Minireview

Mycorrhizal fungal establishment in agricultural soils: factors determining inoculation success

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Summary

Soil biota provide a number of key ecological services to natural and agricultural ecosystems. Increasingly, inoculation of soils with beneficial soil biota is being considered as a tool to enhance plant productivity and sustainability of agricultural ecosystems. However, one important bottleneck is the establishment of viable microbial populations that can persist over multiple seasons. Here, we explore the factors responsible for establishment of the beneficial soil fungi, arbuscular mycorrhizal fungi (AMF), which can enhance the yield of a wide range of agricultural crops. We evaluate field application potential and discuss ecological and evolutionary factors responsible for application success. We identify three factors that determine inoculation success and AM fungal persistence in soils: species compatibility (can the introduced species thrive under the imposed circumstances?); field carrying capacity (the habitat niche available to AMF); and priority effects (the influence of timing and competition on the establishment of alternative stable communities). We explore how these factors can be employed for establishment and persistence of AMF. We address the importance of inoculum choice, plant choice, management practices and timing of inoculation for the successful manipulation of the resulting AMF community.

Introduction

One of the greatest challenges of the 21st Century is to feed an increasing world population without exacerbating current environmental problems (Fitter, 2012). One promising approach is to increase the utilization efficiency of scarce nonrenewable fertilizers. This has the potential to simultaneously increase plant productivity and reduce pressures on the environment. Soil microbes offer largely unexplored potential to increase agricultural yields and productivity in a low-input manner.

Evolutionary and ecological research is unveiling the various mechanisms by which soil microbes can stimulate plant productivity (Van der Heijden *et al.*, 2008). In particular, rhizosphere symbionts named arbuscular mycorrhizal fungi (AMF) have received considerable attention as a potential low-input solution

to increasing the nutrient uptake efficiency of crop hosts. The majority of plant species, including most agricultural crops, enter into a symbiosis with mycorrhizal fungi, exchanging plant sugars for fungal-derived nutrients, such as phosphorus and nitrogen. Apart from nutritional benefits, they are also known to increase soil structure and suppress diseases.

Given the potential benefits to agricultural productivity (see Lekberg & Koide, 2005 for a review), it is not surprising that manipulation of AMF communities (either by inoculation with particular strains or through management of resident communities) has been attempted at the field scale. The implicit assumption of inoculation is that these systems are limited in either abundance or functioning of AMF, and that this limitation can be reversed through application of fungal inoculum. However, limitation may arise not only from insufficient availability or quality of AMF

propagules, but also from complex ecological and evolutionary dynamics of plant–fungal interactions. Here we synthesize the current knowledge on AMF establishment and loss, analyzing the success and failure of field inoculations using an ecological and evolutionary vantage point. Our ultimate goal is to predict how this symbiosis may be best optimized at the field level to increase plant productivity.

Are agricultural fields limited by AMF?

An important starting point is to determine whether AMF are limiting to processes in agricultural settings. Limitation has the potential to occur in at least two different forms: abundance and diversity. Abundance of AMF has been found to be negatively associated with intensive agricultural production (Smith & Read, 2008). Tillage, high levels of nutrients (particularly phosphorus) and frequent fallow periods are all predicted to decrease the absolute abundance of viable AMF propagules, such as spores and infective mycelium (Karasawa & Takebe, 2011; Schnoor *et al.*, 2011). If sufficient root colonization is not achieved, suboptimal plant growth can occur. Under such circumstances, inoculation offers a potential solution to increase colonization and benefits to crop hosts.

The other form of limitation is genetic, meaning levels of AMF diversity. Agricultural systems typically harbor lower AMF diversity than natural systems (Verbruggen *et al.*, 2010), and these systems are often dominated by a few select taxa within the AMF order *Glomerales* (Oehl *et al.*, 2010). For example, one particular genotype of *Funneliformis mosseae* was found to have a global distribution, potentially related to its spread and successful adaptation to agricultural conditions (Rosendahl *et al.*, 2009). A reduction of diversity can limit AMF-derived benefits if either different AMF species or genotypes provide complementary benefits, or the potentially highest yielding plant–fungal combination is not formed. Both of these mechanisms are known to occur when AMF diversity is manipulated (Wagg *et al.*, 2011). Adding inoculum has the theoretical potential to alleviate these types of limitations.

