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Research review

Unearthing the plant–microbe *quid pro quo* in root associations with beneficial fungi

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Summary

Mutualistic symbiotic associations between multicellular eukaryotes and their microbiota are driven by the exchange of nutrients in a *quid pro quo* manner. In the widespread arbuscular mycorrhizal (AM) symbiosis involving plant roots and Glomeromycotina fungi, the mycobiont is supplied with carbon through photosynthesis, which in return supplies the host plant with essential minerals such as phosphorus (P). Most terrestrial plants are largely dependent on AM fungi for nutrients, which raises the question of how plants that are unable to form a functional AM sustain their P nutrition. AM nonhost plants can form alternative, evolutionarily younger, mycorrhizal associations such as the ectomycorrhiza, ericoid and orchid mycorrhiza. However, it is unclear how plants such as the Brassicaceae species *Arabidopsis thaliana*, which do not form known mycorrhizal symbioses, have adapted to the loss of these essential mycorrhizal traits. Isotope tracing experiments with root-colonizing fungi have revealed the existence of new ‘mycorrhizal-like’ fungi capable of transferring nutrients such as nitrogen (N) and P to plants, including Brassicaceae. Here, we provide an overview of the biology of trophic relationships between roots and fungi and how these associations might support plant adaptation to climate change.

Quid pro quo principle in mutualistic host–microbe interactions

Mutualistic symbioses, as defined by the German botanist and mycologist Heinrich Anton de Bary in 1878 (Oulhen *et al.*, 2016), are interactions between organisms in which there is a reciprocal benefit for the symbionts. This type of interspecies interaction is present among many life forms and is a key factor that drives the functionality and evolution of natural ecosystems. In the case of mutualistic symbioses between microorganisms and multicellular eukaryotes, they are primarily associated with a nutritional trade between the partners in a *quid pro quo* (‘giving and taking’) manner.

In mutualism, both partners must constantly regulate the symbiotic association in order to maintain the highest gain relative to their own investment. From an evolutionary point of view, the ability of the symbionts to coordinate the flow of resources according to their partner’s input determines the sustainability of

the mutualistic symbiosis. The oldest and probably most widespread mutualistic symbiosis world-wide is the arbuscular mycorrhizal (AM) symbiosis (Karandashov & Bucher, 2005). It is an ancient mutualistic partnership based on the principle of reciprocity between host and symbiont, which was probably crucial for symbiosis stabilization during evolution.

It is hypothesized that in the AM symbiosis, both partners can equally control their contributions to the symbiosis, depending on what the other provides, but there is obviously some danger of anthropomorphic interpretation when describing these ‘*quid pro quo*’ mechanisms. The ‘biological market theory’ underlying these premises assumes that individuals prefer interactions with partners that provide more nutrients (Kiers *et al.*, 2016). To this end, plants specifically direct the increased carbon (C) flux to the fungus that has the highest benefit, *that is* the highest phosphorus (P) supply. Accordingly, the AM fungus rewards the plant that is able to supply the most C with an increased P flux (Kiers *et al.*, 2011). In support

of this concept, it has also been shown that when plant C flux is low, the fungus can confiscate P, which then accumulates in the fungal hyphae (Kiers *et al.*, 2011), or is diverted to nutrient-poor patches where the host's resource requirements are higher (Whiteside *et al.*, 2019).

The biological market theory should allow scientists to make testable predictions about resource allocation patterns and underlying molecular mechanisms in mutualistic symbioses and how they vary across time, species, genotypes and environmental scales. Despite convincing experimental support, this theory was recently challenged in two studies on the effect of elevated CO₂ and aphid herbivory on the bidirectional exchange of C and P in the AM symbiosis of wheat. While elevated CO₂ and aphids significantly reduced C transfer from host to mycobiont, P transfer from the fungus to the host plant remained largely unaffected (Charters *et al.*, 2020). In older work using different experimental settings, the terms of trade between different hosts with arbuscular mycorrhizal fungi (AMF) did not conform to the biological market theory, thus questioning the broad applicability of this theory (van der Heijden & Walder, 2016) (and references therein). In summary, a widely applicable theory to explain resource exchange in mutualistic symbioses, including and beyond the AM symbiosis, and an underlying genetic framework are still needed to understand how mutualistic symbioses actually work.

