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REGULAR ARTICLE

Multiple factors influence the role of arbuscular mycorrhizal fungi in soil aggregation—a meta-analysis

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Abstract
Background and aims Soil aggregation is a crucial aspect of ecosystem functioning in terrestrial ecosystems. Arbuscular mycorrhizal fungi (AMF) play a key role in soil aggregate formation and stabilization. Here we quantitatively analyzed the importance of experimental settings as well as biotic and abiotic factors for the effectiveness of AMF to stabilize soil macroaggregates.
Methods We gathered 35 studies on AMF and soil aggregation and tested 13 predictor variables for their relevance with a boosted regression tree analysis and performed a meta-analysis, fitting individual random effects models for each variable.
Results and conclusions The overall mean effect of inoculation with AMF on soil aggregation was positive and predictor variable means were all in the range of beneficial effects. Pot studies and studies with sterilized sandy soil, near neutral soil pH, a pot size smaller than 2.5 kg and a duration between 2.2 and 5 months were more likely to result in stronger effects of AMF on soil aggregation than experiments in the field, with non-sterilized or fine textured soil or an acidic pH. This is the first study to quantitatively show that the effect of AMF inoculation on soil aggregation is positive and context dependent. Our findings can help to improve the use of this important ecosystem process, e.g. for inoculum application in restoration sites.

Keywords Arbuscular mycorrhizal fungi · Water stable soil aggregates · Meta-analysis · Boosted regression tree analysis

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Introduction

Arbuscular mycorrhizal fungi (AMF) are widespread and multifunctional members of the soil biota. In addition to their generally acknowledged functions of nutrient transfer and amelioration of abiotic and biotic stresses of their plant hosts (Auge 2001; Sikes et al. 2010; Veresoglou and Rillig 2011), AMF play a key role in soil aggregate formation and stabilization (Rillig and Mummey 2006; Tisdall and Oades 1982). Soil aggregates are defined as particles that adhere to each other more strongly than to surrounding particles (Kemper and Rosenau 1986). They are a main component of soil structure, which is a term used to describe the size, shape and arrangement of solids and pores,

hence affecting pore continuity, water holding capacity and infiltration (Bronick and Lal 2005). AMF hyphae entangle soil particles and thus mainly stabilize macroaggregates (>250 μm) (Tisdall and Oades 1982), whereas bacteria, polysaccharides and organo-mineral complexes mainly stabilize microaggregates (<250 μm) (Tisdall 1994). Because soil structure influences physical, biological and chemical parameters of the soil (reviewed in Diaz-Zorita et al. 2002; Six et al. 2004), it is a crucial aspect of sustainability in agriculture and ecosystem functioning. In nonagricultural ecosystems a favorable soil structure can contribute to the restoration of disturbed lands, erosion prevention and soil carbon storage (Rillig and Mummey 2006).

The functioning of AMF can differ based on a number of biotic and abiotic factors (Johnson et al. 1997; Klironomos 2003; Smith and Read 2008). The context-dependency in the effects of AMF on host growth was recently revealed by a meta-analytical approach (Hoeksema et al. 2010). However, no such analysis exists for the AMF function of soil aggregation. We thus examined here a number of biotic and abiotic parameters with likely effects on mediating the influence of AMF on soil aggregation.

It is commonly assumed that AMF have a positive effect on soil aggregation (Amézketa 1999; Lynch and Bragg 1985; Rillig and Mummey 2006; Six et al. 2004; Tisdall and Oades 1982). We first tested the potential overall effect of AMF on aggregation and then we addressed more detailed hypotheses, which we develop in the following sections.

It has been shown that AMF species differ in their root colonization rate and, depending on the AMF family, colonization may take up to 8 weeks (Hart and Reader 2002). We expect that the development of the extraradical mycelium (ERM) takes at least the same time as the colonization of the root does and that only after the ERM has been developed AMF may affect soil aggregation. Depending on the pot size and experiment duration the roots can grow to such an extent that they are pot-bound or the roots become very crowded in the soil (Poorter et al. 2012). If roots are crowded, effects of AMF on soil aggregation might be covered by the roots. An overall optimal time span for experiments does not exist because potential soil aggregation depends on the development of extraradical mycelium, and thus on the AMF species used; and it depends on root growth and therefore on the plant host used and the space available for root growth (see below) (Piotrowski et al. 2004). We therefore tested the following hypothesis: i) Experiments with intermediate duration will have more pronounced effects of AMF on soil aggregation than experiments with short or long durations.

In addition to the experimental duration, the biotic and abiotic experimental settings can have an important effect on the functional performance of AMF. Several studies demonstrated lower spore and extraradical mycelium development in lower pH, with varying response among isolates (Helgason and Fitter 2009). Varying soil pH can change species richness and community composition (Clark 1997; Toljander et al. 2008). However, in many studies the interpretation of pH effects on AMF functioning is difficult due to confounding factors. AMF functions and abundance (soil hyphal length, percent root colonization) are more pronounced in soils with low nutrient availability, especially under P limiting conditions, (Johnson et al. 2003; Parniske 2008; Pietikäinen et al. 2009). Because nutrient availability in sandy soils is typically low, AMF hyphae will have more pronounced effects on soil aggregation in coarsely textured soils (Six et al. 2004). This effect, however, can be mitigated by the presence of organic matter (OM) or clay. Both OM and clay can be major components of soil aggregation either as direct binding agent or as components of an abiotic process where aggregates are formed through shrink and swell cycles, respectively (Oades 1993; Tisdall and Oades 1982). We therefore tested the following hypothesis: ii) The influence of AMF on soil aggregation should be stronger for nutrient poor soils that have low intrinsic aggregation capacity, e.g. low clay content or low content of OM, and favorable conditions for AMF growth such as optimal soil pH.

