**Mycorrhizal-induced growth depression in plants**

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**Abstract**

As plant mutualists, one would not expect arbuscular mycorrhizal fungi (AMF) to cause growth depression of their host plants. The mechanism responsible for negative effects of AMF is still debated and so here we review the possible abiotic and biotic reasons for AMF-induced growth depression in plants: 1) The Phytocentric explanations, include: a) AMF and non-mycotrophic plants, b) different growth stages of plants. 2) The Mycocentric explanations, include: a) Low effective AMF species, b) The existence of vesicles, c) Genetic variability of AMF, and d) Geographic origin of AMF.3) Unbalanced C-for-nutrient-trade, involving both partners and 4) Indirect effects of other organisms. We note deficiencies in previous studies and suggest improvements in experimental designs such as the use of realistic mixtures of AM fungal species, and growing plants in mixtures in field situations, rather than single pot studies, with and without fungi. Determining whether and how AM fungi cheat on their hosts will enable a better understanding of their roles in natural communities and their use as biofertilizers in agriculture.

**Keywords:** abiotic and biotic stress; arbuscular mycorrhizal fungi; growth depression; negative effect; parasite

**1 Introduction**

Arbuscular mycorrhizal fungi (AMF) comprise one of the most important groups of micro-organisms in terrestrial ecosystems, forming a symbiosis with more than 80% of vascular plants (Wang and Qiu 2006). It is generally accepted that AMF are obligate biotrophs and have zero fitness in the absence of a host plant (Berruti et al. 2016). With the widely distributed external hyphae, AMF can increase nutrient acquisition and water absorption (Smith and Read 2008). They can also alleviate environmental stresses (Chandrasekaran et al. 2014) and enhance plant resistance to pests and pathogens (Yang et al. 2014). Thus, AM symbiotic associations can influence the fitness of individual plants (Koide and Dickie 2002), the composition of plant communities (Hartnett and Wilson 2002), inter-specific competition (Jin et al. 2011), and productivity within terrestrial ecosystems (Klironomos et al. 2000; van der Heijden et al. 2008).

Plants supply AMF with photosynthetic products, while the fungi enhance the ability of plants to obtain nutrients, particularly P and N (Treseder 2013; Hodge and Storer 2015). Thus, AMF can enhance the growth and survival of host plants, as well as increasing biomass production. However, it is not true that all host plants gain net benefits from symbiosis with the AMF. Some of the AM fungi cause negative effects in host plants, such as nutrient outflux (Mariotte et al. 2013) or growth depression (Graham 2000). As plant mutualists, this is unexpected and begs the question: Why do some AMF appear to cheat on their host plants? Janos (1985, 1987, 1996) and Smith and Smith (1996) first examined the potential for parasitism by mycorrhizal fungi in the context of "cheating". Subsequently, Johnson et al. (1997) and Gange and Ayres (1999) discussed the mutualism-parasitism continuum, including negative effects of AMF on the performance of the host plant. A mechanistic explanation for the negative effects of AMF on the performance of the host plant was provided by Smith and Read (2008) and Johnson (2010), who proposed a trade balance model, further advanced by the review of Smith and Smith (2011). A recent paper (Jones et al. 2015) suggests that while there may be evidence for low-quality partners in mycorrhizal mutualisms, there is actually little evidence for cheating by the fungi. Yet abundant theoretical work shows that such negative effects are required to prevent Robert May’s famous ‘orgy of mutual benefaction’ from occurring (Holland 2015). Here, we explore the mechanisms by which negative effects of mycorrhizas might occur (and illustrated in Fig 1), our aim being to suggest a series of research questions that should address the question as to whether mycorrhizal fungi can cheat on their partners. It is generally accepted that plants and AMF symbiotically trade the commodity that they can most readily procure - plants trade carbon and fungi trade mineral ions and water. But the effects of mycorrhizas are far more complex than this, so what other factors might play a role in cheating?