Mycorrhizal symbioses in AM nonhost lineages

Are AM symbiosis principles applicable to other growth-promoting plant–fungal interactions? Mycorrhizal evolution gave rise to AM in early land plants; however, there is good evidence that mycorrhizal associations with Mucoromycotina fungi, a sister lineage to the Glomeromycotina fungi, also facilitated colonization of Earth's land by plants (Field *et al.*, 2019), maybe even pre-dating the AM symbiosis (Field & Pressel, 2018). In AM nonhost liverworts from the Haplomitriopsida (*Haplomitrium* and *Treubia*, the earliest diverging land plants), the Mucoromycotinal mycorrhizal symbiosis seems to have been selected over the AM symbiosis as the sole mycorrhizal association in these plants (Field & Pressel, 2018) (Fig. 1a). Since its emergence, the AM symbiosis has been subjected to evolutionary selection in plant lineages, which are now AM hosts, and has been abandoned in AM nonhost lineages, which either became nutritional specialists (e.g. carnivorous plants), developed new root–fungus mycorrhizal symbioses including intracellular associations (orchid and ericoid mycorrhiza) and extracellular associations (e.g. ectomycorrhiza, in short ECM), or remained 'non-mycorrhizal' lineages, that is not establishing any plant–fungus symbiosis that we know of (e.g. Brassicaceae) (Brundrett & Tedersoo, 2018; Werner *et al.*, 2018) (Fig. 1a). With the exception of orchid mycorrhiza, all these associations, such as the AM symbiosis, are based on a nutritional *quid pro quo*. Transport of nutrients from one partner to the other has been evidenced by the tracing of isotopes (e.g. ³³P, ³²P, ¹⁴C, ¹³C and ¹⁵N), in compartmentalized experimental systems, which allow the separation of a 'root compartment' from a 'fungal compartment', connected only by fungal hyphae (Pearson & Jakobsen, 1993). In the Mucoromycotinal mycorrhizal symbiosis of Haplomitriopsida liverworts,

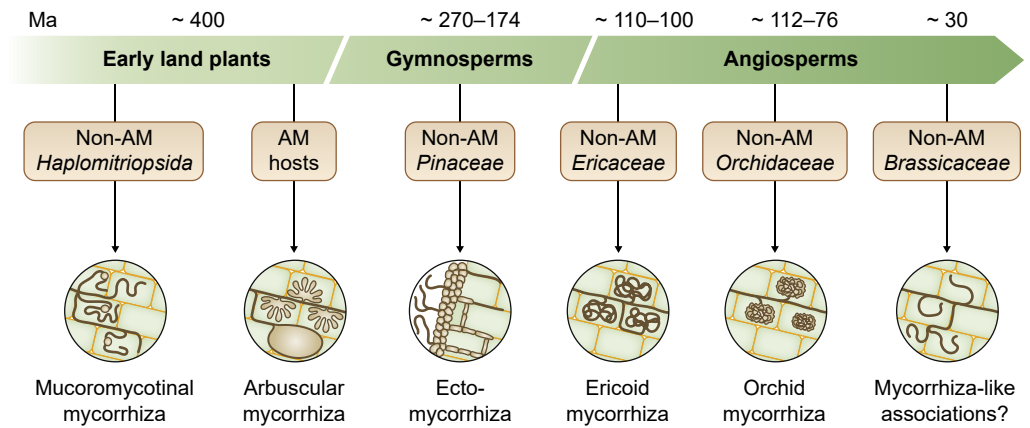
Mucoromycotina fungi provide nitrogen (N) and P to the plant in exchange for C (Field *et al.*, 2015). In the ECM symbiosis with Basidiomycota fungi and pines, fungi provide P (Becquer *et al.*, 2018) and N (Finlay *et al.*, 1988) to the plant in exchange for plant C (Wu *et al.*, 2001). In the case of the orchid mycorrhizal symbiosis, orchids from the family Orchidaceae appear to use Basidiomycota fungi for obtaining C (Bougoure *et al.*, 2014), N (Cameron *et al.*, 2006) and P (Cameron *et al.*, 2007) for seedling development or for heterotrophic growth, in the case of nonphotosynthetic orchids. The ericoid mycorrhizal symbiosis is only observed in Ericaceae plants, and mutual exchange of C and P has been demonstrated in Basidiomycota fungi of the genus *Clavaria* and Rhododendron plants (Englander & Hull, 1980). In addition to this nutritional *quid pro quo*, these mycorrhizal associations have in common the formation of specific fungal–plant interfaces within host roots, that is intracellular arbuscules or arbuscule-like structures (AM and Mucoromycotina mycorrhiza), intracellular pelotons (orchid mycorrhiza), intracellular coils (ericoid mycorrhiza) and the intercellular Hartig net formed in ectomycorrhiza (Werner *et al.*, 2018; Genre *et al.*, 2020) (Fig. 1a).

Adaptive gene selection is the driving factor that, from an evolutionary perspective, leads to the emergence and maintenance of a plant's ability to harbour a successful AM symbiosis. Interestingly, all plant genes essential for AM symbiosis are not systematically absent or were lost in all AM nonhost lineages. In orchid and ericoid mycorrhiza, genes involved in presymbiotic communication and intracellular fungal accommodation are retained, while genes involved in nutrient exchange seem to have been lost (Fig. 1b) (Radhakrishnan *et al.*, 2020). This suggests that in these mycorrhizal associations, intracellular fungal colonization of root cells relies on communication and infection mechanisms co-opted from the AM symbiosis pathway. In the case of ECM and in nonmycorrhizal plant lineages such as Brassicaceae, most genes that are essential in the AM symbiosis have been lost, except for genes involved in strigolactones biosynthesis (D27, CCD7 and CCD8) (Radhakrishnan *et al.*, 2020) and in the regulation of symbiotic nutrient exchange (CBX1) (Fig. 1b). Thus, these symbiotic functions could play an important role in the ECM and in mutualistic mycorrhizal-like associations.