In pot experiments most confounding factors are excluded but there are edge effects of the pots that include exposure to higher temperatures and impedance. These edge effects can represent unfavorable environmental conditions that could negatively impact the growth of the plant and alter the behavior of microorganisms (Poorter et al. 2012). Field experiments typically are not subject to edge effects (no container boundaries) but there are many confounding factors such as changing precipitation, irradiation, temperature and small scale soil properties (Six et al. 2004). Sterilizing the soil eliminates living organisms in the soil and thus enables the researcher to create the treatments with only the desired organisms present in the

soil. This can be particularly important in experiments with AMF to establish an AMF free control (Endlweber and Scheu 2006). In the field, mycorrhizal treatments are established by either increasing AMF abundance through AMF inoculation procedures in the AMF treatments or through controlling AMF abundance in the non-mycorrhizal treatment through, e.g. fungicides (e.g. Alguacil et al. 2008; Wilson et al. 2009). In these field experiments the controls are not completely AMF-free, which represents a confounding factor for the analysis of the treatment differences. We therefore formulated the following hypothesis: iii) In laboratory pot experiments aggregation will be higher than in field experiments because controlled experiments exclude most confounding factors and thus effects of AMF on soil aggregation are easier to detect.

In small pots nutrient availability may be limited and therefore plant growth can be smaller, but root density might be higher due to scavenging (Herold and McNeil 1979; Poorter et al. 2012), Mycorrhizal colonization decreases with increasing root length in the pot (Baath and Hayman 1984) and hence the AMF effect on plant growth decreases when pot size decreases or root density increases (Koide 1991; Kucey and Janzen 1987). The reduced effect of AMF on plant growth at small rooting volumes (pot sizes) might also extend to the effect on soil aggregation. Furthermore, comparatively low root densities in large pots or in the field might again return small effects of AMF on soil aggregation as hyphal density declines with increasing distance from the roots (Jakobsen et al. 1992). We formulated the following hypothesis: iv) AMF effects on soil aggregation in pots will depend on the space available for root growth. AMF effects on soil aggregation might be absent or difficult to detect in small pots which result in high root densities as well as in large pots where root and hyphal density can be comparatively low.

The degree to which single AMF species contribute to the various functions can vary but increased AMF species richness generally has positive effects on the promotion of plant productivity, probably mediated by increases in hyphal length and P transfer (Jansa et al. 2008; Klironomos 2003; van der Heijden et al. 1998). Whether functional complementarity among AMF species also induces synergistic effects on soil aggregation has not been broadly studied (Rillig and Mummey 2006). A number of studies on soil aggregation addressed the influence of single fungal species and the role of fungal diversity (Enkhtuya and Vosatka 2005; Klironomos et al. 2005). Schreiner and Bethlenfalvay (1997) found that a mix of three species was more beneficial to plant growth promotion and soil aggregation than the single species alone. We therefore tested the following hypothesis: v) Some single AMF species will have more pronounced effects on soil aggregation than others and higher levels of AMF richness will have more beneficial effects than single species.

Moreover, the identity of the fungal species, the community composition, as well as the combination of fungal species and host plant, appear to be important for the extent to which soil aggregation is promoted (e.g. Piotrowski et al. 2004; Schreiner et al. 1997). Plant roots themselves are important for soil aggregation. Roots create biopores, exude soil binding compounds and fine roots enmesh soil particles and thereby stabilize soil aggregates (Milleret et al. 2009; Oades 1993). Aggregation tends to increase with increasing root length density and aggregation is higher in rhizosphere soil than in non-rhizosphere soil. Plant species can differ in their effects on soil aggregation as root properties such as root architecture or number of fine roots can differ substantially between different plant groups like grasses and shrubs or trees for example (Oades 1993). The colonization of a host plant by AMF can change root properties such as the root physical force, rhizodeposition, root entanglement of soil particles and also the soil water regime; parameters that are all related to soil aggregation (Rillig and Mummey 2006). Leguminous host plants, for example, tend to have higher microbial biomass and water stable aggregates compared to non-legumes where aggregation is instead related to root mass (Bronick and Lal 2005). Woody species have less fine roots and a slower root growth than grasses or herbaceous species, thus providing less opportunity for infection with AMF. This could slow the progress of colonization (Smith and Read 2008) and potentially also the development of extraradical hyphae, which would be important for soil aggregation. We formulated the following hypothesis: vi) The host plant identity will be important for the effect of AMF on soil aggregation as it can affect AMF hyphal growth and functioning via various mechanisms. The association of AMF with trees will produce smaller effects than the association with herbaceous or leguminous plants.

Soil aggregate stability can be assessed by several methods: dry sieving, wet sieving and rainfall simulation

(Diaz-Zorita et al. 2002; Lax et al. 1994). If a rewetting step is included in the method, this step can be slow (by vapor or capillary rewetting) or fast (by slaking), in which fast rewetting represents the maximum level of disruption (Diaz-Zorita et al. 2002). The macroaggregate size classes considered in the literature vary substantially from 0.25 mm up to 10 mm (Bearden and Petersen 2000; Garcia-Cruz et al. 2007) and the chosen fraction can be small, e.g. 0.25–0.5 mm or encompass a larger range from 0.25 to 4 mm (Enkhtuya et al. 2003; Kohler et al. 2009a). However, beneficial effects of AMF on soil aggregation have been found in numerous studies across a broad range of laboratory procedures (e.g. Alguacil et al. 2004; Auge et al. 2001; Bethlenfalvay and Barea 1994; Siddiky et al. 2012). We formulated the following hypothesis: vii) The detection of a potential effect of AMF on soil aggregation will not be influenced by the chosen laboratory procedures such as the method of aggregation assessment, including rewetting of samples, and the chosen aggregate size fraction.

The effectiveness of AMF at aggregating soil can therefore depend on a range of factors, whose individual effects cannot always be disentangled. To date there are several narrative reviews addressing AMF and soil aggregation (e.g. Oades 1993; Rillig and Mummey 2006; Six et al. 2004; Tisdall 1994). Here we aim to quantitatively synthesize the importance of experimental settings and multiple biotic and abiotic factors for the effect of inoculation with AMF on soil macroaggregates.

