised by (very) low P availability, we may predict plants with relatively low P:Mn mass ratios develop under those conditions. The recent analysis by Lambers et al. (2021) indeed showed significantly higher leaf Mn mass fractions of NM than of AM plants. As mycorrhizal plants, and especially the AM plants (i.e., mycorrhizal plants under mycorrhizal condition), likely have higher leaf P mass fractions than non-mycorrhizal plants or plants in the non-mycorrhizal condition on these impoverished soils, they are predicted to exhibit significantly higher leaf P:Mn mass ratios. While the comparison above pertains to NM versus mycorrhizal plants, a comparison of normally mycorrhizal plants in the mycorrhizal and NM condition also shows an AM effect on leaf Mn mass fractions. Lehmann and Rillig (2015) found a marginally significant negative effect of the AM symbiosis on Mn mass fractions (a decline of 4%). This negative effect was significantly stronger in P-deficient soils than in soils with higher P availability and was independent of soil Mn content. Subsequent studies are in agreement with this meta-analysis. Watts-Williams and Gilbert (2021) reported significantly lower Mn mass fractions (reduction by more than 50%) in grain of wheat (*Triticum aestivum*) and barley (*Hordeum sativum*) under the mycorrhizal than NM condition. Similar mycorrhizal effect on Mn root and leaf fractions of maize was described by Ramírez-Flores et al. (2017). Baslam et al. (2012) noted lower Mn mass fractions in leaves of lettuce (*Lactuca sativa* L.) under mycorrhizal than NM conditions. However, their data show Mn mass fractions in outer leaves that are 4–6 times higher than established adequacy levels and close to the highest values ever reported, while their data equally raise questions about K content. Two mechanisms may be envisaged to explain lower Mn mass fractions in plants under the mycorrhizal condition. Kothari et al. (1991) proposed an AM fungi-induced shift in the composition, abundance and activity of Mn-reducing bacteria. An alternative hypothesis is an AM fungi-induced reduction in carboxylate exudation as was demonstrated in the majority of species of the legume genus *Kennedia* (Ryan et al. 2012), although no data on leaf Mn mass fractions were provided. A subsequent study by Nazeri et al. (2014) demonstrated a lower amount of carboxylates in the rhizosphere and lower Mn leaf mass fractions of five legumes but higher leaf P mass fractions when plants were under mycorrhizal compared with NM conditions. We are not aware of any studies that have applied this ratio in ecological studies, but the published data allow a preliminary assessment. The shoot P:Mn mass ratio was around 8 in the NM condition and almost doubled to 15 in five legumes in the mycorrhizal condition (Nazeri et al. 2014). Wheat and barley grain P:Mn mass ratios were 23 respectively 55 in the NM condition and increased to 82 resp. 205 when the plants were mycorrhizal in the study by Watts-Williams and Gilbert (2021), whereas Ramírez-Flores et al. (2017) reported P:Mn mass ratios in maize of 2.7 and 4.0 in the NM and mycorrhizal condition respectively. Investigating links between the AM symbiosis, plant P:Mn mass ratios, and strategies to acquire limiting nutrients through different mechanisms is thus a potentially rewarding research topic.

Arbuscular mycorrhiza and the carbon cycle

AM fungi are obligate biotrophs and lack saprotrophic capability (Tisserant et al. 2013). They cannot complete their life cycle except in the presence of a host plant that provides organic C to the fungus as energy source and as skeleton for biomolecules. Sugars (hexoses) were for a long time reported to be the major component that plants provide. However, the last decade has shown that AM fungi lack the genes for long-chain fatty acid biosynthesis and are fully dependent on the fatty acids synthesised by the host

plant (Luginbuehl et al. 2017). These fatty acids that are delivered by the plant both serve as signals and as major nutritional source, as triacylglycerols are a major storage component in AM fungi (Bago et al. 2002). Instances have been reported of successful co-cultivation of certain AM fungi and the bacterium *Paenibacillus validus* in the absence of a host plant (Hildebrandt et al. 2006) and a recent study by Sugiura et al. (2020) showed that *Rhizophagus irregularis* (Błaszk. et al.) C. Walker & Schüßler exhibited limited asymbiotic growth under artificial conditions if myristate was externally supplied which could be taken up and further processed and utilised by the fungus. However, the spores formed under these conditions remained smaller compared with those formed under symbiotic conditions and it remained unclear whether such alternative forms of artificial cultivation of AM fungi would provide a viable way to study their physiology. Tanaka et al. (2022) recently reported mass production of viable spores in the absence of a host plant by one strain of *Rhizophagus clarus* (T.H. Nicolson & N.C. Schenck) C. Walker & Schüßler, provided with a complex suite of hormones and the fatty acids.

Even though AM fungi lack efficient exoenzymes to degrade even simple forms of organic matter, there are several mechanisms through which AM fungi could affect C cycling and C storage in ecosystems (Hodge 2014; Wei et al. 2019). The first three mechanisms do not impact decomposition processes, but still affect the sizes of soil C pools, while others stimulate or retard decomposition. Here we provide an overview of potential mechanisms, while admitting that the diversity of mechanisms currently make any generalisation very difficult.

- Enhanced plant productivity. Most plant species benefit from the AM symbiosis (at least under certain conditions) by increasing their biomass, and this consequently results in higher inputs of aboveground and belowground litter in the soil.
- Addition of hyphal necromass. It has become increasingly clear that the contribution of microbial necromass in mineral-protected SOM is more important for soil C storage than that of recalcitrant plant material (Hoffland et al. 2020). It is therefore relevant to assess the extent to which AM fungal hyphae possess properties that make it likely that they also contribute to SOM protection and hence sequestration. Schäfer et al. (2019) determined the decomposition rate of AM fungal hyphae and noted a decline of decomposition rate over time with a maximum value of the decomposition constant k of 2.5 $month^{-1}$ and a minimum value of 0.1 $month^{-1}$. The coarse hyphae decomposed on average twice as rapidly as the fine hyphae which seems counterintuitive considering the larger surface of smaller hyphae per unit mass. Whether these differences therefore reflect functional and chemical differentiation in the AM mycelium (Friese and Allen 1991) or species-specific differences in decomposition rates remains to be studied. Zhang et al. (2020) reported somewhat slower turnover of AM fungal necromass, with $k = 0.1$ $month^{-1}$, similar to the minimum values reported previously by Schäfer et al. (2019). There are only few studies that assessed the chemical composition of the AM mycelium. Huang et al. (2022) noted considerable chemical differences in the decomposability of hyphae of AM and EcM fungi, with AM fungi possessing a much higher fraction that is acid-hydrolysable, suggesting a higher decomposition rate of AM fungi than of EcM fungi (and possibly also of other Basidiomycota and Ascomycota). However, following the logic above that more easily degradable substrates allow a higher microbial C-use efficiency that ultimately translates into more mineral-associated microbial necromass, the contribution of AM fungal necromass to soil C storage could be higher than that of EcM fungal biomass. Schultz et al. (2022) demonstrated a special class of cell surface proteins that are unique to the Glomeromycotina. Whether these surface proteins play a role in the interactions with the environment and stabilisation of mycorrhizal fungal necromass is currently not known. Further interactions with the mineral phase of soil could be due to the charge on hyphal walls. Joner et al. (2000) noted a much higher CEC for hyphae of AM fungi than for plant material (200 mmol kg^{-1} for hyphae and 10–30 mmol kg^{-1} for roots respectively). However, it is unclear whether the CEC of AM fungal hyphae differ from those of EcM fungi, where Marschner et al. (1998) reported values between 100 and 300 mmol kg^{-1}.
- Production of glomalin. Glomalin was only reported less than thirty years ago as a very sta-

ble proteinaceous or glycoproteinaceous compound produced by AM fungi (Wright et al. 1996; Wright and Upadhyaya 1996). It was supposed to cause aggregation or stabilisation of aggregates of soil particles and to possess a low decomposability, making it a soil C fraction that makes a major contribution to soil C sequestration. Following these first reports the study of glomalin rapidly gained momentum. However, subsequent research casted considerable doubts about its uniqueness for AM fungi. The term glomalin tended to be replaced by glomalin-related soil proteins (GRSP; Rillig 2004). Glomalin or GRSP is primarily operationally defined through extractions of the SOM pool in citrate buffer at high temperatures, but its chemical nature (or rather the diversity of its chemical natures) is still poorly known. While a number of studies indicated correlations between soil GRSP contents and independent estimates of AM fungal abundance, other studies showed that even in extractions where little or no AM fungi would be expected, considerable amounts of GRSP were observed (Nie et al. 2007). The very significant correlations between SOM content and GRSP contents in nearly all studies would further cast doubts on its uniqueness as a compound produced by AM fungi (Holátko et al. 2021). Holátko et al. (2021) and Irving et al. (2021) reviewed the current knowledge on GRSP and identified a number of pertinent questions, starting with the (obvious) one what GRSP actually is and what its chemical composition is, followed by questions about its origin and temporal dynamics (stability). They raised also more fundamental questions whether GRSP is produced by soil microbes and what the fitness effects, if any, are of its production. While Agnihotri et al. (2022) stated that GRSP production by AM fungi is a strategy for survival in poorly structured soils by acting as a binding agent, other properties of GRSP, such as the ability of GRSP to bind or adsorb metals, including heavy metals (see above), are likely an afterlife effect and less likely related to microbial fitness. If, as seems likely, GRSP is a heterogeneous mix of SOM compounds, only some of which are produced by AM fungi, it is likely that estimates of the AM fungal contribution to soil C storage via glomalin are generally overestimated.

- Changes in litter quality. Schädler et al. (2010) and Urcelay et al. (2011) demonstrated that AM plants showed higher leaf decomposition rates than their counterparts under NM conditions, likely due to the fact that AM plants generally have larger mass fractions of N and P in their leaves. Interestingly, Urcelay et al. (2011) did not observe effects of mycorrhization on the decomposition of root litter, which was not explained. One possible explanation for this difference between leaf and root litter is that part of root mass is in fact fungal (mycelium) mass, which might exhibit different decomposition rates than plant tissues. As roots contribute more to soil C storage than leaf litter (Rasse et al. 2005), separating plant and intraradical hyphal mass losses over time appears ecologically relevant and demands further study.
- Modifications of soil properties that can either enhance or retard decomposition. The main mechanism related to retarded decomposition is likely enhanced formation of soil aggregates that protect organic material against decomposition. Reduced decomposition rate and increased C retention in soil were described by Verbruggen et al. (2016), who suggested that reduced nutrient availability could underlie the observed slowdown. Leifheit et al. (2015) equally demonstrated retarded decomposition of woody litter. As these authors also noted increased soil aggregation in the mycorrhizal treatment, it seems likely that the slower degradation was caused by protection of organic materials within aggregates. Modifications could also include impacts on the saprotrophic bacterial and fungal communities (Gui et al. 2017b, 2020; Herman et al. 2012; Chowdhury et al. 2022; Nuccio et al. 2013; Xu et al. 2018). Finally, competition between AM fungi and saprotrophs for mineral nutrients, in cases where decomposition is nutrient-limited, could reduce decomposition, an example of an AM fungal-driven Gadgil effect, the suppression of decomposition by mycorrhizal fungi (Bukovská et al. 2018). Effects of modification of root exudation and hyphal exudation could both result in a stimulation and a retardation of decomposition of litter or SOM (positive or negative priming). Cheng et al. (2012) reported enhanced decom-

position of soil organic C in a mycorrhizal compared with NM treatment; however, we think their data should be dealt with caution, as their Fig. 1 shows unrealistically high decomposition rates of soil organic C, with 30–40% of SOC having been decomposed, depending on AM fungal species, after 10 weeks. Their data on SOC decomposition contrast with those by Gui et al. (2017a), who noted that AM fungi enhanced litter decomposition compared with an NM treatment, but had no effect on the decomposition of soil organic C. Hodge et al. (2001) reported enhanced decomposition of milled litter in the mycorrhizal compared with the NM microcosms. The study showed very high decomposition rates in both treatments, with almost 90% being decomposed in the absence of AM fungi and 96% decomposed with hyphal access after four weeks. As their data suggest that 75% of the N budget was unaccounted for and as it is unclear whether the N found in the plants was in shoots or roots and hence potentially (still) under fungal control, we suggest that these data need to be interpreted cautiously. Mei et al. (2022) observed that after addition of benomyl, a fungicide that specifically targets AM fungi, a larger fraction of two grass litters remained in soil, an effect consistent with a positive effect of AM fungi on litter decomposition. Yet, such an interpretation assumes that benomyl had no or very limited effect on other saprotrophic organisms, which is probably not the case. Kong et al. (2018) noted that the positive effect of AM fungi on litter decomposition was larger under lower levels of soil fertility, but unfortunately their experimental design did not allow separation of the effects of AM fungi and soil fertility. Xu et al. (2018) noted that AM fungi enhanced decomposition at low P availability but reduced it at high P availability. From their stable-isotope data it is evident that especially compounds with very low C:N ratios (C:N = 6 or less) were decomposed.

