

Meta-Analysis of Crop and Weed Growth Responses to Arbuscular Mycorrhizal Fungi: Implications for Integrated Weed Management

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Integrated weed management (IWM) relies upon multiple chemical, physical, or biological weed management techniques to achieve an acceptable level of weed control. Agents that selectively suppress weeds but not crops and that can be manipulated in agriculture will be promising components for inclusion in IWM. We used a meta-analytic approach to investigate the potential of arbuscular mycorrhizal fungi (AMF) to contribute to IWM. We quantified the effect of crop and weed host status (strong and weak AMF hosts are divided in this study by a 10% root length colonization threshold), AMF diversity (single vs. mixed), and soil N and P fertility management on plant mycorrhizal growth responses (MGRs). Our results indicated that weak host weeds had consistently lower MGRs than strong host crops in both controlled and field conditions. Moreover, these differences in MGRs between weak host weeds and strong host crops were more pronounced under mixed AMF inoculum and low N and P nutrient availability. In contrast, MGR of strong host weeds was not different from strong host crops in general. However, we observed a wide range of MGRs among strong host weeds, some of which had much lower MGRs than strong host crops. In addition, in the presence of N and P fertilizers, strong host crops had a stronger positive response to AMF than strong host weeds. Thus, our meta-analysis indicates that AMF have potential to contribute to weed control by direct and indirect pathways: directly suppress weak host weeds, and indirectly suppress some strong host weeds mediating by competitive effects exerted by strong host crops. We suggest that management practices affecting AMF diversity and crop and weed mycorrhizal responses could be chosen to improve the contribution of AMF to IWM. Better understanding is needed of crop–weed–AMF interactions and management practices that enhance this form of weed management.

Nomenclature: Glyphosate.

Key words: Integrated weed management, mycorrhizal growth response, mycorrhizal host status.

The selection for weed genotypes resistant to herbicides and other management practices indicates a need for diversification of weed management through integrated approaches (Heap 2014; Owen et al. 2015). IWM relies upon multiple chemical, physical, or biological weed management techniques, guided by biological and ecological knowledge of weeds, to achieve an acceptable level of weed control (Buhler 2002). The search for promising viral, bacterial, and fungal taxa for weed control

strategies for inclusion in IWM programs has attracted considerable attention (Hallett 2005; Harding and Raizada 2015). However, few such methods have become widely adopted (Charudattan 2001; Harding and Raizada 2015). Two crucial prerequisites when considering whether a new weed management tactic will be effective in IWM include whether the tactic (1) creates a differential impact on the crop and weed, and (2) can be managed consistently.

In this study, we investigate whether AMF meet these criteria, and therefore may have potential as part of an IWM approach. Recent experimental and meta-analytic studies of interactions between AMF and plants provide evidence of differential plant responses to AMF, and context-dependent environmental control over these responses (Hoeksema et al. 2010). In addition, detailed studies of interactions between AMF and a limited number of agricultural weeds have been performed, but have not been synthesized into a more comprehensive quantitative understanding of AMF–weed interactions (Allen et al. 1989; Francis and Read 1994,

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1995; Jordan and Huerd 2008; Rinaudo et al. 2010; Sanders and Koide 1994; Vátovec et al. 2005; Veiga et al. 2011). This range of studies highlights needs for a broad-based assessment of AMF–weed interactions and comparison of those interactions to AMF–crop interactions. Here, we meet those needs via a meta-analytic approach, aiming to improve understanding of the role of crop and weed host status and environmental context in determining AMF–plant interactions. Our objective is to build understanding of whether and under what circumstances AMF may contribute to IWM.

AMF are a globally distributed group of organisms that can form symbioses, in the form of mycorrhizae associated with plant roots, with more than 66% of terrestrial plant and 74% of angiosperm species (Brundrett 2009). They provide many ecosystem benefits to host plants, including facilitation of nutrient and water uptake (Bolan 1991; Marulanda et al. 2003), enhanced stress tolerance (Al-Karaki et al. 2004; Auge et al. 2014; Chandrasekaran et al. 2014; Lehmann and Rillig 2015), and improved defense against pathogens (Borowicz 2001; Cordier et al. 1998). AMF can also have negative or neutral effects on plant growth (Francis and Read 1995; Klironomos 2003; Sanders and Koide 1994). It is now recognized that interactions between AMF and plants fall along a continuum ranging from mutualism to antagonism (Johnson et al. 1997; Klironomos 2003).

The direction and magnitude of the interactions along this continuum can be shaped by various abiotic and biotic factors, such as nutrient levels, sources of AMF inocula, plant invasive status, and plant phylogenetic relationships (Bunn et al. 2015; Hoeksema et al. 2010; Maltz and Treseder 2015; Treseder 2004; Veresoglou and Rillig 2014). Host status, i.e., extent of mycorrhizal colonization of plant root, has been proposed as a mechanism underlying the variation in how different plant species respond differently to AMF (Feldmann et al. 2009; Treseder 2013). Plants with mycorrhizal root colonization rating lower than 20 to 30% were more likely to have nonpositive mycorrhizal responses (Feldmann et al. 2009). Possible explanations for nonbeneficial effects of AMF on weak and nonhost plants include (1) direct inhibitory effects of AMF on nonmycorrhizal root development (Allen et al. 1989; Francis and Read 1994; 1995); (2) direct inhibitory effects of allelopathic exudates released from AMF on the growth of nonhost plants (Francis and Read 1994); and (3) competitive disadvantages of weak and nonhost

plants compared with strong host plants in response to AMF infection (Sanders and Koide 1994).