Methods

Data acquisition

We conducted a literature search with the Web of Knowledge platform on the 29th of November 2012 with the search terms 'soil AND (aggregat* or structur*) AND (mycorrhiz* OR Glom* OR Giga*)'. We additionally traced back citations from review papers on soil aggregation (see Introduction) and altogether retrieved 1,935 papers. We found articles from the years 1986 to 2012. Articles were screened according to the following inclusion criteria:

i) Studies needed to have a treatment with one or more AMF species present. These could be pot or field studies with single species or a mix of species applied (as spores, mixed inoculum with spores, roots and hyphae or whole soil inoculum) or field experiments where AMF host plants were used.
ii) Studies needed to have a non-inoculated control. For inclusion of a study the AMF percent root colonization or hyphal length (m per g soil) in the treatment group needed to be at least twice as high as in the non-inoculated control. Studies that applied fungicides were eligible as control if they met this criterion.
iii) The AMF treatment and the control had to be directly comparable in that either root growth had been inhibited in the assayed compartment or not in both treatments. Studies with a plant present in the AMF treatment but not in the control (e.g. fallow fields) were excluded.
iv) Studies needed to report their response variable referring to aggregate stability as percent water stable aggregates (WSA), mean weight diameter (MWD) or geometric mean diameter (GMD) in the size class of macroaggregates (>250 μm). Studies on microaggregates were excluded.

Studies on soil aggregation and sole inoculation with AMF are comparatively rare; this is why our dataset only included 35 studies. With the abovementioned search terms we found many studies that did not explicitly use AMF (but used the whole soil microbial community or other single non-AMF microorganisms e.g. ectomycorrhizae) in the treatment and were therefore excluded. From the studies that did report values for aggregate stability many did not have a non-mycorrhizal control and were therefore excluded as well. For the majority of the included studies more than one trial could be extracted if, for example, results of parallel experiments were presented in one paper. Multiple trials within each publication were treated as independent when they were drawn from systems differing in at least one of the moderators chosen (see below). Responses from multiple trials sharing a common control were not independent and thus merged to one adjusted value for the response and the variance respectively (Lajeunesse 2011). The dataset of 35 studies yielded a total of 175 trials.

The effect size calculated for all statistical analyses was the log response ratio of the soil aggregate stability in experimental vs. control group. It was calculated as: $\ln(R) = \ln(X_i/X_n)$, where X_i is the soil aggregation in the inoculated AMF treatment group and X_n is the soil

aggregation in the non-inoculated control group. This effect size is positive for a beneficial effect of inoculation with AMF and negative for a detrimental effect on soil aggregation. It was chosen because it is an effect size that requires only mean values, but can be expanded to include additional statistics depending on their availability (Hedges et al. 1999; Lajeunesse and Forbes 2003).

Variance was calculated as in Hedges et al. (1999, eqn (1)). Where not given, the variance was back-calculated from ANOVA results. The median of the given calculated variances (variance of ln(R)) was determined and used as surrogate for those studies with missing data on variance and where a back-calculation was not possible (Corrêa et al. 2012). The inverse of the variance was used for weighting of the studies.

In addition to soil aggregation responses we collected information on 13 factors that could potentially affect soil aggregation. These were used either as continuous or categorical explanatory variables. To maximize the statistical power of our tests we reduced the number of levels of the categorical moderators to a minimum. This was done through either merging information on related categories or, alternatively, excluding poorly represented trials (see below).

The moderators used as covariates were:

Setting: The location of the experiment had two levels: 'field' and 'pot'.

Duration of the experiment: The duration of the experiment was included as a continuous variable. The mean experimental duration of studies with only a single harvest was 6 months. If there was more than one harvest, the sampling closer to 6 months was chosen in order to keep the span of duration of experiments as narrow as possible. For an improved data distribution the duration was ln transformed.

Pot size: The pot size was included as a continuous variable using the soil weight (kg) added to the pots as the parameter. Alternatively we used pot size in liters and converted the value to a weight using the bulk density of the soil. For this moderator analysis all field studies were excluded.

Sterility: The variable had two levels: 'yes' and 'no' and reported whether or not the soil of pot studies was sterilized prior to the experiment.

AMF richness: The number of AMF species present in the experiment. Due to the poor representation, information on experiments with more than one fungus was merged into a single category. The variable thus had two levels: 'one' and 'more'.

AMF species: A single AMF species used for inoculation in the experiment. There were two levels: *Gl. intraradices* and *Gl. mosseae*. All other species were excluded from the analysis because they were only poorly represented.

Plant: The variable had three groups: 'legume', 'herbaceous' and 'tree'. Other plant groups were poorly represented. The poorly represented groups and hyphal compartments were excluded from this analysis.

Soil content of organic carbon: This continuous variable described the content of soil organic carbon in the experimental soil in percent.

Sand content: Values for sand content in the experimental soil were either directly reported or deduced from the information given on texture using the 'texture triangle' according to the classification of the United States Department of Agriculture (Juma 1999). The continuous data were converted to categories with three approximately equally sized classes (in terms of number of trials): 'low', 'medium' or 'high' sand content. These classes correspond to proportions of sand of 7–40 %, 41 % (all soil textures designated as just "loam" in the specific experiment) and 42–82 %, respectively.

Soil pH: Because we expected highest responses for intermediate pH values we converted the continuous data of soil pH to a categorical variable. The data were grouped based on their ranking into three classes with equal sample size: 'low', 'medium' and 'high', corresponding to pH values of 5.05–6.7, 6.8–8 and 8.1–8.9, respectively.

Method of soil aggregation assessment: The variable had two levels: 'wet sieving' (as described by Kemper and Rosenau (1986)) and 'artificial rainfall' (as in Lax et al. (1994)).

Rewetting: This categorical variable described the rewetting step during the measurement of soil aggregate stability. It had two levels: 'fast' (slaking) or 'slow' (capillary rewetting or vapor rewetting).