- Modification of plant exudation by upstream capturing of C, i.e., reducing exudation. In a comparison of plants of the legume *Kennedia* under the mycorrhizal and NM condition, Ryan et al. (2012) showed that mycorrhizal colonisation in most cases reduced the exudation of carboxylates. This reduction might have potential negative consequence for bioavailability of P that is sorbed onto mineral surfaces (see above) as these exudates competitively desorb bound phosphates, but also for desorption of mineral-protected SOM. That mechanism, known for the EcM symbiosis (Keiluweit et al. 2015) has not yet been tested for the AM symbiosis. Studies that implied significant carboxylate exudation by AM fungi such as by Andrino et al. (2021) did not assess whether these carboxylates were produced by the AM fungi themselves or by associated hyphosphere bacteria (see section on hyphosphere microbiome).
- While the general levels of exudation through the plant in the mycorrhizal condition might be reduced, one might argue that hyphal exudation could partly counter this effect. However, AM fungi are unlikely to exude significant amounts of carboxylates as they are considered to be C-limited compared with plants. Evidence for direct hyphal exudation and priming of SOM degradation comes from a study by Paterson et al. (2016) who demonstrated a C flux from the plant through AM fungal hyphae that primed the decomposition of SOM. Exudates not only impact the potential priming of organic-matter degradation but might also contribute to the recruitment of specific bacterial consortia in the hyphosphere [Kaiser et al. (2015); see section on hyphosphere microbiome]. Zhang et al. (2018b) noted that fructose was an important component in hyphal exudation that increased phosphatase activities in hyphosphere bacteria.
- Even though AM fungi cannot live saprotrophically (see above), it does not preclude the possibility that acquisition of nutrients in organic forms delivers some C that these fungi could use for their own metabolism after internalisation. Currently, no evidence exists that AM fungi can directly take up organic P (see section on P). Whereas for N, uptake of the nutrient in organic forms has been demonstrated, the quantitative importance is likely very limited as well (see section on N acquisition). There are scattered reports of AM fungal hyphae specifically proliferating in decaying litter (Bunn et al. 2019; Went and Stark 1968), and the more recent paper suggested that such specific fungal foraging may be a global phenomenon. The studies by Thirkell et al. (2016) and others (Bukovská et al. 2018, 2016) demonstrated foraging of AM fungal hyphae in organic

matter patches and enhanced plant benefit from such selective foraging, thereby explaining mycorrhizal benefits under conditions of additions of organic amendments. The meta-analysis by Jiang et al. (2021b) also indicated that organic amendments generally resulted in an increase of AM fungal biomass. Bunn et al. (2019) hypothesised that certain species of AM fungi may even be specialised for foraging in this specific microhabitat. The implications of their admittedly speculative hypothesis might be that AM researchers should not only study these fungi in the mineral soil, but also in the organic layers above the mineral soil or in organic patches. Further, the AM fungal role in short-circuiting mineral nutrient cycles, as their presence close to saprotrophic microorganisms provides them with rather immediate access to mineral nutrients (but most likely mediated through activity of other saprotrophic microorganisms), may be one mechanism that prevents rapid nutrient leaching in tropical rainforests.

Because of the multitude of mechanisms, and hence the variability of outcomes, it is currently not possible to generalise the effects of the AM symbiosis on litter decomposition. This is not surprising considering the extreme heterogeneity of forms of organic C that have been used in various studies. It is therefore important, both when addressing the role of nutrients in organic forms and in addressing the role of AM fungi in the global C cycle, to work with more defined organic compounds (cf. Jansa and Hodge 2021). Hodge (2014) noted that, whereas several studies showed AM fungal responses to organic patches and measured the magnitude of such a response, the importance of that response for the fungus itself and for the associated plants, remains poorly quantified. Care should finally be taken in interpretations of correlations between changes in AM fungal activity and changes in SOM levels. Such relationships can be misleading as both processes can be caused by a third underlying factor that determines both responses. Such a spurious relationship is evident in case of soil disturbance that both enhances organic matter decomposition, due to a breakdown of aggregates, and reduces AM fungal abundance. A spurious relationship might also pertain in the study by Sochorová et al. (2016). The authors described a reduction in AM fungal hyphal length and a concomitant increase in hay yield after mineral fertilisation including P, but not after mineral fertilisation without P. The authors interpreted these results as correlative evidence that AM symbioses contribute to SOM stocks and speculated about a direct role for AM fungal biomass and necromass or an indirect role through changes in aggregation.

However, it is at least equally plausible that addition of P would create competition for sorption sites on mineral surfaces, thereby displacing organic matter from these sites and this desorption subsequently resulting in increased breakdown of SOM and release of both C and mineral nutrients (particularly the N) from the SOM (Regelink et al. 2015). Studies where both alternative hypotheses have been simultaneously tested have, to the best of our knowledge, not yet been executed.

Finally, AM fungi might contribute to enhanced weathering of silicate materials, a process that consumes bicarbonate ions and leads to inorganic-C sequestration. The AM management has been suggested as a way of enhanced silicate weathering in order to store C in soils by Verbruggen et al. (2021), who listed pathways through which ground silicate, added to agricultural systems, could enhance C sequestration. While no studies are currently available, the increased attention to olivine weathering as a C sequestration option, makes inclusion of AM fungi in this research attractive.

The AM symbiosis and water relations of plants

It is generally accepted that the AM symbiosis provides plants with enhanced abilities to withstand drought (resistance or tolerance) and / or to recover from drought events (resilience); however, the mechanisms underlying drought tolerance or resilience are still subject to debate (Cheng et al. 2021). Generalisations are also difficult because of different ways in which drought has been imposed (He and Dijkstra 2014), the use of different plant species that possess their own mechanisms to adapt to drought, and the use of different AM fungal species and soils with various physico-chemical properties. Whereas Jayne and Quigley (2014) did not observe significant differences between seven species of the Glomerales, they also noted large variation in the data. In a direct comparison between a temperate strain

of *Rhizophagus irregularis* and a strain of *R. arabicus* (Sieverd. et al.) Błaszk. et al. from arid regions, Symanczik et al. (2018) noted that drought induced a reduction of stomatal conductance of plants inoculated with *R. irregularis* by 15%, whereas this parameter remained unaffected in plants inoculated with *R. arabicus*. Interestingly, in a study using synthetic mycorrhizal communities and manipulation of environment including a drought treatment, *Funneliformis mosseae* (T.H. Nicolson & Ged.) C. Walker & Schüßler abundance was promoted via preferential C allocation at the cost of *Claroideoglomus claroideum* (N.C. Schenck & G.S. Smith) C. Walker & Schüßler upon short-term drought. This indicated significant dynamics in AM fungal communities under varying environmental conditions and possibly the ability of plants to preferentially allocate C to the fungus that was more rewarding under given set of conditions (Forczek et al. 2022).

Currently we cannot link specific mechanisms to traits of individual AM fungal species. Beneficial effects of AM fungi are often larger under conditions of water limitation than under well-watered conditions, and in factorial experiments a significant AM fungus × drought interaction is often noted, indicating both generalised and drought-specific effects of the AM symbiosis (Leventis et al. 2021; Püschel et al. 2021). To facilitate discussion about this topic we separate mechanisms that allow plants when growing under mycorrhizal conditions (and plants growing in soils where AM plants grew before) to acquire more water from mechanisms determining how AM plants deal with the negative impacts of drought. The mechanisms related to enhanced water acquisition include both hydraulic properties of AM soils and the role of AM hyphae in better access to water in a pore space inaccessible to roots and transport of that water towards the plant. Mechanisms internal to the enhanced drought tolerance of AM plants include changes in nutrient status, changes in hormonal status that affect photosynthesis, and production of antioxidant enzymes. Many of these mechanisms equally allow AM plants to better deal with salinity, a topic that has been extensively reviewed by Evelin et al. (2009), Miransari (2017), and Porcel et al. (2012), to which we refer. Specific effects of the AM symbiosis on the K^+/Na^+ balance are mentioned in the section on AM and stoichiometry of plants.

Augé et al. (2001) were the first to show that AM soils had different hydraulic properties than NM soils. In a subsequent study, Augé et al. (2007) applied path analysis to separate the effects of soil colonisation and root colonisation by AM fungi, and confirmed a major role for soil colonisation. A recent study, Pauwels et al. (2020) confirmed that AM soils, specifically soils that were colonised by extraradical AM fungal hyphae, possess greater water retention capacity, likely due to increased pore space heterogeneity. Bitterlich et al. (2018a) equally noted that the AM symbiosis alleviated resistance to water movement in soils and speculated that the effect might be due to fungal modification of pore architecture. Next to changes in pore space, the formation of stable aggregates could impact the moisture retention in drying soils (Guber et al. 2004). Further, the hydrophobic nature of AM fungal hyphae (Rillig et al. 2010) could also contribute to the differences in hydraulic properties between AM and NM soils (Querejeta 2017).

The direct role of extraradical hyphae in water uptake is still controversial and the mycorrhizal contribution to plant water acquisition has therefore produced highly variable quantitative estimates (Kakouridis et al. 2022; Püschel et al. 2020). On the one hand, it is commonly stated that due to their small size extraradical hyphae of AM fungi can access soil pores that are too small for fine roots or root hairs, thereby allowing for a better soil–water contact (Allen 2007). Physical principles, on the other hand, such as the Hagen-Poiseuille law for flow through vessels that states that flow rates scale with the fourth power of vessel diameter, would lead to the opposite conclusion, i.e., a small direct effect of AM fungi on plant water acquisition. As the diameter of the finest hyphal branches is very small, these fine hyphae, despite their favourable position to maintain soil–water contact, are in fact too small to allow ecologically relevant amounts of additional water to be transported to the plant. There are not many estimates of flow rates through hyphae in relation to their diameter. Based on P flux data through hyphae of different diameters, Pearson and Tinker (1975) reported P flow rates for small-diameter hyphae (2—4 µm) between 0.3–1.0 10^{-9} mol cm^{-2} s^{-1}, and for large-diameter hyphae [10 µm diameter; hyphal diameter estimates based on Friese and Allen (1991)] of 38. 10^{-9} mol cm^{-2} s^{-1}, roughly in agreement with this law.

