Original article

The impact of arbuscular mycorrhizal fungi on plant growth following herbivory: A search for pattern

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Victoria A. Borowicz*

Behavior, Ecology, Evolution and Systematics Section, School of Biological Sciences, Illinois State University, Normal, IL 61790-4120, USA

ABSTRACT

Arbuscular mycorrhizal (AM) fungi can facilitate nutrient uptake and increase host plant growth but also place constraints on the host's carbon budget. When plants are stressed by herbivory the net effect of the symbiosis may be altered tolerance. Individual experiments manipulating AM fungi and herbivory have demonstrated increased, decreased, and no effect on tolerance but patterns with respect to plant, herbivore, or fungus characteristics have not emerged. Meta-analysis of published results from factorial experiments was used to describe the size of the effects of herbivory and of AM fungi on host growth when factors such as cause of damage, inoculum, and host characteristics are considered, and to determine whether AM fungi alter the effects of herbivory. Also, the correlation between the effect of AM fungi on tolerance and resistance was tested with data from studies that examined insect performance. Herbivory strongly and consistently reduced shoot and root growth, especially in perennial plants and crops. AM fungi increased shoot growth of perennials but not annuals, and when insects caused damage but not when artificial defoliation was applied. Root growth was consistently greater with AM fungi. The interaction of AM fungi and herbivory, which indicates whether AM fungi alter the effects of herbivory, was variable and never significant overall but homogeneity tests indicated underlying structure. In experiments that used single species inoculum, *Glomus intraradices* increased, whereas *Glomus mosseae* reduced, effects of herbivory on shoot growth. Multispecies inocula magnified effects of herbivory on root growth whereas single species inocula ameliorated effects. The impact of AM fungi on resistance to herbivory was positively correlated with the impact on tolerance; however AM fungi reduced both tolerance and resistance in many cases. Review of these results with respect to the types of systems studied suggests directions for future investigation.

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1. Introduction

Arbuscular mycorrhizal (AM) fungi are common root symbionts of plants and ecologically important constituents of soil communities in many habitats (Smith and Read, 2008). Once assumed to be a narrow group of species engaged in mutually beneficial nutritional association with a broad range of hosts, AM fungi are now considered to be taxonomically and functionally diverse (Newsham et al., 1995; Fitter, 2005). Theoretical (Bennett et al., 2006) and empirical studies (van der Heijden and Horton, 2009) present a broader and still evolving view of the role played by these fungi (Fitter, 2005). Nutrient relations remain a major focus and incorporation of carbon cost to the host has produced models depicting an array of effects that better match the reality that these symbionts range from mutualists to parasites (Johnson et al., 1997;

Vannette and Hunter, 2009). In addition to reducing constraints on growth due to P limitation, AM fungi can modify relations between hosts and other organisms including herbivores.

Herbivores chew, scrape, or pierce tissues to obtain photosynthates in shoots, roots, or in transport in vascular tissue. Effects on plants are commonly assumed to be negative and include reduced reproduction and vegetative growth as well as altered population dynamics and competition (Crawley, 1989). However, increased reproduction following herbivory (overcompensation) occurs in some systems (e.g., Paige and Whitham, 1987; Lennartsson et al., 1998). The ability to compensate for losses to herbivores depends upon external factors such as the frequency and timing of herbivory, and resource availability (Maschinski and Whitham, 1989; Turner et al., 1993; Lennartsson et al., 1998) that mediate internal mechanisms of tolerance (Tiffin, 2000).

AM fungi can increase or decrease the ability of a plant to sustain herbivory without loss of fitness, i.e., affect tolerance, if colonization modifies post-damage growth or reproduction. Individual experiments have demonstrated clear effects of AM fungi on

* Tel.: +1 309 438 5208; fax: +1 309 438 3722.
E-mail address: vaborow@ilstu.edu.

tolerance (e.g., Gange et al., 2002; Kula et al., 2005; Bennett and Bever, 2007; Garrido et al., 2010) but general patterns with respect to host, herbivore, or fungus traits have not been identified. Do broad-scale patterns exist? For example, if AM fungi promote host growth, do they also promote tolerance to shoot herbivory? If not broad patterns, do consistent relationships apply to a limited universe, e.g., do AM fungi commonly promote tolerance to shoot herbivory in legumes? Alternatively, is the impact of AM fungi on plant-herbivore relations strictly a function of the combination of host, fungus, enemy, and environment? Identification of clear patterns would better position researchers to pose succinct hypotheses regarding processes underlying effects of this type of symbiont on plant-herbivore relations. Significant, but very restricted patterns might have utility for management purposes.