Mycorrhiza-like associations

The transfer of nutrients from fungal cells to plant roots was thought to be limited to the mycorrhizal associations mentioned above, but recent research suggests otherwise. Indeed, since the discovery of 'mycorrhizal-like' fine root endophytes from the Mucoromycotina (for a review, see Sinanaj *et al.*, 2021), other endophytic fungi from other lineages have been discovered to form mycorrhiza-like associations. Several studies have independently demonstrated N, P, S and iron (Fe) transfers from 'mycorrhizal-like' endophytic fungi to plants, using isotope tracking experiments in compartmentalized systems similar to those used in mycorrhizal research. Such exchanges have been evidenced in a variety of plants with diverse root-colonizing fungi not previously known to form mycorrhizal associations. In these associations, the fungi are capable of intracellular colonization of plant roots and nutrient

(a) Root–fungus (mycorrhizal) associations



(b) AM symbiotic genes

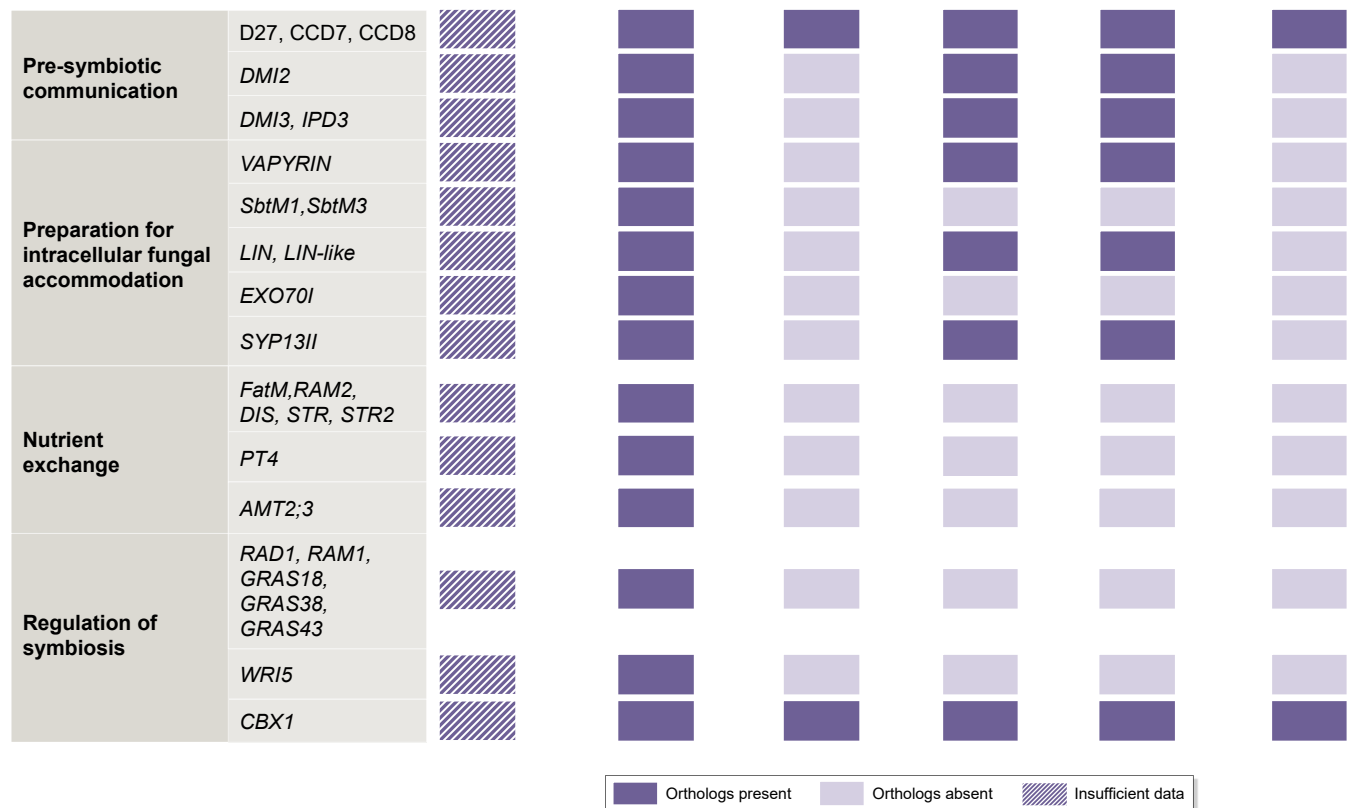


Fig. 1 (a) Root–fungus (mycorrhizal) associations in plant lineages having lost the capacity to establish the ancestral arbuscular mycorrhizal (AM) symbiosis (non-AM). Cropped images show distinctive cellular structures associated with the mucoromycotinal symbiosis, AM symbiosis (arbuscules), ectomycorrhizal symbiosis (mantle, fungal sheath), ericoid mycorrhizal symbiosis (coils) and orchid mycorrhiza (pelotons). The particular case of nonmycorrhizal Brassicaceae is shown, including hypotheses about their association with mycorrhizal-like fungi. (b) Conservation of AM-symbiosis essential plant genes in non-AM host plant lineages. Missing genomic data are shown with a hatched pattern. Reference proteins (Uniprot database) from *Lotus japonicus* and *Medicago truncatula* were BLASTED against genomes of species establishing ectomycorrhizal (*Picea glauca*, NCBI Taxonomy ID: 3330; *Pinus pinaster*, 71 647), ericoid mycorrhizal (*Rhododendron* sp., 4346) and orchid mycorrhizal associations (*Dendrobium catenatum*, 906 689; *Phalaenopsis equestris*, 78 828), as well as non-AM hosts (*Arabidopsis thaliana*, 3702; *Brassica rapa*, 3711) using BLASTP with default parameters.

transfer into the plant (major mycorrhizal features), but they do not form specific cellular structures specialized in nutrient trade, and the bidirectional nature of nutrient exchange has not been studied in most of them. Research on mycorrhizal-like fungi is relatively recent, and many important questions are still unanswered. Are the amounts of nutrients transferred to the plant relevant for plant

growth under natural conditions? Is there a systematic *quid pro quo*, that is do these fungi receive significant amounts of plant-derived C in return, or are these associations exploitative, that is without mutual nutrient exchange? How do these fungi interact with mycorrhizal fungi and more generally with the rest of the root microbiota? What is their quantitative contribution to nutrient

cycling in the rhizosphere? Is there a chemical dialogue and a common genetic toolkit supporting root colonization and symbiotic functions? How old are these associations from an evolutionary perspective? And are they in the 'waiting room' to evolve into true mycorrhizal associations, as suggested elsewhere (Strullu-Derrien *et al.*, 2018)? In the following paragraphs, we will describe newly discovered (non Mucoromycotina) mycorrhizal-like fungi and their contribution to plant nutrition.