Among studies in which AMF have antagonistic effects on weak and nonhost plants, many of the focal plants are weedy and invasive species (Allen et al. 1989; Francis and Read 1995; Jordan and Huerd 2008; Rinaudo et al. 2010; Veiga et al. 2011). For example, the growth of four agricultural weeds was reduced by 22 to 35%, when colonized by AMF (Veiga et al. 2011). There have also been anecdotal reports that weed species are more likely to be weak and nonhosts than are crop species (Brundrett 2009; Francis and Read 1994). In a comprehensive summary of plant AMF host status (Wang and Qiu 2006), weeds had higher representation among nonhosts (20% of nonmycorrhizal angiosperms) than did crops (3% of nonmycorrhizal angiosperms). These patterns underscore the need for systematic analysis of previous studies to assess whether weak and nonhost plants consistently show negative responses to AMF and whether weak and nonhost species are more common among weeds than among crops. If so, the differential vulnerability of weeds to AMF, relative to crops, could be exploited in IWM strategies.

Another knowledge gap, with respect to the potential impact of AMF on crops and weeds, is the degree to which management of agricultural soils affects crop and weed responses to AMF. Agronomic practices can affect soil properties and cause changes in the abundance and diversity of AMF and their effects on plant growth. For example, AMF richness and abundance in soils can be increased by reducing the intensity of tillage, so as to avoid severing pre-established mycelial networks, and diluting spores and hyphal densities (Kiers et al. 2002). Crop systems incorporating diverse plant species, such as crop rotation and cover crops, can change soil AMF community compositions and maintain high abundance of AMF across successive growing seasons (Hijri et al. 2006; Karasawa and Takebe 2012; Oehl et al. 2003; Ramos-Zapata et al. 2012). In contrast, high soil P and N inputs can reduce the abundance and diversity of AMF, and cause a reduction in plant mycorrhizal responsiveness (Hoeksema et al. 2010; Peng et al. 1993; Treseder 2004). The application of herbicides, especially glyphosate, can reduce the viability of AMF propagules in soils and decrease plant mycorrhizal colonization rates (Druille et al. 2013, 2015; Zaller et al. 2014). In addition, some genetically modified crops were proposed to negatively impact AMF–plant symbiotic develop-

ment and decrease AMF diversity after a long-term cultivation (Liu 2010). With a better understanding of what crop–weed species mixtures are amenable to weed suppression and crop stimulation by AMF, it is possible that agronomic practices can be chosen specifically to enhance the contribution of AMF to IWM.

In this study, we propose that a quantitative understanding of crop and weed host status and their mycorrhizal growth responses (MGRs) in different environmental conditions will help to identify situations that favor AMF in IWM. Meta-analysis offers an approach for combining results and identifying patterns among multiple studies. Although numerous recent meta-analyses have advanced knowledge of AMF–plant relationships (Auge et al. 2014; Bunn et al. 2015; Chandrasekaran et al. 2014; Hoeksema et al. 2010; Jayne and Quigley 2014; Lehmann and Rillig 2015; Lekberg and Koide 2005; Lin et al. 2015; Maltz and Treseder 2015; Treseder 2004; Veresoglou and Rillig 2014), none have specifically focused on AMF impacts on weeds. The growing body of literature examining AMF–crop and AMF–weed interactions under controlled and field conditions makes such a meta-analysis possible. Our experimental approach was framed by two research questions. First, can AMF have different effects on weeds and crops based on their host status? Second, can the effect of AMF on weeds and crops be affected by environmental variables such as location, AMF inoculum richness, and nutrient application?

Materials and Methods

Data Source. We carried out an initial search in the ISI Web of Science database (1990–2013) using keywords “arbuscular mycorrhiz* and inocul*” on July 31, 2013. Supplemental searches were conducted from November 6 to November 12, 2015, using keywords “arbuscular mycorrhiz*, incol*, and weed”, “arbuscular mycorrhiz*, inocul*, field experiment and cropping”, and “arbuscular mycorrhiz*, field, and weed”. Respectively, these searches retrieved 3,197; 178; 1,075; and 273 articles. Articles were then screened for the following criteria: (1) either crop or weed species was reported; (2) yield, whole plant biomass, or shoot biomass was reported; (3) sample sizes and variances (e.g., standard deviation [SD], standard error [SE], or confidence interval [CI]) were reported; (4) if multiple levels of environmental factors were reported in one study, data from the treatment level closest to ambient conditions were