Kothari et al. (1990) calculated that only a small amount (slightly over 10%) of the increase in water flow from soil to AM over NM plants could be attributed to the active hyphal transport of water, as a higher water flux through hyphae should have resulted in a considerably higher P inflow rate than observed. In their experimental design, water was supplied in the root compartment and there was very little water consumed in the hyphal compartment. However, a study by Kakouridis et al. (2022) calculated that around 30% of water transpired by host plants was delivered through the hyphae of AM fungi. This recent study was based on a system where water was withheld from the plant compartment before the treatment started, whereas the compartment that could only be accessed by the AM fungal mycelium received a considerable amount of water. The conclusion that water flow through hyphae might be quantitatively unimportant was also supported in a study by Püschel et al. (2020) who used deuterium as a tracer for water uptake. They concluded that plants under the mycorrhizal condition increased water uptake compared with plants under the NM condition. However, they also concluded that the effect was largely indirect, caused by differences in plant size and more extensive root system of the AM plants. Water transport via AM fungal hyphae was slow compared to the transpiration demand of the plants and to water uptake via roots. The conditions under which such experiments are executed have a potentially large role on the outcome and hence on the quantitative assessment of the importance of water flow through hyphae. Kakouridis et al. (2022) also stated that the water might have travelled either outside the hyphal wall or extracellularly within the hyphal cell wall matrix; however, it seems difficult to reconcile that statement, based on the behaviour of the dye used as tracer, with the observation that mycorrhizal P uptake was very high in that experiment.

Whereas the role of the extraradical mycelium in water flow may be quantitatively limited, mycorrhization of the plant could influence water flow inside the plant root. Bárzana et al. (2012) noted that roots of AM plants showed significantly more apoplastic water flow than those plants under the NM condition, an effect that occurred both under drought and well-watered conditions. They also suggested that the ability of AM plants to modify water transport pathways allows the AM plant to respond more flexibly to water limitation. It remains to be clarified whether root hydraulic conductivity or hydraulic conductivity at the soil-root interface are more affected by AM symbiosis formation and which of them is more relevant to plant drought tolerance (M. Abdalla Ali, personal communication).

Meta-analyses of the effects of the AM symbiosis on stomatal conductance and on chlorophyll fluorescence have been published by Augé et al. (2015) and Wang et al. (2019b). Augé et al. (2015) noted a stronger increase due to mycorrhization under moderate and severe drought (positive effects of + 51% and + 111% respectively) than under well-watered conditions (an effect of + 23%). The mycorrhizal effect was larger under conditions of a mycorrhizal growth benefit (+ 53%), although even in cases where plants in the AM condition did not outperform plants when non-mycorrhizal, the positive mycorrhizal effect on stomatal conductance was significant (from + 11 to + 21%). The same pattern occurred in leaf P status: The AM plants that had higher leaf P mass fractions showed a significantly stronger positive effect on stomatal conductance (+ 52%) than plants that did not exhibit higher P mass fractions (from + 8 to + 29%). Plants with C_3 photosynthesis type showed a larger beneficial effect than plants with C_4 photosynthesis type (+ 28% versus + 12%). Legumes responded more strongly than herbs, and monocots showed the smallest positive response, an effect likely partly due to the inclusion of C_4 plants among the monocots. It is likely ecologically relevant that the beneficial effect of the AM symbiosis on stomatal conductance was larger in field experiments (+ 55%) than with plants grown in a greenhouse (+ 17%); however, due to the large variation in field experiments the effect was only marginally significant. Wang et al. (2019b) concluded that most components of photosystem II were more abundant in plants under the mycorrhizal than NM condition when exposed to salinity, which likely also reflects mycorrhizal effects under drought. Their data on apparent quantum yield of photosystem II (F_v/F_m) have to be interpreted with caution, though, as their Fig. 1 showed a positive effect size due to the mycorrhizal symbiosis of close to 20%, whereas the text and Table 1 refer to a beneficial effect of only 4% (Wang et al. 2019b). Their data show that the mycorrhizal benefit is larger for C_4 than for C_3 plants, which is in contrast to the mycorrhizal benefits for stomatal conductance (see above).

The mechanistic basis for this difference is currently unknown.

Hormonal changes in AM plants include changing levels of abscisic acid (ABA), the hormone that regulates stomatal closure and thereby reduces water loss. However, results are contradictory with some studies showing that AM plants under drought had lower concentrations of ABA than plants with lower levels of AM colonization or when in the NM condition (Chareesri et al. 2020; Chitarra et al. 2016), and other studies showing the opposite (Ding et al. 2022). Earlier research (Duan et al. 1996) showed that plants under the mycorrhizal and NM condition did not differ in stomatal sensitivity to ABA, meaning that AM symbiosis may not necessarily affect the mechanism of stomatal closure but may actually postpone the activation of that mechanisms throughout soil drying (Bitterlich et al. 2018b). A role for strigolactones in conferring drought tolerance of AM plants has equally been described (Ruiz-Lozano et al. 2016). Hormonal changes under the influence of AM fungi could modify root hydraulic conductivity where the drought-induced decrease in hydraulic conductivity is mitigated by AM fungi (Bárzana et al. 2012; Sánchez-Romera et al. 2016).

Drought has a strong impact on the acquisition of nutrients whose uptake is diffusion-limited, like P, but can also be important for nutrients for whose uptake by plants mass flow is important. As P is preferentially allocated to reproductive organs (seeds), it can be predicted that assessments of beneficial effects of AM fungi in conferring drought tolerance and enhancing plant performance and fitness under drought will demonstrate larger positive effects based on yield than on plant biomass. Somewhat surprisingly, the meta-analysis of Jayne and Quigley (2014) provided no support for this notion, possibly due to the fact that different plant functional groups showed very different responses to AM fungi with respect to reproductive performance. Reproductive performance of legumes under drought hardly showed additional benefits of AM fungi compared with well-watered conditions. However, the above meta-analysis also showed that there were far more studies that considered plant (or shoot) biomass than yield, a bias that should be addressed in future studies. Interestingly, the meta-analysis by Hoeksema et al. (2010) also indicated that N_2-fixing plants tend to be less responsive to AM fungi than other plant functional groups. In order to explain that low effect, the authors suggested two explanations: (1) experiments with legumes are usually done in soils with generally higher P availability which would then reduce relative mycorrhizal benefit; and (2) C costs of both the mycorrhizal symbiosis and the N_2 fixation limit plant biomass increases. However, in their meta-analysis both explanations could not be evaluated. A further explanation could be the large seed mass (and large nutrient reserves therein) of legumes, which makes growth responses in experiments of a short duration more dependent on the reserves in seeds that on external acquisition of nutrients.

Recovery of plants after drought, and the role of AM fungi therein, has been far less studied than the direct impacts of drought on plant performance and fitness. Studies on rice (Ruiz-Sánchez et al. 2010; A. Chareesri, personal communication) showed higher drought resilience of plants in the mycorrhizal than in NM conditions. Considering the high sensitivity of rice compared with other cereals to drought, this effect may critically extend the window of opportunity for recovery after drought periods. As climate change makes weather extremes more likely, enhanced opportunities to recover from drought may become increasingly relevant for future agricultural production.

Water relations in intercropping systems with AM plants might also be affected by the role of AM fungi in hydraulic redistribution, a topic that has received only limited attention, but that could be relevant for dryland cropping systems with intercropped plants that differ in vertical root distribution (Allen 2007; Singh et al. 2019, 2020). For further details see the section on ecological effects of common mycorrhizal networks (CMN).

Interactions between AM symbiosis and plant-soil water relationships appear a particularly hot topic with respect to ongoing climate change. Yet, the understanding of underlying mechanisms is still in its infancy, particularly because the research needs strong expertise in both botany and soil sciences. For example, modulation of the soil (e.g., aggregation) needs to be studied in conjunction with plant physiological response, often in a timely resolved manner.

Hyphosphere microbiome

For a long time, it has been customary to look at the AM symbiosis as pertaining to just two organisms, the AM plant and the AM fungus. While there has been awareness about plant effects on the immediate vicinity of their roots (the rhizosphere effect) and the role of mycorrhiza in modifying this rhizosphere effect (the mycorrhizosphere effect), attention to the microbial community around the hyphae, the hyphosphere, the zone immediately surrounding the extraradical hyphal network and under the influence of hyphal exudates, has only recently become an area of very active research (Zhang et al. 2022; Wang et al. 2022a, b). Similar to the rhizosphere microbiome research, a similar set of questions is pertinent, amongst which the most important are:

- To what extent does the fungus exert influence over the composition of the hyphosphere microbiome?
- To what extent are there AM fungal species-specific differences in the hyphosphere microbiome?
- What are the functional consequences of the bacterial/fungal/protistan consortia establishment that constitute the hyphosphere microbiome for the AM fungus, the plant, and the ecosystem?
- How tight is the association between different species of AM fungi and the microbial taxa within the associated hyphosphere microbiome?
- How can we reconstruct the hyphosphere microbiome under simplified experimental conditions?
- What are the consequences of a specific hyphosphere microbiome for experiments involving AM plants under mycorrhizal and NM conditions?

The hyphosphere constitutes a specific habitat with specific microbial consortia and these consortia are AM fungal species-specific (Zhang et al. 2018c, 2022; Zhou et al. 2020). While several studies have provided overviews of the more abundant prokaryotes in this microhabitat (See et al. 2022 for a brief overview), translating such species lists to a functional interpretation has remained largely elusive (Faghihinia et al. 2023). Compared with the rhizosphere microbiome, currently available evidence suggests that the effect of soil properties is less important, and that of AM fungal taxonomy and phylogeny more important (Emmett et al. 2021), which could be an indication for a much closer association between AM fungi and bacteria in the hyphosphere than in the (mycor-) rhizophere. Hyphosphere bacteria receive their C as energy-rich compounds exuded by the hyphae (Kaiser et al. 2015; Paterson et al. 2016); however, quantitative data on hyphal exudation rates do not seem to be available. The role of these exudates in priming the decomposition of SOM has been discussed above; here we focus on the cycles of N and P.