**2 Phytocentric explanations**

**2.1 AMF and non-mycotrophic plants**

In natural ecosystems, there are some non-mycotrophic plants which do not form a symbiosis with AMF, including species in the families of Amaranthaceae, Brassicaceae, Caryophyllaceae, Polygonaceae, Urticaceae, Cyperaceae, Haemodoraceae, Proteaceae and Restionaceae (Lambers and Teste 2013). *Arabidopsis thaliana* is one of these plants in the Brassicaceae. It has been reported that most of the plants in this family do not form a symbiosis with AMF (Brundrett 2009). However, Veiga et al. (2013) found that in some cases, *A. thaliana* can be colonized with a mycorrhizal species (*Rhizophagus irregularis*). The interaction did not bestow positive benefits on *A. thaliana*, but had a negative influence, shown by growth depression in the colonized plants (Veiga et al. 2013). The reason may be that when AMF mycelia make contact with the roots of these plants, costly chemical defences are produced using resources that might otherwise have been directed to plant growth (Song et al. 2011). In the case of non-mycotrophic plants, the roots may perceive a need to defend against the potential colonization, e.g., by changing morphology for physical protection or producing secondary metabolic products (e.g. Hetrick et al. 1990; Vierheilig et al. 1996). Such growth or production requires extra photosynthetic products and may result in growth depression if resources are limited. It would be most instructive to pursue more studies like the one by Veiga et al. (2013) and to challenge a range of non-mycorrhizal plants with different AM fungi species. Metabolomics could then be used to examine the chemical mechanisms involved.

**2.2 Seedling growth stages of plants and competition**

Growth depressions may also be seen at different stages in the life of a plant. Janoušková et al. (2011) showed that *Tripleurospermum inodorum* plants responded positively to mycorrhiza when grown in a nutrient-deficient soil, the responses being more significant with P uptake than with nitrogen uptake or growth. In contrast, growth of nearby seedlings of this species and of the non-mycorrhizal *Sisymbrium loeselii* was inhibited in the mycorrhizal treatments. Importantly, the plants were grown in boxes in which seedlings were establishing in soil containing hyphae, but not roots. This suggests that the growth of the seedlings was depressed by nutrient depletion (particularly P) in the extra radical mycelium radiating from the large plants (Janoušková et al. 2011). Further evidence for this effect was provided by Del Fabbro and Prati (2014). These authors found that seedlings of *Senecio inaequidens* and *S. vernalis* were smaller in the presence of AM hyphae in soil, even though no fungal colonization of the seedlings could be detected. The results of these studies point to an important aspect of mycorrhizal effects on the coexistence of large plants and seedlings in nutrient deficient substrata. Similarly, the identity of the nearby large plant is also an important determinant with respect to whether AM fungi may negatively affect the growth of seedlings. Seedlings can connect to a common mycelial network in the soil and their growth can be reduced if establishing near an adult plant of a different species, compared with those that establish near to a conspecific plant (Burke 2012). This further emphasizes that future experiments need both to grow plants in mixtures, and to take account of the identity and ages of plants in those mixtures too.

Competition between plants is likely to be of paramount importance in determining the outcome of the interaction between AMF and the host. For example, Allsopp and Stock (1992) found that *Aspalathus linearis* was non-responsive at low plant density, but negatively responsive to AMF at high density. The intensity of intra specific competition and the distribution of plant sizes in populations can be shifted by AMF, resulting in many small individuals if colonization is high (Ayres et al. 2006). Interspecific competition is also influenced by AMF, particularly if competing species differ in their responsiveness to the fungi (Watkinson and Freckleton 1997). A knowledge of the responsiveness of different crops and weeds is essential if AMF are to be of use in agricultural situations (Daisog et al. 2012).

**3 Mycocentric explanations**

**3.1 Low effective AMF species**

It is well known that AMF species differ in their ability to be a ‘good’ partner for a plant, but quite what constitutes ‘good’ or separating such measurement from environmental influences presents many challenges (Werner and Kiers 2015). Indeed, the frequency of poor AM partners may be very hard to discern in natural communities, when their presence may be masked by other, more effective fungi (Hart et al. 2013). These mycorrhizal species may provide no or only a few benefits to the host plant, such as a little P, N nutrients or water, even though they form mycorrhizal structures within plant roots. The inefficiency of the fungi may be due to either poor development of fungal structures or to a lower rate of transfer per unit area of the symbiotic interface (i.e. flux across the interface). Hart et al. (2013) reported that there were several low effective AMF species, including *Entrophospora colombiana*, *Glomus aggregatum*, *Glomus etunicatum*, *Rhizophagus irregularis* (*Glomus intraradices*) and *Scutellospora calospora*. However, the context-dependency of such interactions is again illustrated by the fact that there are many reports of *R. irregularis* conferring beneficial effects on plants, including increased yield, (e.g. Hijri 2016) resistance to pathogens (e.g. Mora-Romero et al. 2015) and tolerance to toxic substances, such as arsenic (e.g. Cattani et al. 2015). However, such beneficial effects can also be plant genotype-specific (Mora-Romero et al. 2015).