Aggregate size fraction: There was a large heterogeneity of macroaggregate size classes in the studies. In order to detect differences between size classes we summarized them in the order of size:

'small' (0.25–1 mm), 'medium' (1–2 mm) and 'large' (>2 mm). Aggregate size classes that did not fit in these categories were excluded from this analysis, e.g. size classes encompassing 0.25–4 mm.

Data exploration: boosted regression trees

Boosted regression tree analysis (BRT) is a relatively new technique of machine learning that combines regression trees with boosting, a method for improving model accuracy by additively fitting and combining many simple models (trees) in a forward step-wise procedure (De'ath 2007). For a detailed description of the application of this method in ecological contexts see Elith et al. (2008). The BRT was performed with the packages 'dismo' and 'gbm' (Hijmans et al. 2013; Ridgeway 2012) in the R software (R Development Core Team 2012). We used this method as an exploratory tool that allowed us to make statistical inferences while relaxing the assumptions of meta-analysis, including the simultaneous assessment of more than one predictor variable and their interactions as well as the fitting of complex nonlinear relationships. This step may reveal whether single moderator models could sufficiently explain variability in the dataset. In order to identify the optimal settings for the model we performed a 10× cross-validation for every setting of the 'gbm.step' function using suggestions by Elith et al. (2008). The error distribution was set to "Gaussian" (Ridgeway 2012). The setting with the highest predictive performance was selected. The criterion we used to assess performance of the settings was their ability to minimize residual deviance (Elith et al. 2008); among all settings increasing the proportion of data that was selected at random had the largest influence on model performance. The deviance of the initial model was lowest with the following settings: number of interactions (*tree complexity*)=*6*, contribution of each tree to the model (*learning rate*)=0.01 and random proportion of data (*bag fraction*)=0.75. The average number of trees was 1,150. This model was simplified using the 'gbm.simplify' function suggested by Elith et al. (2008). Non-informative variables were dropped one at a time in a backward selection starting with the least important using a 10× cross-validation. This process was repeated until the model deviance could not be reduced further.

Meta-analysis

The meta-analysis was performed through fitting random-effects models separately for each moderator using the statistical software MetaWin v. 2.1 (Borenstein et al. 2009; Rosenberg et al. 2000). Significance of comparisons was based on a permutation procedure (3,999 iterations) and means and confidence intervals (CI) were calculated based on a bootstrapping procedure (Adams et al. 1997). To correct for errors due to small sample size (classes with a small number of studies) we used the bias-corrected bootstrap CI, which corrects for distributions where more than half of the bootstrap replicates are above or below the observed mean. Categorical moderator levels were considered statistically different if the significance level of the random probability value of the Q statistics was <0.05. For continuous data the significance was tested using the significance level of the probability value for the slope of the regression. For significant moderators we checked the proportional influence of single studies with a sensitivity analysis to identify studies that had a disproportionally high impact on the effect size (Copas and Shi 2000) (see Supplementary material). To better visualize the relationship between the moderator 'duration of the experiment' and the effect size we additionally implemented a loess regression on unweighted data (Zuur et al. 2009). This specific model was fitted in the statistical software R (R Development Core Team 2012) with the 'gam' package (Hastie 2011).

Results

Data exploration: boosted regression trees analysis

The simplified model included the four most influential moderators and ranked them according to their relative contribution to the explanation of variation in the effect size (Fig. 1). The experiment duration (*N*=172) had the largest influence on the effect size, explaining 31.6 % of variation in the data. The effect size started to increase at 2.2 months, had a peak at approximately 4 months and strongly declined after 5 months (back calculated from ln transformed values). The moderator 'soil pH' explained 27.6 % of variation in the data. 'Medium' pH values (range 6.8 to 8, *N*=51) clearly induced the highest responses compared to both lower (*N*=55) and higher (*N*=54) values. The

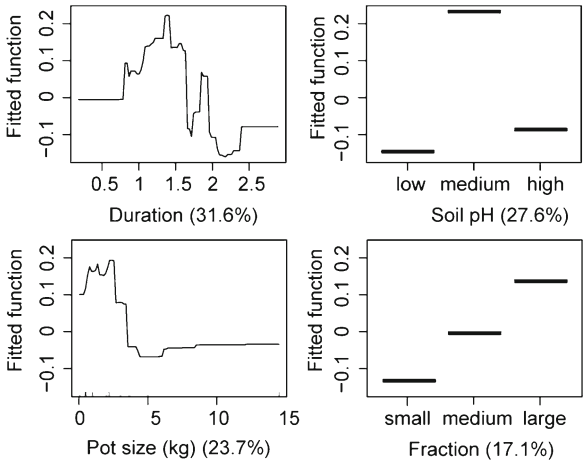

Fig. 1 Partial dependence plots for the four most influential variables in the model for the effect size. *Y-axes* represent the fitted functions that are centered around the mean. For explanation of categorical variables and their units see Methods section. The *X-axis* for the experiment duration is on a ln transformed scale. *Numbers in parentheses* refer to the percent of variation in effect size explained by this variable

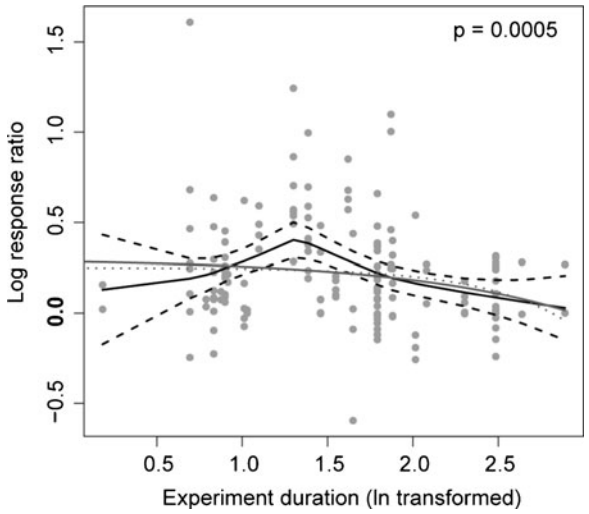

Fig. 2 Scatterplot for data points of ln transformed 'duration of experiment' ((*N*=172), original unit: months) and the effect size (log response ratio). *Dotted and solid grey lines* represent linear fits of first and second order, respectively. The *solid black line* represents the smoothed line of the loess regression with ± standard errors as *dashed black lines*. The reported *p*-value was obtained from the loess regression

moderator 'pot size' (*N*=136) explained 23.7 % of variation. Smaller pot sizes gave higher effect sizes than large pot sizes with a peak between 0.6 and 2.5 kg. The moderator 'fraction' explained 17.1 % of variation in the data. There seemed to be a decreasing trend from larger aggregate sizes (*N*=32), inducing higher responses, to smaller aggregate sizes inducing lower responses (medium: *N*=26, small: *N*=32).

