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RESEARCH ARTICLE

Crop-specific and single-species mycorrhizal inoculation is the best approach to improve crop growth in controlled environments

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Abstract Arbuscular mycorrhizal fungi are root symbionts that play a key role in crop growth. A systematic quantitative analysis of the response of crops to arbuscular mycorrhizal inoculation, however, remains to be done. Additionally, little is known regarding the role of mycorrhizal specificity and the diversity of the inoculum on crop growth. Therefore, we collected data from 115 inoculation studies, including 435 experiments. We then used meta-analysis to examine the effect of crop identity, arbuscular mycorrhizal fungus identity, and mycorrhizal diversity on crop biomass increase, following inoculation. Our results show that total crop biomass was on average 34.9 % higher in inoculated versus non-inoculated plants. We found that specific combinations of arbuscular mycorrhizal fungus genera and host plant families were more beneficial for growth promotion as compared to other combinations. Moreover, a single-species inoculum increased crop growth response on average by 41.2 % compared to a multi-species inoculum. Overall, our findings show that a broad range of crops highly benefit from the inoculation with arbuscular mycorrhizal fungi. They also strongly suggest that selecting specific arbuscular mycorrhizal taxa for specific crops is the most promising approach to enhance crop growth. There is no "one-size-fits-all" arbuscular mycorrhizal fungus. Finally, and at least in stable and controlled environments, inoculation with a single arbuscular mycorrhizal species is more effective, compared to inoculation with a mixture of different arbuscular mycorrhizal taxa. This may be explained by fungi superior in extraradical growth, but less beneficial to the host, that outcompete the more mutualistic fungi. Therefore, it may be beneficial to maintain a high dominance of one beneficial arbuscular mycorrhizal taxon in simplified agricultural systems.

Keywords AMF · Biodiversity · Host preference · Host selectivity · Meta-analysis · Specificity

1 Introduction

Arbuscular mycorrhizal fungi (Glomeromycota) are widespread and obligate plant symbionts known to play a key role in the functioning of agricultural ecosystems and crop productivity (Verbruggen et al. 2010). These fungi establish a symbiosis with the majority of the land plants and generally provide mineral nutrients to the host plant in exchange for plant-assimilated carbohydrates (Smith and Read 2008). Furthermore, they form a large network of hyphae and have a great impact on soil formation and soil aggregation (Wilson et al. 2009). Finally, arbuscular mycorrhizal fungi can provide protection of the host plant against fungal and nematode pathogens (Veresoglou and Rillig 2012). Overall, arbuscular mycorrhizal fungi have been shown to increase host plant biomass production (Hoeksema et al. 2010), although a systematic analysis on the response of crop species in particular remains to be done (Fig. 1). However, whereas the symbiosis is often seen as an unambiguous mutualism where especially the host plants often benefit from the association, arbuscular mycorrhizal fungi have also been reported to be of little benefit to the host plant and even to be parasitic by causing a net carbon cost for the host (Johnson et al. 1997; Graham and Eissenstat 1998).

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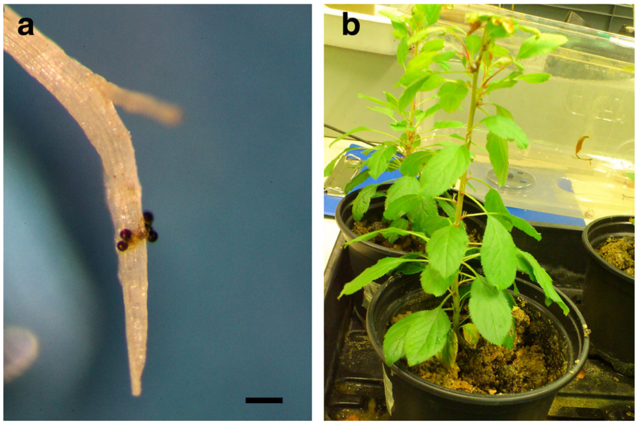

Fig. 1 An example of an inoculation experiment, related to the study of Van Geel et al. (2015), to compare the growth response of mycorrhizal to non-mycorrhizal apple seedlings. In order to establish a single-species culture, arbuscular mycorrhizal fungal spores were first isolated from the field. Next, spores with similar morphology were carefully applied to the root tips of *Plantago lanceolata* (**a**), a good host plant known to form a symbiosis with a broad variety of arbuscular mycorrhizal fungi. After 6 months of growth in the greenhouse, the cultures were used to inoculate apple seedlings (**b**) and to evaluate the growth response to AMF inoculation in comparison to non-mycorrhizal seedlings. *Bar* indicates 200 μm

