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Host plant quality mediates competition between arbuscular mycorrhizal fungi

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ABSTRACT

Arbuscular mycorrhizal fungi exchange soil nutrients for carbon from plant hosts. Empirical works suggests that hosts may selectively provide resources to different fungal species, ultimately affecting fungal competition. However, fungal competition may also be mediated by colonization strategies of the fungi themselves. To test whether host quality drives fungal colonization strategies, we allowed competing fungi access to the roots of plants that varied in quality (manipulated by shading). We used quantitative PCR and microscopy to assess fungal competitive dynamics and found that shaded plants were not left as an open niche for less competitive fungi. However, while competitive fungi outcompeted less competitive fungi, the intensity of this effect depended on the quality of the host, with the strongest differences found on low-quality (shaded) hosts. Our results suggest that environmental conditions for the host aboveground play a role in the competitive interactions among fungi belowground.

Introduction

Over 70 % of all known plant species form partnerships with arbuscular mycorrhizal fungi (AMF), exchanging mineral nutrients for carbohydrates from plant hosts (Smith and Read, 2008). From an ecological and evolutionary perspective, these exchange processes exhibit interesting dynamics. First, both plant and fungal partners can vary in mutualistic quality (Kiers and Denison, 2008). The degree to which AMF benefit their hosts is highly context-dependent (Hoeksema et al., 2010), and in extreme cases AMF can even reduce host growth (Klironomos, 2003; Jones and Smith, 2004). Plant hosts

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can also vary in mutualistic quality, for example by providing less carbon to fungal partners when soil nutrient levels are high or when plant hosts are shaded and carbon limited (Treseder and Allen, 2000; Grman, 2012; Grman and Robinson, 2013). Second, fungal competition can be intense (Herrera Medina et al., 2003; Kennedy, 2010; Engelmoer et al., 2014). Initial colonization by fungi can prevent later colonization by others (Werner and Kiers, 2014), even of the same species (Vierheilig, 2004). Third, the mycorrhizal mutualism typically involves complex networks of simultaneous interactions among plant and fungal partners (Giovannetti et al., 2004; Mikkelsen et al., 2008). At any given time, plants are colonized by multiple AMF species (Jansa et al., 2008) and conversely, one AMF network can colonize multiple host plants and species (Selosse et al., 2006; Mikkelsen et al., 2008; Lekberg et al., 2010). Because of these many-to-many interactions, neither partner can be forced to cooperate; no single plant or AM fungus exclusively controls the nutrient supply of its symbiotic partner (Denison and Kiers, 2011). Lastly, research has suggested that some AMF species that are beneficial at promoting host growth can be less competitive than AMF that are less beneficial, suggesting a fitness trade-off in plant growth promotion and competitive ability (Bennett and Bever, 2009). Competition between AMF could thus lead to a decreased abundance of high-quality mutualistic partners for plants (Thonar et al., 2014).

Given these various constraints, researchers have asked how individual plants and fungi maintain high-quality interactions, i.e. with partners that provide most nutrients or otherwise enhance fitness (Bever et al., 2009; Lekberg et al., 2010; Denison and Kiers, 2011; Hammer et al., 2011; Walder et al., 2012). One possibility is that partners can mediate competition in such a way that high-quality interactions are favored, leading to an increase in abundance of particular partners. It has been hypothesized that fungal competition is largely a host-driven process, with hosts providing different amounts of resources to fungal species, ultimately affecting the outcome of fungal competition (Pearson et al., 1993; Kennedy, 2010; Werner and Kiers, 2014). Recent work supporting this idea has shown that host plants can differentially allocate resources in their root systems, preferentially supporting the fungal species that provide the most nutrients (Bever et al., 2009; Kiers et al., 2011). In turn, fungal partners appear to increase nutrient transfer to high-quality plants, i.e. plants that provide more carbohydrates (Lekberg et al., 2010; Hammer et al., 2011; Kiers et al., 2011; Fellbaum et al., 2012), resulting in dynamics of trade between plants and fungi that resemble a biological market (Grman et al., 2012; Werner et al., 2014; Fellbaum et al., 2014). However, it is not well understood how these preferential rewarding mechanisms operate under natural conditions. Previous studies following nutrient exchange dynamics have largely relied on *in vitro* root organ cultures lacking a photosynthetic shoot (Bücking and Shachar-Hill, 2005; Hammer et al., 2011; Kiers et al., 2011; Fellbaum et al., 2012). These have been criticized for underplaying the role of photosynthetic tissues, hormone regulation and source–sink relationships between plant organs (Fortin et al., 2002; Smith and Smith, 2011). A second problem is that resource exchange studies generally use only one fungal species (but see Engelmoer et al., 2014), while in nature fungal communities rarely are monotypic (Kivlin et al., 2011). Given these limitations, it remains unknown how partner quality affects competitive dynamics in the mycorrhizal mutualism. Is host quality an important factor driving fungal colonization strategy? Will fungi compete to preferentially colonize a higher quality host or will a low quality plant host serve as a niche for less competitive fungi?

To answer these questions, we studied the competitive dynamics of closely related fungal species when fungi had access to high and low quality plant hosts. We manipulated plant quality through shading: when photosynthetic rate is reduced, plants are potentially less attractive to AMF for resource exchange (Heinemeyer et al., 2003; Fitter, 2006; Kiers and Van der Heijden, 2006), as it reduces net carbohydrate assimilation rates (Loach, 1970). AMF colonizing the roots of shaded plants contain fewer structures for nutrient exchange (arbuscules), a potential indication of a reduced nutrient exchange with the host (Whitbeck, 2001; Hodge and Fitter, 2010).

We constructed experimental setups with two plants in a single microcosm, of which one plant was shaded. While the roots of host plants were separated with a mesh, hyphae were able to cross this barrier, allowing fungal networks to be formed between the two host plants. We inoculated plants with various combinations of two AMF species that differed in their colonization strategy (Table 1), and tested whether shading affected competitive interactions. Although colonizing a shaded host plant may still be beneficial for AMF, we expected the fungi to preferentially compete for a non-shaded host.

Methods

Plant, fungal and soil material

Medicago truncatula seedlings (variety Jemalong A17, courtesy of Dr. B. Hause, Leibniz Institute of Plant Biochemistry, Halle, Germany) were germinated following standard protocols (http://www.noble.org/medicagohandbook/), and transferred to sterilized peat-based soil to grow for 8 d. Seedlings were assigned to three size classes (small, middle, large) and

Table 1 – Experimental treatments. Single species treatments contained only one AMF species, plants in the mixed treatments were inoculated with a mix of both AMF species, while in the crossover treatments the shaded plant was inoculated with one AMF species and the non-shaded plant with the other. Each treatment contained 10 replicates

Treatment	Non-shaded	Shaded
Non-mycorrhizal	None	None
Single species	*R. irregularis*	*R. irregularis*
Single species	*G. aggregatum*	*G. aggregatum*
Mixed	Mix	Mix
Crossover	*R. irregularis*	*G. aggregatum*
Crossover	*G. aggregatum*	*R. irregularis*

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