collected (e.g., if multiple copper levels were reported, only the study with the ambient copper concentration was included in the database); and (5) if multiple harvest points were reported, data from the final time point were included. The resulting database contained 114 publications, comprising 410 studies (see Appendix S1 in the supplementary material for publication list; <http://dx.doi.org/10.1614/WS-D-16-00050.AS1>). Weed species were not restricted to agricultural weeds, but included weeds found in highly disturbed and nonarable early successional environments. Among the 410 studies, 233 and 177 were of crops and weeds, respectively; 120 were field studies, and 290 were greenhouse studies. Plants have been divided into strong hosts, weak hosts, and nonhosts based on their percent root length colonized by AMF (Vatovec et al. 2005). However, the mycorrhizal status of many plants was not clearly distinguished and some so-called nonhost species can have very low mycorrhizal colonization rate (< 10%) in some cases (Vatovec et al. 2005; Wang and Qiu 2006). In our meta-analysis, plants with percent root length colonized by AMF (%RLC) greater than 10% were classified as strong hosts, whereas nonhost plants and those with %RLC no greater than 10% were classified as weak hosts. For few studies which %RLC were not reported, we consulted Wang and Qiu (2006) and at least two other papers with the same species. Detailed species information is included in Appendix S2 (<http://dx.doi.org/10.1614/WS-D-16-00050.AS2>).

Data Analysis. Effect size was calculated as the natural log of the response ratio of the mean biomass of inoculated plants in comparison to that of control plants, also known as plant “mycorrhizal growth response” (MGR) (Hoeksema et al. 2010). Whenever possible, whole plant biomass or shoot biomass was used to determine MGR; however, for some papers focused on crop species, only economic yield (e.g., grain or fruit mass) was reported, and yield was therefore used to calculate MGR in these cases. Effect size was calculated as:

$$\text{Effect size} = \ln(X_t/X_c) \quad [1]$$

where X_t was the mean biomass of the AMF group and X_c was the mean biomass of the corresponding control group.

For each study, measures of dispersion (SD, SE, or CI) and sample size (n) were collected. Dispersion measures were converted to SD before doing meta-analysis. SE was converted to SD using the equation: $SE = SD/\sqrt{n}$. If 95% CI was

reported, it was converted according to the equation:

$$SD = \sqrt{n^*}(\text{upper limit} - \text{lower limit})/3.92.$$

Mean squared error was converted to SD using the equation: $SD = \sqrt{MSE}$. If least significant difference (LSD) was reported, then the MSE was first computed by $LSD = t_{\alpha/2} \sqrt{2MSE/n}$, where n was the sample size and $t_{\alpha/2}$ followed the t distribution with a significance level of α and n degrees of freedom. MSE was then converted to SD.

We used the random-effects meta-analysis model to calculate the summary effect size of plant MGR. In a random-effects model, the variation of any given study consists two parts: within study variance and between-studies variance. Within study variance depends on the SD, which is collected from the given study, and between-studies variance depends on the variation of the distribution of effect sizes across all studies. We used the DerSimonian and Laird method to estimate the between-studies variance value (DerSimonian and Laird 1986), and this same value applied to all studies in the meta-analysis. In order to down-weight studies with highly variable data, each study was assigned with a weight, which was the inverse of within and between-studies variances (Hedges et al. 1999). Individual effect sizes were weighted by the given weight, and the mean effect size across all studies was obtained by the sum of weighted effect sizes divided by the sum of weights (Borenstein 2009a).

Mixed-effect meta-regression models were used to estimate the effect size of subgroups. CIs (95%) were calculated for each mean effect size. All pairwise comparisons were carried out using Tukey's method, along with Holm-Bonferroni corrected P-values. When P-value for the corresponding comparison was less than 0.05, mean effect sizes were considered as significantly different from each other. Omnibus tests were carried out for all models to test the significance of model coefficients (Q_m). In addition, Q_e was reported to estimate residual heterogeneity for each analysis (Borenstein et al. 2009b). All analyses were conducted using the package "metafor" in R version 3.3.2 (Viechtbauer 2010).

Results and Discussion

Overall Effect. The effect of AMF on plant growth spanned a broad range, with negative MGR indicating plant growth reductions, and positive

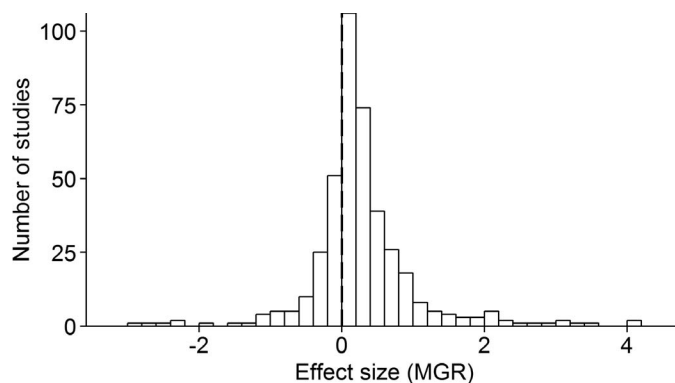


Figure 1. Distribution of mycorrhizal growth response effect sizes for studies compared in this meta-analysis ($n = 410$). Positive effect sizes indicate that plants grow better when colonized by arbuscular mycorrhizal fungi (AMF) than nonmycorrhizal controls. Negative effect sizes indicate that plants grow worse when colonized by AMF than nonmycorrhizal controls.