Meta-analysis

There was a positive overall effect of inoculation with AMF on soil aggregation (ln(R) = mean effect 0.2028 (bias-corrected CI: 0.1645 to 0.2425) for *N*=175).

For the continuous moderator 'duration of the experiment' a significant negative relationship was detected (*p*-value of 0.0094 for the slope of the linear regression, *N*=172). To better visualize the relationship between the effect size and this moderator we present the scatterplot for the unweighted average model with first and second order fits, which did not appropriately represent the data distribution, and additionally the result of the loess regression, which clearly showed a better fit to the data (Fig. 2). The smoothing function of the loess regression (span width 0.65) produced a graph with a non-monotonic function that showed a clear increase in the effect size until a peak at 3.7 months in duration (back calculated from ln transformed values) was reached. Afterwards the smoothing line decreased. There was a negative linear relationship between the effect size and the pot size (Fig. 3).

Significant categorical moderators were 'soil pH', 'sand content', 'setting' and 'sterility' (Fig. 4). As in the exploratory BRT model, the bootstrapping procedure produced the highest effects for 'medium' soil pH values compared to 'low' and 'high' values. The analysis of the texture classes showed that inoculation with AMF had the highest effects on soil aggregation in soils with a high sand content (42–82 %) (*N*=58), compared to soils with 'low' (*N*=29) or 'medium' (*N*=54) sand content. Laboratory studies using pots (*N*=151) had higher effect sizes than field studies *N*= 24). The field studies were the only class having a CI that overlaps zero. Sterilization of the soil prior to an experiment (*N*=89) resulted in higher effect sizes compared to non-sterilized soils (*N*=71).

The permutation test showed no significance for the moderators 'AMF richness', 'AMF species', 'aggregate size fraction', 'soil organic carbon', 'method of aggregation assessment', 'rewetting' and 'plant' (see Table 1). In order to compare only woody plants (trees) and non-woody plants (legumes and herbaceous plants) we merged the two levels legume and herbaceous of the

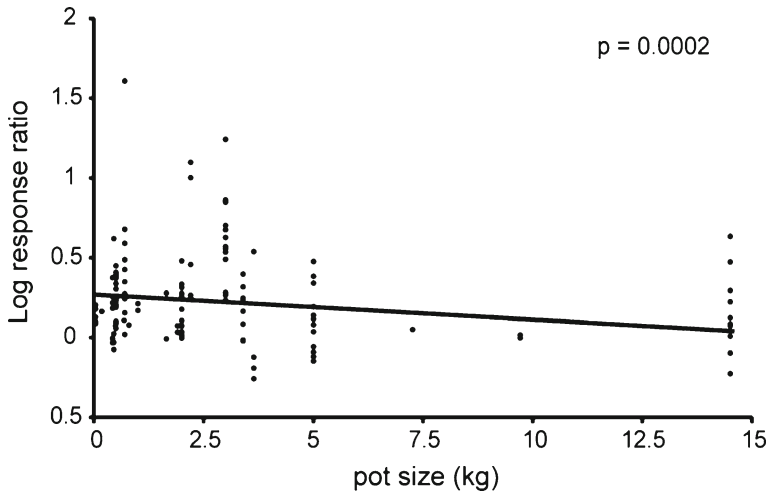

Fig. 3 Scatterplot for data points of the pot size (kg) (N=136) and the effect size (log response ratio) and linear regression line. The reported p-value was obtained from the permutation test

moderator 'plant' into one group. The permutation test returned a significant p-value of 0.0343 for the difference between the two groups, where non-woody plants had a higher estimated mean effect size (see Table 1). The conversion of the moderator 'plant' did not change the result of the BRT analysis.

Discussion

This is the first study to quantitatively synthesize effects of AMF inoculation on soil aggregation. Our finding of an overall positive mean effect of AMF corroborates previous narrative reviews. Moderator means and CIs were—with one exception—all in the range of beneficial effects, i.e. above zero. Our results provide insight into how the experimental outcome depends on specific experimental settings and abiotic and biotic factors. We found support for four of our hypotheses but there was no support for two of them.

Hypothesis (i): experiments with intermediate duration will have more pronounced effects than short or long experiments

Our analyses suggest that there is a minimum time span of approximately 2 months after which positive effects of AMF on soil aggregation are more likely to occur. We could additionally show that there is also a maximum time span for aggregation experiments of about 5 months, after which positive effects of AMF on soil aggregation become less likely to occur. There was a non-monotonic relationship between the duration of an experiment and the effect size with the highest response after approximately 3.7 months (Fig. 3, N= 172). The first part of the smoothed curve is rather flat and can likely be attributed to the time it takes the fungus to colonize the plant and to subsequently develop extraradical mycelium (Hart and Reader 2002). After this initial phase the effect size increases, probably parallel to changes in hyphal or root proliferation. After the peak, the response progressively decreases, showing a reduced influence of AMF, possibly as a result of the decomposition and degradation of the hyphae or increased root growth that gradually overwhelms the AMF effect. The BRT analysis (Fig. 1) supports this pattern. These results support our hypothesis and we therefore conclude that the duration of an experiment appears to be of exceptional importance for the detection of AMF effects on soil aggregation.

