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The Costs and Benefits of Plant–Arbuscular Mycorrhizal Fungal Interactions

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Abstract

The symbiotic interaction between plants and arbuscular mycorrhizal (AM) fungi is often perceived as beneficial for both partners, though a large ecological literature highlights the context dependency of this interaction. Changes in abiotic variables, such as nutrient availability, can drive the interaction along the mutualism-parasitism continuum with variable outcomes for plant growth and fitness. However, AM fungi can benefit plants in more ways than improved phosphorus nutrition and plant growth. For example, AM fungi can promote abiotic and biotic stress tolerance even when considered parasitic from a nutrient provision perspective. Other than being obligate biotrophs, very little is known about the benefits AM fungi gain from plants. In this review, we utilize both molecular biology and ecological approaches to expand our understanding of the plant–AM fungal interaction across disciplines.

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1. COSTS AND BENEFITS IN THE PLANT–ARBUSCULAR MYCORRHIZAL FUNGAL INTERACTION

Approximately 72–80% of all angiosperms at least partially outsource nutrient uptake and form a symbiotic relationship with arbuscular mycorrhizal (AM) fungi (24) belonging to the subphylum Glomeromycotina (138). Because of their thin hyphae and extensively branched hyphal network, AM fungi improve plant host acquisition of limiting mineral nutrients: Hyphae increase the absorbing surface area and can access smaller soil cavities than root hairs. The interaction between plants and AM fungi was established more than 450 million years ago (139); therefore, the interaction has a long common evolutionary history and was crucial for the colonization of land by plants (24). AM fungi require fixed carbon (C) from plants, and plants provide 4–20% of their photoassimilates (84) in the form of carbohydrates and lipids to the fungus (68, 76). Plants receive more than 50% of their nitrogen (N) and more than 90% of their phosphorus (P) from AM fungi (135), as well as potassium; trace minerals such as manganese, magnesium, and zinc (57); sulfate; and water (54). The relationship between most plants and AM fungi is unbalanced: AM fungi are obligately dependent on host plants, while most plants can survive and reproduce without AM fungi. This imbalance contributes to our calculation of costs and benefits for plants and AM fungi.

Cost: the relative loss in comparison to the lack of association (plants) or the average fitness of an association (for AM fungi)

Benefit: the relative gain in a trait in comparison to the lack of association (plants) or the average association (for AM fungi)

Common mycorrhizal network (CMN): a network of mycorrhizal fungal hyphae that connects plants of the same and different species and shares nutrients and other compounds

Costs and benefits influence the fitness of an organism and are calculated for individuals in a population, but the definition of an individual is not clear for AM fungi. If benefits are greater than costs, then individual fitness increases, and if multiple individuals in the population experience the same balance of costs and benefits, then we can expect the population to increase. However, unlike plants, AM fungi do not produce discrete units that can be defined as individuals. When associating with plants, AM fungi produce hyphae internal and external to the roots, and external hyphae can be connected to multiple plants simultaneously, forming a common mycorrhizal network (CMN). Hyphae are coenocytic and cytocellularly stream their contents, including multiple nuclei, to locations of need (135). Thus, individual hyphae are important structures but can lack genetic material. How do we define an AM fungal individual, and if we cannot, then how do we assess individual fitness? This remains an open question in the field, although in this review we

refer to AM fungal fitness as a composite of root length colonized by AM fungi, external radical hyphal length, and spore abundance. Thus, costs and benefits are relatively straightforward to calculate for plants, but less so for AM fungi.

1.1. Plant Benefits

The research emphasis on costs and benefits for plant growth was established early in the field. The first common experiments on AM fungal–plant interactions often involved plants grown with and without AM fungi and measured morphological characteristics, primarily growth and biomass (29). This approach was adapted in the 1990s to develop a so-called response metric (e.g., 62, 154). The response metric was originally the relativized difference between plants grown with and without AM fungi (a nonlinear metric) but is now commonly calculated as the ratio of those variables (a linear metric). This metric can be positive (representing beneficial interactions), neutral, or negative (representing parasitic interactions). Tests of costs and benefits have appeared primarily in the ecological literature and, therefore, have relied on physical and chemical mechanisms of AM fungal exclusion, such as inoculating sterile soil, excluding AM fungal hyphae by using fine mesh or rotating cores, and adding fungicide (**Table 1**). None of these approaches allow us to test the presence or absence of AM fungi in situ because all of them also alter the natural microbiome or disturb the soil by introducing meshes. However, mutants and transgenic plants resistant to AM fungal colonization in comparison to isogenic wild-type lines (93) may solve this problem and allow us to compare AM fungal–colonized and –noncolonized plants under the same conditions, which in turn would enable the quantification of costs and benefits under field conditions. Researchers have used the response metric to place particular plant–AM fungal interactions on the mutualism-parasitism continuum on the basis of nutritional and growth effects. The traits measured are often proxies (biomass, growth rate, or nutrients) for fitness or reproductive output,

Response: the capacity of a plant to respond to AM fungal colonization; AM fungal–inoculated and –noninoculated plants are compared for specific parameters, usually growth and fitness, and the difference between the two is considered the response

Mutualism: a species interaction in which partners belonging to different species often benefit from association with each other

Parasitism: a species interaction in which one organism gains resources from a second organism, resulting in a fitness loss for the second organism

Table 1 Common protocols for creating controls that lack AM fungi used in cost-benefit experiments

Nonmycorrhizal fungal controls	Limitations
Physical manipulations	
Sterilized soil (with or without soil filtrate)	Requires soil filtrate to emulate natural microbial community
Autoclaving	Nutrient flush; not feasible in the field
Microwaving	Nutrient flush; not feasible for large volumes or in the field
Gamma irradiation	Expensive; not feasible in the field
In-field clear plastic covering	Effective only for surface soil
Mesh[a]	Microfauna and other fungi may also be excluded
Soil core rotation to break hyphal connections	Does not prevent AM fungal colonization
Chemical manipulation	
Fungicide	Removes most fungal species, not only AM fungi; frequent reapplication required
Biological manipulations	
Plant mutants or transgenic plants resistant to AM fungal colonization	Available for only a limited number of species; mutations may influence other, non–AM fungal colonization traits

[a]Refers to mesh with holes smaller than the diameter of AM fungal hyphae.
Abbreviation: AM, arbuscular mycorrhizal.

instead of fitness traits (seed number, viable seed number, pollen production, or asexual ramets). For plants, the response metric has been a powerful tool; however, at present this metric is used to describe responses to only one plant trait (e.g., biomass). Recent studies have begun to address this concern and have proposed the accumulation of secondary metabolites or tolerance-related transcript levels as additional measures of response (16).