Based on morphological characteristics of spores, 244 arbuscular mycorrhizal species have been described so far (Schüssler 2014). Direct sequencing of fungal ribosomal RNA genes from the soil on the other hand has revealed the existence of 341 virtual arbuscular mycorrhizal taxa so far (operational taxonomic units (OTUs)) (Öpik et al. 2013). Consequently, the number of known arbuscular mycorrhizal species/virtual taxa is very low, compared to the *c.* 200.000 plant species they associate with (Brundrett 2009), suggesting that arbuscular mycorrhizal specificity to the host plant is very low (Mosse 1975; McGonigle and Fitter 1990). Nevertheless, some studies found evidence that co-existing plant species harbor different arbuscular mycorrhizal communities (Vandenkoornhuyse et al. 2003; Torrecillas et al. 2012). Furthermore, specificity in the arbuscular mycorrhizal symbiosis may also occur at a higher level, such as the ecological group (Öpik et al. 2009) or family (Torrecillas et al. 2012) of the host plant.

In addition to the extent of arbuscular mycorrhizal fungi specificity, little is known regarding the role of arbuscular mycorrhizal diversity on host plant growth. In a more general context, there is now convincing evidence that higher species diversity is generally beneficial for a range of ecosystem functions (Cardinale et al. 2012). For example, a higher plant species or pollinator species richness may result in higher biomass production and crop pollination, respectively, either through the sampling effect or through the complementarity effect. The sampling effect refers to having a greater chance of including a very effective species with respect to the ecosystem functioning, whenever there is a higher species diversity (Turnbull et al. 2013). The complementarity effect refers to resource partitioning through functional complementarity, which leads to a more efficient exploitation of resources in the system (Tilman 1997). Also, arbuscular mycorrhizal taxa are known to be functionally different, for example, regarding the formation of extra-radical hyphae, colonization rates and their phosphorus foraging strategy (Hart and Reader 2002). This may result in a more efficient exploitation of soil resources in case of the presence of different arbuscular mycorrhizal taxa and a direct fitness benefit for the host plant. For example, compared to colonization by a single arbuscular mycorrhizal fungus, colonization by two arbuscular mycorrhizal fungi with different spatial abilities to acquire soil phosphorus induces a larger growth response in the host plant (Smith et al. 2000). Although van der Heijden et al. (1998) already provided insights in the relation between mycorrhizal diversity and ecosystem functioning, their results were based on microcosms and macrocosm mimicking European calcareous grasslands, and are as such difficult to transpose to crops in an agricultural context. Even though there have been many experimental studies testing the growth response of a broad range of crops to single and multiple mycorrhizal inoculations, the results obtained appear to be inconsistent. On the one hand, many studies have shown an increased growth benefit of crops to inoculation with multiple arbuscular mycorrhizal fungi compared to inoculation with a single arbuscular mycorrhizal fungus (e.g., Ortas and Ustuner 2014; Pellegrino and Bedini 2014a). On the other hand, Hart et al. (2013), for example, showed that high fungal diversity in the roots of a plant can facilitate the persistence of low-quality symbionts, resulting in a very limited growth benefit to their host. Consequently, it is still unclear to what extent mycorrhizal diversity can promote growth in the host plant.

Meta-analysis is a statistical technique used to summarize and quantify a selected set of studies (Borenstein et al. 2011). Given the large number of studies, performed with different crops and different arbuscular mycorrhizal fungi, a meta-analysis now allows to integrate their results and provide quantitative answers regarding the outcome of different arbuscular mycorrhizal taxa-host plant combinations and to what extent mycorrhizal diversity can promote crop growth. More specifically, the objectives of this study were to (i) quantify the overall growth response of crop species to arbuscular mycorrhizal inoculation, (ii) assess the importance of arbuscular mycorrhizal specificity on the growth response of crop species, and (iii) evaluate to what extent arbuscular mycorrhizal diversity can promote crop growth.