***Metarhizium* and closely related insect pathogenic endophytes** Ascomycota fungi from the *Metarhizium* and *Beauveria* genera are entomopathogenic root endophytes found in association with diverse plants including grasses, shrubs and trees (Wyrebek *et al.*, 2011). Using ^{15}N -labelled insect larvae, it was shown that these fungi are able to extract N from the dead larvae and transfer it to their host plant (Behie *et al.*, 2012), carrying it over 10–20 cm distances (Behie & Bidochka, 2014). Reciprocally, C from ^{13}C -labelled plants was traced into fungal biomass and more specifically in fungal chitin and trehalose compounds (Behie *et al.*, 2017). Interestingly, it was shown that the transfer of N from insect larvae is a prerequisite to observe reciprocal C exchange from the plant, verifying the *quid pro quo* principle observed in other plant–fungus beneficial associations. Although N transfer seems to be widespread across tested fungal isolates and hosts plants (Fabaceae and Poaceae), higher amounts of transferred N tend to be observed in Poaceae (Behie & Bidochka, 2014), which suggests some level of preference in the association with monocots. The amounts of N transferred by the fungus are likely to be relevant for plant growth amounting up to 88% of total N in plant leaves (Behie & Bidochka, 2014). Fungal genetics has been used to identify genes involved in N transfer, but the results are not completely clear. Indeed, contrary to expectations, deletion of ammonium transporters (*MepC* and *Mep2*) and a urease gene in *Metarhizium robertsii* showed increased N transfer to barley, probably related to compensatory mechanisms in the N metabolism of the fungus (Moonjely *et al.*, 2019).

***Serendipita indica* (syn. *Piriformospora indica*)** *Serendipita indica* is a basidiomycete fungus from the Sebaciales order, first isolated from a spore of the AM fungus *Glomus mosseae* in desert soil. Although *S. indica* has been rarely found in nature, sister species from the Serendipitaceae have been described world-wide as endophytes in monocotyledons and dicotyledons (including trees), and in mycorrhizal associations with green orchids. Upon inoculation, *S. indica* is able to endophytically colonize the roots and promote the growth of several monocot and dicot plant species, with virtually no plant species characterized as nonhost for *S. indica* (Weiß *et al.*, 2016). In *A. thaliana* (Brassicaceae), the fungus has been shown to increase root growth, leaf biomass as well as P uptake. The observation that *S. indica*-inoculated plants could take up three times more P than control plants, over a short period of time (6 h), suggested P transfer capacities in the fungus (Shahollari *et al.*, 2005), which were later confirmed using P isotope-tracing in compartmentalized systems (Bakshi *et al.*, 2015). Further isotope-tracing studies showed that *S. indica* is also capable of transferring P and sulphur (S) to maize (Kumar *et al.*, 2011; Narayan *et al.*, 2021), and Fe to rice (Verma *et al.*,

2021). Although the molecular bases for these nutrient transfers on the fungal side are not yet clear, the involvement of the fungal sulphate transporter SiSulT (Narayan *et al.*, 2021), the iron transporter PiFTR (Verma *et al.*, 2021) and the phosphate transporter PiPT (Kumar *et al.*, 2011) is strongly suspected. Reciprocal C transfer from the plant to the fungus has not been proven, but it is known that the fungus alters C metabolism in *A. thaliana*, which could mediate the uptake of monosaccharides from the plant by the fungus (Opitz *et al.*, 2021).