Changes in morphological traits such as biomass are often attributed to changes in nutrient uptake, but there are other important benefits. AM fungal colonization increases photosynthesis rates, thereby increasing the total C fixed by a plant (e.g., 23). This increase may modulate the losses of C to the AM fungal partner (55) under optimal growth conditions.

AM fungi can promote plant tolerance to abiotic and biotic stresses. AM fungi promote abiotic benefits such as drought tolerance (6) and salinity tolerance (45). Most impacts of AM fungi on biotic stresses are thought to occur indirectly via changes in host plants. For example, AM fungi are known to prime plant innate immunity, resulting in faster and more efficient immune activation upon attack by pathogens and arthropod herbivores (97). Thus, there are multiple potential benefits, aside from growth and nutrient delivery, for plant hosts of AM fungi.

1.2. Plant Costs

As with benefits, the costs for plants have been calculated primarily for growth-related traits. AM fungi act as a carbon sink even while they increase rates of photosynthesis (75). Depending on the context, the balance of these two forces on C within the plant may not be in equilibrium. For example, multiple shading studies have shown a reduction in AM fungal root colonization that is likely associated with the increased C costs for plants associated with AM fungi (83). This balance may also depend on community composition (e.g., 80) and developmental stage (e.g., 132). Costs may also arise if AM fungi provide benefits, but not the benefits needed in a given environment.

1.3. Arbuscular Mycorrhizal Fungal Benefits

There is no equivalent metric for assessing the response of AM fungi to association with plants, which has created a bias in the literature. The bias is due in part to biology: AM fungi cannot be cultivated both with and without plants, and there is no one clear AM fungal trait to measure. We often assume that "parasitic" AM fungi (determined using the plant metric) provide less nutrients (P) for C to the plant in comparison to other, "beneficial" strains, but we have no consistent metric with which to demonstrate differences in benefit. AM fungal traits include root length colonized by AM fungi, external radical hyphal length, spore abundance, or a combination of all three. The determination of benefit or cost is estimated from the relative performance of this fungal trait in association with different host plants or in comparison to other fungal taxa. This metric is limited in many of the ways the plant metric is limited, but it does provide an initial starting point for discussion of benefits and costs for AM fungi.

Very few benefits other than C and growth have been identified for AM fungi, yet we can imagine several. For example, plant roots provide protection against predators and abiotic stresses, and information about a pathogen or herbivore attack transported in hyphal networks (e.g., 69) could also provide defensive benefits for AM fungi themselves. Thus, there is potential for a better understanding of how AM fungi benefit from symbiosis.

1.4. Arbuscular Mycorrhizal Fungal Costs

Few well-defined costs for AM fungi exist, aside from variation in C delivery among plant hosts. However, we know that abiotic (92) and biotic stresses (48) can reduce root colonization by AM

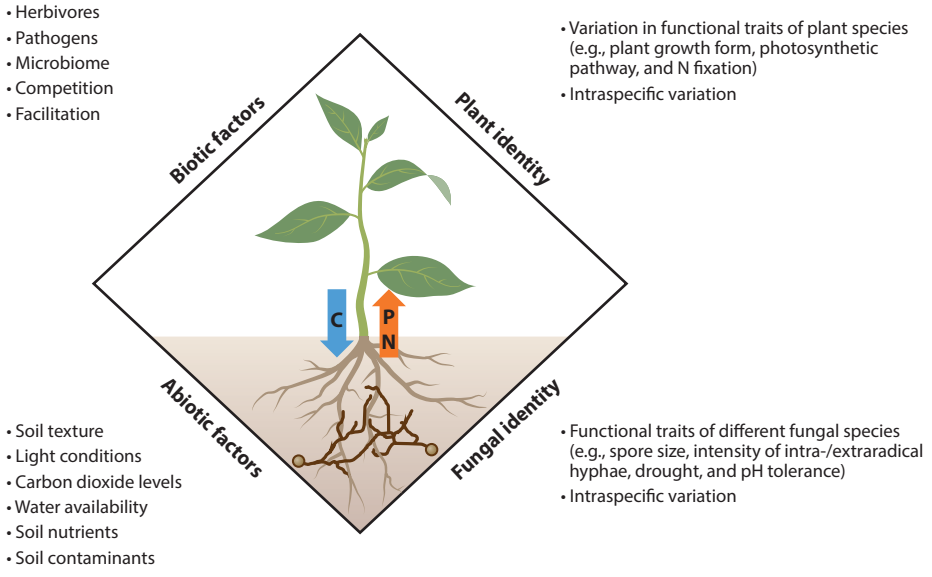

Figure 1

Context dependency of costs and benefits of plant–AM fungal interactions. The outcome of the interaction between plants and AM fungi (*brown*) is shaped by biotic and abiotic factors as well as plant and fungal genotype. Arrows show the flow of nutrients. Abbreviations: AM, arbuscular mycorrhizal; C, carbon; N, nitrogen; P, phosphorus. Plant image created with BioRender.com.

fungi. Might plant host–promoted tolerance to these stresses by the fungi come at a cost? To our knowledge, this question has never been explored. In addition, plants and AM fungi require many of the same limiting nutrients (especially N) and therefore may compete with each other.

The costs and benefits of the plant–AM fungal interaction are context dependent (64). Here we focus on the contexts that drive outcomes of the interaction (**Figure 1**). We aim to address outcomes for both the plant and the fungi, though less research has focused on outcomes for the fungi. Finally, we discuss the future of plant and AM fungal research.

2. THEORIES OF COSTS AND BENEFITS IN PLANT–ARBUSCULAR MYCORRHIZAL FUNGAL INTERACTIONS

Predicting the costs and benefits of the plant–AM fungal mutualism has led to significant theoretical development. In this section, we introduce and describe some of these theories.

A common theme is a focus on host costs and benefits via nutrient exchange and/or growth benefits. To date, aside from research on parasitic plants that siphon resources via mycorrhizal fungal hyphae (100), theories have rarely included other costs and benefits or incorporated costs and benefits for AM fungi. Below, we describe two groups of theories: (*a*) how costs and benefits of AM fungi for plants are derived and (*b*) how plants (and, occasionally, AM fungi) manage the costs and benefits of associating with a partner, and we explore how these costs and benefits may be translated to understand the impacts of functional groups and within communities.

We can divide theories related to how costs and benefits are predicted to be derived for plants into two categories: environmentally derived and functionally derived. Functionally derived benefits are not individual-based benefits, so we discuss them in Section 2.2.

2.1. Environmentally Derived Theories

The theory predicting that AM fungal benefits to plants are environmentally derived is based on resource stoichiometry (70, 87). Resource stoichiometry, the balance of nutrients in organisms and the environment, is attractive because we expect the interchange of nutrients between plants and AM fungi to be at least partially related to it, and we can test that hypothesis using relatively straightforward approaches. Tests of this theory have provided clear evidence that AM fungal growth promotion is determined by regulation of C, N, and P allocation within the plant and is related to environmental variation in N and P (72, 120).