MGR indicating plant growth increases when colonized by AMF (Figure 1). According to our results, the mean effect size across all studies was significantly positive (MGR = 0.23, $P < 0.0001$) (Supplemental Table 1 <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>), indicating a mean plant growth increase by 26% when colonized by AMF. This result was similar to results of previous meta-analytical papers in which plant–AMF relationships were investigated (Chandrasekaran et al. 2014; Hoeksema et al. 2010; Yang et al. 2015). In addition, effect sizes of individual studies ranged widely from negative to positive (Figure 1), following the mutualism–parasitism continuum previously shown for AMF–plant relationships (Johnson et al. 1997).

Responses of Crops and Weeds to AMF. In the following two subsections, we compare the relative MGR of weak and strong host weeds, respectively, with those of weak and strong host crops. We saw similar MGR for greenhouse and field studies (Figure 2; Supplemental Table 1; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>) and therefore present analyses for data aggregated across these conditions. This corroborates a previous report, in which growth environment (greenhouse compared to field conditions) was relatively unimportant to AMF–plant interactions (Hoeksema et al. 2010). General correlations of AMF effects on plants between field and greenhouse experiments have also been reported in individual studies (Pringle and Bever 2008). The consistent results between greenhouse and field data suggest that the mycorrhizal growth response of a plant in the field may

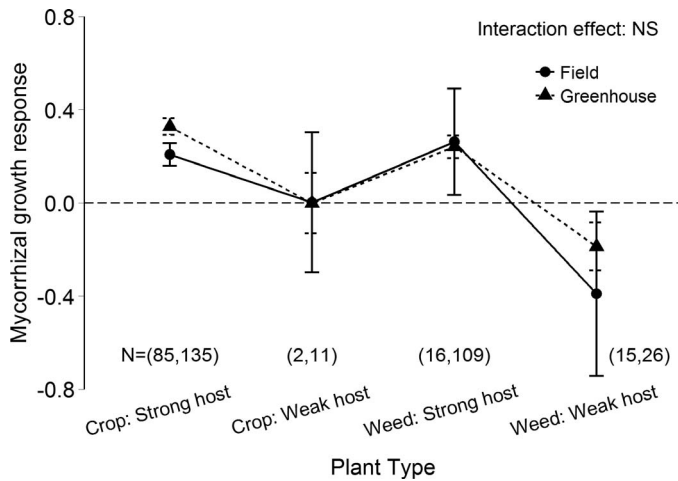


Figure 2. Mean mycorrhizal growth response effect sizes showing the interaction between location and plant type. Error bars represent the 95% confidence interval. Explanation of symbols: solid circles and solid lines = field experiments; solid triangles and dashed lines = greenhouse experiments.

roughly be predicted by its response to AMF in controlled experiments.

Weak Host Weeds Compared to Crops. AMF had generally negative effects on weak host weeds (weak hosts contained nonhosts and host species with the percent root length colonization rate from 0 to 10%). According to our results, weak host weeds showed negative growth responses to AMF (MGR = -0.19, 95% CI = -0.29 to -0.10, $n = 41$) (Figure 3). In addition, we found a higher number of studies with weak host weeds ($n = 41$ from 19 different species) than that of weak host crops ($n = 13$ from 8 different species) in our data set. Weak host crops displayed no differences in mycorrhizal growth responses from zero (MGR = 0, 95% CI = -0.11 to 0.11, $n = 13$) (Figure 3). Moreover, the effect of AMF on weak host weeds was significantly lower than the effect of AMF on strong host crops (strong hosts included plant with the percent root length colonization rate greater than 10%) (MGR = 0.28, 95% CI = 0.26 to 0.31, $n = 220$) (Figure 3; Supplemental Tables 1 and 2; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>).

These results indicate that weak host weeds respond negatively to the colonization of AMF, and that AMF weak hosts are more prevalent among weeds than crops. The detrimental effects of AMF on weak host weeds suggest that managing for abundant AMF communities can be part of a generally “weed-suppressive” strategy in fields where dominant weeds are weak hosts. In addition, the considerable difference in MGR between weak host weeds and strong host crops holds out the

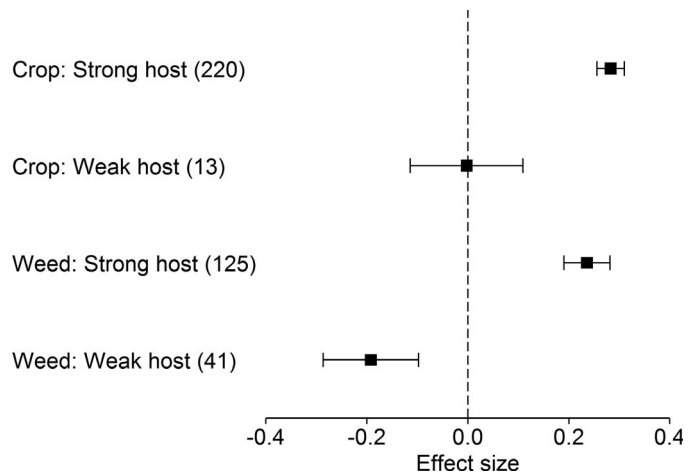


Figure 3. Mean mycorrhizal growth response effect sizes for studies grouped by plant type and host status (crop strong host, crop weak host, weed strong host, and weed weak host). Error bars represent the 95% confidence interval.

possibility that the use of AMF in the weed management of weak host weeds may contribute to IWM approaches, especially when major strong host crops are planted. Controlled and field studies are needed to test these hypotheses.