***Heteroconium chaetospora* and other dark septate endophytes** Dark septate endophytes (DSE) are a paraphyletic group of endophytic ascomycetes characterized by the formation of dark-pigmented hyphae often found inside plant roots. Plant–DSE associations have been described for more than 600 plant species and dozens of fungal taxa (Rodriguez *et al.*, 2009). Isolation/reinoculation experiments with DSE have shown that they can promote plant growth through several mechanisms, including enhanced nutrient acquisition by the plant. The DSE *H. chaetospora* was shown to promote growth of its natural host *Brassica rapa* (Brassicaceae, Chinese cabbage) under N- and P-limited conditions. While the fungus was unable to promote plant growth in the presence of plant-available mineral N, it was able to increase plant biomass fourfold when an organic N source (amino acid) was present in the medium (Usuki & Narisawa, 2007). This is in line with findings on pleosporal and calosphaerial DSE associated with tomato (Vergara *et al.*, 2017), which suggest that DSE can access and use organic N sources that are not available to the plant, and trade this resource with the plant in exchange for C. Indeed, N transfer between fungus and plant in the *H. chaetospora*–*B. rapa* association is coupled with reciprocal C transfer from the plant, as observed by tracing plant-derived ^{13}C into the fungal mycelium (Usuki & Narisawa, 2007). Although the ecological significance of DSE remains enigmatic, DSE colonization of Cyperaceae and Caryophyllaceae plants under natural conditions appears to correlate with natural ^{15}N enrichment in these plants, suggesting that DSE fungi mediate N uptake from organic sources in these nonmycorrhizal plant families (Giesemann *et al.*, 2020).

Colletotrichum tofieldiae *Colletotrichum tofieldiae* was isolated from *A. thaliana* growing in a xeric grassland in central Spain on a low P soil (García *et al.*, 2013). Although it has rarely been detected in other European *A. thaliana* populations (Hiruma *et al.*, 2016), it has been isolated from other dicotyledonous and monocotyledonous plants on different continents (Jayawardena, 2016). The fungus was shown to promote the growth of *A. thaliana* under low P conditions. Tracking of ^{33}P in compartmentalized systems showed that the fungus was capable of transferring P to the plant under low but not under high P conditions. This suggests that, as in the AM symbiosis, in this mycorrhiza-like association fungus-to-plant P transfer is regulated by the plant's phosphate starvation response (PSR). Indeed, PSR-deficient plant mutants did not express fungus-inducible PHT1 P transporters and showed reduced root colonization and P transfer by the fungus (Hiruma *et al.*, 2016). On the fungal side, P transporters with high affinity for phosphate and similarity to the PHT1 family have been

described, but studies with gene knockout strains are needed to prove their involvement (Hacquard *et al.*, 2016). Reciprocal C transfer from the host has also not been described for this association, yet.

Helotiales sp. The strain Helotiales sp. F229 was isolated from the roots of *Arabis alpina* (Brassicaceae) growing in the French alps in a very low-P soil. When reinoculated into its host in sterile soil microcosms (consisting of the original low-P soil), the fungus was able to promote shoot growth and P uptake of *A. alpina* by 52% and 60%, respectively. P-tracing studies using the ^{33}P radioisotope in compartmentalized systems showed that the fungus was able to transfer P to the plant under both high and low P conditions, suggesting that in this case, P transfer from fungus to plant is not regulated by the phosphate status and PSR of the plant (Almario *et al.*, 2017). No reciprocal C transfer from the plant has been described for this association. Closely related Helotiales taxa have been isolated in another Brassicaceae *Microthlaspi perfoliatum* (Glynou *et al.*, 2016). Although fungi from the order Helotiales (Ascomycota) are widely distributed, they seem to be particularly important in alpine and arctic environments where they dominate fungal communities in plant roots (Almario *et al.*, 2017; Botnen *et al.*, 2020) and soil (Broadbent *et al.*, 2021), interestingly reflecting the high abundance of nonmycorrhizal plant species in these habitats (Botnen *et al.*, 2020).