It has been demonstrated that low effective AMF are widely distributed in natural habitats. Increasing the diversity of plant species could reduce the negative effects on individual host plants (Hart et al. 2013). Burrows and Pfleger (2002) found that high diversity of host plants could mitigate the growth depression of host plants with AMF. When diversity was high, those species antagonized by AMF were less affected, implying that mycorrhizal growth responses of individual plants may not translate to the population or community level. We again suggest that all future experiments that seek to investigate fungal partner ‘quality’ should take place in realistic scenarios of plants growing in mixtures (or monocultures for crops) rather than individuals in pots.

A further problem with the literature is that it is replete with experiments involving ‘control’ (non-mycorrhizal) plants being compared with inoculated individuals. In many cases, the latter involves one species of fungus. Yet such scenarios are most unrealistic, and such controls for the most part inappropriate (Partída-Martinez and Heil 2011), because uncolonized plants are virtually absent in nature, and thus the ‘normal’ ecological outcome of the interaction between AMF and host plant may be obscured. Such experimental designs are of course useful when trying to elucidate the interactions between mycorrhiza and plant at the molecular level, but they may provide a misleading ecological outcome. Future ecological experiments need to involve combinations of fungi, to determine whether functional redundancy or cheating exists amongst mycorrhizal species in any particular association (Treseder et al. 2012). Perhaps of most importance is that molecular techniques need to be used to quantify the different fungal species in the roots at the end of such experiments. Fungal abundance may then be correlated with various host plant traits, leading to testable hypotheses regarding the roles of the various species (Partída-Martinez and Heil 2011). On the rare occasions when this has been done (Robinson Boyer et al. 2015), relative fungal abundance has been shown to be affected by water availability. It is highly likely that other environmental parameters, such as nutrients, will similarly affect the outcomes and could go a long way to explaining the variable effects seen in previous studies (Table 1).

**3.2 The existence of vesicles**

Growth depressions may also be attributed to the occurrence and functioning of the various AM structures. It is remarkable that even today, the majority of studies express AM colonization as ‘total percent root length colonized’, giving little indication of the occurrence of the different kinds of structures within roots, namely hyphae, arbuscules, vesicles, and spores. The vesicle is one of the most obvious structures which can be observed in tissues of plant roots. However, the function of vesicles is still debated today. There are two opinions about it. One is that vesicles have a propagule function and can support the regrowth of intercellular hyphae when appropriate conditions occur (García et al. 2008). More vesicles were formed under stress conditions showing the tendency of AMF to invest more energy in storage structures for survival (García et al. 2008). When adverse conditions prevailed, such as drought stress, salt stress or high temperature, vesicles could survive in these conditions. After the conditions improved, vesicles could be activated and new fungal structures could be regenerated. The second opinion is that the vesicles are purely storage tissue for AMF (Li 2007). No matter which is correct, it is suggested that the existence of vesicles may decrease the growth rate of plants (Johnson 1993), through direction of resources to these structures. Perhaps of more interest is the observation that *R. irregularis* (as *G. intraradices*) reduced the growth of a non-host plant only when hyphae and vesicles were present (Wagg et al. 2011). The reason maybe that when vesicles grow, the fungus needs to obtain more photosynthetic products from the host plant, resulting in plant growth depression. We suggest that in all future studies that report AM colonization of plants, data for the different structures should be included. Simply presenting total colonization may hide a lot of useful and interesting data.

