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SHORT NOTE

Evidence for functional redundancy in arbuscular mycorrhizal fungi and implications for agroecosystem management

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Abstract Arbuscular mycorrhizal (AM) fungi provide benefits to host plants and show functional diversity, with evidence of functional trait conservation at the family level. Diverse communities of AM fungi ought therefore to provide increased benefits to the host, with implications for the management of sustainable agroecosystems. However, this is often not evident in the literature, with diversity saturation at low species number. Growth and nutrient uptake were measured in onions in the glasshouse on AM-free phosphorus (P)-poor soil, inoculated with between one and seven species of AM fungi in all possible combinations. Inoculation with AM fungi increased shoot dry weight as well as P and copper concentrations in shoots but reduced the concentration of potassium and sulphur. There was little evidence of increased benefit from high AM fungal diversity, and increasing diversity beyond three species did not result in significantly higher shoot weight or P or Cu concentrations. Species of Glomeraceae had the greatest impact on growth and nutrient uptake, while species of *Acaulospora* and *Racocetra* did not have a significant impact. Failure to show a benefit from high AM fungal diversity in this and other studies may be the result of experimental conditions, with the benefits of AM fungal diversity only becoming apparent when the host plant is faced with multiple stress factors. Replicating the complex interactions between AM fungi, the host plant and their environment in the laboratory in order to fully understand these interactions is a major challenge to AM research.

Keywords Arbuscular mycorrhiza · Fungal diversity · Phosphorus · Onion

Introduction

Morphological similarity of arbuscular mycorrhizal (AM) fungi within roots was for many decades a significant barrier to understanding their ecology. However, application of molecular techniques has allowed active AM fungi to be identified in plant roots, revolutionising understanding of their ecology (Helgason et al. 1998). AM fungi were once thought to have low diversity, global distribution, little functional diversity and little or no host preference. This paradigm has now been overturned, with strong evidence of functional diversity and host preference as well as classical biogeographical distribution patterns (Munkvold et al. 2004; Maherali and Klironomos 2007; Opik et al. 2009; Van der Gast et al. 2011; Gosling et al. 2013). In addition, renewed effort to identify novel AM fungal species, combined with frequent reassessments of their taxonomy (e.g. Schüßler et al. 2001; Schüßler and Walker 2010; Oehl et al. 2011; Redecker et al. 2013), has revealed greater and more complex diversity. These revelations mean that questions of ecosystem assembly and function, addressed for many decades by ecologists, have become relevant to AM fungi.

One such question central to ecological theory is the role of biodiversity in maintaining ecosystem functions (Hector and Bagchi 2007), which has important implications for conservation and for maintaining ecosystem services. The question is

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particularly pertinent for agroecologists. It is often assumed that long-term sustainability of agroecosystems is reliant on maintaining high diversity across trophic levels, with some evidence for this in the literature (Schlapfer and Schmid 1999). However, agroecosystems have degraded diversity compared with natural ecosystems, with more intensively managed agroecosystems showing the greatest degradation (Hole et al. 2005). This extends to AM fungi, which have reduced diversity in agroecosystems compared with natural ecosystems, with more intensive agricultural systems generally showing the greatest reductions in diversity (Helgason et al. 1998; Oehl et al. 2004; Hijri et al. 2006; Van der Gast et al. 2011; Dai et al. 2014). Whether high AM fungal diversity is required in these systems for sustainability is still open to question (Verbruggen and Kiers 2010). Nevertheless, the suggestion that increasing AM fungal diversity in agroecosystems can boost crop growth, nutrient uptake and ultimately sustainability is widespread (Hart and Forsythe 2012).

The notion that low AM fungal diversity in agroecosystems is a problem has driven the development of commercial products containing AM fungi, intended to boost colonisation of crop plants (Vosatka et al. 2012). However, results of inoculum use in the field have been variable and they have so far failed to have much impact in the agricultural industry (Tarbell and Koske 2007). Fertilisers and plant protection products remain relatively cheap and their use is straightforward, with relatively predictable results compared with the uncertainties of a biological product like AM fungi. Nevertheless, the increasing cost of fertilisers and plant protection products, and stricter environmental regulations controlling their use (Schultea et al. 2010), means that mycorrhizal fungi are likely to play an increasingly important role in crop production. If they are to be used effectively, then a fundamental understanding of their ecology will be required (Rodriguez and Sanders 2015). A central question is whether a diverse community of AM fungi is required to obtain maximal benefit for a crop, or whether in agroecosystems, high populations of one or two well-adapted species is sufficient.