The second group of theories that focuses on managing costs and benefits of the association is extensive. Poor host plant growth promotion by AM fungi has been termed "cheating" (143) and is typically characterized by low nutrient delivery and/or high C demand by the fungus. Most of the theories in this area have focused on plants sanctioning cheaters, and these sanctions are often derived from established theories that have been applied to the plant–AM fungal system. Sanctions fall into two categories: denying resources such as C or root space to the cheating partner (77) and providing more resources to the best partner. An empirical test of sanctions suggested that the ability to sanction (in this case, suppress root colonization) is related to the plant functional group and plant response to AM fungal colonization (59).

Theories incorporating the strategy of allocation to the best partner build on broadly explored mutualism theories. Partner Choice models hypothesize that organisms will choose the best partner and reinforce that choice with sanctions (143). In these models, plants choose partners and sanction underperformers with reduced C allocation (2, 50). Partner Fidelity Feedback suggests that repeated associations between partners will lead to positive feedbacks between those partners such that a loss of the association will reduce fitness (25, 123). This theory, as applied to plant–AM fungal interactions, suggests the following positive feedback loop: Increases in abundance of AM fungi are likely to promote plant fitness, and increases in plant abundance are likely to increase AM fungal fitness (51).

Biological Market Theory (108) is a type of game theory model that has proven a popular and somewhat debated approach (79, 144, 148) to understanding the plant–AM fungal relationship. Plants and AM fungi trade resources (primarily C and P), and if access to these resources via the AM fungal partner (e.g., P) is less costly than access via roots, then plants are assumed to engage in resource trade with AM fungi (78, 109, 131). In this model, sanctions and rewards are implicit: Plant and AM fungal partners know the "fair market price" for their resources (unit of C for unit of P) and are rewarded or sanctioned on the basis of the resources provided. Preferential allocation to the most beneficial partner has been argued to help stabilize the symbiosis over evolutionary time frames (63). Studies from in vitro systems and glasshouse experiments often support Biological Market Theory (20, 145; but see 147), though testing in more complex systems may be challenging.

2.2. Theories About Functional Groups and Communities

Costs and benefits describe individual responses, but many of the cost-benefit concepts have been extended to develop theories about how communities and functional groups of AM fungi and plants vary when associated, as the interaction may directly or indirectly affect diversity, dispersal, and abundance. The theory predicting that AM fungal benefits are functionally derived is based on an adaptation of Grime's Competitor–Stress Tolerator–Ruderal framework (27, 58) and is the only theory to incorporate AM fungal benefits other than plant growth and nutrient defense. Ruderal fungi are expected to exhibit high growth rates and better protection against pathogens and herbivores, whereas competitive fungi have high soil hyphal densities and are expected to promote greater plant growth rates via improved P delivery to hosts (27, 115). Stress tolerators

are less well studied but are expected to associate with stress-tolerant plants. The vast majority of research on AM fungi has examined primarily ruderal AM fungi such as *Rhizophagus irregularis* and *Funneliformis mosseae*, both from the family Glomeraceae (27, 115); we know less about competitive fungi such as members of Gigasporaceae (115) or stress tolerator fungi such as some *Acaulospora* species and *Gigaspora* isolates that have a higher tolerance to low-pH and high-aluminum soil content (33). However, this theory has not yet been fully tested.

Functional trait: a feature of an organism that contributes to ecological processes either directly or indirectly

We expect future theories and analyses of plant- and AM fungal functional group–relative costs and benefits to more fully incorporate both plant and fungal traits. Plant traits have proven useful for understanding community assembly and ecosystem functioning, and we expect the recent publication of the Fun$^{(Fun)}$ (161), FungalRoot (137), and TraitAM databases (28) and similar efforts on fungal functional traits to be a starting point for analyses and theoretical development, including fungal functional traits.

The basic underlying theory behind plant–AM fungal feedbacks was proposed almost two decades ago (19) and is based on our understanding that AM fungi do not promote all plant species equally. Research supports this theory (e.g., 18). The theory is based on frequency dependence and argues that common plants promote more costly AM fungal partners, leading to a decline in the abundance of the common plant over time. In this way, the frequency dependence of parasitic AM fungi maintains plant diversity temporally. This is one proposed mechanism for the well-documented effects of negative plant-soil feedbacks (8, 36, 119).

3. COSTS AND BENEFITS ARE CONTEXT DEPENDENT

As briefly outlined above, the costs and benefits of plant–AM fungal interactions are not fixed terms. They strongly depend on plant and fungal genetic background (species and genotype) and on the abiotic and biotic environment.

3.1. Plant and Fungal Genetic Background

In this section, we discuss the importance of the plant and fungal genetic backgrounds with regard to the costs and benefits of the interaction for each partner separately.

3.1.1. Plants. We can identify two levels of plant genetic background that influence the costs and benefits which control shifts along the mutualism-parasitism continuum in this symbiosis: species and genotype (**Figure 2**). First, plant species are well known to vary in their mycorrhizal response (29). Root traits vary with plant species' strategy for acquiring nutrients. Root type is also often a predictor of association with AM fungi. On the basis of root trait data from 1,810 species across the globe, plants that rely at least partially on AM fungi for nutrient acquisition usually have a higher specific root length and larger cortex fraction to accommodate the fungus (17), as has also been demonstrated for 21 different grassland species (141). A transcriptome analysis of *Medicago truncatula* associated with *R. irregularis* 09 showed elevated expression of mycorrhiza-specific P, ammonium, and nitrate transporters as well as genes relevant for providing nutrients to the fungus (the mycorrhiza-induced sugar transporter *SWEET1.2* and the lipid biosynthesis gene *RAM2*) (35). This analysis presents an opportunity to examine whether expression of these genes varies among plant genotypes. In contrast, the low-benefit fungus *Glomus aggregatum* 165 was presumably recognized as a pathogen because biotic stress-response genes were induced. Alternatively, this fungal species may better defend plants against pathogen attack (35). Additional studies under natural conditions are needed to determine whether so-called low-benefit fungi from a plant's nutritional perspective play key roles in defense.