In the case of abundance, there is strong evidence that AMF colonization and spore number can be stimulated by altering management practices, for example mediating fertilization regime (Smith & Read, 2008), reducing fallow and/or growth of nonmycorrhizal crops (Karasawa & Takebe, 2011) and introducing organic management schemes, including the planting of temporary grass–clover pastures (Verbruggen *et al.*, 2012b). Loss of the AMF gene-pool may be harder to reverse, as this requires spread to and establishment in the system. In a recent meta-analysis of 111 sites (which included a variety of habitats), AMF dispersal was estimated to be very low; a large majority of taxa were only found at single sites (Kivlin *et al.*, 2011). Limited movement (as a result of underground spore formation) and strong local adaptation (Johnson *et al.*, 2010) will potentially amplify each other, and may strongly hamper invasibility of local AMF assemblages by nonlocal strains.

Because the type of limitation (genetic vs abundance) may have important implications for the merits of AMF application, it is important to distinguish between the types. Experiments in which AMF are applied to agricultural fields usually manipulate both abundance and species composition of AMF, making it difficult to disentangle their independent effects. However, in a thorough meta-analysis of various trials, effect of inoculation was explicitly compared with changes in indigenous AMF abundance via specific management changes (Lekberg & Koide, 2005). The results demonstrated that, on average, inoculation increased root colonization by 29%, resulting in a significant plant biomass increase of 23%. This suggests that the introduced strain performed a nonredundant function, resulting in increased plant nutrition. However, these effects were similar in trials where AMF abundance was increased by alternative management, particularly by shortening of the fallow period. Thus, plant responses to inoculation may to a large extent be driven by increases in AMF abundance, rather than the introduction of new strains. This is in line with recent work suggesting that native and exotic inocula can be similarly effective in increasing plant growth (Pellegrino *et al.*, 2011).

Collectively, this evidence supports the idea that inoculation effects may often be transient, and related to abundance, rather than identity effects. Nonetheless, if an agricultural field is, in principle, conducive to a better functioning AMF community but is limited by dispersal, inoculation may have long-term beneficial effects. This would require successful establishment on a crop and, for long-term benefits (e.g. throughout a crop rotation sequence), persistence of an introduced AMF strain. In the next section we will explore which processes determine whether AMF will establish.

Which factors contribute to establishment?

Compatibility

How compatible are introduced species with local agricultural conditions? Agricultural fields are subject to intense selection pressures from management practices (Rosendahl *et al.*, 2009). As a result, they are often occupied by fewer taxa than more natural systems, and these taxa are presumably well adapted to agricultural conditions (Oehl *et al.*, 2010; Schnoor *et al.*, 2011). Establishment of new taxa may be difficult if they are to compete with well-adapted local communities. One promising approach would be to match potential inoculants with specific field conditions, such as tillage environment (Schnoor *et al.*, 2011), soil type and pH (Oehl *et al.*, 2010) and breadth of potential hosts (Öpik & Moora, 2012). This last point in particular deserves attention, because it is becoming more and more apparent that some AMF taxa can be host or habitat 'specialists', while others are 'generalists' (Öpik & Moora, 2012). Because crops are usually rotated, and weeds can serve as additional inoculum sources, an AMF strain that is a plant-host generalist, all else being equal, is likely to have an enhanced establishment and persistence.

Sites that have a low AMF species diversity because of historical mismanagement are expected to particularly benefit from inoculation, as these are the cases in which AMF limitations are most likely to occur (Wagg *et al.*, 2011). Moreover, these sites may also exhibit an increased compatibility with inoculated species, provided that the low diversity means that there are more unoccupied

niches available. If the low complexity of agricultural systems is responsible for relatively low species diversity (i.e. dominance is no longer countered by nonequilibrium dynamics typical of more complex ecosystems), this may actually favor, instead of limit, establishment of particularly suitable strains. In order to still maintain a diverse AMF community, circumstances (e.g. management regimes) responsible for the low diversity have to be modified to a certain extent.