2 Materials and methods

2.1 Data compilation

Data were compiled based on articles retrieved from a Web of Knowledge search on the 15th of October 2015, using the search string "arbuscular mycorrhiza* AND inoculat*" (resulting in 1701 articles). Articles were then included in the meta-analysis when they included at least one experiment that met the following criteria: (i) a crop was inoculated with one or more arbuscular mycorrhizal taxa and the vegetative or generative response (root, shoot, or fruit biomass) was compared with the non-mycorrhizal crop (control) and (ii) both a measure of variance in plant response and the number of replicates were reported. Furthermore, when multiple phosphorus levels were compared within a study, we only included the "normal" treatment in our meta-analysis, and not the fertilized treatment.

From each experiment that met these criteria, we retrieved data on plant growth (root, shoot, total, and/or fruit biomass), with and without mycorrhizal inoculation. If not reported, standard deviations were calculated from sampling sizes and standard errors. When results were only reported in figures, the raw data were extracted using GetData Graph Digitizer (version 2.26; http://getdata-graph-digitizer.com). From each experiment, also crop species, arbuscular mycorrhizal fungi taxon (species names were annotated according to Schüssler and Walker (2010)) and inoculum type (single-species vs. multi-species inoculum) were recorded.

2.2 Statistical analysis

For each experimental comparison between inoculated and control treatments, an effect size for plant biomass response was calculated. We used total plant biomass when available or calculated it as the sum of root and shoot biomass. In the minority of cases where total plant biomass was not available or could not be calculated, we used shoot biomass as a proxy for total plant biomass. We then used the response ratio $\mathrm{Ln(R)} = \mathrm{Ln}(X_{\mathrm{AMF}}/X_{\mathrm{c}})$ as the effect size, where X_{AMF} and X_{c} are the mean total biomass values for the inoculated and control treatments, respectively (Hedges et al. 1999). A positive value of Ln(R) indicates a positive effect of arbuscular mycorrhizal fungi inoculation on total plant biomass. A value of $\mathrm{Ln(R)} = 0$ indicates that arbuscular mycorrhizal fungi inoculation had no effect. For each experimental comparison, both Ln(R) and the variance of Ln(R) were calculated using MetaWin v2.1 (Rosenberg et al. 2000). Because only a limited number of experimental comparisons between arbuscular mycorrhizal fungi inoculation and control treatments (66 out of 435, 15 %) reported a measure of fruit biomass, no meaningful analysis was possible on the effect of arbuscular mycorrhizal fungi inoculation on fruit biomass.

We then used general linear models (GLMs) in SPSS 20.0 (SPSS Inc., Chicago, IL, USA) to simultaneously estimate the effects of multiple explanatory variables on total plant biomass to arbuscular mycorrhizal fungi inoculation. Two models were ran with Ln(R) as the response variable and the following fixed explanatory variables: arbuscular mycorrhizal fungi genus, crop family, arbuscular mycorrhizal fungi genus × crop family (model 1) and inoculum type (single-species or multi-species inoculum) (model 2). The observations with multiple AMF taxa were omitted in model 1. The Bayesian information criterion (BIC) was used to select the most parsimonious model out of a suite of reduced models compared with the full model (i.e., with the lowest BIC). In all cases, we used the full model which had the lowest BIC. The high number of crop species and arbuscular mycorrhizal taxa in our dataset did not allow to conduct a meaningful analysis at the species level. It is normal conduct in meta-analysis to give higher weight to more accurate effect sizes (Borenstein et al. 2011). Therefore, a weight factor (1/variance of the effect size) was included in all models.

When a study reported more than one experiment, these experiments were included as separate data records. To test whether this approach may have led to an overrepresentation of the effect of studies that included a high number of experiments, we randomly chose one observation from each study and conducted the same analysis (He and Dijkstra 2014). The mean effect sizes that were calculated this way were similar to the effect sizes based on the whole dataset, suggesting that overrepresentation did not occur (He and Dijkstra 2014). Finally, the presence of a publication bias was tested using scatter plots of effect size versus their variance and the sample size of each experiment. No patterns indicative of publication bias could be discovered (data not shown).