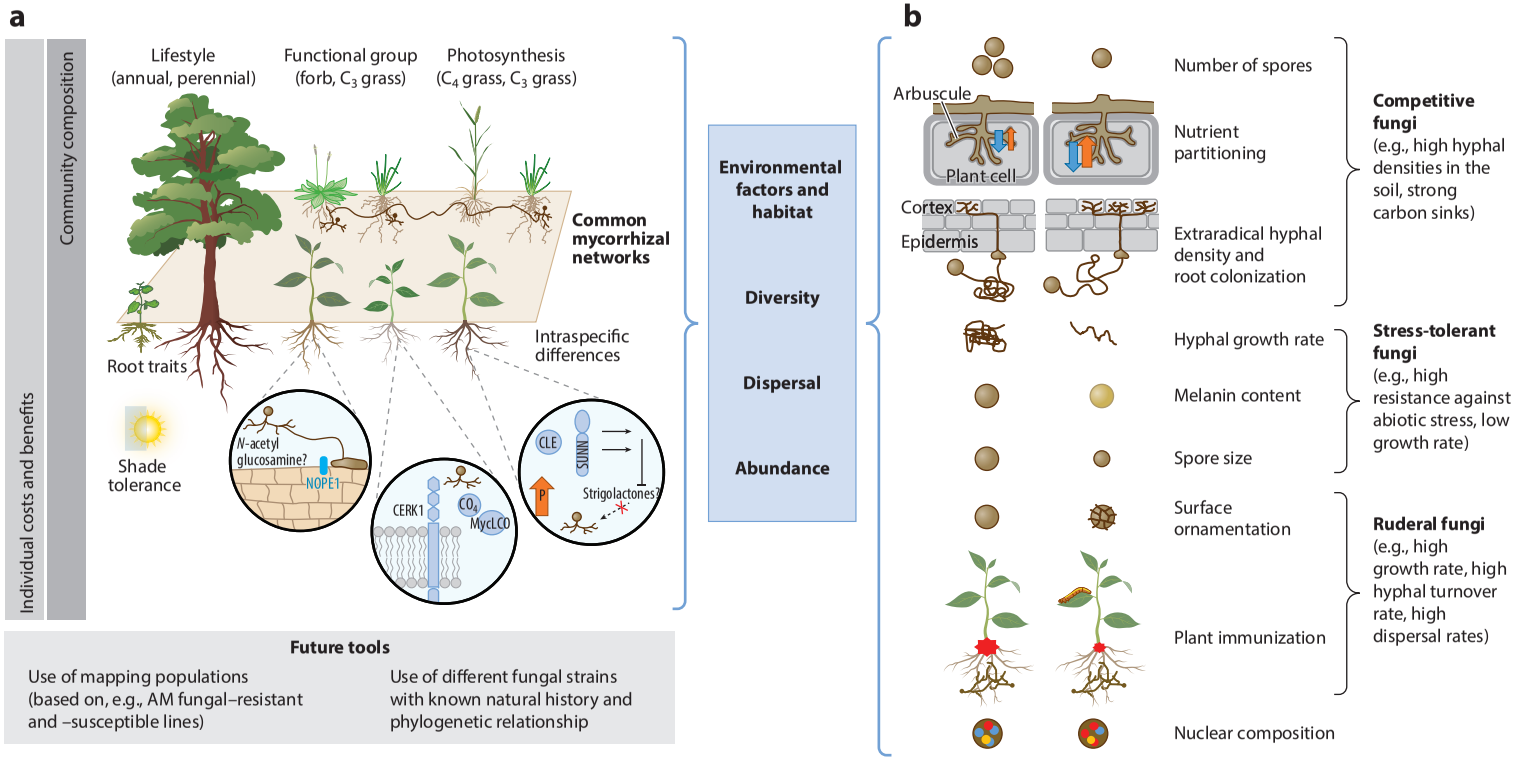

Figure 2

Plant and fungal genotypes play an important role for the costs and benefits of plant–AM fungal interactions. The outcome can be measured as individual plant fitness or at the community level. The interaction affects the population dynamics, diversity, and abundance of both plant and fungal communities. (*a*) Plant functional traits that modulate the interaction exist at both the species and genotype levels. Intraspecific differences may be based on genes involved in early signaling during plant–AM fungal interactions. For instance, NOPE1 is required for initiation of the AM fungal symbiosis and was found on a QTL related to mycorrhizal colonization (106, 149); variation in rice CERK1 affects AM fungal colonization (66); and CLE-SUNN negatively controls AM fungal colonization (74, 105). In nature, plants are connected to a common mycorrhizal network with their neighbors, affecting the exchange of nutrients and information. (*b*) Fungal traits relevant for the fungal benefit can be independent of the interaction or also modulated by the plant partner. Plant-independent traits may still be important for the interaction, considering that they affect fungal dispersal and abundance and, hence, co-occurrence with plants. Quantification of benefits of individual fungi is difficult, whereas effects on AM fungal communities can be more easily measured. AM fungi can also be classified according to the Competitor–Stress Tolerator–Ruderal framework, depending on their phenotype (27). A recent study showed that, in addition to general traits at genus level, the nuclear composition of AM fungi is important (81). Abbreviations: AM, arbuscular mycorrhizal; QTL, quantitative trait locus. Panel a adapted from images created with BioRender.com.

Second, genotypes and cultivars differ in their mycorrhizal response (16). For example, wheat and barley cultivars can differ in their C-for-nutrient exchange (43), and maize cultivars differ in their interaction with AM fungi on the basis of soil nutrient content (128). Domestication may have resulted in reduced response to AM fungi (13), but there is conflicting evidence in support of this hypothesis (94).

What are the mechanisms responsible for the variation between genotypes and cultivars? The genetic and mechanistic basis is still largely unknown (16). On the basis of current knowledge, we propose intraspecies variation in symbiosis initiation genes as a putative mechanism. The interaction between plants and AM fungi is initiated by a conserved set of genes involved in the fungal recognition and signaling required for the establishment of a functional symbiosis (e.g., 88, 114, 155, 159). We speculate that variation in fungal recognition and early signaling may play a role in modulating the plant response to AM fungi, as the successful establishment of the fungus is a prerequisite for nutrient exchange. The importance of variation in early signaling has been demonstrated by use of a mapping population of AM fungal–susceptible and –resistant maize plants that contain mutations in the mycorrhizal signaling pathway (*CASTOR* gene) (117). This elegant approach revealed a trade-off between quantitative trait loci (QTLs) associated with AM fungal growth benefits and yield in the absence of AM fungi (117). Furthermore, a leucine-rich repeat receptor–like kinase in *M. truncatula* [Super Numeric Nodule (MtSUNN)] with known homologs in other species regulates the proportion of root length colonized by AM fungi (**Figure 2*a***). This gene is regulated by specific peptides [CLAVATA3/ESR-related (CLE) peptides], which in turn are regulated by P levels (74, 105). This is the first mechanism describing how plants may control AM fungal colonization in relation to available P. Variations in this mechanism could help explain cultivar-specific responses under different P regimes. Another receptor, the lysin motif–containing receptor–like kinase CHITIN-ELICITOR-RECEPTOR KINASE 1 in rice (OsCERK1), and especially its second lysin motif domain, is the reason for the differences in AM fungal colonization levels, P uptake, and yield among rice cultivars (65) (**Figure 2*a***). OsCERK1 is required for the activation of the AM fungal signaling pathway and root colonization–recognizing mycorrhiza-specific lipochitooligosaccharides and chitinoligomers, but it also regulates chitin- and oligosaccharide-triggered immunity in rice against fungal pathogens (31, 164). Thus, OsCERK1 seems to act as a switch activating different responses depending on the type of infecting fungus (162). Furthermore, the *N*-acetylglucosamine (the monomer of chitin) transporter *NOPE1* (*no perception 1*) was found within a QTL related to the levels of a metabolic marker for arbuscular colonization (blumenols) in recombinant inbred lines of wild tobacco (*Nicotiana attenuata*) (149). An early study showed that *NOPE1* plays a role in the initiation of root colonization by AM fungi in maize and rice (106), and the parental lines of the *Nicotiana*-mapping population differ in expression of *NOPE1* and mycorrhizal colonization (149). Despite these promising results, root colonization is not always a reliable factor for growth and nutrient status (e.g., 129, 151). Further mapping efforts should take P content or fitness parameters into account to elucidate the genetic basis of the variability in mycorrhizal responses.