Carrying capacity and abundance

Two aspects of AMF abundance are strongly interrelated, and are expected to strongly affect establishment: inoculum quantity and the extent to which the particular system supports AMF populations. Some agricultural soils may have a reduced 'carrying capacity', caused by low plant allocation towards AMF. This is thought to occur as a response to culturing of nonhost plants, high nutrient levels, or other adverse environmental factors. For instance, high phosphorus levels do not typically favor a large AMF community because these conditions often suppress root colonization and thus growth of AMF (Fig. 1; Smith & Read, 2008; Verbruggen *et al.*, 2012b). For introduced AMF, this may be a problem: if AMF suffer from reduced fitness at low population sizes, they will be easily outcompeted by native AM fungi. Mechanisms through which this can occur include demographic stochasticity or 'Allee effects', where abundant AMF experience a higher fitness. The latter phenomenon is common across a wide diversity of organisms, and may operate in AMF if abundant strains
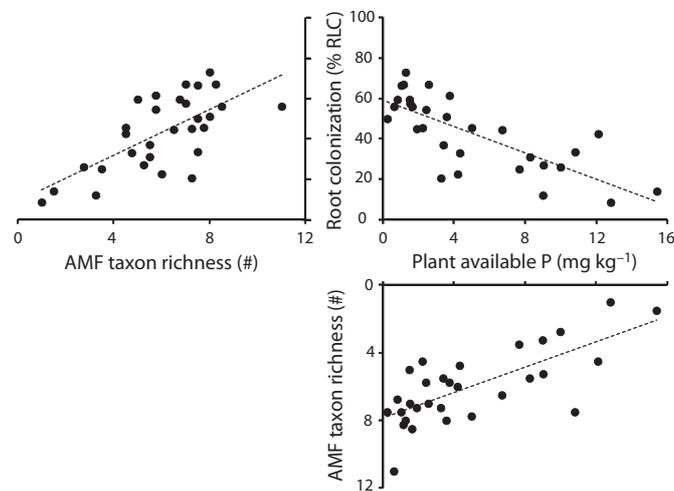
have a strong tendency to engage in anastomosis; that is, hyphal fusion resulting in direct physiological links between mycelia. At higher density AMF will be better able to reach conspecific strains. This will increase the volume of soil and plant roots colonized, more than proportionally (Rosendahl, 2008). However, even in the absence of anastomosis, there may be an abundance threshold below which taxa are disadvantaged. Relatively abundant taxa may be favored through a positive feedback. For example, if intact mycelia are present early in the season, abundant taxa can simultaneously colonize multiple plants, leading to strong dominance of such taxa in AMF assemblages (Dumbrell *et al.*, 2011).

There are few studies that have assessed AMF establishment multiple years after inoculation. This means that information on the critical propagule abundance that ensures successful establishment is currently lacking. In recent years, the possibility of tracking inoculum strains over multiple years has greatly increased through the development of molecular methods (Table 1). For instance, in one multi-year tracking study, there was strong evidence of persistence of at least one of two *Funneliformis mosseae* isolates (Pellegrino *et al.*, 2012). However, levels of inoculum applied were roughly equivalent to native population densities (Pellegrino *et al.*, 2012). If such doses are a requirement for successful establishment and persistence of AMF, this seriously reduces the feasibility of inoculation approaches: the amount applied in this study would scale up to application rates of 7 tons per hectare of soil (Table 1).

