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Plant pathogen protection by arbuscular mycorrhizas: A role for fungal diversity?

Jeannine Wehner, Pedro M. Antunes, Jeff R. Powell, Jana Mazukatow, Matthias C. Rillig*

Freie Universität Berlin, Institut für Biologie, Plant Ecology, Altensteinstr. 6, D-14195 Berlin, Gemany

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ABSTRACT

Arbuscular mycorrhizal (AM) fungi can confer protection to host plants against some root pathogens, and several mechanisms for these phenomena have been proposed. If AM fungal taxa vary in the ways that they limit the negative effects of pathogens on host plants, additive and/or synergistic interactions among members of diverse AM fungal assemblages and communities may result in a greater pathogen protection than is currently predicted. However, in a review of the literature on interactions between AM and pathogenic fungi, we found few examples that compared the effectiveness of single- and multi-species AM fungal assemblages. Here, we briefly recount the generally recognized mechanisms of pathogen protection by AM fungi and present evidence, where appropriate, for functional diversity among AM fungal taxa with regard to these mechanisms. We propose that functional complementarity of AM fungal taxa in interactions with pathogens could mimic, or even be the cause of, previously observed relationships between AM fungal diversity and plant productivity.

Why consider diversity?

The role of below-ground soil organisms interacting with plant roots has gained increased attention in recent years (e.g. Reynolds et al. 2003; van der Putten 2003; Callaway et al. 2004), and the interactions between beneficial and pathogenic organisms have been identified as being particularly relevant due to their important implications for plant fitness (e.g.Schippers et al. 1987; Fitter and Garbaye 1994; Bever 2003). Most studies, however, focus on interactions between a single pair of species (i.e. one beneficial and one pathogen) and do not take into consideration the vast microbial diversity within these functional groups that coexist in, on, and near plant roots. This means that the existing body of knowledge is rather unrealistic and not concordant with the emerging view that many communities include guilds of interacting species (Stanton 2003).

This is particularly evident with the arbuscular mycorrhizal (AM) fungi, which are obligate symbionts of a majority of all plant species and common across most terrestrial biomes (Smith and Read 2008). Although not necessarily the primary function of the symbiosis, AM plants have been observed to receive protection from pathogens relative to their non-mycorrhizal counterparts in experimental studies (e.g.Newsham et al. 1995a; Filion et al. 1999, 2003; Borowicz 2001). Several mechanisms have been proposed to explain how this protection arises (Azcón-Aguilar and Barea 1996; Whipps 2004; Dalpé 2005). Studies suggest that AM fungal taxa vary both in the expression of traits associated with some of these mechanisms (Hart and Reader 2002; Pozo and Azcón-Aguilar 2007) and in their ability to protect host plants against pathogens (Newsham et al. 1995b; Klironomos 2000; Maherali and Klironomos 2007; Sikes et al. 2009). Therefore, it is plausible that assemblages of AM fungi derived from multiple species may exhibit greater potential to protect host plants against pathogens than a single AM fungal species; this concept could be analogous to (or even contribute to) the positive relationships observed between the richness of AM fungal assemblages and the growth of individual plants or the diversity and productivity of plant communities associating with these assemblages (van der Heijden et al. 1998; Maherali and Klironomos 2007).

Most research on AM fungal-mediated pathogen protection, especially studies addressing the mechanisms of this interaction, fails to consider the richness of AM fungal communities in natural systems (Azcón-Aguilar and Barea 1996; Borowicz 2001; Whipps 2004; Dalpé 2005). We propose that it is timely to revisit the mechanisms known to mediate pathogen protection and consider ways through which AM fungal diversity may influence the outcomes of these interactions.

Improved nutrient status of the host plant

It is well known that AM fungi can improve the nutrient status of their host plants (Smith and Read 2008). Several mineral

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* Corresponding author.
E-mail address: matthias.rillig@fu-berlin.de (M.C. Rillig).

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nutrients, especially P, are allocated through the symbiosis to the plant in exchange for carbon (e.g. Pearson and Jakobsen 1993). There is evidence that plants that took up larger amounts of nutrients through their AM fungal symbiont (e.g. *Glomus intraradices* and *Glomus mosseae*) have an increased tolerance for pathogenic infections (e.g. Bodker et al. 1998; Karagiannidis et al. 2002). However, it is not clear whether this increased tolerance was a direct consequence of improved nutrition. In other studies not involving the AM symbiosis, increased nutrient uptake did not result in improved pathogen tolerance (Shaul et al. 1999; Fritz et al. 2006). Maherali and Klironomos (2007) found taxonomic variation within the AM fungal phylum Glomeromycota, both in terms of nutrient responses and pathogen protection. While members of the Gigasporaceae enhanced nutrient uptake to a larger extent than those of the Glomeraceae, the latter reduced pathogen abundance in roots to a greater extent. This suggests that an enhancement of P by the AM symbiosis may increase plant development, but not decrease pathogen infections (Trotta et al. 1996). Accordingly, Newsham et al. (1995a) found no effects of AM fungi on the P level of host plants, only pathogen protection against *Fusarium oxysporum*.