Variation in nutrient use efficiency may be another important mechanism (16). Furthermore, genotype × genotype combinations induce largely specific plant and fungal gene transcriptional responses and genotype-specific reprogramming during symbiosis (e.g., 96). This research, based on genetic variation of the plant and fungal partners, should be extended to reveal additional mechanisms explaining the variation in responses.

3.1.2. Plant communities. While costs and benefits are measured for individuals within a population of an individual species, there are also clear differences in plant performance between plant functional types associating with AM fungi. The plant response metric can be used to assess

differences between plant functional types, and there is significant evidence that different plant functional groups vary in plant biomass and nutrient uptake when associated with AM fungi. For example, non-N-fixing forbs, woody plants, and C_4 grasses respond more positively to mycorrhizal fungal inoculation than do plants with N-fixing bacterial symbionts and C_3 grasses (64). Plant functional groups may also be associated with distinct AM fungal communities, which may aid adaptation to different environments (38). The successional stage of a plant has also been hypothesized to predict response to AM fungi. Specifically, early-stage successional plants are expected to be less reliant on AM fungi than are later-stage successional plants, likely because of the fast r-selected lifestyle of early-stage successional species (86).

3.1.3. Arbuscular mycorrhizal fungi. To date, almost all research on the implications of AM fungal genetic background variation has focused on implications for plant growth promotion and nutrient delivery (but see 122 and 156). No studies have examined how genetic variation influences costs and benefits for AM fungi. This is a significant gap in the literature.

The AM fungal genetic background (species and genotype) influences costs and benefits for plants. AM fungal species vary in nutrient delivery to host plants (155), probably because of variation in life history traits among AM fungal species (27, 115). Members of Glomeraceae tend to be strong root colonizers and sporulate early, members of Gigasporaceae tend to develop more external mycelium and sporulate late, and members of Acaulospora are overall poor soil and root colonizers that preferentially live in acidic soils (115). Thus, AM fungal species vary not only in intraradical and extraradical hyphal growth, as well as in the number of spores and timing to sporulation, but also in melanin production, a trait associated with stress tolerance (42) (**Figure 2*b***). We expect each of these traits to influence plant benefit: Intraradical hyphal growth should have greater C costs, whereas extraradical hyphal growth requires C but provides nutrients. The number of spores and the timing of spore production likely create different C and N gains at different time points in the plant–AM fungal relationship. Melanin production may further influence C and the nutrients that AM fungal species must direct to their maintenance versus plant growth. Thus, there are multiple reasons why AM fungal species may influence plant growth and nutrient content.

AM fungal isolates vary in their influence on plant growth promotion, but most of the research demonstrating this variation has been performed with *R. irregularis* (99). A pioneering study revealed that "mating" two strains of AM fungi could produce fivefold changes in the promotion of rice growth (5)—variations that, previously, one might have expected to see only between species. Cassava (*Manihot esculenta*) inoculated with 12 different phylogenetically characterized strains of *R. irregularis* (127) varied in the proportion of root length colonized, which correlated with the phylogenetic relationship between strains. In addition, fungal isolates with low root colonization were greater inducers of the fatty acid pathway, while isolates with high root colonization resulted in lower levels of fatty acid pathway induction (127). Thus, this variation may be due to a trade-off between root colonization and fatty acid synthesis. This study provides strong support for a link between AM fungal genetic variation and plant responses.

Most studies on AM fungal genetic background variation have focused on implications for plants. No studies, to our knowledge, have examined how genetic variation has influenced costs and benefits for AM fungi themselves. This remains a gap in the research. Plant genotype can modulate the ratio of dikaryotic to monokaryotic AM fungi (81) and alter allocations to internal and external fungal hyphae (129), thereby influencing AM fungal genotypes and phenotypes.

We expect plant and AM fungal genetic background to influence preference. We do not yet know whether preference is exhibited by host plants, AM fungi, or both, but most studies assume that preference is exhibited by host plants. For example, plant and AM fungal communities

associate with one another on the basis of their functional group (38). However, most of these studies sampled a single time point, although we know that AM fungal community composition changes in host plant roots throughout the growing season (e.g., 12). Thus, there is likely more to learn about preference.

3.1.4. Arbuscular mycorrhizal fungal communities. As discussed above, AM fungi have been categorized into functional groups (27) that are predicted to vary in plant growth promotion. These traits have been suggested to drive plant selection of AM fungal partners (26).

3.2. The Abiotic Context

As outlined above, the costs and benefits of plant–AM fungal interactions are also modulated by abiotic context.

3.2.1. Plants. Both nutrient availability and abiotic stresses alter costs and benefits for the plant–AM fungal interaction. The most commonly studied abiotic context is P availability. The availability of soil P can determine costs and benefits in the plant–AM fungal interaction. Under high-P conditions, AM fungi become redundant: Plants can gain the necessary P without allocating C to their partners, so AM fungi become a carbon sink and often have little impact on growth or nutrient uptake. In these conditions, plants can restrict AM fungal colonization (150, 155). However, even under high P, positive effects of AM fungal inoculation can be observed (e.g., 32), and nonnutritional benefits have been less frequently examined. While we understand how plants sense the soil P status (46), we do not know how C delivery to the fungus is regulated by the host plant. One hypothesis is that lipid transport might be linked to P status. Furthermore, high soil P reduces strigolactone biosynthesis gene expression, which in turn reduces AM fungal spore germination and hyphal branching and, as a consequence, may reduce root colonization (4). The expression of a mycorrhiza-specific phosphate transporter is also downregulated under high-P conditions in *Petunia* (150). Yet even under high-P conditions AM fungi still colonize host plants. Thus, the interaction between AM fungi and plants can lead to costs for plants because most plants continue to deliver some C to their fungal partner.