**3.3 Genetic variability of AMF**

Variation in the outcome of mycorrhizal colonization of plants may be partially based on fungal genetic variability and there can be high rates of genetic variability in AMF populations (Koch et al. 2004). Koch et al. (2006) found that different AMF isolates exhibited different influences on host plants even though they belonged to the same species (*R. irregularis* (*G. intraradices*)): some of them promoted the growth of host plants, and some of them decreased growth. This means that genetic variability in an AMF population can cause a range of different outcomes of plant growth, which could also be ecologically relevant at the ecosystem level and be important for the development of potent AMF inocula as successful biofertilizers (Rouphael et al. 2015). Such variability was further emphasized by de Novais et al. (2014) who demonstrated that 41 AMF-plant combinations had responses ranging from functionally compatible interactions to essentially neutral with their host plants. Furthermore, Klironomos (2003) also found that plant growth responses to different AMF inoculation within an ecosystem can range from highly parasitic to highly mutualistic. Clearly, genetic variability of AM fungi is very important in determining the outcome of the interaction with the host. Indeed, this may be as important as fungal phylogeny itself. However, relatively few studies have explored the importance of fungal phylogenetic effects on growth depressions in plants (but see Mummey et al. 2009). It would be instructive to examine the role that phylogeny plays in AMF-induced plant growth depression, particularly as plants in natural communities tend to be associated with a variety of fungal species (Davison et al. 2011).

**3.4 Geographic origin of AMF**

That populations of AMF from different geographic areas vary genetically has been known for some time (Giovannetti et al. 2003). Indeed, Mummey et al. (2009) show that growth depressions in plants may occur depending on the geographic origin of the fungus. Other good examples of this type of problem come from trials of commercial inoculants, not all of which are successful, and which often produce undesirable effects (Herrmann and Lesueur 2013). For example, Williams et al. (2013) found that commercial inoculation with AMF did not increase the growth of *Podocarpus cunninghamii*, but instead caused growth depression and decreased P and N concentrations in plant tissues. Furthermore, Faye et al. (2013) found that only three out of 12 different commercial inoculants had a beneficial effect on growth of maize. The reason maybe that although there is little significant specificity in the relationship between AMF and their host plants, local adaptation occurs, whereby plants may select the most beneficial partners (Werner and Kiers 2015). Because most native AMF have co-evolved with their host plant in any given areas, they may have a closer relationship with each other, than combinations that are geographically isolated. These interactions are most likely driven by variation in local resources, primarily soil fertility (Johnson et al. 2010). To date there are relatively few studies that have investigated the consequence of AM geographic origin on host plant performance, and this would be another fruitful area for research. One example is that of Antunes et al. (2011), in which six AMF species were collected from cool and warm climatic conditions and used to colonize cool-adapted *Poa pratensis* and warm-adapted *Cynodon dactylon* grasses. With *P. pratenis*, five (83%) of the cool-adapted fungi in warm conditions resulted in growth depression, while with *C. dactylon*, four (67%) warm-adapted fungi produced growth depressions in cool conditions. This clearly shows how abiotic conditions, such as climate and ecotype variability of the fungi, can interact to affect plant growth.

Such problems with geographic origin or genetic variation in AMF may well be why these fungi have yet to realise their potential as biofertilizers (Herrmann and Lesueur 2013, but see also Rouphael et al. 2015). A better understanding of how and why AMF may cause growth depressions in plants would enable the production of inocula that can be used in a wide variety of agricultural or horticultural situations.

**4 Unbalanced C-for-nutrient-trade**

C-for-nutrient trade is certainly the most obvious key factor in predicting the outcome of AMF symbioses. It has long been known that AM benefits to plant growth tend to be lower when soil P is high (e.g. McArthur and Knowles 1992) and similar effects seem to hold true for soil N (Correa et al. 2014) (Table 1). It is now becoming clear that the ‘cost/benefit’ approach is more complex than previously thought. Hoeksema et al. (2010) and Werner and Kiers (2015) pointed out that AMF-host plant relations are context-dependent and can be mediated by abiotic factors, including soil nutrients, pH, water and sunlight. Light availability (i.e. photosynthetic activity) has long been thought to be the limiting factor of symbiont activity and plant growth (Reinhard et al. 1993), though this is not always so and is dependent upon plant identity (Stonor et al. 2014). Carbon cost analyses of plants suggest that the effectiveness of AMF ranges from mutualistic to parasitic depending mostly on soil nutrient supply in natural or artificial ecosystems. It is clear that future studies of the effects of AMF on plants should take place along gradients of soil nutrients and that current levels of knowledge regarding C/N dynamics in particular are poor (Correa et al. 2015). Yet, a remarkable amount of the literature has involved experiments that have not varied the soil nutrients, even though natural soil levels are known to be extremely heterogeneous.