Ecological relevance of the hyphosphere microbiome has been clearly demonstrated for P cycling. The focus on the hyphosphere microbiome came as a logical outcome from two contrasting sets of observations: On the one hand, empirical studies that demonstrated the ability of AM fungi to acquire P from organic sources through phytases and various phosphatases that showed higher activity in soils under mycorrhizal than under NM condition (Koide and Kabir 2000); On the other hand, genome sequencing of AM fungi that demonstrated that these fungi did not possess the genes for those extracellular enzymes (Tisserant et al. 2013). These contrasting data were reconciled when it was shown that it were the bacteria in the hyphosphere that were responsible for mineralisation of organic P. Studies indicate that the hyphosphere microbiome bacteria are more efficient in releasing P than the bacteria in the mycorrhizosphere (Qin et al. 2022; Taktek et al. 2015). Hyphosphere bacteria allow desorption and subsequent mineralisation of various organic P sources into orthophosphate, which then can be taken up by AM fungi (Jiang et al. 2021a). Through their activities, certain AM fungi and associated hyphosphere bacteria can thus increase the potentially available P in soils, qualifying them as P miners (Lambers et al. 2008). The importance of this process compared with carboxylate exudation by plants in the mycorrhizal condition needs further study, especially under field conditions. Genetic analyses of these hyphosphere bacterial communities showed the presence of genes for the relevant enzymes (Wang et al. 2019a). These hyphosphere microbiomes differ among species of AM fungi (Zhou et al. 2020) but can also differ among isolates of the same species (Wang et al. 2022a). Zhou et al. (2023) noted that these different hyphosphere microbiomes associated with different species of AM fungi allowed niche differentiation, as AM fungal species that were weaker colonisers of

the soil environment were associated with bacteria that were more efficient in desorbing and mineralising P from phytate than more efficient soil-colonising AM fungi. Also, the study of intraspecific variation of *Rhizophagus irregularis* showed that one isolate produced larger amounts of extraradical mycelium, but that ability was traded off against a more efficient hyphosphere microbiome (Wang et al. 2022a). The extent to which AM fungal species-specific hyphosphere microbiomes allow niche differentiation and hence coexistence of different AM fungal species on the same root system demands further study. Another question that should be further investigated is the extent to which the AM fungal phylogeny can be used as a predictor for certain functions executed by the hyphosphere microbiome; and, in case there is a clear phylogenetic signal, whether such a strong phylogenetic signal constitutes evidence for coevolution of AM fungi and their associated microbiota. The closer the coevolution between AM fungal species and their hyphosphere microbiomes, the more important it becomes to reflect on how to control for such different hyphosphere microbiomes in mycorrhizal research and possibly also in mycorrhizal applications.

The role of the hyphosphere microbiome for N acquisition, especially from more recalcitrant organic N sources, has been discussed by Jansa et al. (2019), and experimental evidence for the involvement of certain chitinolytic bacteria in the utilisation of chitin-N in AM fungal hyphosphere has been recently published by Bukovská et al. (2021) and Rozmoš et al. (2022). Hyphosphere bacteria also play a major role in the denitrification pathway. Lower denitrification in the presence of plants under mycorrhizal than NM conditions has been previously reported by Storer et al. (2018). Direct AM fungal mechanisms (i.e., the AM symbiosis results in larger plants that have higher N contents and therefore leave less N in the soil for denitrifiers) have been discussed above, and here we specifically focus on the role of the hyphosphere microbiome. Both changes in the associated communities of nitrifying (ammonia-oxidising) and denitrifying (nitrate-reducing) bacteria have been reported (Bender et al. 2014; Okiobe et al. 2022; Storer et al. 2018; Veresoglou et al. 2019; Zhao et al. 2021; Dudáš et al. 2022). Data by Li et al. (2023) showed that the AM symbiosis specifically promoted bacteria that increased the ultimate step of the denitrification pathway, resulting in reduced formation of the greenhouse gas N_2O while emitting more N_2 through complete denitrification. Shi et al. (2021) finally demonstrated the presence of the NifH gene in bacteria of the hyphosphere microbiome, implying the possibility for N_2 fixation close to the hyphal cell walls. Rates of N_2 fixation have not yet been determined and so we can only speculate about ecological relevance of this finding.

Less tight associations between AM fungal species and hyphosphere microbiomes might have effects outside the direct hyphosphere. See et al. (2022) hypothesised that the hyphosphere microbiomes could well extend into bulk soil and that these microbiomes could specifically reach patches of mineral-associated organic matter [possibly using the hyphal highways for migration towards such patches (Jiang et al. 2021a)] and thereby contribute to both the breakdown of mineral-associated organic matter and, through the formation of bacterial and fungal necromass, to the formation of new mineral-associated organic matter.

However, the bacteria with the functions specified above constitute only a minor part of the total bacterial biomass. The activities of the other bacteria have been less studied. Jansa et al. (2013) took a more critical approach towards an exclusive functional assignment of these hyphosphere bacteria, allowing for a larger diversity of effects of these bacteria, including mutualistic interactions with AM fungi (qualifying these bacteria as hyper-symbionts) but also opportunistic bacteria attracted by the energy-rich hyphal exudates without a direct benefit for the fungus. Also, negative interactions between AM fungi and bacteria of these consortia deserve more attention [such as ammonia oxidizers, as their activity would increase mobility of the soil N to the plant and hence potentially reduce mycorrhizal benefit, see Bukovská et al. (2018, 2021) and Veresoglou et al. (2019)]. Further experiments are needed to obtain a complete understanding of the hyphosphere microbiome community assembly, developmental dynamics and functions, without privileging hypotheses on beneficial functionality. Obviously, some bacteria in the hyphosphere microbiome also act as mycorrhizal helper bacteria. Previous research focused merely on the interactive effects on AM fungi and bacteria in promotion of root colonisation or host plant performance, often without specifically investigating the development of the bacteria and / or AM fungi in

the soil [reviewed by Deveau and Labbé (2016) and Drigo and Donn (2017)].

Given the above, the set-up of NM condition in model experiments appears a complex and complicated task by adding one more layer – the accompanying microbiomes of the AM fungus. In a NM treatment, the microbiome composition in the soil is very different from that of the mycorrhizal treatment, even after adding a microbial wash. There virtually is no way to develop comparable microbiomes in mycorrhizal and NM pots, considering various microbial wash and mock inoculum additions (Gryndler et al. 2018). Using a microbial wash from or soil-based NM mock inoculum may likely lack the microbes that constitute the AM hyphosphere microbiome. Thus, it seems that adding both microbial wash from a field soil or from mycorrhizal inoculum (containing potential AM fungal hyper-symbionts) together with significant amounts (several percent of substrate mass) of NM mock inoculum, incubated for a sufficient time before starting an experiment (e.g., 2–3 years) should provide a more realistic setting for comparing mycorrhizal and NM treatments, particularly with respect to slow-growing microbes such as ammonia oxidizers (Bukovská et al. 2018). However, such time periods as alluded to might be considered prohibitively long by many researchers or research programs.

Mycorrhizal and non-mycorrhizal plants – pre-determination or opportunity?

In a recent, provocative paper, Albornoz et al. (2021) critically evaluated our knowledge and our generalisations, based on that knowledge, about the mycorrhizal symbiosis. They referred to 'dogmas', widely accepted claims that have been insufficiently empirically validated, on the ecology of the mycorrhizal symbiosis. While they mainly focused on Ericaceae and Orchidaceae, two plant families with their own unique mycorrhizal types, they included in their critical review the question about the commonness and taxonomic distribution of the AM symbiosis. Their first dogma refers to the statement that 80–90% of all extant plant species are mycorrhizal – a claim that the authors do accept, with the addition that they urge researchers to both validate the occurrence of the fungus *in planta* and, when statements are made about the functionality of the symbiosis, that those are backed up by experimental demonstration of its functioning. One major explanation why the first dogma is almost certainly correct is that the AM symbiosis is very ancient, predating the evolution of plant roots and thereby constraining plant roots to evolve in a mycorrhizal fungal world. Despite a significant trend of fine roots becoming thinner over evolutionary time (Comas et al. 2012; Ma et al. 2018) and hence a lower mycorrhizal fungal presence [and likely benefit from these fungi (Valverde-Barrantes et al. 2016)] in the fine roots, a switch to a permanent NM condition has occurred only rarely, with the heterogeneous group of (constitutively) NM plants making up some 10–20% of all plant species only. (However, in certain parts of the globe, the fraction of NM plants is considerably larger.) That group contains plants both at the most nutrient-poor and the nutrient-rich side of the nutrient availability spectrum (Lambers and Teste 2013).

The second dogma is about the phylogenetic underpinning of the mycorrhizal symbiosis, where the mycorrhizal status of a plant can often be inferred from its taxonomic position, either on family or generic levels. The authors point out several cases where the trait is not constant within families or within genera. Such cases, including both reports of NM plants belonging to species or genera that are normally considered mycorrhizal and of mycorrhizal species belonging to genera that are normally considered non-mycorrhizal, demand further scrutiny. Brundrett (2021) scrutinised the literature that had accumulated over more than a century. He concluded that around 10% of the records are incorrect. While that may seem a reassuringly low number, he also pointed out the risk of error propagation in databases. From the analysis it also became clear that there was a very large degree of phylogenetic conservatism with respect to the AM symbiosis.

Because of cases of inconsistency in reports of plant mycorrhizal status, a third category, next to mycorrhizal and NM plants, has been introduced, namely that of facultative mycorrhizal plants. These have been defined by Moyano et al. (2020) as plants that have the potential to form mycorrhiza but do not require mycorrhiza for their nutrition, growth, or survival. However, in practice the concept is interpreted more broadly. First, survival of plants under ecologically relevant natural conditions is only very infrequently assessed and so the concept is applied when plants are found in the field without fungal

colonisation. Second, the concept is also applied for plants that are considered non-mycorrhizal but where under certain conditions mycorrhizal fungal structures may be observed (or otherwise detected) in roots.

Bueno et al. (2017) and Pyšek et al. (2019) interpreted facultative mycorrhizal plants as plants that are sometimes but not always colonized by AM fungi. A different definition was provided by Smith et al. (2009) where facultative mycorrhizal plants were plants constitutively unresponsive to the AM symbiosis in terms of their P uptake. Cases of so-called facultative AM symbiosis [sensu Moyano et al. (2020)] are frequent. Moyano et al. (2020) noted that 17% of the plant species in their analysis were facultatively mycorrhizal, whereas Pyšek et al. (2019) and Hempel et al. (2013) reported 24% and 31%, respectively, and Bueno et al. (2017) even reported that 41% of their plants were facultatively mycorrhizal, which fraction was actually 20% higher than the fraction of obligate AM plants in the latter study. Table S1 provides an overview of the 26 most commonly reported "facultative mycorrhizal plant" species.

Most studies devote little attention to methodological problems surrounding the application of the concept of facultative mycorrhizal plant. The first problem is of a statistical nature. Plants for which there only is one record in the database are per definition obligatorily mycorrhizal (or non-mycorrhizal) and the chances that the database contains records of a plant species with and without mycorrhiza increase with the number of records (Dickie et al. 2017) that likely scales with the commonness of a plant species. The dataset by Moyano et al. (2020) shows that of the 50 most frequently listed plant species, which are generally considered as forming the AM symbiosis, 48 are listed as facultative (combining the AM and NM status, sometimes added with an EcM status); only two species, *Lolium perenne* L. and *Nardus stricta* L., are listed as exclusively AM plants. Moyano et al. (2020) tried to correct for this potential problem by using the number of references to a plant's mycorrhizal status as a proxy for the number of observations, and by using that number of references as an additional predictor variable. Unfortunately, references to mycorrhizal status cannot be treated as independent observations.

A second problem relates to reliability of data, especially old data, when staining techniques were less well developed, a problem potentially of large influence in the data that are more than a century old (Brundrett 2021). Sampling in various seasons could also lead to incorrect conclusions, as shown by Brundrett and Kendrick (1988) who sampled *Solanum dulcamara* L. twelve times during the growing season and reported an NM status at four sampling dates. Insufficient attention for root age might also lead to reports of an NM status as both pioneer roots (Zadworny and Eissenstat 2011) and old fine roots (Lynch et al. 2021) could normally be devoid of mycorrhizal colonisation. Bueno et al. (2017) reported that an error rate of 20% in reports would not strongly affect their conclusions, but their randomisation method could not effectively test for the specific question whether or not the concept of facultative mycorrhizal plants is problematical.