3 Results and discussion

In total, 115 publications met our criteria, resulting in 435 experimental comparisons between arbuscular mycorrhizal fungi inoculation and control treatments. Both models showed an overall positive response of total biomass to inoculation with arbuscular mycorrhizal fungi. Our first model estimated the overall response ratio of total biomass at 0.290 (95 % CI 0.133 to 0.448), the second model at 0.307 (95 % CI 0.248 to 0.366). Although our first model found no overall significant main effect of arbuscular mycorrhizal fungi genus, the 95 % confidence intervals of the mean effect sizes for the genera *Glomus* and *Funneliformis* did not include zero, indicating a positive growth response to inoculation with arbuscular mycorrhizal fungi (Fig. 2a). Similarly, although there was no main effect of crop family, the crop families Cucurbitaceae and Poaceae showed the strongest positive response to arbuscular mycorrhizal fungi inoculation and the 95 % confidence intervals of the effect sizes did not include zero (Fig. 2a). Whereas no main effects of arbuscular mycorrhizal fungi genus and crop family on total plant biomass were found, the significant interaction between arbuscular mycorrhizal fungi genus and crop family indicated that the effect of arbuscular mycorrhizal fungi genus is dependent on crop family (Table 1) and that the main effects discussed above have to

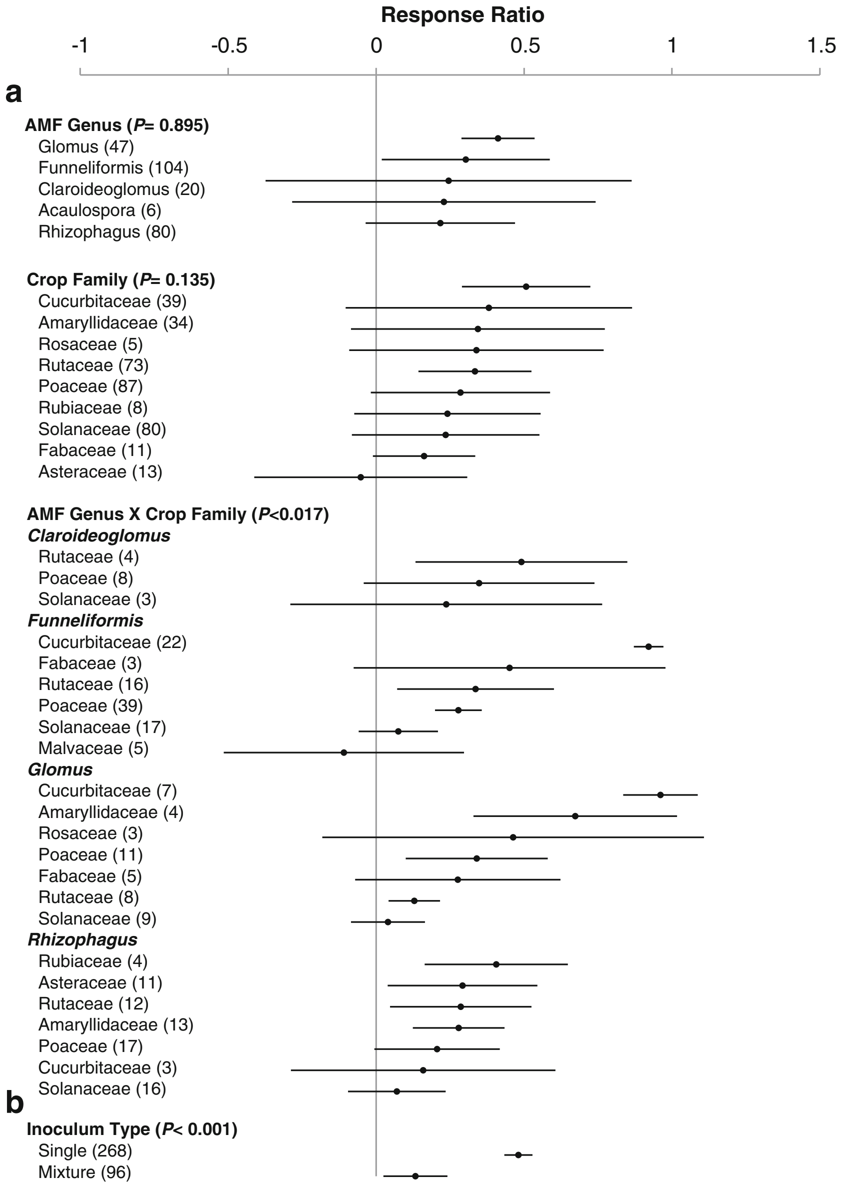

Fig. 2 The estimated marginal means (±95 % confidence intervals) of the general linear model analyses relating the effect size for the total plant biomass to the identity of the inoculated arbuscular mycorrhizal fungi (*AMF*) and the identity of the crop (*a*) and to the inoculum type (*b*). The effect of arbuscular mycorrhizal inoculation was considered statistically significant if the 95 % confidence intervals of the mean effect size did not overlap with zero. A positive response ratio (Ln(R)) indicates a positive effect of arbuscular mycorrhizal inoculation on total plant biomass. *P* values reported are those obtained in both general linear model analyses (Table 1). The number of observations in each group is shown in *parentheses*. Groups with less than three observations are not shown. Arbuscular mycorrhizal fungi is abbreviated as *AMF*