Growth depressions may be caused by AM fungi when the demands for organic carbon (C) from the host plant outweigh any benefits which might be produced from phosphorus or nitrogen transfer via the common mycelial network (Table 1). In this way, the mycorrhiza is essentially acting as a parasite or a ‘cheater’ (Johnson et al. 1997). However, the situation is complicated greatly by there being much variation in the ‘quality’ of the fungal partners and the degree to which plants can control the carbon outflow to the mycorrhiza (Grman 2012; Werner and Kiers 2015). It is also quite possible to observe a positive or negative effect of colonization of a plant by a fungal species (or combination), depending on the prevailing environmental conditions and fungal abundance (Gange and Ayres 1999). There is a real need to use molecular techniques that quantify the amount and metabolic activity of each fungal species over time in root systems during experiments, and to relate their presence to growth effects in the plant, linked with measurements of nutrient inflows and carbon outflows (Thonar et al. 2012). A good example of the latter, in a controlled experiment, is the study by Robinson Boyer et al. (2015). We suggest that similar molecular studies be performed on plants that grow along nutrient gradients, so as to understand better the C for P tradeoffs in different fungi and in different host plants. Furthermore, it is now possible to use genetically modified plants that allow different amounts of carbon transfer to the fungus, enabling an understanding of the degree to which the fungi reprogram sugar transporation in plant roots (e.g. Manck-Gotzenberger and Requena 2016).

**5 Indirect effects of other organisms**

A final biotic factor that may result in growth depression as a result of mycorrhizal colonization is through the influence of these fungi on the insect and fungal antagonists of plants. AM fungi generally increase the resistance of their host to attack by insects and plant pathogens (Borowicz 2001; Koricheva et al. 2009). However, this is not always the case, especially with sucking insects, where AMF can lead to increases in insect performance. However, remarkably few studies have followed the effects of AM fungi on insect population dynamics in the field (but see Ueda et al. 2013). Barber et al. (2013) found that pollinators exhibited taxon-specific responses, with honeybees, bumblebees, and Lepidoptera all responding differently to AMF treatments. Koricheva et al. (2009) hint at different responses amongst insect feeding guilds, which is to be expected from controlled experiments. Gange et al. (2003) demonstrated that some AM fungal combinations increased parasitism by insects, some decreased it, while others had no effect. To date, no study has examined the effects of AMF on insect community structure and the population dynamics of herbivorous species. Without such knowledge, it is impossible to say whether AMF effects on plants exhibit negative feedback as a result of enhanced populations of herbivores causing growth depressions. Thus, long-term studies of mycorrhizal-plant-insect interactions in field situations are urgently needed.

**Acknowledgements**

This study was supported by National Natural Science Foundation of China (31270558) and the Research Funds for the Introduction of Talents of Shanghai Science and Technology Museum. We are grateful to the anonymous referees whose comments greatly improved the manuscript.

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Fig 1 Mechanisms of mycorrhizal-induced growth depression in plants

Table 1 Results of the relationship between AM fungi and C-for-nutrient trade for host plant

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Plant | AM fungi | Nutrients | Effects of AM on plant | Reference |
| *Vetiveria zizanioides* | *Acaulospora**scrobiculata*, *Glomus aggregatum*,*Glomus sp.* | No P-supplied, | + | Techapinyawat et al. 2002 |
| 30, 60, 90 kg P2O5/ ha | - or 0 |
| *Macaranga denticulata* | *Glomus spp*., *Glomus fasciculatum*, *Acaulospora spp.* | Low P | + | Youpensuk et al. 2005 |
| High P (25-150 mg P/kg soil) | - or 0 |
| *Oryza sativa* | *Rhizophagus irregularis*,*Funneliformis mosseae* | Limiting N (0.15, 0.23, 0.45,0.79 mM (NH4)2SO4 | + | Correa et al. 2014 |
| High N (1.88, 3 mM (NH4)2SO4) | - or 0 |
| Wheat | *Paraglomus sp., Glomus sp.* | Conventional production | + | Dai et al. 2014 |
| organic production | - |
| *Oryza sativa* | *Glomus mosseae* | Low N level (20 mg pot-1) | More positive effects from AM to plant in low N than high N level | Liu et al. 2013 |
| High N level (50 mg pot-1) |
| Wheat (*Triticum aestivum*) | *Funneliformis ssp.*, *Rhizophagus ssp.,Claroideoglomu ssp.* | Adverse soil condition | More benefits under adverse soil condition than favourable soil conditions | Aghili et al. 2014 |
| Favourable soil conditions |

Note: "+" means positive effects, "-" means negative effects, "0" means neutral effects.