A third problem relates to the fact that the category of facultative mycorrhizal plants includes both species generally considered mycorrhizal with at least one report of an NM status, and species generally considered non-mycorrhizal but with at least one report of colonisation, even when such reports stated that the symbiosis was likely non-functional.

Functional consequences for plants that are called facultative mycorrhizal have received emphasis in the studies of plant invasions, where this feature has been linked to invasiveness as a trait that makes it more likely that an introduced plant becomes a successful invader. Questions have been raised whether NM plants [because of frequency of invasions in disturbed habitats where NM plants are more common, cf Peat and Fitter (1993)], obligate mycorrhizal plants (because of their ability to become integrated in and benefit from CMN) or facultative mycorrhizal plants (because of their versatility) are more likely to become invasive. The studies published to date (Moyano et al. 2020) concluded that mycorrhizal plants are more likely to become naturalised and subsequently invasive than NM plants, except on continental islands. Facultative mycorrhizal plants have a higher likelihood to become successful invaders than obligate mycorrhizal plants. That conclusion was also reached in earlier studies by Menzel et al. (2017), Menzel et al. (2018) and Pyšek et al. (2019). We analyse a few cases in Box 2 and like to argue that the current databases contain too many uncorrected errors to allow addressing this question properly.

Box 2 Problems with the concept of facultative mycorrhizal status

A study of databases with plant species that have been treated as facultative mycorrhizal did uncover a number of problems that to us indicate that the current concept of facultative mycorrhizal plants is not a very useful category in ecological research. In this text box we refer to a number of cases that highlight problems with that category.

***Alchemilla* spp.** There are 41 species of that genus listed in Moyano et al. (2020), with 13 species being obligate and 28 species being facultative mycorrhizal. The database indicates 6–10 references per species. One of the references (Akhmetzhanova et al. 2012) listed the facultative AM status for *A. vulgaris* L. (in one of 10 sites it was non-mycorrhizal). They also listed two species as EcM / AM (depending on a field site), and one species as EcM / non-mycorrhizal (NM). Harley and Harley (1987) listed two publications from 1900 and 1929 where *A. vulgaris* (a species aggregate of many apomictic species) was reported as NM. Hempel et al. (2013) disaggregated the apomictic species of *Alchemilla* resulting in 28 recorded facultative mycorrhizal species which seems to us a very liberal interpretation of the literature

***Allium oleraceum* L.** The references about an NM status are derived from Harley and Harley (1987), who cited a (difficult to access) paper from 1912 in support of that claim

***Anthericum ramosum* L**. Listed as facultative mycorrhizal by Moyano et al. (2020) based on Bidartondo et al. (2004), where the species is indicated as AM / NM, but no plant species in that paper is listed as exclusively AM, as the only categories used are AM / FIX and AM / NM. It is highly likely that the statement AM / NM refers to the ^{13}C and ^{15}N signal that would be expected for both AM and NM plants, compared with AM and N_2-fixing legumes (as that explains logically the use of both categories; the paper also refers to AM or NM), rather than as an empirical statement of the mycorrhizal status of the sampled plants

***Arabidopsis thaliana* (L.) Heynh.** While for many authors this species is the model for an NM plant because of the antagonistic interaction between plant and the AM fungus (Fernández et al. 2019), it is listed as facultative mycorrhizal in these analyses. The reference goes back to Kruckelmann (1975), who noted mycorrhizal colonisation in seven weed and three crop species that belong to families that are currently considered non-mycorrhizal (Brassicaceae, Caryophyllaceae, Amaranthaceae, Polygonaceae) and remarked that there is "some susceptibility to mycorrhizal infection in some plant families previously reported to contain few or no mycorrhizal species."

Our criticism of the concept of facultative mycorrhiza does not imply that we overlooked that many AM plants are co-colonised or sometimes exclusively colonised by dark septate endophytes (DSE). These DSE might compete with AM fungi for space and / or C provided by the plant, and may also show nutritional benefits, especially with members of the Poaceae (Malicka et al. 2022; Mayerhofer et al. 2013; Newsham 2011). It seems that in arctic and alpine environments, where there could be inoculum limitation of AM fungi or where low temperatures reduce their physiological activity (Acuña-Rodríguez et al. 2020; Kytöviita 2005), DSE can be the sole colonising mutualists in roots, and such plants would then be classified as facultative mycorrhizal. Under such cold environments, N mineralisation might be slow, and the low availability of mineral N could privilege DSE with their saprotrophic abilities. The relevant question would be to understand the costs and benefits of having one or both kinds of symbiotic fungi in the roots and how the plants regulate C allocation to either of them.

Nor does it imply that we consider the concept of facultative mycorrhizal plants sensu Smith et al. (2009) that do not benefit from AM fungi in terms of biomass production or P uptake as relevant. We discuss this issue in the next section.

Why do so many plants seem not to benefit from the arbuscular mycorrhizal symbiosis?

It is generally accepted [a dogma sensu Albornoz et al. (2021)] that most plant species are able to associate with AM fungi. At the same time, a fairly large number of plant species do not seem to benefit from the AM symbiosis. The meta-analysis by Hoeksema et al. (2010, supplementary figure) showed that in 25% of all studies there was no difference in growth performance between plants in the mycorrhizal and NM condition. While these studies included both AM and EcM plant species, it is likely that the same pattern would emerge for AM plants only. This raises the question why so many plants associate with AM fungi if they are apparently able to perform as well without these fungi? Several plant traits (root diameter, root hair length and abundance) have been correlated with mycorrhizal benefit (Jakobsen et al. 2005; Schweiger et al. 1995). Species with thin roots and frequent, long root hairs usually do not or hardly benefit from the AM symbiosis in those studies.

Two kinds of explanations are often brought forward for lack of responsiveness of plants to AM fungi. One explanation refers to experimental

conditions (small pots, low light availability, short duration of experiments, soil nutrient supply regime). Soil properties (the relative supply of N and P) are a major determinant of mycorrhizal responsiveness, with plants with a low leaf N:P ratio (indicative for being N-limited) showing generally a much weaker response to AM fungi than plants with high leaf N:P ratios (Hoeksema et al. 2010). However, there could also be experimental conditions that privilege findings of significant responsiveness. Koide (1991) demonstrated that mycorrhizal benefits decline with increasing intraspecific density, and as many experiments have been executed with single plants, it is plausible that mycorrhizal benefit tends to be overestimated under such conditions. The increased overlap in depletion zones of immobile nutrients with increasing plant and root densities constitutes a logical explanation for this effect.

The second kind of default explanations refers to mycorrhizal multifunctionality (Newsham 2011), the range of additional benefits beyond enhanced P acquisition that the mycorrhizal symbiosis confers to plants such as enhanced Zn, Cu or N acquisition, improved tolerance of drought, higher tolerance to heavy metals in high concentrations, improving soil structure, reducing nutrient losses, conferring greater tolerance of or resistance to herbivores and pathogens, etc. Individual components of multifunctionality are evidently testable experimentally. Delavaux et al. (2017) provided a meta-analysis of AM benefits and noted, apart from beneficial effects on uptake of P and N and hence a beneficial effect on growth, also significant effects on water fluxes, soil aggregation, and disease resistance. However, testing multifunctionality itself is complicated, as the number of possible alternative benefits is not specified and therefore falsification of the hypothesis can always be explained away by referring to another function that had not been measured. (A third explanation for reduced performance of plants under the mycorrhizal compared to the NM condition points to C costs of the symbiosis, but as C costs are invoked rather than measured, it is likely that the concept is used to describe the outcome of reduced performance rather than in a mechanistic sense which makes such an explanation merely circular.)

The density dependence of mycorrhizal responsiveness prompts a further question about the default explanations for lack of responsiveness (or even a negative growth response). Is the way in which we assess mycorrhizal responsiveness (i.e., plants grown singly or at low density in the absence of interspecific competition) correct if our aim is to understand lack of growth benefits? Might it be possible that benefits of being mycorrhizal (or conversely disadvantages of being non-mycorrhizal) are manifested (only or mainly) in multispecies plant communities? Under that logic the important question would be whether an NM strategy in a mycorrhizal plant community constitutes an evolutionarily stable strategy; and whether a mycorrhizal plant could successfully invade an NM plant community. Addressing this question demands a game-theoretical approach. Game theory was explicitly used by Franklin et al. (2014) who suggested that the EcM strategy could persist even if it did not yield benefits compared with an NM strategy; and by Lu and Hedin (2019) who demonstrated that invasion of an EcM plant community by an AM plant or invasion of an AM plant community by an EcM plant was unlikely in the presence of plant-soil feedbacks (PSF), a result empirically confirmed for North American forests by Averill et al. (2022). Halloway et al. (2022) equally applied game theory to understand coexistence of mycorrhizal and NM plants in a community. Based on their description of the traits of an NM plant, they likely referred to the Brassicaceae type sensu Albornoz et al. (2021); in the Proteaceae type of NM plants their model might well be different. Their model assumes that there must be benefits of being mycorrhizal and precludes conditions where plant performance is reduced in the mycorrhizal condition by the N trap. Their model also assumes that the cost of root production is the same for mycorrhizal and NM plants. Their model predicts that the region where the mutualistic strategy is non-invadable by a non-mutualistic strategy declines with increasing plant species richness, a prediction that is testable for species-rich grasslands. However, it seems that in such species-rich grasslands (that usually occur on nutrient-poor sites), NM plants (of the Brassicaceae type) are competitively inferior (Francis and Read 1995) and can only persist in the presence of regular disturbances that create larger gaps. We think there is a bright future for game theoretical models that describe interactions between NM and mycorrhizal plants and plant communities with different mycorrhizal types [as replacement of EcM forests by AM forests is likely occurring under climate

change and due to the effects of N deposition, contrary to the feedbacks implied by the model of Lu and Hedin (2019) – see section on AM and EcM ecosystems below].

Game-theoretical approaches would also be useful in understanding concepts like cooperative and less-cooperative fungal species, and plant potential sanctions towards less cooperative species. The stability of the AM symbiosis has seemed a conundrum – would "selfish" fungi that benefit more in terms of C taken from the plant or that deliver less nutrients to the plants, gain in fitness compared with more cooperative fungi? Could that eventually result in collapse of the mutualistic symbiosis? Does the same argument apply to plants? Would plants that provide less C to the fungus or receive (or take) more nutrients not gain in fitness compared with competitors? The fact that the symbiosis has persisted for more than 450 million years shows that the scenario of collapse is implausible. Researchers therefore sought explanations for this conundrum and suggested that the concept of plant sanctions would provide an elegant solution. While pursuing this path, they sought for analogies in the legume – rhizobium symbiosis, where the concept of cheaters (bacterial strains that lack leghemoglobin, considered a proxy for the ability to fix atmospheric N_2) was developed before. Kiers et al. (2011) showed that selective rewards by a plant towards a more cooperative AM fungal species compared with a less cooperative species could stabilise the symbiosis. However, that study and similar studies showing suchlike effects also raised a number of questions. If AM fungal species differ in their degree of cooperativeness, is cooperativeness a genetic trait that can be selected for? If so, would one most cooperative fungus ultimately be selected by the plant? Would that result in either reduced species richness globally or a very high level of selectivity, if every plant selects its own most cooperative fungus? The study by Kiers et al. (2011) suggested that cooperativeness was a fungal trait as the ranking of growth benefits by the three AM fungi studied was similar for a monocot (*Allium porrum* L.) and a dicot (*Medicago truncatula*). These data suggest that cooperativeness forms a transitive hierarchy and, combined with plant sanctions, would result in reduced AM fungal species richness globally as the less cooperative species would then be selected against. However, cooperativeness turned out not to be a context-independent species trait. Argüello et al. (2016) observed the less cooperative AM fungal species *Funneliformis mosseae* became more cooperative in the presence of a (generally) more cooperative species, *Rhizophagus irregularis*, suggesting that interspecific fungal competition could modify the cooperativeness trait. One would expect that long-term sanctioning and rewarding would have resulted in optimal fungal genotypes; however, data by Angelard et al. (2010) and Feldmann (1998) showed large untapped genetic variation that potentially resulted in enhanced plant benefit.