Table 1 Results from the general linear model analysis relating the effect size for total plant biomass to the genus of the inoculated arbuscular mycorrhizal fungi (AMF) and the crop family (model 1, and to the inoculum type (model 2)

Explanatory variables	df	*F*	*P*
Model 1			
Intercept	1	3.815	0.052
AMF genus	9	0.469	0.895
Crop family	13	1.451	0.135
AMF genus × crop family	29	1.690	0.017
Model 2			
Intercept	1	104.265	<0.001
Inoculum type	1	33.545	<0.001

be interpreted in this context. Especially, the symbiosis between arbuscular mycorrhizal fungi from the genera *Funneliformis* or *Glomus* and crops from the Cucurbitaceae and arbuscular mycorrhizal fungi from the genus *Rhizophagus* and crops from the Rubiaceae resulted in a strong plant growth response (Fig. 2a). On the contrary, the symbiosis between arbuscular mycorrhizal fungi from the genera *Funneliformis* or *Glomus* and crop plants from the family Solanaceae did not result in a positive growth response (95 % confidence intervals did overlap with zero). Also, the symbiosis between arbuscular mycorrhizal fungi from the genera *Rhizophagus* and crop plants from the family Cucurbitaceae did not result in a positive growth response.

Whereas arbuscular mycorrhizal fungi were originally considered to be non-specific (Mosse 1975; McGonigle and Fitter 1990), more recent studies demonstrated an affinity of certain arbuscular mycorrhizal taxa for specific plant species or cultivars (e.g., Vestberg 1992; Vandenkoornhuyse et al. 2003; Torrecillas et al. 2012). Our results demonstrate that specific combinations of arbuscular mycorrhizal fungi genera and host plant families are more efficient for growth promotion of crops as compared to others. We showed that arbuscular mycorrhizal specificity may also translate into differing growth responses of crops. Insufficient available data in the literature did not allow us to systematically evaluate specificity at the species level. Nevertheless, when the most frequently occurring arbuscular mycorrhizal species in our dataset was considered, *Funneliformis mosseae* ($n = 104$), still large differences in plant growth were found between crop species ($P < 0.001$). Cucumber, for example, showed a significantly higher growth response compared to cotton, maize, tobacco, or tomato when inoculated with *F. mosseae*, suggesting a trend of arbuscular mycorrhizal specificity at the species level as well.

Our second model resulted in a significant effect of inoculum type on the effect size for total plant biomass (Table 1). Although both inoculum types (single-species vs. multi-species inoculum) resulted in a positive growth response, the single-species inoculum had a mean growth response of 0.481 (95 % CI 0.433 to 0.528), compared to only 0.133 (95 % CI 0.025 to 0.241) for the multi-species inoculum (Fig. 2b). These results were somewhat counter-intuitive as it was expected that sampling and complementarity effects would result in higher plant growth following inoculation with multiple arbuscular mycorrhizal taxa. On the contrary, our analysis indicates that crop plants that could have been colonized by multiple arbuscular mycorrhizal taxa perform less, compared to crop plants colonized by a single arbuscular mycorrhizal taxon. These findings resemble those of Veresoglou and Rillig (2012) who found that a host plant colonized by multiple arbuscular mycorrhizal taxa suppresses fungal pathogens less efficiently than when colonized by a single arbuscular mycorrhizal species.

van der Heijden et al. (1998) found that increasing the arbuscular mycorrhizal diversity in artificial mesocosms led to increased plant productivity. The proposed mechanism for this effect, however, was based on variable plant growth responses of different arbuscular mycorrhiza-host plant combinations. In our model 1, we also demonstrated variable growth responses of different arbuscular mycorrhiza-host plant combinations, and therefore, our results, based on growth responses of individual crops, are consistent with van der Heijden et al. (1998). Additionally, the lower effect on the growth response of crops of the multi-species compared to the single-species inocula can be explained by the nature of the studies included in our meta-analysis, which were mainly short-term inoculation studies performed in controlled artificial environments. Indeed, a higher magnitude and stability of ecosystem functions associated with diversity are likely most evident under changing and/or heterogeneous conditions that crops experience in the field. In plant communities, the stabilizing effect of diversity on ecosystem properties can be explained by temporal complementarity between species (Loreau and de Mazancourt 2013). In stable controlled experiments, however, temporal complementarity can hardly play any role.