Priority effects

One phenomenon that can strongly affect community composition is priority effects; that is, the process by which initial species present in a community determine the eventual community composition. This process can amplify or negate any inherent competitive superiority. For instance, in fungi involved in wood decay, order of arrival has a critical effect on eventual community composition (Dickie *et al.*, 2012). These priority effects even outweighed the effect of fertilization, which is considered among the strongest determinants of species sorting in these fungi (Dickie *et al.*, 2012). In AMF, Lekberg *et al.* (2012) measured whether physical disturbance affects communities in a predictable way, by testing if it benefits some AM fungal taxa over others. While disturbance was not found to directly predict species composition, they proposed that priority effects were responsible for community differences after disturbance. If eventual community composition is contingent on small differences in initial conditions, they may be influenced relatively easily. Such stochasticity has been argued to be a major determining factor in several studies on AMF communities (Dumbrell *et al.*, 2011; Caruso *et al.*, 2012).

Estimates of the strength of priority effects on AMF communities are limited, but indirect evidence suggests that they can be important: Hausmann & Hawkes (2010) found that the order in which host plants (colonized by different AMF) established was a decisive factor in determining the resulting taxa of the community. Likewise, when plants already colonized by a particular AMF were introduced to a natural AMF community, the eventual diversity and composition of the resulting community were largely altered compared with uninoculated plants (Mummey *et al.*, 2009). One

Fig. 1 Tripartite relationship between root colonization, soil P fertility (plant available phosphate; $CaCl_2$ – extractable) and arbuscular mycorrhizal fungus (AMF) taxa richness in roots at 30 sites in the Netherlands. The three parameters are all strongly interrelated; higher soil P availability relates to reduced root colonization (percentage root length colonized) and reduced AMF richness (estimated number of taxa). Data to produce this figure are described in Verbruggen *et al.* (2010, 2012b). Root colonization and AMF taxon richness estimated by T-RFLP are averaged over July and September sampling in 2007; sites include 26 maize (*Zea mays*) fields and four semi-natural grasslands. Correlation coefficients and *P* values are for richness–colonization ($r^2 = 0.47$; $P < 0.001$), available P–colonization ($r^2 = 0.53$; $P = 0.001$) and available P–richness ($r^2 = 0.57$; $P < 0.001$).

Table 1 Specifics of four field inoculation trials where root colonization of introduced arbuscular mycorrhizal fungus (AMF) species was assessed through molecular methods

Host species	Means of application	Amount applied	Success per species/strain		Time course	References
Potato (*Solanum tuberosum* L.)	Pre-inoculation of seedlings with soil containing spores, roots and hyphae, yearly	2.3×10^3 kg ha^{-1} ($> 2.3 \times 10^7$ propagules ha^{-1} estimated by MPN)	*R. intraradices* *F. mosseae* *C. etunicatum*	+/−[a] +/− +/−	Only measured 6 weeks after planting, 2 consecutive years	Farmer *et al.* (2007)
Reed canarygrass (*Phalaris arundinaceae* L.)	Expanded-clay carrier containing spores, roots and hyphae, once	5×10^3 l ha^{-1} number of propagules not known, mixture of 2 species and strains	*R. irregularis* (1) *R. irregularis* (2) *C. claroideum*	+ +/− −	Measured 3 times per year over the course of 3 years	Sýkorová *et al.* (2012)
Lucerne (*Medicago sativa* L.)	Soil containing spores, roots and hyphae, once	7×10^3 kg ha^{-1} for two AMF strains separately; number of propagules not known (spores: 1.3×10^7 ha^{-1} and 1.3×10^6 ha^{-1}; see main text)	*F. mosseae* (1) *F. mosseae* (2)	+ −	Yearly, for 2 consecutive years	Pellegrino *et al.* (2012)
Olive (*Olea Europaea* L.)	Soil containing spores, roots and hyphae, mixed with local soil, once	1.7×10^4 kg ha^{-1} ($= 5.8 \times 10^8$ propagules ha^{-1} estimated by MPN)[b]	*R. intraradices* *Rhizophagus* sp.	+/−[c] +/−[d]	Measured 3 times, latest after 14 months	Alguacil *et al.* (2011)