Results of experimental work are contradictory, with some suggesting increased plant productivity with increased AM fungal diversity (e.g. Klironomos 2003) and others indicating that a single AM fungal isolate can be as effective as mixtures (e.g. Lekberg et al. 2007). As understanding of the relationships between AM fungi, their hosts and their environment increases, the complexity of the interactions is becoming apparent (Dickie et al. 2015). Thus far, experiments exploring the role of AM fungal diversity have generally been simple, often involving a single plant species and two or three AM fungal species (e.g. Pellegrino et al. 2011), though there are exceptions (e.g. Klironomos 2003). More complex experiments with a larger number of species may offer greater insights, but they require substantial resources and their results may be more difficult to interpret.

Agroecosystems are generally characterised by low plant diversity and low AM fungal diversity, thus resembling the simplified model systems used in most experiments. This might suggest that agroecosystems should respond in a similar way to many simple experimental systems. Understanding AM function in agroecosystems could be a stepping stone to understanding more complex natural and semi-natural ecosystems, although even the most depleted AM fungal communities in agroecosystems contain multiple species, often from several families (Oehl et al. 2004), while few experimental systems have considered this so far.

The aim of the present work was thus to determine (1) if growth and nutrient content of an AM-dependant crop, onion, are increased by a more diverse AM fungal community and (2) whether some AM fungal species are more effective than others at improving crop growth and nutrient content.

Methods and materials

The impact of AM fungal diversity on crop growth and nutrient uptake was tested in pots in the glasshouse using a low-P soil and a responsive crop, onion (*Allium cepa* L) cv Bedfordshire Champion. As with other alliums, onion is strongly dependent on AM fungi and maintains high levels of root colonisation even in intensive agricultural systems (Galvan et al. 2009). The soil was taken from the top 20 cm in a field at Ryton-on-Dunsmore, Warwickshire, England (latitude 5221′ 58″ N, longitude 1° 24′ 4″ W). It is designated as Arrow series (Soil Survey of England and Wales) and as an inceptisol in the USDA Soil Taxonomy classification system, with a sandy loam texture and a low concentration of extractable P. pH was 6.1 (in water), organic carbon 20.1 g kg^{-1} (acid dichromate wet oxidation), total N 2.1 g kg^{-1} (dry combustion autoanalyser, CB-2000, Leco Corporation, MI, USA), total P 459 mg kg^{-1} (acid digestion aqua rega/HF), extractable P 8.1 mg kg^{-1} (Olsen et al. 1954), extractable Mg 145 mg kg^{-1}, extractable K 156 mg kg^{-1} and extractable S 15.4 μg g^{-1} (ammonium acetate extraction). Soil was sieved through a 6-mm sieve and gamma-irradiated (10 kGy) to kill native AM fungi.

Seven species of AM fungi were sourced from either IBG or INVAM, to represent species found regularly in even the most intensively managed agricultural soils: *Funneliformis caledonium* (BEG20), *Funneliformis mosseae* (BEG12), *Rhizophagus manihotis* (FL879), *Rhizophagus irregularis* (BEG144), and species rarely found in highly intensive systems but common in less intensively managed systems: *Paraglomus occultum* (WV224), *Racocetra fulgida* (VA103B) and *Acaulospora spinosa* (NC501). Inoculum for the experiment was prepared as described in the Supplementary Material.

A preliminary experiment was conducted to determine colonisation potential of the inoculum. This indicated that the final colonisation of onions after 10 weeks was not significantly influenced by the initial amount of inoculum added (1–20 g), but the final level of colonisation differed between species. The main experiment was set up as follows. For each combination of AM fungi, moist soil (900-g fresh weight) at 60 % WHC was placed into polythene bags and mixed by shaking. The design was a fully factorial 2^7 design with a single replicate of all possible combinations of AM fungi in equal proportions on a weight basis. Controls and all seven species combined were replicated for three times. Controls received 20 g of twice-autoclaved AM inoculum (mixed species).