Meta-analysis has been used to examine the role of arbuscular mycorrhizal fungi in plant resistance to herbivory (Koricheva et al., 2009) and resistance and tolerance to root pathogens (Borowicz, 2001), to evaluate plant growth responses to mycorrhizal colonization as a function of plant and environment characteristics (Hoeksema et al., 2010) and whether herbivory suppresses colonization (Barto and Rillig, 2010), and to compare the magnitude of effects of mycorrhizal fungi to other plant mutualists and antagonists and test for interactive effects among these agents (Morris et al., 2007). Hoeksema et al. (2010) demonstrated that variation in the direct effects of mycorrhizal fungi on plant growth can be explained by factors such as the functional group of the plant, complexity of inoculum, and soil nutrients. These authors argued that future syntheses should continue to examine how the environment determines plant response to the mycorrhizal symbiosis. The analysis presented here specifically focuses on the interplay between herbivory and mycorrhizal fungi in determining plant growth.

This paper reports the results of meta-analysis of factorial experiments that examined the impact of mycorrhizal fungi on plant growth in response to natural and simulated herbivory. Pros and cons of simulated herbivory (Lehtilä and Boalt, 2004) as well as imposed vs. uncontrolled natural herbivory (Tiffin and Inouye, 2000) have been debated. Simulated herbivory may induce different biochemical pathways and subsequently alter patterns of growth and biotic interactions (Hjältén, 2004). Nonetheless, simulated herbivory is commonly employed and arguably provides a more tightly-controlled treatment measuring plant growth. Dismissing these studies would ignore a significant body of work. This analysis includes a test for differences between natural and simulated herbivory.

The main objectives were to: (1) describe the size and consistency of the main effects of herbivory and of AM fungi on host plant growth when factors such as cause of damage, inoculum, and host characteristics are considered, and (2) determine whether association with AM fungi generally alters the growth of plants challenged by herbivores, i.e., alters tolerance. In addition to tolerance, mycorrhizal fungi may affect resistance to herbivory (Koricheva et al., 2009). As alternative defense strategies resistance and tolerance are predicted to be negatively correlated if they draw upon the same pool of resources (reviewed in Strauss and Agrawal, 1999; Leimu and Koricheva, 2006). If AM fungi increase nutrient availability they may boost both tolerance and resistance to herbivory. A subset of the studies included in the present analysis of tolerance also evaluated effects of AM fungi on plant resistance to herbivory by measuring insect performance on colonized vs. AM-free plants. Thus objective (3) was to evaluate the association between effects of AM fungi on tolerance vs. resistance to herbivory.

This analysis of the effects of AM fungi on plant growth response to herbivory is limited to non-woody flowering plants;

nonetheless, this is a broad group that can be parsed in many ways. Patterns, or lack thereof, need to be evaluated against the context of the available data. In assessing this body of work, objective (4) was to highlight under-examined groups in order to suggest fruitful directions for future research.

2. Methods

2.1. Data

Almost all publications used in these analyses were accumulated as they were published. A search of Web of Science Citation Index Expanded data base (from 1985) was conducted in June 2012 with keywords used by Barto and Rillig (2010): mycorrh*and (mow* or clip* or defoliat* or cut* or insect* or graz* or feed* or brows* or pastur* or herbivor* or cattle or cow* or sheep or horse* or rabbi*, in addition to other keywords such as toleran*, resist*, and AM fung*. This search produced only two additional papers that met criteria for inclusion. To be included studies had to: 1) use a full factorial design manipulating herbivory and AM fungi, 2) provide the means, sample sizes, and clearly identified measures of variance, 3) control for effects of other factors, and 4) exhibit differences in colonization between control and experimental AM fungus treatments. The search produced a total of 23 papers that reported one or more experiments, all published between 1990 and 2011 (see Appendix S1 in Supporting Information). Twenty-one papers reported results for potted plants inside and two were field experiments. In the single study in which multiple plant species were included in each replicate, the total biomass across all species was analyzed because the individual species were not independent.

For individual experiments, means and a measure of error about the means were obtained from tables or were extracted from figures using the program ImageJ (Abramoff et al., 2004). In these full factorial experiments AM fungi were manipulated (added/ambient vs. absent/suppressed with fungicide) and plants were damaged or left intact. An "experiment" thus produces means for four treatments. A number of studies reported the results of multiple levels of a factor, such as alternative AM fungus species or several intensities of herbivory. These different levels of a factor are not statistically independent when compared to a common control. One study measured the same plants repeatedly, and these measurements are not independent. Excluding levels of a factor by random selection or by averaging potentially misses important effects. Because the main emphasis of this review is on the range of interactions, each analysis of the most comprehensive data set that included these non-independent data was followed with two additional analyses that retained only one experiment from each set of non-independent experiments. First, only the experiment that yielded the largest positive (or least negative) interaction effect size was retained for each set of two or more non-independent experiments. This was followed by an analysis in which the experiment that yielded the smallest positive (or greatest negative) interaction effect size was retained.

Many plant species respond to resource limitation by increasing investment in the part that gathers the resource in shortest supply (Bloom et al., 1985) and so the effects of AM fungi and herbivory could differ depending on the response variable that was measured and the plant part that was damaged. Most investigators reported a measure of shoot growth (usually shoot mass) and some also reported root growth, but approximately half of the studies examining non-legume forbs reported only total mass. In a preliminary analysis, the outcome of meta-analysis was qualitatively similar for a data set that included total mass with shoot mass and a data set that excluded total mass. Hence, I included experiments that

reported shoot growth or total mass in the same analyses (full data set $n = 59$). Experiments that measured root growth were analyzed separately (full data set $n = 28$).