Success is defined as whether a species or strain (as specified) is found in the majority of samples and not in the controls (+), found in some samples, but more than in controls (+/−), or not found at all (−). Data are from Farmer *et al.* (2007) and Pellegrino *et al.* (2012) (agricultural fields) and Sýkorová *et al.* (2012) and Alguacil *et al.* (2011) (re-vegetation projects). Abbreviations of genera: *R*, *Rhizophagus*; *F*, *Funneliformis*; *C*, *Claroideoglomus*. MPN, most probable number. Estimated amounts are calculated by extrapolating the density applied at plot level to field level.
[a]All species in this studies have qualification of +/− because longer term detection is not ascertained.
[b]Weight of inoculum is estimated assuming a bulk density of 1 g cm^{-3}, and assuming a distance between plants of 1.2 m, planted in rows.
[c]This species was not found in the control plants, but was highly abundant in the treatment where the other species was applied, and not this species.
[d]This species was also found in the control plants, but at lower abundance (number of screened clones) than in the treatment.

important question is whether effects of priority are symmetric: if plant colonization by one taxon has a prohibitive or stimulatory effect on a subsequent colonizer, does the same apply if the order is reversed? If this is the case, the effect on community dynamics might be relatively straightforward to predict. If, however, there is less regularity in priority effects, these effects will be very complex and community-specific, limiting the possibility to predict establishment chances without extensive prior knowledge of the system.

How can these processes affect inoculation success?

Species compatibility, carrying capacity, and priority effects are all processes that directly or indirectly affect competition for root or soil space, and therefore are important in determining the persistence and success of specific fungal taxa. If we understand how these processes operate in plant–AMF interactions, we can optimize management to stimulate the establishment of introduced strains (for a schematic overview of these processes, see Fig. 2).

One potentially successful approach may be to find which AMF families or functional types are missing from particular habitats and add agriculturally 'compatible' representatives. Such inoculation attempts may have an increased establishment success because of 'unoccupied niches'. For example, in one study, the AMF species *Claroideoglomus etunicatum* was particularly successful (Table 1; Farmer *et al.*, 2007). Of the three inoculants assessed, this species was the only one for which the field lacked any other representatives of its particular family, which is likely to have contributed to its
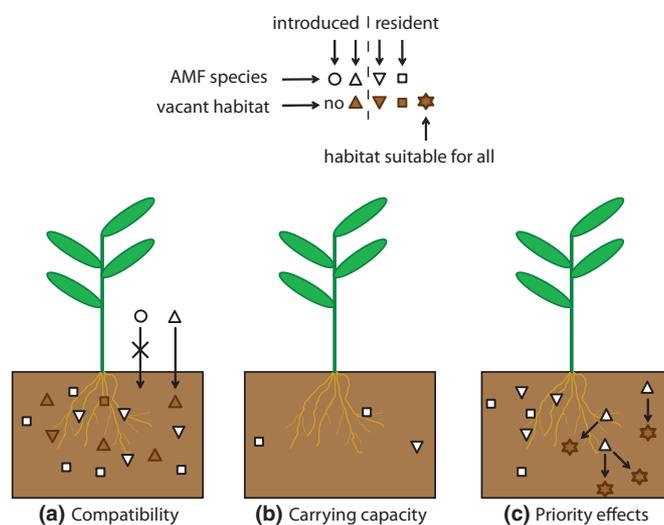

Fig. 2 Conceptual illustration of factors affecting species introduction success. White symbols represent species, and brown symbols represent vacant habitat for that particular species. (a) Compatibility: species must be compatible with the environment, including crop host, soil type, tillage and nutrient levels, as well as with the resident community where competition may be fiercer when it has higher species diversity. (b) Carrying capacity: if the carrying capacity (i.e. the habitat quality) for AMF of the system is low (as represented by a low number of symbols), persistence of low-abundance AMF such as the introduced species may be particularly at risk. (c) Priority effects: if the introduced AMF can reach unoccupied patches sooner than competing species it may benefit from priority effects, which can be through spatial (as presented) as well as temporal processes (not presented).

success. When there is no prior knowledge about what niches remain unoccupied, which will often be the case, one could consider applying a mixture of species which will increase the likelihood that at least one species is able to establish and persist. However, because this will simultaneously decrease the absolute amount of this species in the inoculum, species inclusion should be carefully considered.