All mixtures plus controls received 10 ml of a soil/water suspension (1.5 kg of moist unsterilised soil mixed with 1.5 l of de-ionised water, left overnight then filtered through a 38-μm sieve). Addition of the filtrate ensured that soil contained a range of native soil microorganisms but excluded AM fungal propagules (Koide and Li 1989). Each soil/inoculum mixture was added to 11-cm pots and covered with sterilised perlite to reduce water loss and algal growth. Three pre-germinated seeds of onion were added to the pots then thinned to two per pot after 1 week. Pots were placed in a glasshouse in a 20/15 °C day/night temperature regime. After 15 weeks, the onions were harvested, roots were removed from the soil by washing, and shoots and roots separated. Approximately 500 mg of fresh roots was retained for quantification of colonisation and the rest dried at 90 °C for 48 h, along with shoot material before weighing. The sub-sample of fresh roots was stained with aniline blue according to Grace and Stribley (1991) and AM fungal colonisation quantified using the gridline intersect method (McGonigle et al. 1990). Shoot material (50 to 300-mg dry weight) was subjected to microwave-assisted nitric acid digestion. Phosphorus, calcium (Ca), magnesium (Mg), sulphur (S), copper (Cu), boron (B), iron (Fe), manganese (Mn) and zinc (Zn) were then quantified by an inductively coupled plasma optical emission spectrometer (ICP-OES; HORIBA Jobin-Yvon, France).

Statistical analyses were carried out in GenStat (GenStat version 13, VSN International 2013). Analyses of variance (ANOVAs) were carried out on shoot and root dry weight, percentage colonisation and nutrient content, with variance-stabilising transformations where necessary. An initial analysis examined only the number of AM fungal species added to each pot, ignoring species identity (for number of replications, see Table S1). In order to examine the effect of individual AM fungal species, the factorial element of the experimental design was used with individual AM fungal species as factors. Sums of squares from the higher order interactions and treatments with replicates (none or all species) were pooled to give a better estimate of the residual mean squared error. Fits for the relationship between species number and dry weight/nutrient content were compared according to McDonald (2009).

Results

Root colonisation

Colonisation varied from 0 to 75 % between plants, with a mean of 20.5 % excluding controls, which were not colonised. All inoculated plants appeared colonised except the *P. occultum* treatment. Colonisation by *Paraglomus* species is difficult to visualise by staining as they stain only weakly. Positive colonisation by *P. occultum* was confirmed by a molecular method (Gosling et al. 2014), though it was not possible to quantify colonisation. Figure 1a shows that there was no significant difference in the average level of root colonisation after inoculation with different numbers of AM fungal species.

Onion dry weight

Addition of AM inoculum significantly increased shoot dry weight compared with controls (Fig. 1b) but had no significant effect on root dry weight (not shown). The effect of AM fungal diversity on shoot dry weight was significant. Although addition of a single AM fungal species had no significant effect on average, application of two or more species did result in a significant increase. Furthermore, application of two or more AM fungi resulted in significantly greater shoot dry weight than application of one species, although further increases in fungal diversity did not result in a further significant increase. Examination of variance ratios (Table S2) indicated that three species were having a significant influence on shoot dry weight: *F. caledonium* and particularly *F. mosseae* and *Rh. irregularis*. Figure 2a shows the influence of these three species on shoot dry weight. Increasing the number of these species included in the inoculum resulted in an increase in shoot dry weight, with species number and shoot dry weight significantly correlated (r 0.51, $P<0.001$). However, there was diversity saturation, even with these species, as fitting a quadratic curve gave a significant improvement of fit compared with a linear curve ($P<0.001$).

Shoot nutrient analysis

The addition of AM fungi had no significant effect on onion shoot concentrations of Ca, Mg, B, Fe, Mn or Zn, but the concentrations of P, K, S and Cu were significantly altered by inoculation. Shoot P concentration was increased by at least 60 % as a result of inoculation, with the concentration being significantly higher at all levels of diversity compared with controls (Fig. 1c). In addition, there was a significant ($P<0.05$), though weak, trend for increasing shoot P concentration with increasing AM fungal diversity. Maximum mean P concentration was achieved with combinations containing six species of AM fungi, where mean P concentration was