Eco-evolutionary origins of mycorrhizal-like fungi

The mycorrhizal-like fungi described above belong to different phyla and have all evolved from different phylogenetic lineages. In the genus *Metarhizium*, endophytism and N transfer to the plant seem to be highly conserved. This lineage appears to have evolved 100 Ma (million yr ago) from beneficial epichloë grass endophytes that subsequently developed a secondary entomopathogenic lifestyle (Barelli *et al.*, 2016). Similarly, *S. indica* belongs to the Sebaciales order, which includes many orchid mycorrhizal fungi, ECM fungi and ericoid mycorrhizal fungi, suggesting that root endophytism is ancestral in this group that emerged 250–300 Ma (Tedersoo *et al.*, 2014). By contrast, in the case of *C. tofieldiae*, this beneficial endophytic lineage appears to have diverged only 8.8 Ma from a pathogenic *Colletotrichum* group that includes the taxon *C. incanum*, which is pathogenic to Arabidopsis (Hacquard *et al.*, 2016). These results suggest that the ability to transfer nutrients to the host plant has convergently emerged from both beneficial endophytic fungal lineages and pathogenic fungal lineages. Comparative genomics studies of mycorrhizal-like fungi such as Helotiales sp. F229, *S. indica* and *C. tofieldiae*, have shown overall that these fungi have maintained or even expanded their repertoire of plant cell wall-degrading (PCWD) genes associated with their endophytic lifestyle (Kohler *et al.*, 2015; Hacquard *et al.*, 2016; Almario *et al.*, 2017). This is in contrast to ECM and AM fungi, where evolution towards mutualism is associated with the loss of PCWD genes from fungal genomes (Tisserant *et al.*, 2013; Kohler *et al.*, 2015). Mycorrhizal-like fungi may therefore be better able to utilize complex nutrient sources from the decomposition of organic matter by their exoenzymes.

Mycorrhiza-like associations and nonmycorrhizal plants

Although mycorrhizal-like fungal associations have been described for both AM host and AM nonhost plants, they are thought to be key to understanding the evolutionary success of, for example, nonmycorrhizal Brassicaceae plants, which lost the trait of functional AM symbiosis with their emergence *c.* 30 Myr ago (Werner *et al.*, 2018), and do not form any other mycorrhizal association that we know of (Cosme *et al.*, 2018). The question of how Brassicaceae and other non-mycorrhizal plant families including Chenopodiaceae, Polygonaceae, Amaranthaceae, Caryophyllaceae and Cyperaceae (Wang & Qiu, 2006; Werner *et al.*, 2018) have adapted to the loss of the mutualistic AM symbiosis is unresolved. The discovery of the mycorrhizal-like fungi *S. indica* (Shahollari *et al.*, 2005), Helotiales sp. F229 (Almario *et al.*, 2017) and *C. tofieldiae* (Hiruma *et al.*, 2016), transferring P to Brassicaceae plants (Table 1), suggests that there are previously unaccounted interactions between mycorrhizal-like fungi and nonmycorrhizal plants. Furthermore, recent studies on ^{15}N signatures in wild Cyperaceae and Caryophyllaceae also suggest trophic interactions with DSE fungi (Giesemann *et al.*, 2020). We hypothesize that nonmycorrhizal plants rely on these plant–fungal associations for their nutrition as a replacement strategy for AM symbiosis loss. Similar to the emergence of ECM, ericoid mycorrhiza and orchid mycorrhiza, after the loss of the AM symbiosis in certain plant lineages (Fig. 1), these associations could be on their way to becoming intimate mutualistic mycorrhizal associations. It is tempting to speculate that further molecular studies of the symbioses of Brassicaceae species with beneficial endophytic fungi may soon indicate that there is an evolutionarily conserved toolkit for establishing true mutualistic interactions. We would then be inclined to call these ‘brassicoid mycorrhizas’ by analogy with ericoid and orchid mycorrhizas.

Impacts of climate change on nutritional *quid pro quo* in plant–fungus associations

In the current climate change scenario, rising CO₂ concentrations in the atmosphere will lead to increased temperatures, drought episodes and outbreaks of plant pathogens around the world. The question of how these changes will impact the plant–fungus nutritional *quid pro quo* remains unsolved, as literature is scarce and available studies have focused exclusively on mycorrhizal associations with no information on mycorrhiza-like associations. Elevated CO₂ is considered a key factor as it has been shown to promote C exudation by plant roots (Calvo *et al.*, 2017), thereby stimulating microbial activity around roots (Usyskin-Tonne *et al.*, 2021), with an overall positive effect on mycorrhizal colonization in roots (Treseder, 2004). In the case of AM symbiosis in wheat, elevated CO₂ conditions for the plant do not seem to translate into higher C fluxes to the fungus, but they can still increase the nutrient flux of P and N to the plant depending on the properties of host cultivars’ mycorrhizal roots (Thirkell *et al.*, 2020). A study on ECM pine seedlings showed that elevated CO₂ increases the rate of root exudation by twofold, with a higher increase observed in

Table 1 Studies reporting fungus-to-plant nutrient transfers in mycorrhiza-like plant–fungus associations.