N may be as important as P in the plant–AM fungal interaction. Like most organisms, AM fungi have a higher N demand than plants do, and they may compete with plants for this resource. A fungal nitrate transporter could regulate bidirectional fluxes (155). Thus, if N is limiting, we can expect AM fungi to put resources into N gain instead of P gain, as predicted by stoichiometry (72).

C limitation can also alter costs and benefits for plants when interacting with AM fungi. Studies have taken two approaches (shading and manipulation of CO_2) to alter C availability for plants and their associated AM fungi. Shading is expected to decrease, and elevated CO_2 to increase, the availability of C in the system. As expected, shading results in reduced investment in AM fungi, and preferential allocation to the most beneficial fungal partner for growth promotion under unshaded conditions declines (83). Although we know that different AM fungal species and groups vary in their C needs (earlier-derived AM fungal species deliver less P per C unit; e.g., 49), no study has tested whether the growth or nutrient delivery benefits provided by different AM fungal species shift as C becomes limiting. Given that plant detection of the red/far-red ratio dictates the plant's responses to shading, the use of photoreceptor mutants could allow us to disentangle the costs of a carbon drain under shading conditions (e.g., 107).

Studies examining elevated CO_2 are inconclusive (11), perhaps because of differences in function between plant species and genotypes. For example, C_4 and C_3 plants often differ in their responses to elevated CO_2 and AM fungal colonization: C_3 plants may benefit more from elevated CO_2 levels because photosynthesis and the use of CO_2 by C_4 plants are saturated at ambient CO_2

conditions (52). In a recent study of the C_3 grass barley, elevated CO_2 led to increased P transfer via AM fungi, although results varied by cultivar, but C transfer to *R. irregularis* was not altered despite plant growth stimulation (142).

One of the most frequently studied abiotic stresses is water availability, primarily drought (126). Many, but not all, of the same responses to AM fungal colonization that have been identified for drought have also been identified for salinity (45). AM fungi promote water uptake through multiple mechanisms (6). For example, hyphae are much thinner than roots and can reach and transport water from much smaller pores, and AM fungi promote stomatal openings that increase transpiration and water uptake, although this process can depend on the AM fungal partner (e.g., 30). AM fungi cause many changes in plant signaling and chemistry under drought. They reduce the abundance of reactive oxygen species in host plant tissues generated during drought (126) and alter distributions of the plant hormones salicylic acid, jasmonic acid, abscisic acid (ABA), indole acetic acid, auxin, and strigolactones, as well as aquaporins (45, 125, 126). The impact of these hormonal changes is likely to depend on many factors. For example, levels of both strigolactones and ABA can increase in the roots of plants during drought, perhaps as a mechanism to increase AM fungal colonization, but effects on strigolactones are inconsistent across systems and plant species (104).

Changes in ABA associated with AM fungal colonization have also been suggested to play a role in stomatal density and openings (e.g., 157). QTL regions associated with mycorrhizal response under drought stress have been identified on the basis of 94 lines of maize, but they still need to be validated (90). AM fungi also improve soil structure, which may further facilitate water uptake. Thus, AM fungi can promote drought tolerance through multiple intertwined mechanisms, and variation in these mechanisms likely contributes to the variation in results.

3.2.2. Arbuscular mycorrhizal fungi. We expect AM fungi to be both directly and indirectly (via their plant hosts) affected by abiotic stress. Changes in soil conditions like nutrient concentrations and drought are changes in the environment in which external AM fungal hyphae grow; therefore, we expect the responses of AM fungi to be independent of their hosts. For example, drought stress impairs AM fungal spore germination, sporulation, and extraradical hyphal elongation (89). There are two hypotheses for how AM fungal communities will respond to abiotic stress. First, species that cannot tolerate the abiotic stress will be eliminated, and second, the remaining species will adapt to the abiotic stress (102). In support of the first hypothesis is the finding that non-Glomeraceae taxa disappear under high-nutrient conditions, likely due to competition via differences in foraging speed and precision (134). In addition, under elevated CO_2, Claroideoglomeraceae germinate and colonize hosts first (52, 133). A global analysis of AM fungi has proposed that Acaulosporaceae occur most frequently in low-pH and low-temperature conditions, while Gigasporaceae prefer high precipitation (39). In support of the second hypothesis is the finding that variation in water availability promotes melanin content in AM fungal spores (42). There are fewer explicit tests of the second hypothesis, and to date no studies have looked for signatures of evolution in response to abiotic stress in AM fungi. Thus, there are unique opportunities for further exploration of how AM fungi respond to abiotic stress independently of host plants.

3.3. The Biotic Context

In the following subsections, we discuss the effects of key biotic factors (pathogens and herbivores as well as plant-plant interactions) on plant–AM fungal interactions.

3.3.1. Pathogens and herbivores. A number of studies have investigated how pathogens and herbivores affect plant–AM fungal interactions. Most focused on the plant partner, whereas knowledge about the costs and benefits for the fungal partner can be scarce.

3.3.1.1. Plants. The defense and tolerance benefits that AM fungi provide against primarily arthropod herbivores and pathogens are thought to arise indirectly via changes in host plants. When challenged by an antagonist, plants employ two strategies, and AM fungi can influence both: (*a*) Plants can tolerate attacks and simply regrow replacement tissue for damaged structures, and (*b*) plants can invest in immune responses or structural changes. AM fungal promotion of plant tolerance is well established, but a meta-analysis suggests that AM fungal communities are less likely to promote tolerance than single isolates (22). However, there have been few tests of single isolate versus community impacts on plant tolerance (but see 9).

Plant investment in immune responses can be categorized into direct and indirect responses, and AM fungi can promote both strategies. Direct responses are changes in plant chemistry or structures that directly influence herbivore performance by slowing herbivore metabolic processing of or limiting access to plant tissues (e.g., thick leaf cuticles). Direct responses can be further categorized as either constitutive or induced. Constitutive direct responses are present from early in plant ontogeny, and induced defenses represent increases in secondary chemistry or changes in plant structures following initial damage. Many examples exist in which AM fungi modulate direct immune responses, both constitutive and induced (14, 111).

A growing body of research is exploring how AM fungi influence indirect defenses against primarily arthropod herbivores. Indirect defenses typically involve plant signaling to a third organism, most frequently a parasitoid or predator of an herbivore. This signaling typically occurs via volatile organic compounds such as fatty acid and amino acid derivatives, terpenes, and aromatic compounds (34) released from plant tissues into the air or soil, and it attracts herbivore enemies (130). AM fungi alter the release of volatile organic compounds and modulate the attraction of herbivore enemies to host plants both above- and belowground (118).