Studies unrelated to pathogen protection have shown wide variation in terms of AM fungal-mediated nutrient uptake among AM fungal species (Jakobsen et al. 1992; van der Heijden et al. 1998, 2003; Smith et al. 2000; van Aarle et al. 2002). This can be explained to a certain extent through the variation of traits such as mycelium development both in soil and roots and P uptake efficiency (Jansa et al. 2005). Consequently, it is possible that increased AM fungal richness may result in improved nutrient supply of their host plants, due to trait variation and complementarity. If multiple AM fungal species are better able to enhance the nutrient status of a host plant (also for different nutrients, such as N, Ca, and P), compared to a single fungus, host defenses of AM plants may be enhanced.

Competitive interactions with pathogenic fungi

Direct (via interference competition, including chemical interactions) and indirect (via exploitation competition) interactions have been suggested as mechanisms by which AM fungi can reduce the abundance of pathogenic fungi in roots. These have generally been proposed in response to observations of negative correlations in the abundance of AM fungal structures and pathogenic microorganisms in roots and soil (St-Arnaud et al. 1994; Bodker et al. 2002; Filion et al. 2003) or on growth medium (St-Arnaud et al. 1995). Presumably, pathogenic and AM fungi exploit common resources within the root, including infection sites, space, and photosynthate within the root (recently reviewed in Whipps 2004). Interference competition may also arise if carbon availability within intercellular spaces and the rhizosphere (Graham 2001) or the number of infection loci within the root system (Vigo et al. 2000) is reduced as a result of AM fungal colonization.

Increasing the richness of AM fungal taxa colonizing the root system may result in more intense competition with a pathogenic fungus. AM fungi in multi-species assemblages vary in competitive ability, but the total level of colonization generally does not exceed that of the most abundant fungus when grown in isolation (Abbott and Robson 1981; White 1984; Jansa et al. 2008). *Glomus fasciculatus* 92 and *Glomus constrictus* 122, when inoculated in combination, did not increase the frequency of AM fungal root colonization or reduce symptoms of *Phytophthora parasitica* on citrus relative to when each were inoculated in isolation (Davis and Menge 1981). In another study, inoculation with a multi-species AM fungal assemblage from a field soil increased the intensity (and, to a lesser extent, the frequency) of AM fungal colonization of date palm roots, when compared with *Glomus monosporus*, *Glomus clarum*, or *Glomus deserticola* in isolation, but this did not result in enhanced amelioration of the negative effects of *F. oxysporum* f. sp. *albedinis* on plant growth (Jaiti et al. 2007). Recent research suggests that if competition between AM and pathogenic fungi is occurring, it is for resources other than just the occupation of space within the root system. The majority of variation in root colonization by AM fungi is explained by the divergence of the two most species-rich fungal clades: the extensively colonizing Glomerales and the poorly colonizing Diversisporales (Powell et al. 2009; Hart and Reader 2002). Surveys of the ability of various AM fungal taxa to reduce the abundance of *F. oxysporum* and/or a *Pythium* sp. in host root systems also suggest that variation in this trait is largely constrained to this divergence, with low levels of pathogen abundance in root systems inoculated with various *Glomus* species relative to those inoculated with various *Gigaspora*, *Scutellospora*, and *Acaulospora* species (Powell et al. 2009; Sikes et al. 2009). Using comparative methods that account for the statistical nonindependence of taxa within these clades, these studies found no evidence that higher frequency of AM fungal colonization within the host root system resulted in a linear reduction in colonization by the pathogenic fungi. This suggests that variation in traits other than the extent of root colonization should be a focus of future surveys. For example, variation exists among AM fungal species in the frequency of infection points within root systems (Liu and Luo 1994), but this has not been subject to widespread, systematic survey. Predicting the contributions of AM fungal assemblages to reduction of pathogen loads will require the identification and characterization of traits that contribute to AM fungal competitive abilities.

Anatomical or architectural changes in the root system

AM fungal colonization influences root architecture of the host plant in most studies by causing a more profusely branched root system (Price et al. 1989; Yanoet al. 1996; Paszkowski et al. 2002; Olah et al. 2005; Gutjahr et al. 2009).

Interactions between changes in the root system and protection of plant roots from pathogen attack have been demonstrated for several AM species. Matsubara et al. (1995) have shown that eggplants colonized by *Glomus etunicatum* or *Gigaspora margarita* contained higher lignin concentrations in first order and second order roots compared to non-mycorrhizal plants, when *Verticillium dahliae* was present. In addition, those AM fungi caused the plant to produce thicker third order roots. In contrast to the induced higher branching of the root system, *G. mosseae* decreased the root branching of tomato under high P conditions if a plant was attacked by *Phytophthora nicotianae* (Trotta et al. 1996). Alternatively, branching of the tomato root system was not affected by inoculation with *G. mosseae*, but decreased the number of infection loci of *Phytophthora parasitica* (Vigo et al. 2000).

Newsham et al. (1995b) proposed that an abundance of lateral root tips and developing meristems make highly branched root systems more susceptible for pathogen attack, resulting in an increasing demand for AM fungi to protect them. Norman et al. (1996) could support this hypothesis as they compared plants with inherently highly branched root systems and found that mycorrhizal plants had fewer necroses compared to non-mycorrhizal ones. If mycorrhizal fungi frequently cause increased branching of the roots, but increased branching in itself leads to higher susceptibility to root pathogen attack, AM fungi must confer protection through additional mechanisms.