Hypothesis (ii): the influence of AMF on soil aggregation should be stronger in nutrient poor soils that have favorable conditions for AMF growth

To test our hypothesis (ii) we used the moderators 'sand content', 'soil pH' and 'soil content of organic carbon'.

Our tests highlight the role of abiotic settings in experiments such as texture and soil pH. The preference of AMF for a near neutral or alkaline soil pH (Helgason and Fitter 2009; Marschner et al. 2005), reflected in a more extensive extraradical network, could be directly correlated with an increase in soil aggregation. Likewise, AMF effects are more pronounced in nutrient poor soils, as are coarsely textured

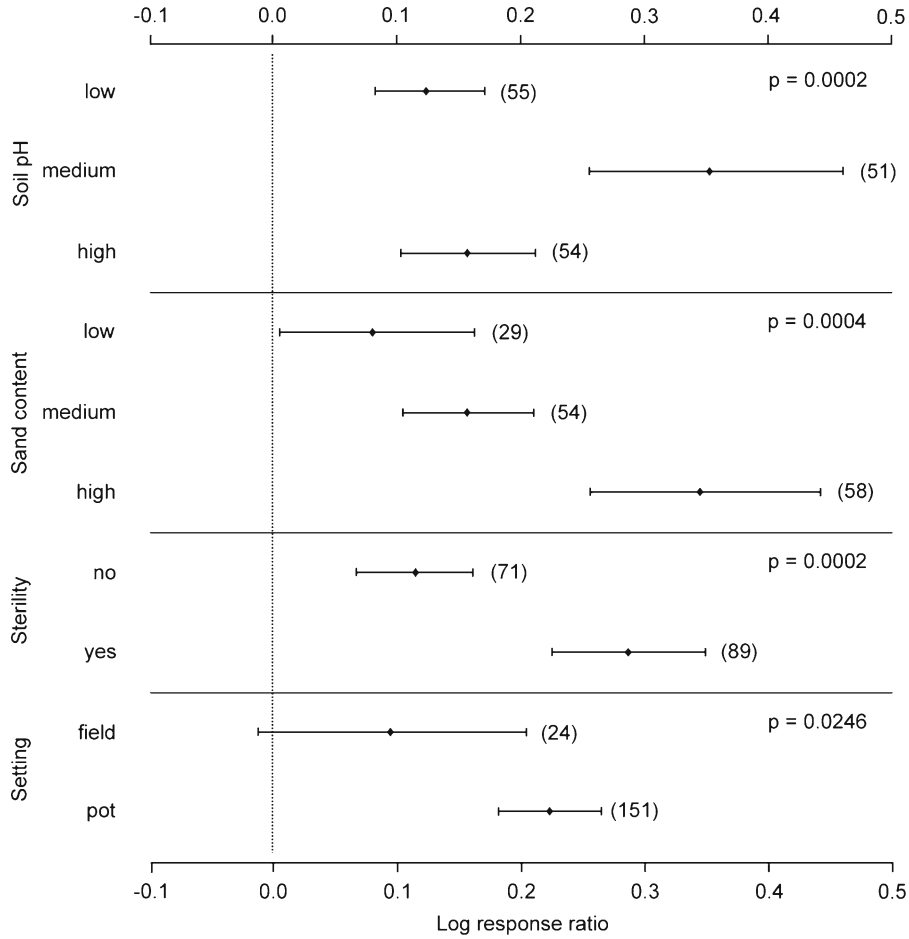

Fig. 4 Means and bias-corrected CIs of the effect size for the levels of the moderators 'soil pH', 'sand content', 'sterility' and 'setting'. *Numbers in parentheses* refer to the number of trials present in the class. For the definition of the classes see 'Methods'. The *p*-values were obtained from the permutation test

soils or soils low in OM (Parniske 2008). For sandy soils we could show an increased effect size, giving strong support for our hypothesis. For soil OM there was no significant trend on the effect size. This may suggest that AMF effects on soil aggregation are more strongly influenced by texture than by OM. Soil aggregation was previously found to be positively influenced by SOM, but also neutral effects have been reported (Chaudhary et al. 2009; Six et al. 2004; Tisdall and Oades 1982). In the literature, both increases and neutral effects of the presence of OM on AMF hyphal length have been found (e.g. Atul-Nayyar et al. 2009; Herman et al. 2012; Hodge 2001). The influence of OM on AMF may depend on the amount of OM added to the soil, the composition of the OM and the different methods of assessing organic Carbon in the soil (Barto et al. 2010). The complexity of interactions between microbes such as AMF, the soil fauna, roots, inorganic binding agents (e.g. metal oxides) and environmental factors (e.g. soil pH) may also lead to the variability of OM effects on AMF and soil aggregation (Six et al. 2004).

Hypothesis (iii): in laboratory pot experiments aggregation will be higher than in field experiments

To test our hypothesis (iv) we used the moderators 'setting' and 'sterility'. The meta-analysis revealed a higher effect size for pot experiments (N=151) compared to field experiments (N=24), corroborating our hypothesis. Potential edge effects of pots (Poorter et al. 2012) do not appear to affect the positive effect of AMF on soil aggregation. The 'field' group is the only

Table 1 Results of permutation tests which yielded non-significant *p*-values (α=0.05; for significant moderator effects please refer to figures) and for the additional analysis of the moderator 'plant'

Moderator level (N)	*p*-value
Plant	
'Tree' (*N*=44), 'legume' (*N*=67), 'herbaceous' (*N*=29)	0.0778
Plant	
'Woody' (*N*=44), 'non-woody' (*N*=96)	0.0343
AMF richness	
'One' (*N*=110), 'more' (*N*=65)	0.3826
AMF species	
'*Gl. intraradices*' (*N*=34), '*Gl. mosseae*' (*N*=48)	0.8624
Soil organic carbon (%) (*N*=86)	0.1244
Method of soil aggregation assessment	
'Wet sieving' (*N*=125), 'artificial rainfall' (*N*=50)	0.1244
Rewetting	0.4564
'Slow' (*N*=97), 'fast' (*N*=50)	
Aggregate size fraction	
'Small' (*N*=32), 'medium' (*N*=26), 'large' (*N*=32)	0.8112