Strong Host Weeds Compared to Crops. Agroecosystem design for selective management of strong host weeds by AMF may be aided by information on crop and weed host status and community composition. The mean growth response of strong host weeds (MGR = 0.24, 95% CI = 0.19 to 0.28, $n = 125$) was positive, and was not different from that of strong host crops (MGR = 0.28, 95% CI = 0.26 to 0.31) (Figure 3; Supplemental Tables 1 and 2; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). However, we observed a wide range of MGRs among strong host weeds, some of which were minimally responsive to AMF symbiosis, and had a much lower MGR than strong host crops (Figure 3). In addition, variation in the MGR of strong host weeds ($\sigma^2_{\text{MGR}} = 0.07$) was 1.6 times greater than that of strong host crops ($\sigma^2_{\text{MGR}} = 0.04$). We hypothesize that the difference in the distribution of MGRs between weeds and crops forms the basis for a potential approach to using AMF in weed management: in cropping systems in which high MGR crops co-occur with low MGR weeds, changes in management to promote AMF diversity and abundance would be predicted to differentially benefit crop growth, thus indirectly suppressing the low-MGR weeds through enhanced crop competition. In essence, AMF may contribute to IWM by indirectly suppressing weed species that are low-MGR strong hosts. A key condition for this effect is the use of

high-MGR crop varieties and management methods that support diverse and abundant AMF communities in agroecosystems (e.g., minimal tillage).

It is worth noting that the positive MGR of strong host weeds also indicates a possibility that AMF may increase the interference of strong host weeds against weak host crops. However, competitive suppression of weak host crops in the field may lead to disruptions of symbiotic associations between AMF and strong weed hosts, because some nonhost plants are able to release allelochemicals, which could suppress AMF in soils (Koide and Peoples 2012; Kremer 2014). Conventional agricultural practices that reduce AMF abundance could also be used for weak host crops, such as crops from *Brassicaceae* family (e.g., canola or broccoli). In light of these results, knowledge of crop and weed host status and community composition on a particular farm may help producers to decide whether management actions that favor AMF will enhance IWM.

Biotic and Abiotic Effects on AMF–Weed and AMF–Crop Interactions. In addition to plant host strength and AMF community, environmental context must also be taken into account in deciding whether managing AMF for contributions to IWM will be successful. Here, we consider the question of the environmental conditions under which weed management with AMF is most likely to succeed. These conditions may include soil biological and chemical properties that could be manipulated by producers, such as AMF species richness and soil nutrient levels.

Inoculum Species Richness. Plant types and AMF inoculum richness showed a significant interaction effect ($Q_m = 42.28$, $df = 3$, $P < 0.0001$) (Figure 4; Supplemental Table 1; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>), indicating that crops and weeds have differential response patterns when interacting with single and mixed AMF inoculum species. Strong host crops showed a higher MGR when colonized by mixed AMF species than when colonized by single AMF species ($P < 0.0001$) (Figure 4; Supplemental Table 3; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). In contrast, weak host weeds showed a lower MGR when colonized by mixed AMF species than single AMF colonized ones ($P = 0.0003$) (Figure 4; Supplemental Table 3; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). In addition, weak host weeds displayed a lower MGR than strong host crops when inoculated with mixed AMF species ($P < 0.0001$) (Figure 4;

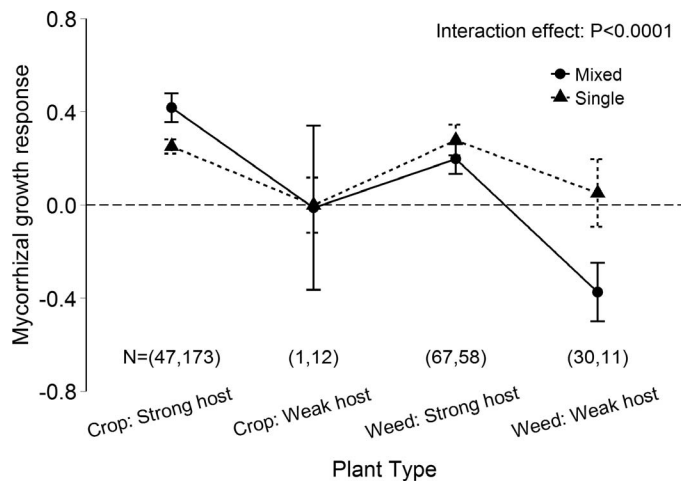


Figure 4. Mean mycorrhizal growth response effect sizes showing the interaction between inoculum richness and plant type. Error bars represent the 95% confidence interval. Explanation of symbols: solid circles and solid lines = mixed arbuscular mycorrhizal fungi (AMF) inocula; solid triangles and dashed lines = single AMF inoculum.