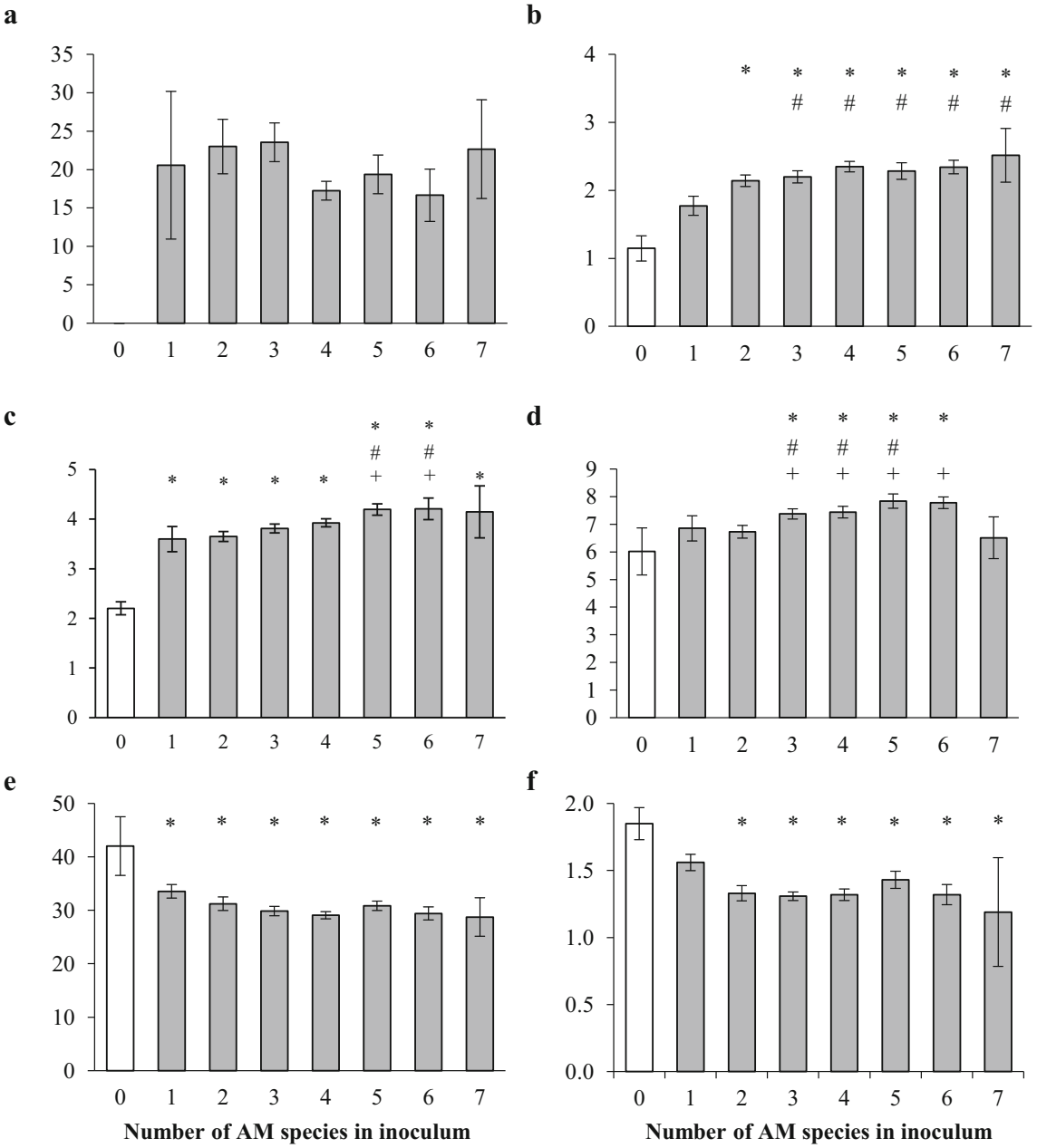

Fig. 1 Response of onion to inoculation with between one and seven AM fungi in all possible combinations, compared with no inoculation: **a** per cent root colonisation, **b** shoot dry weight (g), **c** shoot P concentration (mg g^{-1} dry wt), **d** shoot Cu concentration (μg g^{-1} dry wt) and **e** shoot K concentration (mg g^{-1} dry wt), **f** shoot S concentration (mg g^{-1} dry wt). *Significantly different from no inoculation, #significantly different from inoculation with one fungal species, +significantly different from inoculation with two fungal species

greater than with one or two AM fungal species. However, there was almost no difference between shoot P concentration with five and six species, and seven species gave a slightly lower concentration of P, suggesting diversity saturation. Examination of variance ratios (Table S3) indicated that addition of *A. spinosa*, *P. occultum* and *F. caledonium* had a significant effect on shoot P concentration, although the effect of *P. occultum* was marginal. Figure 2b shows that as the number of these species in the inoculum increased, P concentration in shoots increased (r 0.58, $P<0.001$).