An assumption underlying the trade resource model is that C is costly to the plant. However, that assumption may be problematical. Mycorrhizal fungi, which can use up to 10% (and occasionally more) of photosynthetic C production, may increase photosynthesis due to sink stimulation (Gavito et al. 2019; Kaschuk et al. 2009), although such sink stimulation has not been reported in all studies (Slavíková et al. 2017). Finally, there is an inherent risk of oversimplification as the experiments were mostly carried out in an artificial medium with orthophosphate as the sole P source. Differences between fungal species in the extent to which they associate with hyphosphere bacteria that can desorb (organic) P from mineral surfaces (see section on AM and the hyphosphere microbiome) would therefore play no role in such simplified settings. Although it is widely known that AM fungi can confer multiple benefits to host plants, often the experimental system is reduced to test for just one specific benefit. However, with multiple benefits depending on context it is not evident that there is a context-independent, transitive ranking in terms of cooperativeness. But would plant sanctions work in more complex soil systems? We think two general considerations would cast further doubts on such models. Werner and Kiers (2015) demonstrated that plants may be colonised by the first arriving fungus regardless of its symbiotic quality – either because plants cannot compare the degree of cooperativeness with a later arriving and potentially more cooperative coloniser or because more selective plant genotypes are outcompeted by genotypes that are more rapidly colonised by the mycorrhizal network. The temporal order of colonisation of plants by AM fungi in a mycorrhizal network (Li et al. 2022b) as well as neighbourhood identity (Chagnon et al. 2020; Mony et al. 2021) could also determine the extent to which a fungus is cooperative and argue against one-dimensional

classification of cooperativeness. Landis and Fraser (2008) proposed a model that was based on a disconnect between (instantaneous) C and P trades. Their argument is based on the fact that, whereas C supply to the fungus is relatively predictable because CO_2 is well mixed in the atmosphere (although light availability across temporal and spatial scales may still be an issue), P supply to the plant is not, because of its heterogeneity of soils, which makes a symbiotic encounter not an issue of instantaneous trade but of long-term investment and risk management. Based on these considerations we argue that plants only need to prevent true 'cheaters' (fungi that take C from the plant without delivering any P) and apparently plants have been quite successful in that respect, as true cheaters, which are known in rhizobia, have not been reported in the case of AM fungi. The only example of a 'true' parasitic interaction between plant and an AM fungus was described by Guo et al. (1994) who reported that *Glomus macrocarpum* Tul. & C. Tul. was the cause of tobacco stunt disease. However, no new information on this disease and its putative mycorrhizal fungal causal agent has been published in the last decades.

Plants are usually not colonised by the most beneficial fungus. One implication of that observation would be that there is space for genetic improvement of AM fungi as shown by Angelard et al. (2010) and Feldmann (1998). Another implication is that plants do not necessarily and always associate with the AM fungi from which plants derive the largest growth benefit, creating opportunities for negative PSF by AM fungi as reported by Bever (2002). The role of AM fungi in PSF has been recently reviewed by Semchenko et al. (2022) and thus left out of further discussion here.

Arbuscular mycorrhizal and ectomycorrhizal ecosystems

Plant roots evolved in an AM fungal world. Understanding the conditions under which plants lost the ability to be associated with AM fungi and switched towards other mycorrhizal symbioses (or became non-mycorrhizal) is therefore a relevant research question. Some switches towards alternative mycorrhizal symbioses occurred in phylogenetically narrow clades (e.g., orchid mycorrhiza in the Orchidaceae and ericoid mycorrhiza in the Ericales), but the switch towards EcM occurred likely around 30 times (Tedersoo and Brundrett 2017), raising the question under which historical ecological conditions an AM plant assemblage was invadable by EcM plants.

Read (1991) pointed out that each mycorrhizal type was associated with its own unique set of ecosystems. Subsequent studies suggested that EcM ecosystems were characterised by a closed N cycle and AM ecosystems by an open N cycle (Leake et al. 2004; Read and Perez-Moreno 2003). These ideas were subsequently formalised in the MANE (Mycorrhizal-associated Nutrient Economy) framework (Phillips et al. 2013) that allowed generalisations on coupled C–nutrient fluxes across landscapes dominated by either kind of mycorrhizal associations. In their terminology, AM ecosystems are characterised by an inorganic nutrient economy since AM plants produce litter of high quality that allows rapid mineralisation. In contrast, EcM ecosystems operate under organic nutrient economy dominated by plants that produce poorly decomposable litter that reduces mineralisation rate and privileges symbiotic fungi that can access nutrients in organic forms. Consequences of a more open N cycle in AM forests are a higher risk of nitrate leaching, as observed by Midgley and Phillips (2014). Differences between both kinds of mycorrhizal forests in the nature of the N and P cycles, as evidenced through nutrient resorption, were shown by Zhang et al. (2018a); however, with a strong mycorrhizal type × climate interaction. N resorption did not differ between both forest types in boreal and temperate zones but was significantly higher for AM trees than for EcM trees in the tropics. The P resorption was not different between both forest types in temperate and tropical zones but was significantly higher in boreal EcM forests than in AM boreal forests. These results run counter to the general idea that AM forests are mainly occupying P-limited sites (as one would expect higher P resorption in such sites) while EcM forests are generally N-limited, at least those in boreal and temperate regions. Such difference could be partly attributed to differences in soil properties that select for either mycorrhizal type. Under conditions where both kinds of mycorrhizal trees co-occur, the data did not show any difference in resorption efficiency. Whereas most studies that focus on the contrast between EcM and AM vegetation investigated differences in N cycling, differences

in P cycling have received relatively little attention. Rosling et al. (2016) reported higher P sorption and higher reactivities of phosphomonoesterase and phosphodiesterase in EcM than in AM forests, but the underlying mechanisms were not elucidated. Another major difference between AM and EcM forests could be the relative importance of positive and negative PSF, with EcM forests showing predominantly positive PSF and AM forests negative PSF (Bennett et al. 2017). Such differences might explain why monodominance in forests is much more common in EcM than in AM forests. Averill et al. (2014) reported greater C storage in EcM than in AM forests. While this statement depends on the soil depth over which C is assessed (Craig et al. 2018), the accompanying message of the paper was that per unit of N, EcM forests stored more C than AM forests. Responses to elevated CO_2 (Terrer et al. 2016) where EcM plants responded to elevated CO_2 irrespective of N availability, but where AM plants only responded positively at high N availability, also emphasise this contrast.

Competition between EcM and AM plants, especially trees, is part of the MANE framework (Phillips et al. 2013). Under that framework one would predict that under situations of global change, dominant vegetation can shift from EcM trees towards AM trees if these external drivers have a larger impact than PSF as proposed by Lu and Hedin (2019). Global climate change and higher temperatures will have a larger effect on N mineralisation (a biological process) than on P desorption (partly a physico-chemical process) and therefore result in a shift towards P limitation. N deposition will likewise entail a shift towards P limitation, conditions under which AM trees are more competitive than EcM trees. Averill et al. (2018) and Jo et al. (2019) reported a shift from EcM towards AM trees in North America, driven by higher temperatures and / or increased N availability as a consequence of N deposition. Maharjan et al. (2022) predicted elevational shifts of Himalayan trees under two scenarios of climate change. Their predictions showed a larger elevational shift for EcM than for AM trees and a partial replacement of the former by the latter guild of trees, especially under the bleaker climate change scenario, consistent with the data from North America. The tree flora in Europe has a significantly lower species richness than the tree flora of eastern North America or eastern Asia. Several authors have tried to explain this difference in terms of differential extinction during the Pliocene – Pleistocene transition. Dickie et al. (2014) reanalysed the data on differential extinction of tree genera as a function of mycorrhizal type with a significantly higher extinction risk for AM trees during glacial periods.

Because EcM and AM forests differ in the forms in which soil C is stored (particulate versus mineral-associated) such shifts in mycorrhizal associations could have far-ranging implications. The recent study by Terrer et al. (2021) indicated that under elevated CO_2, EcM plants would increase in biomass (concomitant with a small decline in SOM), whereas AM plants show a small response in plant growth but store significantly more C in soils. Because AM forests store more C (and much more N) in the uppermost 1 m of soil than EcM forests (Craig et al. 2018) such shifts in mycorrhizal type could to some extent mitigate the effects of climate change.

These various studies have tended to distinctly dichotomise between both kinds of ecosystems and allow for very broad generalisations, especially with respect of the ability of EcM trees to mine soil for organic-N sources. What is evident in some, but definitely not all papers, is that the contrast seems to be generally valid for temperate ecosystems, but find far less support for tropical ecosystems, where EcM forests seem to be characterised by an equally open N cycle as AM forests. The causes for failure of an otherwise attractive theory under tropical conditions are currently not understood. Possible explanations are the nature of the plants, the EcM fungi, or the soils (the extent to which soil properties result in N-limited or P-limited plant growth). Such discrepancies suggest that generalisations based on intimate knowledge of mycorrhizal systems in one climatic zone cannot be easily transferred to another zone.

Common arbuscular mycorrhizal networks

Most species of AM fungi exhibit low levels of specificity with respect to the plant host(s) with which they can associate. Newman (1988) was the first author to reflect on the ecological consequence of such mycorrhizal links between conspecific and heterospecific plants [see also Newman et al. (1992)]. Work on these links, which were later relabelled as common mycorrhizal networks (CMNs), received a strong impetus with the publication of the study by

Simard et al. (1997) where possible fluxes of C and nutrients between different EcM tree species were investigated. Critique also appeared, when Robinson and Fitter (1999) asked question about the magnitude (and hence the ecological importance) of this flux and especially the extent to which the mycorrhizal plant or mycorrhizal fungus had control over such fluxes. The concept of CMNs also gained rapid popularity in popular press, helped by anthropomorphic descriptors and metaphors of CMNs such as nurse plants, mutual aid (Kytöviita et al. 2003), and socialism in soil (van der Heijden and Horton 2009). Whereas currently some of the underlying concepts are being reconsidered and data reinterpreted (Karst et al. 2023), research on CMNs has focused on a number of different questions and in the last three decades also certain questions have disappeared from the scientific literature; however, we think that some of these unaddressed issues would benefit from renewed attention.