In these stable controlled environments, the lower effect of arbuscular mycorrhizal diversity on individual host plants may be explained by competition among arbuscular mycorrhizal taxa, with arbuscular mycorrhizal fungi superior in extraradical growth, but less beneficial to the host plant, outcompeting more mutualistic arbuscular mycorrhizal fungi (Werner and Kiers 2015a). Hart et al. (2013), moreover, have shown that diverse arbuscular mycorrhizal communities on *Plantago lanceolata* can support the persistence of a less-beneficial symbiont. Complementary, also priority, effects, i.e., the impact of species arrival on subsequent community development, may negatively affect host plant growth following inoculation with different arbuscular mycorrhizal taxa. Werner and Kiers (2015) argued against space limitation as the mechanism allowing priority effects to emerge in the arbuscular mycorrhizal fungal system. Instead, their data supported an active downregulation of specific mycorrhizal partners by the host. Such systemic suppression of arbuscular mycorrhizal fungi by the host has also been observed in split-root experiments in which an established arbuscular mycorrhizal symbiosis suppressed subsequent colonization by different arbuscular mycorrhizal species in the second side of the split-root system (Vierheilig et al. 2000). Although arbuscular mycorrhizal species were inoculated simultaneously in all studies in our dataset, certain taxa may be more efficient colonizers and may consequently inhibit colonization by arbuscular mycorrhizal fungi that are more beneficial to the host plant.

As said, our meta-analysis is based on results from short-term inoculation studies performed in controlled artificial environments. Plants are grown separately in a soil that has been kept moist, autoclaved, mixed with sand, and placed in plastic pots. The soil is inoculated with a single arbuscular mycorrhizal fungus that may not naturally interact with the host. Also, the host is not exposed to naturally occurring arbuscular mycorrhiza, pathogens, or plants. Therefore, caution is required before extrapolating our results to natural settings with complex community interactions and changing environmental conditions (Lekberg and Koide 2014).

We used a multi-factor model with two categorical predictors to assess the role of different arbuscular mycorrhizal taxa and crop families on the response of crops to mycorrhizal inoculation. Because data availability was dependent on what was found in the literature, some combinations of levels of predictor variable occurred more than others, generating incomplete orthogonality between the explanatory variables of our model 1. In such an unbalanced design, the fitted parameter values may be different from the observed parameter values. Although some small differences between fitted and observed parameter values occurred in our dataset, the data from the observed parameter values generally supported the same conclusions.

4 Conclusion

Our findings may have important implications regarding applications of arbuscular mycorrhizal fungi in agriculture. They could serve as a general guideline towards selecting arbuscular mycorrhizal strains to be used as inocula in agriculture and potentially guide agricultural management practices. On the one hand, they confirm that a broad range of crop plants can benefit from the inoculation with arbuscular mycorrhizal fungi and that there is a high potential for additional growth. On the other hand, our results suggest that specific arbuscular mycorrhizal taxa-host plant combinations enhance the growth of a crop and that, at least in stable and controlled environments, inoculation with a single arbuscular mycorrhizal species may be more beneficial to crop species, compared to inoculation with a mixture of different arbuscular mycorrhizal taxa. In other words, our results indicate that there is no “one-size-fits-all” arbuscular mycorrhizal fungus, and suggest that there may be potential benefits in maintaining high dominance of one very beneficial arbuscular mycorrhizal taxon. Yet, caution is required when extrapolating our results to natural field conditions with more complex community interactions and variable environmental conditions. Further research should focus on finding the particular arbuscular mycorrhizal taxon-host plant combination that will maximize growth response, both ex situ and under field conditions. Finally, we encourage researchers conducting arbuscular mycorrhizal inoculation experiments to report also on the marketable part of the plant and not only on the root and shoot biomass.

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