Supplemental Table 3; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). However, this is not the case with single AMF inoculum studies, in which the mean MGR of weak host weeds showed no difference in comparison with strong host crops ($P = 0.10$) (Figure 4; Supplemental Table 3; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>).

The reason for higher MGRs for strong host crops under mixed AMF inoculation than single AMF inoculation may be that various AMF species interacted to produce complementary effects (Koide 2000; Maherali and Klironomos 2007; Smith et al. 2000). Different AMF species have different functional effects, which may combine to produce an overall greater benefit to their hosts (Hart et al. 2003). We speculate that mixed AMF inoculum may have similarly diverse functions when interacting with weak host weeds, in which effects of various AMF species in the community combine to produce a more pronounced negative impact on the weak host weeds. For example, in a previous AMF–weed experiment, green foxtail [*Setaria viridis* (L.) Beauv.] showed a stronger negative growth response to inoculum mixtures of AMF species than to those comprising a single AMF species (Veiga et al. 2011). The positive relationship between AMF richness and MGRs of strong host crops, and the negative relationship between AMF richness and MGR of weak host weeds, emphasize the need to protect and conserve AMF diversity in production situations in which AMF weed management benefits are desired (Table 1).

Table 1. Recommended management decisions based on host status, and crop–weed community composition for use of arbuscular mycorrhizal fungi (AMF) in integrated weed management (IWM) approach.

Dominant crop	Dominant weed	Management for greater AMF weed control
Strong host Crop	Weak host Weed	AMF are most weed suppressive under these conditions. Practices supporting high AMF diversity and low N and P fertilizer addition are suggested.
	Strong host Weed	Practices supporting high AMF diversity and relatively high N and P fertilizer addition are suggested.
Weak host Crop	Weak host Weed	Low N and P fertilizer addition is suggested.
	Strong host Weed	AMF suppression of weeds is not favored.

Farmers seeking to harness AMF for weed management purposes can manipulate AMF diversity in their soils through tillage, vegetation, and nutrient management. Soil disturbance intensity is inversely proportional to AMF diversity; for example, AMF diversity was higher in soils managed without tillage than in soils managed with moldboard plowing or subsoil-tillage (Alguacil et al. 2008). Floristic diversity has been found to be proportional to AMF diversity, with crop rotation promoting a more diversified AMF community compared to soils under continuous mono-cropping systems (Oehl et al. 2003). The adoption of cover crops, especially the mixture of different cover crops, could provide diverse and continuous living hosts to increase AMF propagule numbers in soils (Kabir and Koide 2002; Lehman et al. 2012). Avoiding long-term high inputs of mineral fertilizers, especially phosphorus, can protect AMF diversity in soils (Lin et al. 2012; Oehl et al. 2004). Finally, diversified organic production systems, which feature a combination of absence of inorganic fertilizers with long crop rotations that

include forage legumes, have been found to promote suppression of weeds by AMF (Vatovec et al. 2005). We speculate that agricultural management practices, such as those mentioned here, that increase AMF diversity may, in turn, contribute to suppression of weak host weeds. More field studies are needed to quantify the effect of AMF in weed control under different management practices to determine how stable this effect is under variable growing environments.

Nutrient Levels. Weed response to AMF showed a strong interaction effect between host status and nutrient addition (N and plant type interaction: $Q_m = 37.15$, $df = 3$, $P < 0.0001$; P and plant type interaction: $Q_m = 54.46$, $df = 3$, $P < 0.0001$) (Figures 5 and 6; Supplemental Table 1; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). When N and P were applied, there was no difference in MGR between strong and weak weed hosts, whereas when these nutrients were withheld, the MGR of strong weed hosts increased greatly and the MGR of weak weed hosts decreased greatly (Figures 5 and 6;

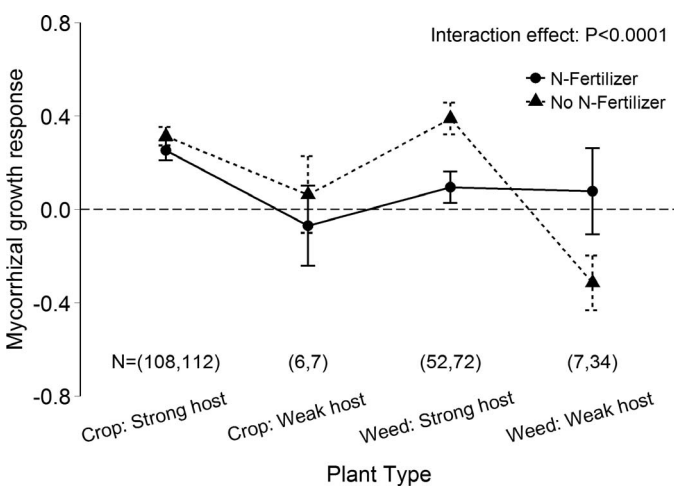


Figure 5. Mean mycorrhizal growth response effect sizes showing the interaction between soil N fertility treatments and plant type. Error bars represent the 95% confidence interval. Explanation of symbols: solid circles and solid lines = N-fertilizer application; solid triangles and dashed lines = no N-fertilizer application.