For the moderators 'plant' and 'aggregate size fraction' see also Fig. S13. Moderator levels are followed by the number of trials present in the level. For definition of the classes see 'Methods'

moderator level having a CI overlapping zero, indicating that detrimental effects are more likely to occur in field studies. There are multiple possible reasons that could affect the functional performance of the inoculated AMF species in the field: a) increased competition among AMF species or with saprotrophic decomposers (Verbruggen et al. 2012), b) greater variability due to small-scale heterogeneity in soil properties such as texture, water holding capacity, nutrient levels or pH (Chen et al. 2006; Kumar et al. 2006; Zhou et al. 2008) or c) the lack of controlled conditions (possible plant neighbors that affect aggregation, changing precipitation and irradiation). The naturally higher heterogeneity in the field, but also the low sample size in the 'field' group causes differences in variance between this and the 'pot' group. We conclude that the location of an experiment is crucial for soil aggregation experiments that include AMF. The result of more beneficial effects of AMF in pot experiments corroborates findings of a meta-analysis on plant growth in the field vs. laboratory studies, where more beneficial effects of AMF on plant growth were reported for greenhouse or growth chamber experiments (Lekberg and Koide 2005). It is important to note that both settings have drawbacks: results from pot experiments have reduced reality while field experiments include confounding factors that both limit the interpretation and extrapolation of results. More research in the field could improve our knowledge on the quantification of the effects of AMF on soil aggregation under realistic conditions, which would be important for practical applications of AMF inoculum such as in the restoration of degraded areas or erosion prevention (Rillig and Mummey 2006).

Sterilized soils (*N*=89) yielded higher effect sizes than non-sterile (*N*=71) soils. Sterilizing the soil prior to an experiment removes any priority effects of other AMF species, leaving only the newly inoculated species (Mummey et al. 2009). The species added can proliferate without competing species and are more likely to produce an effect. Non-sterilized pot or field experiments include priority effects (Verbruggen et al. 2012), and measure only the effect of the addition of propagules; the effect size would thus automatically be expected to be smaller due to less pronounced treatments. This result shows that sterilizing the experimental soil is important to clearly disentangle effects of an inoculated AMF species and other microorganisms and that the detection of an effect is more likely in sterilized soils. For future pot experiments studying effects of interactions with other microbiota or effects of diversity it is inevitable to use sterilized soil, especially when molecular techniques or other techniques to assess diversity are involved (see below).

Hypothesis iv) AMF effects on soil aggregation in pots will depend on the space available for root growth

In smaller pots the development of a hyphal network throughout the whole soil is faster compared to large pots. Thus it is not surprising to see a significant impact of the moderator 'pot size' on the effect size. However, it is interesting to observe that this relationship is non-monotonic. There seems to be a plateau with an "optimal" pot size yielding the highest effect sizes. One reason could be that in very small pots (<0.6 kg) the effect of plant roots aggregating soil more rapidly covers up the direct hyphal effect. Root density was found to correlate negatively with mycorrhizal infection (Baath and Hayman 1984). Therefore, a high root density in a small pot may lead to low infection rates with AMF and small effects of AMF on soil aggregation. In very large

pots (>3.5 kg) on the contrary, hyphal proliferation may not be fast enough to yield comparable results in soil aggregation and root mass could be relatively smaller (as root mass per rooting volume) due to increased available amounts of nutrients and water (Poorter et al. 2012). For future soil aggregation experiments the pot size or rooting volume, in conjunction with experiment duration, should carefully be taken into account to avoid pot-bound roots or extremely high root densities, which might impair the interpretation of AMF effects on soil aggregation.

Hypothesis (v): some single AMF species will have more pronounced effects on soil aggregation than others and higher levels of AMF richness will have more beneficial effects than single species

In the literature both positive and negative effects on soil aggregation have been found for *Gl. intraradices* and *Gl. mosseae* (e.g. Alguacil et al. 2004; Ambriz et al. 2010; Enkhtuya et al. 2003). However, in our meta-analysis these species yielded similar positive mean responses. We had high replication for *Gl. intraradices* (N=34) and *Gl. mosseae* (N=48) and the permutation test produced a high p-value (non-significance: p=0.8624). We can therefore confidently state that there is no difference in soil aggregation capability between *Gl. intraradices* and *Gl. mosseae*. These two *Glomus* species are commonly used in AM experiments and often showed positive effects on soil aggregation (e.g. Auge 2001; Bethlenfalvay and Barea 1994; Kohler et al. 2008), but AMF functional effects generally depend on the combination of fungus and host plant species (Klironomos 2003). Studies yielding negative effect sizes were mostly field experiments, which are less likely to detect AMF effects on soil aggregation, as discussed above. Therefore, we think that the setting is a more important factor influencing soil aggregation than the AMF species identity. Furthermore, the lack of species of other genera (*Gigaspora*, *Scutellospora*), which can have more dissimilar lengths in extraradical hyphae than *Glomus* (Hart and Reader 2002), might be the reason why we did not find support for our hypothesis.

The analysis for the moderator 'AMF richness' returned no effect, i.e. no difference between the groups 'one' and 'more'. Studies on effects of different levels of diversity or richness of AMF on soil aggregation are rare as this is a relatively new topic (Rillig and Mummey 2006). To improve our statistical power it was necessary to merge studies with more than one fungus into a single group, necessitating that studies with only two AMF species and studies with the entire AMF community adapted to the specific soil were classified together. Also the field studies were included in this group, which tend to have lower aggregation values. This might have caused variability in the group 'more' that reduced the probability of finding effects.