What is the mechanism by which AM fungi alter direct and indirect plant immune responses? Plant innate immunity can be primed by AM fungi. Priming primarily activates jasmonic acid–mediated signaling and is therefore expected to be most effective against chewing herbivores and necrotrophic pathogens; the impact of priming on chewing herbivores is well documented (85). When first colonized by AM fungi, plants initiate an immune response that leads to increased cytosolic calcium and a burst of reactive oxygen species (97). However, AM fungi and other beneficial microbes can stop this immune response, leaving plants in a primed state (95, 97) without fitness costs. Priming sensitizes the immune system (73) and allows plants to retain an immune memory (similar to a vaccine in humans), resulting in faster and more efficient immune activation upon attack (61, 113). We are still identifying the factors that lead to this state of alert in plants; however, there are common changes in primed plants that result in improved immune responses to multiple antagonists. Transcriptional changes occur in approximately 4% of genes and include changes in signaling, transport, and hormone-related genes (73, 97). Primed plants also exhibit enhanced sensitivity to immune regulatory signals, chromatin modifications, and accumulation of inactive mitogen-activated protein kinase (95, 97). This plastic immune response has many advantages, including low energy costs, and results in increased tolerance and resistance to herbivory and other stresses (116, 121, 124).

3.3.1.2. Arbuscular mycorrhizal fungi. We are still learning the costs and benefits of antagonists for AM fungi. The vast majority of studies assessing plant–AM fungal–antagonist interactions measured AM fungal colonization, but very few of them assessed other traits, such as extraradical hyphae or spores (but see 10 and 153). A meta-analysis has shown that insect herbivory marginally reduces AM fungal colonization, but it questioned the biological significance of such small shifts in colonization (7). A recent study in barley explored the possibility that herbivory alters the community composition of AM fungi, but it found no significant impacts on composition (153). Thus,

there appear to be minimal costs for AM fungi due to plant antagonists, but this area deserves further exploration.

Functional diversity: refers to the portion of diversity that alters ecosystem operations and/or functions; a subset of biological diversity, measured as the variation in organismal traits that alter ecosystem functioning

In contrast, mammalian grazing confers both costs and benefits for AM fungi. Few studies have reported impacts of AM fungi on mammalian herbivores, but several studies have examined the reverse impact of grazers on AM fungi. Heavy grazing tends to negatively affect AM fungal root colonization, but light to moderate grazing can promote AM fungal root colonization (160). A framework for the impacts of grazers on AM fungi has recently been proposed (48). This framework suggests that, in addition to soil nutrients and edaphic properties, host plant identity, host plant functional diversity, mycorrhizal response of host plants, and AM fungal identity/functional diversity are likely to alter the costs and benefits for AM fungi (48).

3.3.2. Plant-plant interactions. Plants can interact directly via competition or indirectly via AM fungal hyphal networks, and in both cases AM fungi are often expected to promote plant coexistence (36). Plant competition is often a result of the differential acquisition of limiting resources (e.g., N, P, C, or sunlight), and AM fungi acquire and redistribute many of these resources. Negative plant-soil feedbacks involving AM fungi have been proposed to mediate plant competition and promote plant coexistence by redistributing resources temporally (**Figure 3*a***). AM fungi, plant competition, and plant-soil feedbacks may interact to promote coexistence, as better competitors tend to experience more negative feedbacks (91). Plant competition theories have been adapted to explain the AM fungal contribution to coexistence (15, 71). Intraspecific competition is greater than interspecific competition when plants are colonized by AM fungi (98).

AM fungi transport nutrients, C, and other compounds and connect plants through the CMN. There are many purported benefits to being connected to the CMN: delivery and relocation of nutrients (e.g., 152), transfer of C to seedlings, and transfer of information (69). Connections to the CMN may act as insurance that ensures nutrient delivery in a constantly changing environment (66).

How do benefits change when plants are connected via a CMN? The benefits of connection to a CMN are context dependent. Here, we highlight some of the factors that provide context. The difference in resource needs (dissimilarity) between plant individuals and/or species (103) may explain why CMNs differentially influence intra- versus interspecific competition. P may also be preferentially transferred in the network to plants that provide the most C (e.g., 101), which may increase competitive interactions between plants.

The CMN can also transport nonnutritional signals, which inform connected hosts about pathogen and herbivore attacks. In comparison to unconnected plants, plants connected to a CMN containing a plant attacked by an antagonist demonstrate greater resistance to the same antagonist when challenged (3, 110, 136). What (and how) signals are transported in CMNs remains elusive. Are they produced by plant immune responses? Are they transported in solution, as liquid films on the hyphal surface, or as electrical signals (56)? Is the signal species specific or universal? Immune responses are beneficial only in the face of an antagonist, and the spatial distribution of immune responses on the landscape may influence herbivore dispersal patterns (56). The nongrowth benefits of CMNs are an exciting avenue for further exploration.

3.4. The Microbial Context

The root and the rhizosphere are a highly dynamic environment that hosts multiple AM fungal species and other microorganisms fueled by C and root exudates (40). Plants transfer up to 30% of their fixed C to roots, and much of this C ends up as exudates in the soil (135). The rhizosphere is full of microorganisms that feed on these exudates, and roots host an endophytic