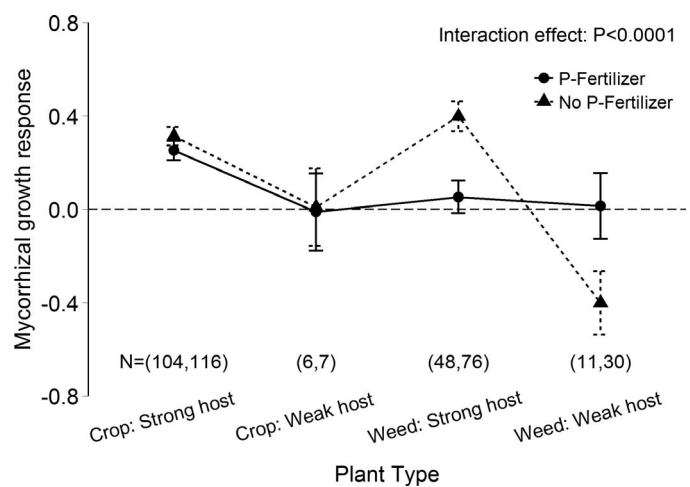


Figure 6. Mean mycorrhizal growth response effect sizes showing the interaction between soil P fertility treatments and plant type. Error bars represent the 95% confidence interval. Explanation of symbols: solid circles and solid lines = P-fertilizer application; solid triangles and dashed lines = no P-fertilizer application.

Supplemental Table 3; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). The large differential impact of nutrient addition on the MGR of weak and strong weed hosts helps to identify contrasting nutrient management strategies for obtaining weed suppression by AMF under different combinations of crop and weed host strength.

First, adding or withholding N and P fertilizer strongly affected mycorrhizal responses of weak host weeds and strong host crops. Weak host weeds showed consistently lower MGRs than strong host crops in the absence of N fertilizers ($P < 0.0001$); however, there was no difference between these two groups when N fertilizers were applied ($P = 0.49$) (Figure 5; Supplemental Table 3; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). Similarly, weak host weeds showed a lower MGR than strong host crops in the absence of P fertilizers ($P < 0.0001$), but the difference reduced drastically when P fertilizers were applied ($P = 0.016$) (Figure 6; Supplemental Table 3; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). High concentrations of plant-available N and P have been found to reduce the abundance of mycorrhizal inoculum in soils (Peng et al. 1993; Treseder 2004). As a result, both beneficial and detrimental effects of AMF on crops and weeds may have decreased because of the reduced AMF inocula under high fertility levels. Thus, soils with low N and P fertilizer application will favor AMF suppression of weak host weeds among strong host crops, compared to soils receiving high N and P (Table 1). Clearly, creating nutrient-poor soils is not a recommended practice for production agriculture; therefore, this strategy may be most beneficial to both weed suppression and crop yield in organic systems, where nutrient levels are typically lower than in conventional systems (Seufert et al. 2012), and under soil management practices that concentrate nutrients in the crop row, such as ridge tillage, narrow in-soil bands and point-injected fertilizer application (Blackshaw et al. 2004b; Kane et al. 2015).

Second, the presence and absence of fertilizer N and P also had a pronounced, but opposite, effect on responses of strong host weeds and strong host crops to AMF. The mean MGR of strong host weeds was lower than that of strong host crops across studies in which N was applied ($P = 0.002$), however, this effect was not observed in the absence of N fertilizers ($P = 0.46$) (Figure 5; Supplemental Table 3; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). Likewise, across studies in which P was applied, the mean MGR of strong host weeds

was lower than that of strong host crops ($P < 0.0001$); however, there was no difference in the absence of P fertilizer ($P = 0.20$) (Figure 6; Supplemental Table 3; <http://dx.doi.org/10.1614/WS-D-16-00050.ST1>). These results indicate that strong host crops may obtain more benefits from AMF than do strong host weeds in the presence of N and P fertilizer. However, high concentrations of plant-available N and P may reduce the abundance of mycorrhizal inoculum in soils (Peng et al. 1993; Treseder 2004). In addition, high fertilizer application brings with it the risk of improving the competitive ability of weeds against crops, because some weeds can absorb more fertilizer-sourced macronutrient, such as N, P, K, and S, through their finely branched root systems than crops (Blackshaw et al. 2003, 2004a; Grant et al. 2007). Therefore, this strategy may be most beneficial to weed control under nutrient management practices that optimize nutrient application rate and timing in relation to the main crop. For example, delayed nutrient application can offer a growth advantage for crops over weeds at the initial stage (Blackshaw et al. 2004b; Di Tomaso 1995; Liebman and Davis 2000). This initial growth advantage of crops may be further assisted by AMF, which disproportionately benefit crops, compared to weeds, in the presence of N and P fertilizers. A better understanding of the interaction between crop and weed host status and soil nutrient availability will help to evaluate when nutrient application will contribute to greater weed control by AMF (Table 1). Incorporating both weed management and soil fertility considerations may be especially helpful for producers to make decisions to achieve better weed control while maintaining good crop yields.