In order to influence carrying capacity, crop choice and fertilization may be particularly important. There is a strong connection between soil phosphorus (P) levels and root colonization, where root colonization decreases strongly with increasing P (Fig. 1). Decreasing root colonization corresponds with active down-regulation of mycorrhiza formation by plants, and thus carbon allocation, when plants are less dependent on AMF for P supply (Lekberg & Koide, 2005; Smith & Read, 2008). Moreover, there is high variation among plant species in their reliance on AMF (Smith & Read, 2008). Thus, choosing a highly mycorrhizal-dependent crop and optimizing the nutrient environment are two management factors that are very likely to increase the establishment success of new strains.

To take advantage of priority effects, timing of inoculation may be crucial, although already in most trials the inoculum is added directly to the soil during plant germination (Pellegrino *et al.*, 2011). In some instances, seedlings could be inoculated before planting (Farmer *et al.*, 2007; Mummey *et al.*, 2009), potentially acting as reservoirs to facilitate spread of new material. Likewise, particular strains could be given a head start, by applying inoculum in a very patchy manner in the field instead of distributing it evenly. When distributed in this manner, high-density areas would experience reduced inter-specific competition, potentially increasing chances of establishment.

Tillage is a management practice that could be optimized to increase successful establishment of AMF. Tillage greatly influences spatial aggregation, and thereby competitive interactions. In two recent studies where spatial distribution of two AMF species was varied (more or less mixing of soil), strong differences in respective species proliferation were found (Bever *et al.*, 2009; Verbruggen *et al.*, 2012a). Future studies should test whether there is an 'optimum' spatial structure that increases the establishment success of 'rare' introduced AMF. This could be determined under realistic conditions (i.e. at the field scale with different tillage levels) to assess the optimal level of soil mixing. Given the potential importance of spatial aggregation of both resident and introduced AMF, 'intensive' tillage before inoculation will reduce aggregation of the resident fungi, and strongly affect the success of the introduced new one. Mixing can increase the number of competitors present at any given place, thereby potentially increasing the chances the new fungus will be displaced (*sensu* Verbruggen *et al.*, 2012a). However, if introduced strains are applied patchily after tillage, it is possible that the new fungus will be locally much more abundant than others because the latter are 'diluted' through mixing. This may enhance the competitive edge of the new fungus, through abundance and priority effects. These are only two of many potential outcomes, all of which deserve to be tested in AMF application trials.

Perspectives

Here we have reviewed emerging scientific work on processes that influence the success of introduced AMF strains. Using this information, we have highlighted new approaches that hold potential to enhance chances of successful inoculation and warrant further investigation. Research efforts should also be directed towards negative (side-) effects of introducing AMF: concerns about introducing nonnative microbes have been raised, and caution should be employed with regard to distributing inocula over large geographical areas (Schwartz *et al.*, 2006). Another potential concern is the risk that introduction of AMF will cause 'outbreeding depression' through genetic exchange of resident and introduced strains. Colard *et al.* (2011) found that genetic exchange between AMF can both increase and decrease mutualistic quality. The effects of genetic exchange between native and alien strains on mutualistic quality remain a research priority.

Another important avenue of research is that of indirect effects. Sometimes positive results of inoculation occur that are not related to root colonization by the introduced AMF (Alguacil *et al.*, 2011; Pellegrino *et al.*, 2012). These may be driven by indirect effects on plant–soil interactions. We must have a better understanding of how these indirect and direct effects of 'new' species interact in order to fully profit from inoculation, while minimizing negative side-effects. It is important to consider that effects of AMF on plants range from antagonistic to mutualistic and that several plants, including several agricultural weeds and some crops, can be suppressed by AMF when conditions are unfavorable. Moreover, in order to make commercial application of AMF feasible, a general framework is required which predicts under which conditions inoculation will contribute to enhanced yield and agricultural sustainability in an explicit economical context.

Acknowledgements

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