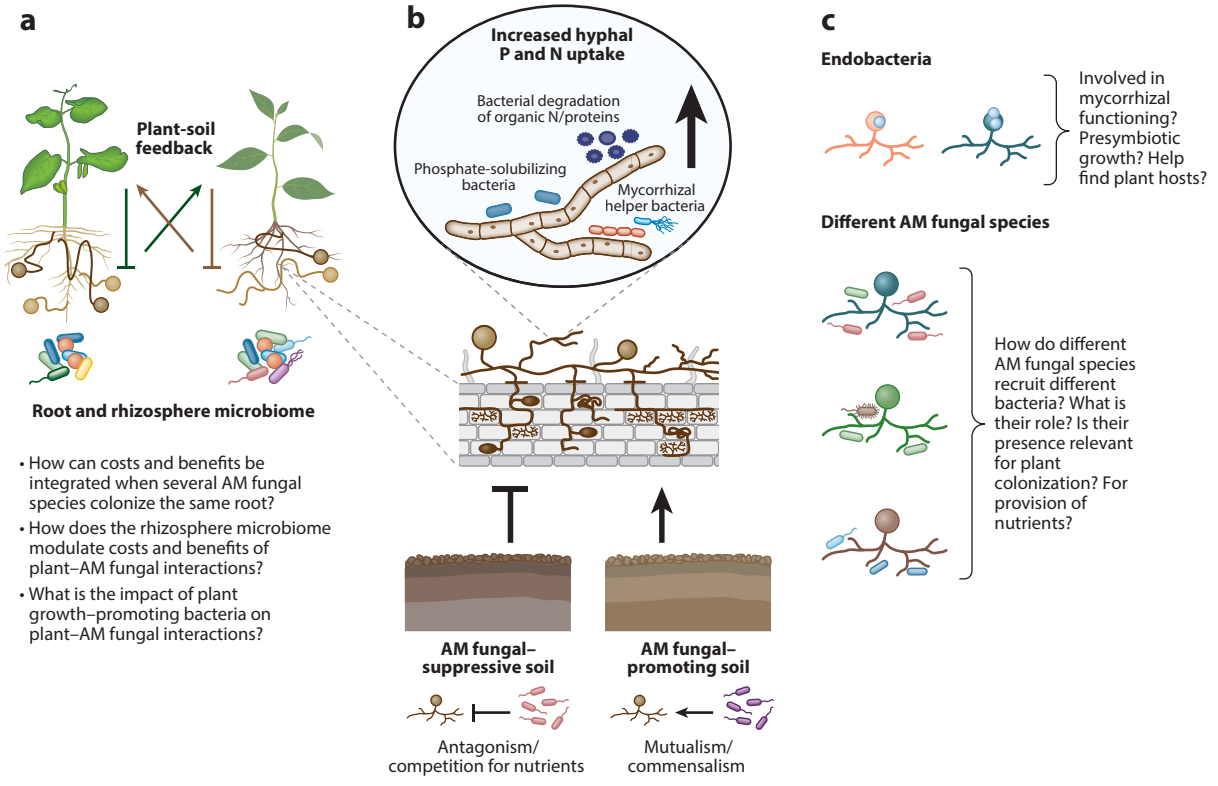

Figure 3

Summary of the interactions among AM fungi, bacteria, and roots, along with key open questions. Different root parts can be colonized by different AM species with different effectiveness. Plant-soil feedback is considered to be mostly negative due to intraspecific competition, species-specific pathogen accumulation, and AM fungal species frequency, while species differing in mycorrhizal guilds and pathogens may benefit (19, 36, 92). (*a*) Soils can be beneficial or suppressive for AM fungal root colonization and the fitness of plants, likely due to specific bacteria and depending on pH. (*b*) Fungal hyphae act as microbial highways for phosphate-solubilizing bacteria, enhancing the fungal uptake of P. (*c*) Different AM species host different microbiomes in their hyphosphere, and some species host endobacteria, though the role of these bacteria for fungal growth and fitness are still largely unknown. Abbreviations: AM, arbuscular mycorrhizal; N, nitrogen; P, phosphorus. Figure adapted from images created with BioRender.com.

microbial community, so many microbes occupy the same habitat as AM fungi. Even commercial AM inocula host a microbiome (1, 82). We are only beginning to determine how rhizosphere and endophytic microorganisms and microbiomes interact with AM fungi (**Figure 3**). For example, a plant growth–promoting rhizobacterium produces ACC deaminase, thereby lowering cucumber ethylene emissions and leading to increased AM fungal root colonization (53). Phosphate-solubilizing bacteria use AM fungal hyphae as a "highway" (67). Soil microbiomes associated with AM fungi that host a high abundance of Acidobacteria (potential antagonists of AM fungi) are suppressive and reduce extraradical mycelium in soil and P transfer to hosts (37, 140). Data are currently limited regarding whether plants may be able to influence the interaction between AM fungi and other organisms in the rhizosphere microbiome. For example, plants lacking the ability to host AM fungi show only small changes in the composition of rhizosphere microbiomes (47, 60, 158).

AM fungi also host their own internal and external microbiomes, and research on both individual components and whole microbiomes is increasing. Individual components of a microbiome

include endosymbiotic bacteria and mycorrhizal helper bacteria. Several AM fungi harbor endosymbiotic bacteria; for example, *Gigaspora margarita* harbors an endosymbiotic bacteria that helps increase fungal primary metabolism and respiration (146), and endosymbiotic bacteria are associated with the earliest AM fungi (Mucoromycota) (112). Several *Pseudomonas* species act as mycorrhizal helper bacteria that enhance hyphal growth and improve plant host colonization (41) (**Figure 3*c***).

Just like plants, AM fungi host their own microbiome (21, 163), but no clearly defined benefits and costs for hosting an AM fungal microbiome have been identified. For example, extraradical mycelia host bacterial communities different from bulk soil, but the function of these communities is not yet known (44). Similar to plants and other organisms, AM fungal microbiomes may vary with host species (44, 165). To date, the costs and benefits of AM fungal microbiomes appear largely context dependent for both AM fungi and plants.

4. FUTURE DIRECTIONS AND OUTLOOK

Many open questions regarding the costs and benefits in the plant–AM fungal interaction remain. We have highlighted that costs and benefits have been explored predominantly for growth and nutrient uptake, not for abiotic and biotic stress. Costs and benefits have also been explored primarily for plants, not for their fungal partners. Growth and nutrient uptake benefits are context dependent, yet we have not fully elucidated the importance of different contexts. Gradients of environmental variables provide opportunities to explore the range of benefits. To date, costs and benefits have been characterized using ecological tools (such as response experiments), and mechanisms that explain variation in costs and benefits have yet to be fully elucidated. Several potential approaches to identifying mechanisms exist, including using mutants impaired in AM colonization (e.g., 117) as controls and using genetically similar isolates of AM fungi that vary in growth promotion (5). Thus, there remain significant opportunities to provide clarity regarding costs and benefits in the plant–AM fungal interaction.

SUMMARY POINTS

1. Costs and benefits have been explored primarily for plants and not arbuscular mycorrhizal (AM) fungi.
2. Costs and benefits have been explored primarily for one set of traits: growth promotion and nutrient delivery, though nonnutritional effects are equally important.
3. Costs and benefits for plants and AM fungi interacting with each other are highly context dependent.
4. The genes that regulate the costs and benefits for AM fungi and plants are largely unknown.
5. Nutrients are a key factor governing the interaction, but higher carbon levels do not necessarily transfer into more nutrient allocation to the fungus.
6. AM fungi alleviate abiotic stress.
7. We are just beginning to learn how the AM fungal microbiome affects the plant–AM fungal interaction.

FUTURE ISSUES

1. Which plant genes govern response? Genes found in quantitative trait locus (QTL) analyses of field-grown AM fungal–colonized and –noncolonized populations should be tested to understand the genetic basis of the response.
2. Costs for nongrowth or nutrient delivery traits should be assessed. For example, is there a cost of immune priming? Do benefits received from AM fungi shift with stress and partner?
3. How is information shared in a common mycorrhizal network (CMN)? Who can perceive and respond to the information? What are the costs and benefits for the donor plant of sharing the information?
4. How do fungi allocate resources among plants? RNA interference of AM fungi could help elucidate how AM fungal isolates and species differ in their colonization and nutrient transfer.
5. Is there a benefit for the fungus to transport information of an attack beyond nutrients? Can fungi decode the information themselves?
6. How does the microbiome modulate costs and benefits for AM fungi? Do AM fungi associate specifically with bacteria providing specific services?

DISCLOSURE STATEMENT

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