Transfer of C The issue of C transfer in ecologically significant amounts has received a positive answer as several mycoheterotrophic plants of various families have been found associated with AM fungi (Bidartondo et al. 2002; Imhof 2009). The involved AM fungi, which usually represent a subset of all AM fungi that occur in the surroundings of these mycoheterotrophic plants, are very well linked with other plant species in their surroundings (Gomes et al. 2022). Partially mycoheterotrophic plants that depend on AM fungi for C gain are known in the Gentianaceae (Suetsugu et al. 2020) and it has recently been suggested that partial mycoheterophy is more widespread among AM plants that form so-called *Paris*-like mycorrhizas in contrast to *Arum*-type mycorrhizas (Giesemann et al. 2021, 2020), although reliance on enrichment with the stable isotopes ^{13}C and ^{15}N has received criticism as well (Murata-Kato et al. 2022). The amounts reported by Giesemann et al. (2021) are substantial, with proportional C gain up to 73% for the angiosperm *Gentiana lutea* L. and up to 93% for the fern *Athyrium filix-femina* (L.) Roth. These data contrast with earlier studies (with AM plants that form the *Arum*-type mycorrhiza) where the amount of C found in the receiver mycorrhizal plants was quite small and mainly located in the roots, suggesting that the larger part or almost all of this C was actually in the AM fungal biomass and hence under fungal control and used for storage (Fitter et al. 1998; Graves et al. 1997; Pfeffer et al. 2004). The authors of those earlier studies therefore concluded that the C transfer does not have an impact on plant fitness, while it is an important element in fungal C budget and hence fungal fitness. A (very) small part of the labelled C from the donor plant could have ended up in the amino acid pool of the receiver but would not constitute ecologically relevant transfer. Experiments with seedlings, where it has been hypothesised that they could benefit from such transfer have been ambiguous, with studies reporting enhanced seedling survival in the mycorrhizal condition but also studies that reported that seedlings were outcompeted when integrated into a CMN, even when the seedlings, when grown alone, clearly benefitted from being mycorrhizal. An analysis by van der Heijden and Horton (2009) showed that in 42% of the cases there was a beneficial effect of CMNs on seedling performance, and a negative effect in 33% of the cases. The causes for this discrepancy have not been elucidated. Independent of any growth benefits, integration of seedlings in a mycorrhizal network may results in faster root colonisation compared with cases where mycorrhizal colonisation was due to newly germinated spores (Varga and Kytöviita 2016).

Apart from some partially mycoheterotrophic plants, there is no evidence that seedlings are C-subsidised by either conspecific or heterospecific plants via the CMN. A different case entails the situation where two plants interconnected by CMN contribute differentially to the shared fungal network. Different C fluxes to the AM fungi by two plants in a CMN have been studied by analysis of stable C isotopes in the case of C_3 and C_4 plants. Walder et al. (2012) demonstrated that in a system with sorghum (*Sorghum bicolor* (L.) Moench) and flax connected by a CMN, the AM fungi obtained around 70% of their C from sorghum. That larger contribution did not necessarily result in larger mycorrhizal nutrient benefits of sorghum; in fact, depending on AM fungal species, flax acquired around 50% to more than 90% of N and P through the CMN, whereas such a proportion was lower for sorghum. In most cases, differential C contributions and nutrient rewards by both plants have not been determined and we only have data on differential plant performance as a consequence of formation of CMN. But as C is in many cases hardly costly to the plant (Kaschuk et al. 2009), it is likely that differential plant performance is due to differential benefits in terms of mineral nutrients. Note that outcomes

where the AM symbiosis amplifies competitive inequalities between plants (rather than foster the establishment of seedlings or allow the persistence of an otherwise competitively inferior species, e.g., Weremijewicz et al. 2016) do not negate the mutualistic nature of the symbiosis; they only show that within that symbiosis, fungal fitness is a parameter that should not be overlooked.

Transfer of allelochemicals and defence compounds Several studies have reported that plants that were integrated in CMNs were better protected against pathogen attack, whereas in the absence of the AM symbiosis this protection did not work, suggesting that these so-called 'talking trees' (Gorzelak et al. 2015) are talking through their mycorrhizal fungi. Song et al. (2010) reported how CMNs allowed tomato (S*olanum lycopersicum* L.) to be better able to deal with both an attack by a fungal pathogen and a leaf-chewing arthropod. Enhanced defence through CMNs was also reported for faba bean (*Vicia faba* L.) by Babikova et al. (2013). In a subsequent study, Song et al. (2014) showed that the upregulation of defence in tomato by the CMN involved the jasmonate pathway. Experiments to test for such protective effects generated though CMNs have focused on experiments with two plants of the same species; as different plant species could also be integrated in a CMN, we may wonder whether in such cases protective effects would also occur, implying that through CMNs, it is mycorrhizal plant assemblages rather than individual plants that may become units of selection. We are not aware of studies that have tested this speculative and potentially far-ranging hypothesis. Not only defence compounds may be transported along CMNs, but also allelochemicals. Barto et al. (2011) reported that CMNs supported the transfer of allelochemicals produced by *Tagetes tenuifolia* Cav., resulting in allelochemical accumulation around targets plants, and through that process reduced the performance of neighbouring plants. While the mechanism of transfer was not studied, the authors in a subsequent publication (Barto et al. 2012) suggested that mainly apoplastic flow along the hyphae might have occurred. For transport of allelochemicals produced by *Juglans regia* L., a similar passive flow over the hyphal surface was suggested as the likely mechanism (Achatz and Rillig 2014).

Transfer of N CMNs formed by a legume and a species that is unable to fix atmospheric N_2 (often cereals) might transfer N from the legume to the accompanying plant. If so, CMN would be actively involved in plant facilitation. The literature on the quantities of N involved in such transfers has been summarised by He et al. (2009). Their data show a tremendous variation ranging from close to zero to almost 80%, although the authors noted that most of the studies reported transfer of less than 10% of the plant N budget, and regularly even less than 1%. Thilakarathna et al. (2016) suggested transfer rates through CMNs below 10% in cases where no N_2-fixing legumes were involved but much higher transfer rates, up to 80% in the case of N_2-fixing legumes. The high estimates of CMN-mediated N transfer, between 31 and 83%, as reported by Moyer-Henry et al. (2006), should in our view be approached with considerable scepticism, because the estimate is based on the assumption that both an AM and an NM plant used the same soil N sources and that there was no subsequent AM fungal-mediated fractionation after N-uptake. A consequence of the calculation based on that assumption was that even an NM plant (*Cyperus esculentus* L.) obtained 31% of its N through mycorrhizal transfer.

Again, it is important to separate assessment of N transfer as measured in shoots (which indicates direct interplant transfer of N) and in roots, as part of the N in the roots may be immobilised in the fungal mycelium, considering that the N mass fraction of the mycelium could be much higher than that of roots (Hodge and Fitter 2010). Currently, most studies are executed with two plants at the same phenological stage and the issue of the order in which the network is formed has not received much attention. Only Li et al. (2022b) tested differences in the order of network formation demonstrating asymmetry in plant performance and nutrient gains depending on the order of formation of the network, where chickpea (*Cicer arietinum* L.) as donor had a stronger beneficial effect on the plant mixture yields than millet [*Setaria italica* (L.) P. Beauvois]. Their data also showed some likely transfer of biologically fixed atmospheric N_2 from the legume to the cereal; however, the magnitude could not be quantified. The order of network formation could also allow temporal niche differentiation belowground, where periods of maximal physiological activity of the different plants

differ. Such temporal aspects could be relevant in case of plants whose roots are dying. Several studies noted rapid transfer of considerable amounts of N and P from dying roots to living plants, both in conspecific and heterospecific mixtures when these different species were able to form CMN (Newman and Eason 1989; Eason and Newman 1990). The authors noted that such rapid transfer was not due to rapid decomposition and mineralisation of these roots, as the transfer also occurred when root material had high C:N and C:P ratios, conditions were one would expect nutrient immobilisation. It is not clear whether the nutrients leaked out of dying roots and the nutrients were then taken up from the soil solution, or whether the AM fungi already took up these nutrients in the dying roots through a backwards flow. Experiments with double compartments and an air gap (that AM fungi can cross but nutrients could not) might allow evaluation of both alternative hypotheses.

Transfer of P Eason et al. (1991) showed that P released from dying roots was transferred in larger amounts to a neighbouring AM plant than a neighbouring EcM plant, indicating preferential P cycling within guilds of plants of the same mycorrhizal type, a process that likely enhances fungal fitness as the costs for P acquisition by the fungus are reduced while the C benefits might remain the same. Quantification of P transfer through CMNs has given variable results. Eissenstat (1990) reported almost negligible amounts of P transferred compared with N transferred throughout the CMNs; however, the ratio of N:P transferred closely followed plant stoichiometry, which we interpret as no evidence for a differential role in CMN in transfers of N and P, contrary to studies cited above that suggest a specific mechanism through which N-rich legumes could transfer N to their neighbours. In the study by Eissenstat (1990), the amounts of nutrient transferred were ecologically marginal. Unequal benefit sharing for both P and N was reported by Walder et al. (2012) but the ratio of N:P transferred again closely followed plant stoichiometry.

CMNs and water It had been hypothesised that a CMN that may be formed between a deep-rooting and a shallow-rooting plant could improve the water status of intercropping systems through hydraulically lifted water. CMNs formed by plants that differ in rooting depth might as a side effect have that water that is acquired by the deep-rooting plants can flow to the shallow-rooting plant, a process that has been called bio-irrigation or hydraulic lift (Allen 2007). Bio-irrigation was hypothesised by Saharan et al. (2018) and tested by Singh et al. (2019, 2020) with the shallow-rooted finger millet (*Eleusine coracana* Gaertn.) and deep-rooted pigeonpea [*Cajanus cajan* (L.) Millsp.]. While these studies provided evidence for access to hydraulically lifted water through CMNs by the shallow-rooted cereal, their data also showed strong competitive interactions under well-watered conditions, and the competitive superiority of pigeonpea was even enhanced in the presence of CMNs, which poses challenges on practical application of this mechanism (Singh et al. 2020).

Control over fluxes The scientific community still seems to be divided over the issue to what extent plants or AM fungi control the fluxes across the mycorrhizal network. We like to argue, as a central tenet of our review, that the case for fungal control is much larger, and that consequently new experiments are crucial to assess the fungal fitness benefits from CMNs, as they have received far less attention than plant benefits.

Integration in CMNs might also be relevant for *clonal plants*, which form networks of ramets. Bittebiere et al. (2020) described that clonality might be a way to either facilitate or escape from the AM symbiosis. Onipchenko and Zobel (2000) hypothesised that clonal plants, due to their "mobility", would generally invest less in mycorrhizal symbiosis than non-clonal plants. AM fungi have been known to modify / manipulate clonal behaviour of plants. Streitwolf-Engel et al. (1997) observed that inoculation with AM fungi resulted in an increase in the number of ramets of two *Prunella* species, with some fungal species-specific effects, thereby increasing the plant's reliance on clonal reproduction with likely positive feedback on fungal fitness as the fungus could spread together with the plant. The large differences in mycorrhizal effects on clonality between both congeneric species shows that we are far from understanding underlying mechanisms. Such effects are not universal, however, and for *Stachys sylvatica* L. some AM fungal species also increased ramet production, whereas other species increased flowering (de la Peña and Bonte 2011). Sudová (2009) studied

five stoloniferous forbs and observed that inoculation with AM fungi increased P content in all five plant species, but had variable effects on biomass and clonality parameters, whereby species with higher stolon length showed smaller mycorrhizal benefit, consistent with Onipchenko and Zobel (2000). This hypothesis of a relationship between stolon length and mycorrhizal colonisation is in need of testing over a larger number of species, including closely related clonal and non-clonal plant species. Variation in clonal strategies and the extent to which clonal plants exhibit various form of division of labour among their ramets (Stuefer 1998) could be further factors that correlate with the AM effect on clonal properties and on possible complementarity in nutrient acquisition by ramets and by underground CMNs, which could actually either increase or suppress physiological integration of the individual ramets.