Implications for AMF in IWM. Our meta-analysis of the variation in crop–weed–AMF interactions indicates that knowledge of crop and weed AMF host status and AMF community composition on a particular farm could help producers to decide when AMF offer useful levels of weed suppression. We have shown that crop and weed MGRs are context-specific, responding to both biotic and abiotic factors that are likely to vary at the farm level. Depending upon the conditions and weed communities of a particular agroecosystem, our results suggest that it may be feasible for producers to use different levels of tillage intensity, vegetation management, and soil fertility inputs to manage AMF–weed–crop interactions and thereby enhance IWM (Table 1).

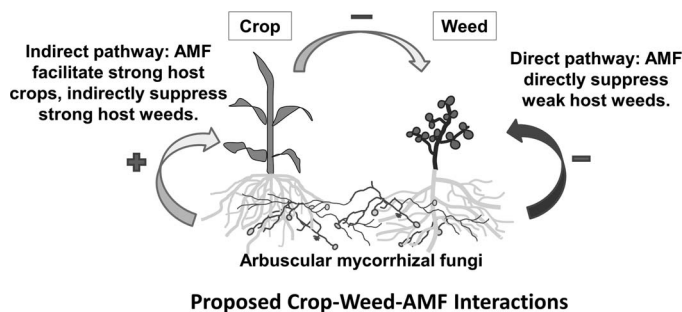


Figure 7. Proposed interactions among crops, weeds, and arbuscular mycorrhizal fungi (AMF). Black arrow: AMF may directly suppress the growth of weak host weeds through impeding their root growth. Grey arrows: AMF may indirectly suppress the growth of some strong host weeds through increasing the competitive ability of their adjacent strong host crops.

Our analysis indicates that weak host weeds show consistent negative responses to AMF. We infer that AMF have potential to directly suppress weak host weeds in fields where host crops are planted, as proposed in Figure 7. Because many weed species are weak hosts, and most major crops are strong hosts, this situation may occur frequently enough to make this approach to IWM useful. Our observations of decreased MGRs of weak host weeds with mixed AMF inocula, compared to single AMF inocula, highlight the need for soil-building management practices which promote AMF diversity, to increase weed control benefits of AMF. In addition, the decreased MGR of weak host weeds in the absence of N or P fertilizer, compared to the condition in which N or P is present, point to the possible value of low input management practices, which also promote AMF diversity, to increase weed control benefits of AMF. Thus, major production practices that establish a relatively vigorous AMF mycelium in soils at the time of weed establishment, such as ridge-till, no-till, application of crop rotation, and less application of synthetic fertilizers and herbicides (Druille et al. 2015; Jansa et al. 2006; Karasawa and Takebe 2012; Zaller et al. 2014), may achieve a strong control over weak host weeds. It is also worth considering that because a number of annual weeds with herbicide resistance biotypes are nonhosts and weak hosts such as the *Amaranthus* species (tall waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer], redroot pigweed [*Amaranthus retroflexus* L.], and Palmer amaranth [*Amaranthus palmeri* (S.) Wats.], common lambsquarters [*Chenopodium album* L.], and wild radish [*Raphanus raphanistrum* L.]) (Heap 2014; Wang and Qiu 2006), the potential benefits of AMF for

weak host weed management may be also useful in areas where given herbicide resistance weeds present (Kremer 2014).

On average, AMF did not differentiate in their impacts on strong host crops and strong host weeds in the studies we analyzed. However, as noted, AMF may differentially benefit high-MGR crops compared to low-MGR host weeds, enhancing indirect weed suppression by crop competition, as proposed in Figure 7. Future work is needed to elucidate the contribution of the specificity of crop–weed–AMF interactions to crop–weed interference within both laboratory and field study systems (Rinaudo et al. 2010; Veiga et al. 2011), given that these interactions may vary in response to physiological, evolutionary, and genetic differences among the species involved. In addition, our results indicate a trend that AMF may benefit strong host crops more than strong host weeds when fertilizer P and N are present. Given the effects of nutrient levels on crops, weeds, and AMF communities, it may useful to develop further strategies for weed control by AMF within an integrated soil fertility–weed management framework (Liebman and Davis 2000).

In summary, our analysis of relevant literature supports proposals (Cameron 2010; Jordan et al. 2000; Kremer 2014; Rinaudo et al. 2010; Veiga et al. 2011) that AMF can contribute to IWM in some situations. Producers make cropping system design decisions, including tillage, fertilization, herbicide application, and diversification practices for a wide range of reasons. Our analysis suggests that improvement in weed control by AMF in IWM could be an additional consideration in decision-making regarding adoption of such practices. Focused research on weed–AMF interactions is needed in a range of agroecosystems to further assess the potential of AMF in IWM.

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