Shoot Cu concentration was increased by as much as 30 % as a result of inoculation with the AM fungi, although the concentration was not significantly greater with only one or two species (Fig. 1d). There was a weak non-significant trend for increasing Cu concentration with increased added AM fungal diversity, with the maximum Cu concentration being achieved with five species. However, the smallest (non-

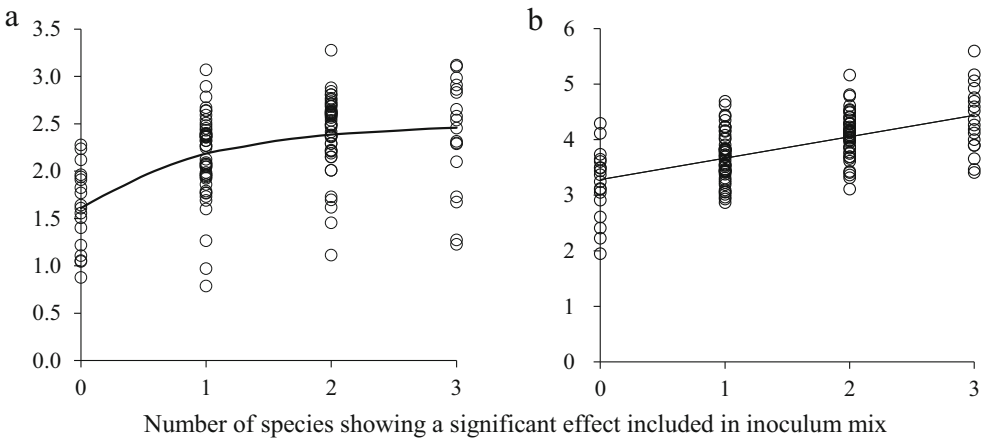

Fig. 2 Relationship between number of AM fungal species showing a significant effect included in inoculum mix and **a** shoot dry weight (g) and **b** shoot P concentration (mg g^{-1} dry wt)

significant) increase in concentration was with seven species. Examination of variance ratios (Table S4) indicated that *F. caledonium* was the only AM fungus associated with higher shoot Cu concentration. The mean concentration in treatments with *F. caledonium* was 7.66 mg kg^{-1} compared with 6.95 mg kg^{-1} in treatments without *F. caledonium*.

In contrast to P and Cu, inoculation with the AM fungi resulted in a significant reduction in shoot K concentration (Fig. 1e). However, there was no significant difference between different numbers of AM fungal species in the inoculum, and only a weak trend was observed for increasing effect with increasing numbers of AM fungi. Examination of variance ratios (Table S5) indicated that *F. mosseae* and *Rh. irregularis* were the two species having the most significant impact on K concentration, with the effect of *F. mosseae* being twice as large as that of *Rh. irregularis*.

Inoculation with the AM fungi resulted in a reduction in shoot concentration of S at all levels of AM fungal diversity, except for inoculation with one species, although the difference between zero and one fungal species was very close to the level of significance (Fig. 1f). Examination of variance ratios (Table S6) indicated that *F. mosseae* and *Rh. irregularis* were the two species having a significant effect on S concentration, with *Rh. irregularis* having the larger effect.

Addition of *Rh. manihotis* or *Ra. fulgida* inoculum had no significant net influence on either growth or nutrient uptake of the onions. The species with the broadest influence was *F. caledonium*, which increased growth as well as uptake of P and Cu. *Rh. irregularis* and *F. mosseae* also had broad effects but included negative impacts on nutrient uptake, while *A. spinosa* and *P. occultum* increased P uptake but had no influence on any other measured parameters (Table S7).

Discussion

The role that species diversity plays in maintaining ecosystem function and ecosystem services is widely debated in the ecological literature (e.g. van Ruijven and Berendse 2005). A paradigm has developed within agroecology that high soil microbial diversity is required for sustainable crop production (Brussaard et al. 2007). This suggestion extends to AM fungi, with functional diversity and host preference suggesting that a diverse AM fungal population will maximise the benefits that the fungi can provide (Munkvold et al. 2004; Maherali and Klironomos 2007; Powell et al. 2009).

Determining the exact role of AM fungal diversity in ecosystem function is difficult. Interactions between host, AM fungi and their environment are complex and context dependant. In manipulated experimental systems such as those used here, competition between AM fungi within the root combined with host/fungi preferences and priority effects—the impact of a species' presence in the root on success of subsequent arrivals—means that the actual realised diversity within the root may not be the same as that added in an inoculum. Ideally, the AM fungal community composition in the roots should be characterised after inoculation to determine actual diversity in planta. Nevertheless, it is possible to gain some understanding of broad principles if not context-specific details, without characterisation.