Fungus (Phylum)	Plant (family)	Transfer direction	Nutrient	Isotope used	Chemical form	Experimental system used	Detection method	Time of transfer detection (dpi)	References
<i>Heteroconium chaetospira</i> (Ascomycota) DSE	<i>Brassica rapa</i> (Brassicaceae)	Fungus to plant	N	¹⁴ N	NaNO ₃ , Gly, Leu, Phe, Val amino acids	<i>In vitro</i> . Agar/rock fibre	Increased plant biomass	60	Usuki & Narisawa (2007)
<i>Pleosporeles</i> sp., <i>Calosphaeriales</i> sp. (Ascomycota) DSE	<i>B. rapa</i> (Brassicaceae)	Plant to fungus	C	¹³ C	CO ₂	<i>In vitro</i> . Agar/rock fibre	¹³ C-NMR in roots and fungal hyphae	28	Usuki & Narisawa (2007)
<i>Metarhizium robertsii</i> (Ascomycota). Insect pathogenic fungus	<i>Solanum lycopersicum</i> (Solanaceae) <i>Phaseolus vulgaris</i> (Fabaceae) and <i>Panicum virgatum</i> (Poaceae)	Fungus to plant	N	¹⁵ N	(NH ₄) ₂ SO ₄ , ¹⁵ N-labelled biomass (NH ₄) ₂ SO ₄ injected in insect larvae (<i>Galleria mellonella</i>)	Soil microcosms	Isotope ratio MS	50	Vergara <i>et al.</i> (2017)
<i>Metarhizium</i> spp. <i>robertsii</i> , <i>acridum</i> , <i>flavoviride</i> , <i>brunneum</i> , <i>guizhouense</i> , <i>Beauveria bassiana</i> and <i>Lecanicillium lecanii</i> (Ascomycota). Insect pathogenic fungus.	<i>P. vulgaris</i> (Fabaceae)	Plant to fungus	C	¹³ C	CO ₂	Soil microcosms	Increased amount of ¹⁵ N (NOI-5 emission spectrophotometer) and ¹⁵ N-labelled amino acids (LC-MS) in plant shoots	7, 14 and 28	Behie <i>et al.</i> (2012)
<i>Metarhizium</i> spp. <i>robertsii</i> , <i>acridum</i> , <i>flavoviride</i> , <i>brunneum</i> , <i>guizhouense</i> , <i>Beauveria bassiana</i> and <i>Lecanicillium lecanii</i> (Ascomycota). Insect pathogenic fungus.	<i>P. vulgaris</i> , <i>Glycine max</i> (Fabaceae), <i>P. virgatum</i> , <i>Triticum aestivum</i> (Poaceae)	Fungus to plant	N	¹⁵ N	(NH ₄) ₂ SO ₄ injected in insect larvae (<i>Galleria mellonella</i>)	Soil microcosms	Increased amount of ¹⁵ N (NOI-5 emission spectrophotometer) in plant shoots	1, 7, 14 and 21	Behie <i>et al.</i> (2017)
<i>M. robertsii</i> (Ascomycota). Insect pathogenic fungus.	<i>Phleum pratense</i> , <i>Bromus inermis</i> , <i>Dactylis</i> spp. (Poaceae)	Fungus to plant	N	¹⁵ N	(NH ₄) ₂ SO ₄ injected in insect larvae (<i>Galleria mellonella</i>)	Field conditions	Increased amount of ¹⁵ N (NOI-5 emission spectrophotometer) in plant shoots	28	Behie & Bidochka (2014)
<i>Serendipita indica</i> (Basidiomycota)	<i>Zea mays</i> (Poaceae)	Fungus to plant	P	³² P	Ortho-phosphate	<i>In vitro</i> . Agar	Radioactivity in fungus-inoculated plants	Data not available	Kumar <i>et al.</i> (2011)
	<i>Arabidopsis thaliana</i> (Brassicaceae)	Fungus to plant	P	³² P	Ortho-phosphate	<i>In vitro</i> . Agar	Radioactivity in fungus-inoculated plants (scintillation counting)	6 or 14	Shahollari <i>et al.</i> (2005)
	<i>Z. mays</i> (Poaceae)	Fungus to plant	S	³⁵ S	Na ₂ SO ₄	<i>In vitro</i> . Agar	Radioactivity in fungus-inoculated plants (scintillation counting)	Data not available	Bakshi <i>et al.</i> (2015) Narayan <i>et al.</i> (2021)

Table 1 (Continued)

Fungus (Phylum)	Plant (family)	Transfer direction	Nutrient	Isotope used	Chemical form	Experimental system used	Detection method	Time of transfer detection (dpi)	References
	<i>Oryza sativa</i> (Poaceae)	Fungus to plant	Fe	⁵⁹ Fe	Data not available	<i>In vitro</i> . Agar	Radioactivity in fungus-inoculated plants (scintillation counting and autoradiography)	Data not available	Verma <i>et al.</i> (2021)
<i>Colletotrichum tofieldiae</i> (Ascomycota)	<i>A. thaliana</i> (Brassicaceae)	Fungus to plant	P	³³ P	Ortho-phosphate	<i>In vitro</i> . Agar	Radioactivity in fungus-inoculated plants (scintillation counting)	17	Hiruma <i>et al.</i> (2016)
<i>Helotiales</i> sp. isolate F229 (Ascomycota)	<i>Arabis alpina</i> (Brassicaceae)	Fungus to plant	P	³³ P	Ortho-phosphate	<i>In vitro</i> . Agar	Radioactivity in fungus-inoculated plants (scintillation counting)	7, 10 and 15	Almaro <i>et al.</i> (2017)