However, the overall replication level in the group was high (N=65) and the analysis returned a highly non-significant p-value (p=0.3826). Hence, we lack support for our hypothesis and for the existence of synergistic effects in the soil aggregation process as was suggested by Rillig and Mummey (2006) and Schreiner and Bethlenfalvay (1997). There are occasions when AMF identity, as well as selection mechanisms, soil type and the specific combination of AMF and the host, may have more pronounced effects on ecosystem functioning than AMF richness (Hoeksema et al. 2010; Koide and Kabir 2000; Vogelsang et al. 2006; Wagg et al. 2011). For the studies considered in our meta-analysis we also found evidence that other factors might be more important for soil aggregation than AMF richness. To gain a better insight into the role of AMF richness on soil aggregation, more single studies on different levels of richness or diversity that incorporate experimentation with variable contexts (location, host plant and soil type) are needed. Knowledge on this topic could help us to improve the use of the ecosystem function soil aggregation (in terms of inoculum application) in, for example, restoration sites (Miller and Jastrow 1992; Sikes et al. 2010).

Hypothesis (vi): the host plant identity will be important for the effect of AMF on soil aggregation. The association of AMF with trees will produce smaller effects than the association with herbaceous or leguminous plants

Root systems among the analyzed plant groups differed considerably (herbaceous including grasses compared to trees for example) and it could be expected to see differences in their influence on soil aggregation. There is evidence in the literature that the combination of AMF with a single plant species—including herbaceous plants and legumes—is important for the influence on AMF functions (Klironomos 2003). Although we observed a trend for the effect size in plant groups

in the expected order herbaceous > legumes > trees (N=29, N=67, N=44, respectively; Fig. S13), this was not significant. If we only analyzed woody (N=44) and non-woody (N=96) plants the difference between the moderator levels was significant (p=0.034). This second analysis corroborates the trend that we found in the first analysis. However, we think that by merging legumes and herbaceous plants that include grasses, we lose information on plant traits such as the number of fine roots (Oades 1993), which probably has an important influence on the result. When keeping more detailed information on plant traits, it seems that the aggregation effect is detectable independently of the host plant type. As AMF functions including soil aggregation usually depend on the specific combination of host and fungus (Piotrowski et al. 2004), the overall influence of a certain plant (root) type or fungus becomes indifferent when meta-analyzed. As the BRT analysis showed, the moderator 'plant' was not influential on the data and therefore we conclude, contrary to our hypothesis, that the differences caused by the host plant identity are not strong enough to have an impact on the effect of AMF on soil aggregation.

Hypothesis (vii): the detection of a potential effect of AMF on soil aggregation will not be influenced by the chosen laboratory procedures

To test this hypothesis we used the moderators 'aggregate size fraction', 'method of soil aggregation assessment' and 'rewetting'. For the moderator 'aggregate size fraction' the permutation test showed a pattern (higher effect sizes for larger aggregate size fractions, Fig. S13), but it was not significant and the CIs widely overlapped. The moderators 'method of aggregation assessment' and 'rewetting' had high replication levels, and thus there probably was a high power to find any effects. It appears that the magnitude of the aggregate stabilizing effect of AMF is not strongly influenced by the method used to measure water stability. However, we only compared water stability of aggregates including rainfall simulation and wet sieving; no studies using dry sieving were included in the analysis. This might be a reason for the similarity in results for the moderator 'method of soil aggregation assessment'.

These results show that the effect of AMF on soil aggregation can be detected in small, medium and large macroaggregates with various methods, corroborating results of previous single studies where positive effects have been shown for various aggregate size fractions and different methods to determine aggregate stability (e.g. Andrade et al. 1998b; Auge et al. 2001; Kohler et al. 2009b; Schreiner et al. 1997; Siddiky et al. 2012). We therefore find support for our hypothesis. Future studies might consider that the entire macroaggregate size range from 0.25 to 10 mm is positively affected by AMF rather than single narrow macroaggregate range classes. They may also use wet sieving and simulation of rainfall interchangeably to determine the water aggregate stability, but—for our dataset we can state that—wet sieving seems to be more commonly used (wet sieving: N=125, artificial rainfall: N=50).

Direct vs. indirect effects of AMF

The majority of results on soil aggregation experiments included in this meta-analysis are from mycorrhizosphere soils, i.e. soils that contain AMF hyphae and roots. The inoculation with AMF can alter the host plant roots, e.g. root morphology and rhizodeposition (Rillig and Mummey 2006), which can hence indirectly affect soil aggregation. The calculated effect size—the log response ratio that compares the inoculated with the non-inoculated control group—cannot account for these indirect effects. However, we were able to detect a positive effect size across all trials, showing a beneficial effect of AMF inoculation on soil aggregation (ln(R)=0.2028, N=175). If we consider only hyphal compartments (excluding root effects), the overall effect across these trials is even higher with ln(R)=0.3039 (N=13), supporting the assertion that AMF hyphae are (at least partly) directly responsible for the increase in aggregation. To clearly show direct AMF mycelium effects, more studies with sterilized soil (AMF free control) are needed that also include hyphal compartments or studies with split root designs that enable us to distinguish between root, hyphae and AMF altered root effects (as in Andrade et al. 1998a).

Conclusions

There is a clear overall positive effect of AMF on soil aggregation when considering the evidence available

to date. With our meta-analysis we showed that the selection of experimental parameters can have an important influence on the outcome of any study testing for AMF effects on water stable aggregates. Pot studies with sterilized sandy soil, near neutral soil pH, a pot size smaller than 2.5 kg and a duration between 2.2 and 5 months are more likely to result in positive effects of AMF on soil aggregation than experiments in the field, with non-sterilized fine textured soil or with an acidic soil pH. The extent to which AMF promote soil aggregation seems to be independent of the number of fungal species present in the system or the soil organic carbon content, and the experimental outcome does not seem to be altered by the selected laboratory procedures for measuring soil aggregation. Differences in soil aggregation caused by host plant identity do not seem to be strong enough to generally influence the effect by AMF, when information on trees, herbaceous plants and legumes is conserved. Future research should include experiments with sterile soil and hyphal compartments or split root designs to clearly distinguish between root and hyphal effects as well as studies on AMF richness and diversity in differing contexts such as location (field vs. laboratory and soil type).

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