Outlook

In a recent paper, Albornoz et al. (2021) discussed four tenets of mycorrhizal research that the authors thought might have been uncritically accepted and therefore could be better described as dogmas. These are:

1. Most vascular plant species are mycorrhizal;
2. Being mycorrhizal or not is a taxonomic trait: plant families are typically mycorrhizal or not;
3. Mycorrhizal colonisation implies plant benefits in terms of enhanced P uptake;
4. Ecology and distribution of mycorrhizal fungi depends on the mycorrhizal type to which they belong.

In this review we have discussed those four dogmas. We conclude that most vascular plant species are indeed forming some forms of mycorrhizal symbiosis, with the AM symbiosis being the most common one. Generally, the level of plant genus seems adequate to predict mycorrhizal status of a plant, while we admit that there are ecologically interesting exceptions that make further reflections on NM plants worthwhile. Many of these NM plants can occasionally be found with AM fungi in their root system, although the functionality of the symbiosis is usually not studied. However, in the case of the so-called facultative *Arabidopsis thaliana* it is clear that the interaction rapidly becomes antagonistic (Fernández et al. 2019). For now we see little benefit for the use of the term "facultative mycorrhizal plants" as the concept apparently is ill-defined and problematical (see also Table S1 for examples). The concept has been interpreted with two different meanings, referring to both the presence of mycorrhizal fungi in roots (as evidenced through staining and currently more and more through metabarcoding approaches, often without due attention to proper quantification) and to a putatively functional symbiosis between plants and the fungi. We agree that it is dangerous to base conclusions on mycorrhizal functioning on the basis of sole presence or morphology. It is therefore imperative that mycorrhizal research does not get lost in pursuing purely descriptive studies of AM fungal species richness and community composition in roots and soils in different ecosystems, but remains firmly rooted in experiments under realistic conditions, aiming at quantification of the various functions that the symbiosis can have.

In a number of cases, plant families have been characterised as non-mycorrhizal but even here exceptions are known. For instance, the Proteaceae contain at least two 'true' mycorrhizal species, viz. *Hakea verrucosa* [a species that grows on high-nickel soils and where a mining strategy through carboxylates might be risky as too much of the heavy metals are then mobilised (Boulet and Lambers 2005)] and *Roupala montana* Aubl. (Detmann et al. 2019). The latter species from South America has almost identical DNA sequences as the Australian genus *Floydia*, suggesting a very close relationship (Hoot and Douglas 1998). It would thus be worthwhile to check *Floydia* for possible mycorrhizal symbiosis. A further check of *R. montana* is equally desirable, as the species was reported as non-mycorrhizal by Steidinger et al. (2015). A larger number of proteaceous plants have been reported with roots that were colonised by AM fungi, but arbuscules or intracellular coils, the indicators for the exchange of C and nutrients, have not been observed (Pattinson and McGee 2004). The plant species from this model NM family show that the ability to form AM symbioses has not completely been lost and that the symbiotic toolkit shows partial conservation. A further candidate plant for functional studies of the AM symbiosis is the plant *Lindenbergia*, belonging to the Orobanchaceae and constituting

a basal clade in that family, which forms functional mycorrhizas (Delaux et al. 2014). Other members of the Orobanchaceae are also worthwhile candidates. Li and Guan (2008) investigated 29 taxa of the hemiparasitic genus *Pedicularis* and noted mycorrhizal colonisation in 26 taxa. Somewhat surprisingly, mycorrhizal colonisation of facultative parasite *P. tricolor* Hand.-Mazz. reduced haustorium formation in the absence and presence of a host (Li et al. 2012). The mycorrhizal symbiosis was apparently functional, as in the absence of a host plant mycorrhizal *P. rex* C.B. Clarke took up more P than plants in the NM condition; there was no mycorrhizal effect on total P uptake for *P. tricolor*. In both species, the hyphal pathway was active, although the contribution to P uptake was limited (< 1%). There also are reports of EcM colonisation in another species, *P. dasyantha* (Trautv.) Hadac (Väre et al. 1992). The genus *Lupinus* has been considered as a prime example of an NM genus (or a facultative mycorrhizal genus without forming functional mycorrhizas as no arbuscules are formed) in an otherwise (almost exclusively) mycorrhizal plant family (Lambers et al. 2013). The genome of *L. angustifolius* L. (Hane et al. 2017) contained 20 out of 38 mycorrhiza-associated genes, many of which are also associated with the rhizobium-legume symbiosis. At least one gene that is exclusively associated with the AM symbiosis, with no known role in the rhizobium symbiosis, has obviously been retained. It may therefore not be surprising that Shi et al. (2017) noted AM colonisation, although often at a low level, for 35 out of 43 species of *Lupinus*, that Moyano et al. (2020) listed three out of five species of *Lupinus* as facultative mycorrhizal (with one NM and one obligate mycorrhizal species), and that O´Dell and Trappe (1992) found AM colonisation in the roots of six out of 10 species of *Lupinus* studied. Not all species of *Lupinus* form cluster roots, which suggests that the AM symbiosis could well be functional in some of the species. Such examples are not introduced to suggest that all plants are potentially mycorrhizal but to suggest that the genetic potential to form mycorrhizas is not easily lost during evolution.

The third dogma, and the one with which the authors of this review most strongly disagree, is that mycorrhizal colonisation implies plant benefits in terms of enhanced P uptake. Contrary to this dogma, we would argue that lack of P uptake benefits is actually often the case. The meta-analysis by Hoeksema et al. (2010, supplementary figure) showed that in 75% of all studies there was an increase of plant biomass in the mycorrhizal condition compared with the NM condition. The analysis also showed that the beneficial effect of mycorrhiza increased with increasing plant P-limitation, as judged from foliar N:P ratios of non-inoculated plants. Unless in many cases enhanced biomass production was achieved by dilution of P mass fractions, higher biomass went together with higher P uptake. As in a number of cases plants in the mycorrhizal condition had higher P mass fractions than when non-mycorrhizal (see above), it is rather likely that plants in the mycorrhizal condition had acquired more P than plants in the NM condition. However, it cannot be excluded that there are hidden problems in the way these studies have been executed and the results interpreted, e.g., by growing single plants in pots and / or by watering the pots with a nutrient solution with a strongly reduced P concentration, or failure to quantify P uptake via direct and indirect (mycorrhizal) pathways. It is also likely that experiments were executed with 'healthy' plants, that is in the absence of visible damage by pathogens, against which AM fungi can provide protection. Many papers have been published that refer to the multifunctionality of the AM symbiosis and the model by Newsham et al. (1995) suggested a trade-off between enhanced nutrient acquisition and growth performance on the one hand and pathogen protection on the other had as a central message of their paper. Powell and Rillig (2018) noted that the concept of multifunctionality may be uniquely suited for understanding the role of AM fungi in ecosystem functioning. While we do criticise the operationalisation of multifunctionality itself as a testable concept, we agree that testing for other effects of mycorrhizal symbiosis than enhanced P acquisition for plant fitness remains important.

A final and major bias could be that most studies have been executed in north-temperate regions and hardly in severely P-impoverished landscapes. These landscapes are biologically very interesting because of the occurrence of plants with specialised nutrient (especially P) acquisition strategies. In such landscapes AM plants are lacking or very rare; on slightly richer soils, NM plants co-occur with AM plants. The question whether on such soils AM plants acquire (additional) P through the symbiosis or whether other mycorrhizal benefits are more important has not yet

been resolved. There are not many studies that have explicitly addressed that question. The study by Parfitt (1979) demonstrated that the mycorrhizal scavenging strategy was effective at soil solution concentrations of P above 0.5 µM; below that concentration only the carboxylate strategy was effective. A general framework to address this issue quantitatively was suggested by Raven et al. (2018). The framework includes constant costs, independent of soil P concentration, and variable costs that increase as soil P concentrations decline. Their model assumes a trade-off that the cheapest P-acquisition mode at high P availability exhibits a steeper increase in costs when P availability decline. As a consequence, cost curves for different acquisition modes cross, implying that at different P availabilities different P acquisition strategies are selected for. The model also implies that with variation in P availability [e.g., through differences in soil moisture or through (rare) events that temporarily increase P availability such as fires] different strategies, such as the AM and NM strategy through carboxylate exudation and root morphological modifications, may co-exist. Other explanations for coexistence could be facilitation of AM plants by NM plants or non-nutritional benefits of the AM symbiosis at low P availability driven by different AM benefits such as enhanced pathogen protection (Lambers et al. 2018). The relative importance of these processes has not yet been assessed and further research is warranted in ecosystems where both strategies co-occur. A further explanation for co-existence of AM and NM strategies at nutrient-impoverished sites could be the fact that AM plants also exude, but at lower rates and hence at lower costs, carboxylates that mobilise sorbed P. Combinations of AM colonisation and cluster roots have been described for *Viminaria juncea* (Schrad.) Hoffmanns. With increasing soil P concentrations both declined (de Campos et al. 2013). From a global perspective it seems that the NM strategy as exhibited by Proteaceae is restricted to a few high-diversity areas such as fynbos (South Africa), campos rupestris (Brazil), and kwongan (Australia; Lambers et al. 2022).

The fourth dogma listed above demands a more general reflection on how ecological disciplines developed and how theories were derived from observations made in temperate regions. The contrast between AM- and EcM-dominated ecosystems and the mechanisms that maintain that contrast (Lu and Hedin 2019; Phillips et al. 2013; Read 1991; Read and Perez-Moreno 2003) seems to be largely based on knowledge derived from temperate ecosystems. Similarly, the relative neglect of extremely P-impoverished sites by mycorrhizal research (Parfitt 1979) might perhaps have resulted in unwarranted generalisations that the mycorrhizal symbiosis is always a superior strategy.

While we do think that the above dogmas in mycorrhizal research are indeed of sufficient generality, we do not want to detract from what we consider risks in current mycorrhizal research. To us these risks consist mainly of an increased focus on descriptive studies, enabled by powerful DNA-based methods, instead of ecophysiological experimentation; and a reduced interest in the peculiarities of soil(s) that result in simplified experiments and their possible over-interpretations that limit our understanding of mycorrhizal function in real ecosystems.

Acknowledgements We are grateful to many colleagues whose work we did cite and apologise to many others whose work we did not cite due to space limitations. We are especially grateful to many colleagues with whom we discussed ideas expressed in this review. While they may not fully agree (or even fully disagree) with some of the provocative statements spelled out here, it was their willingness to share ideas that helped us shape this paper. It is by maintaining a healthy and sceptical attitude to the results of studies on this oldest and fascinating root symbiosis that mycorrhizal research remains a vital multidisciplinary science at the intersection of soil science, mycology, and botany. We also acknowledge critical and constructive comments by Hans Lambers and two anonymous reviewers on an earlier version of this manuscript. Funding to JJ by Czech Science Foundation (project 21-07275S) and Czech Academy of Sciences (RVO61388971) is gratefully acknowledged.

Author contributions Both authors contributed to the conceptualisation of the review, wrote sections, provided feedback to other sections, and approved the final version of the manuscript.

Funding T.W. Kuyper declares that no funds, grants, or other support were received during the preparation of this manuscript. J. Jansa acknowledges funding by Czech Science Foundation (project 21-07275S) and Czech Academy of Sciences (RVO61388971).

Data Availability All data generated or analysed during this study are included in this published article [and its supplementary information files].

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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