mycorrhizal roots (Paterson *et al.*, 1997). However, it is not known whether higher C exudation of ECM plant roots could inversely lead to higher N transfer from the ECM fungus to the plant. Field experiments in pine forests have shown an increase in ¹⁵N flux from soil to plants under CO₂ fertilization (fumigation), but these effects were only detected after 3 years of elevated CO₂ conditions (Hofmockel *et al.*, 2011). This may suggest that high CO₂ conditions favour ECM-mediated ¹⁵N transfer to trees, but *in vitro* experiments under controlled conditions are needed to test this hypothesis. In the case of *Mucoromycotina* mycorrhizal symbiosis, the exposure of liverworts to higher atmospheric CO₂ resulted in some cases in higher fungal C uptake, but this had no positive effect on P or N transfer from the fungus to the plant (Field *et al.*, 2015), suggesting that there is an uncoupling of P-for-C and N-for-C exchanges under high CO₂ conditions.

In addition to the effects of elevated CO₂, extreme temperature variations and drought may also affect nutrient exchange between plants and fungi. As with all microbes, the growth of AM fungi is temperature-dependent, with the extraradical mycelia being more temperature-sensitive than the intraradical mycelia. Using *in vitro* root organ cultures, Gavito *et al.* showed that nutrient exchange between plant and fungi (C and P) is quite robust at temperature variations between 15 and 30° (Gavito *et al.*, 2005), while temperatures of < 10° completely block mycorrhizal P uptake by the plant (Gavito *et al.*, 2003). Several research studies have shown that drought alters the profile of plant C exudation and the amount of compounds excreted by roots (Williams & Vries, 2020), but studies investigating the effects of drought on nutrient transfer between fungi and plants are still limited. As expected, symbiotic P transfer to the plant by AM fungi appears to be sensitive to drought conditions as shown in AM-inoculated *Medicago truncatula* plants, which acquired significantly more P than noninoculated plants, under drought conditions (Püschel *et al.*, 2021). As for C fluxes, under drought conditions AM colonized grasses allocate less C into rhizodeposits, which could suggest that less C was also allocated to the AM symbiont (Wang *et al.*, 2021).

Will mycorrhiza-like associations help plants adapt to global climate change?

The importance of mycorrhizal associations for plant adaptation to climate change is widely recognized, but little attention has been paid to this in the case of the recently discovered mycorrhizal-like associations. It is likely that mycorrhizal-like fungi could play a central role by promoting nutrient uptake by nonmycorrhizal plants and by mycorrhizal plants, in ecosystems with low abundance of mycorrhizal fungi, but also by improving overall plant health (stress tolerance and disease resistance) through mechanisms other than nutrient transfer.

DSE fungi, including Helotiales taxa, are thought to promote local adaptation of plants in Arctic/alpine habitats by feeding on organic nutrient sources (Giesemann *et al.*, 2020), as AM fungal association become increasingly rare in high-altitude environments (Bueno de Mesquita *et al.*, 2018). Climate change is expected to drastically reduce snow cover and thus affect N

bioavailability in the coming years. DSE fungi could therefore become important for the adaptation of alpine plants to reduced snow cover and perturbed N cycling (Broadbent *et al.*, 2021).

Serendipita indica has been shown to promote drought resistance in rice by acting synergistically with *Bacillus* bacteria in the rhizosphere, jointly modulating plant hormone balance and subsequently rhizosheath formation (Xu *et al.*, 2021). In addition, *S. indica* enhances salt tolerance in its host *A. thaliana* via sodium (Na) and potassium (K) efflux transporters, thereby decreasing the Na content in the plant (Lanza *et al.*, 2019). Similarly, some DSE fungi are thought to improve drought resistance and salt tolerance in different plant species (Santos *et al.*, 2021). Under current global change scenarios, the abundance of plant pathogens in soil is predicted to increase (Delgado-Baquerizo *et al.*, 2020), implying that plant protection by endophytic mycorrhizal-like fungi could improve plant adaptation to increased disease pressure. *Serendipita indica* has been shown to promote plant resistance by modulating plant defences, but also by interacting with various rhizosphere bacteria acting through microbial processes involving lytic enzymes (Mahdi *et al.*, 2021). Similarly, *H. chaetospora* induces plant defence and has been described as a plant protection agent (Lahlali *et al.*, 2014).

The mutual exchange of nutrients in plant–microbe interactions is a complex genetic trait. Symbioses between plants and fungi have contributed significantly to the adaptation of plants to new environments and trophic niches, and the bidirectional exchange of nutrients has played an essential role (Rich *et al.*, 2021). We anticipate that this trait will provide genetic sources of adaptation that will help plants resist further impacts of climate change (such as invasion or the development of new pathogens and drought), as well as grow crops that resist climate change.




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Author contributions

JA and MB developed the concept of this review. All authors contributed to the writing. JA and GS generated the figure.

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