Intensively managed agroecosystems characteristic of developed countries are greatly simplified when compared with natural and semi-natural ecosystems and may be functionally different, more closely resembling simplified experimental systems. In such simplified systems, the role that AM fungi have in supporting the host may be greatly reduced. This hypothesis is supported by the work on onion here. Levels of root colonisation were not high, but they were in line with results obtained on this soil previously (Gosling et al. 2010), and they significantly increased shoot growth of onion. However, there was no benefit from applying more than three species of AM fungi. Furthermore, the three species which significantly improved growth are closely related (Glomeraceae). Adding further species from different orders (Diversisporales and Paraglomerales) had no significant impact, despite the fact that phylogenetically distant AM fungi appear to show

stronger functional diversity (Powell et al. 2009). Only three fungal species increased P uptake, although two of the species that increased P uptake did not have an impact on growth, suggesting some functional differentiation. Gigasporaceae have been shown to provide functional complementarity to other AM fungal families in P uptake (Verbruggen and Kiers 2010; Tian et al. 2013), but there was no evidence of *Ra. fulgida* showing this effect here. The failure of *Ra. fulgida* and *Rh. manihotis* to have any net effect on onion growth or nutrient uptake may reflect failure to colonise, in addition to functional redundancy. In terms of nutrients other than P, the AM fungal species that initiated a significant response were species that had also increased onion growth, suggesting functional redundancy even within this small group of AM fungi. Indeed, much of the benefit gained from inoculation (increased shoot growth and increased P and Cu uptake) could have been obtained with the single species *F. caledonium*. These results suggest that apparent benefits from increased AM fungal diversity in experimental systems may be attributed to a 'sampling effect'. That is, greater diversity increases the likelihood of an AM fungus with the appropriate functional attributes and host preference being present in the species mix, in this case *F. caledonium*. This corresponds with results from Bennett and Bever (2007), Vogelsang et al. (2006), Jansa et al. (2008) and Hart and Forsythe (2012).

Even in the context of agroecosystems, the low level at which diversity saturation occurs with AM fungi in this and other pieces of work is in apparent contradiction to results obtained for other trophic groups and is counter-intuitive to the presence of functional diversity in AM fungi and the maintenance of diverse AM communities in the field. It is particularly puzzling that members of the Glomeraceae are often dominant in terms of their impact on host growth and nutrient uptake, while significant functional diversity exists across rather than within AM fungal families (Powell et al. 2009). Why do experiments often fail to show benefits to the host plant from increasing AM fungal diversity, when the fungi can confer significant multiple benefits on the host plant? If highly diverse communities of AM fungi offer no additional benefit to the host compared to single species or small number of species, how are diverse AM fungal communities maintained in nature and are they needed in agroecosystems?

A number of possible explanations exist for this apparent contradiction (Afkhami et al. 2014), although some are likely to be ecologically unstable (Lekberg and Koide 2014). The most likely explanation for the results reported here and elsewhere lies in the experimental conditions used. Most experiments that measure the response of the host to AM fungal diversity examine the response of the symbiosis to a single stress factor, such as low soil P (Vogelsang et al. 2006; Jansa et al. 2008; Aurélien et al. 2013) or a soil pathogen (Sikes et al. 2009), while maintaining otherwise benign conditions. In reality, plants in the field are exposed to multiple stress factors simultaneously, with stress factors also changing with season and in response to stochastic events. Under these circumstances, it will be beneficial for plants to host multiple AM fungal species even if some do not provide an immediate benefit, a so-called bet-hedging strategy (Lekberg and Koide 2014). Where the host plant is exposed to a single stress factor (such as in a controlled glasshouse experiment), two or three AM fungal species functionally suited to alleviate that stress can provide maximal benefit to the host; indeed, more closely related fungi may even be more beneficial than more distantly related (Aurélien et al. 2013). Adding other species with functionally different attributes or more species with the same attribute has no benefit. The results presented here support this hypothesis. Under field conditions with multiple stress factors which change over time, a more diverse community will be required to gain the maximal benefit from AM fungi. Similarly, in diverse crop rotations with many different host species or where changes to management aimed at increasing sustainability result in more stress on crop plants and in natural ecosystems, greater AM fungal diversity may be required.

Understanding of the importance of AM diversity at the level of the host and the ecosystem has advanced in recent years, but there is still much to be determined. Replicating representative AM fungal communities and their interactions with the host and their environment in the laboratory has been a neglected area thus far (Johnson 2015) and remains a significant challenge. In particular, if the role of AM fungal diversity at different scales is to be fully understood, future work must seek to characterise the actual community established in the root, as this is likely to differ from the community established in the soil in a context-dependant way.

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