Data were coded according to year of publication, plant species, part damaged (shoot, root), functional group (legume, grass, or non-legume dicot hereafter called "forb"), life history (annual, perennial), agronomic status (crop, other), agent of damage (insect, simulated), and inoculum (single, multiple species). Such categorizations allows for examination of differences among the classes, such as between simulated vs. insect damage. Although other forms of categorization would be intriguing (e.g., responses to sucking vs. chewing insects), too few experiments were available for useful comparison. The full data set included 25 different host species (10 forbs, 8 grasses, 7 legumes) as well as one mix of three host species. Damage was inflicted by nine different insect species (7 chewers, 1 sucker, 1 scraper), unidentified (presumably insect) herbivory, or three forms of simulated damage (scissors, hole puncher, cork borer). Monospecific inoculum from seven known and one unidentified AM fungus species were used in 30 of the 59 experiments examining aboveground growth. Most of these experiments used one of three species of *Glomus*. To determine whether these most commonly used species evoked similar responses in shoot growth, a data set including only these 23 experiments was created and categorized by species (*Glomus claroideum, Glomus intraradices,* or *Glomus mosseae*).

2.2. Analysis

Meta-analysis was conducted following methods outlined by Gurevitch et al. (2000) for factorial experiments using Hedges' *d*, with modifications by Morris et al. (2007 Appendix B). The latter produces a positive value when presence of the agent improves plant performance and a negative value when plant performance is decreased. A negative interaction indicates that the effect of AM fungi and herbivory together is more detrimental to the plant than predicted based on their individual effects, i.e., AM fungi magnifies the detrimental effect of herbivory. A positive interaction indicates that the effect of AM fungi and herbivory together produce better plant performance than predicted based on individual effects of AM fungi and herbivory. Although Hedges' *d* can overemphasize an effect size if the measure of variance is small (Osenberg et al., 1997), it provides an intuitive measure of direction and relative magnitude of an effect and has been used in similar analyses in the literature. An effect size is deemed significant if its 95% confidence interval does not extend across zero. Bootstrap confidence intervals were generated with the bootstrap option in MetaWin Version 2.0 (Rosenberg et al., 2000) using effect sizes and variance determined from the spreadsheet.

Calculations were performed in an Excel spreadsheet and used a categorical random-effects model. Using the coding described above, data were categorized a number of ways to search for patterns in the response of plants to combined effects of herbivory and AM fungi. A significant homogeneity test using the weighted among-group sum of squares (Q_b) indicated significant differences among classes. Half of the multispecies inoculum involved fungicide-treated soil as the control. Homogeneity test for differences between sterile soil vs. fungicide treatment for the control was not significant and so no distinction was made between these two methods.

Analysis for each manner of categorization proceeded as follows: (1) full (most comprehensive) data set for shoots & total mass, (2) independent data set based on largest (most positive) interaction effect, and (3) independent data set based on smallest (most negative) interaction effect. The procedure was repeated for data on root growth.

To estimate the effect of AM fungi on resistance, Hedges' *d* was calculated with Meta-Win using the difference between the mean performance of insects on AM-free and the mean performance on AM-colonized plants. A positive value indicates that AM fungi increased resistance (=reduced herbivore performance). The correlation between resistance and tolerance (AMF × herbivory interaction) was calculated using the interaction effect size for shoot mass as the measure of tolerance.

3. Results

Means ± 95% CI's for all analyses for the full shoot/total and root growth data sets are presented in Tables S1 and S2, respectively. Whether significant results held for the reduced (independent) data sets are also indicated. Here I present graphical results from the full data sets for analyses in which different ways of categorizing data accounted for significant variance, as indicated by significant homogeneity tests.

3.1. How large and how consistent are the main effects of herbivory and mycorrhizal fungi across a range of factors?

3.1.1. Shoot and total growth

Herbivory caused small to moderately large reduction in growth, and in several experiments, growth was markedly reduced (Fig. 1). The average effect of herbivory in the full data set was consistently large to very large and negative across analyses of shoot growth (Fig. 2, Table S1). Herbivory produced slightly positive or essentially neutral effects on shoot growth in some individual experiments (Fig. 1) and this was most evident when data were categorized by life history (Fig. 2a). The overall effect of herbivory was very large, negative, and significant for perennials but small and not significant for annuals regardless of which data set was analyzed (Table S1).

For the most part, tests for homogeneity for the herbivory effect were not significant when data were categorized in other ways (Table S1), indicating that the response of plants to herbivory was consistent among classes within factors such as cause of damage (simulated vs. insect) and functional group (grass, legume, forb). This was true for the distinction between single vs. multispecies inocula (Fig. 2b) but not when single species inocula were compared. Here the effect size for herbivory was especially large for experiments with *G. claroideum* (Fig. 2c).
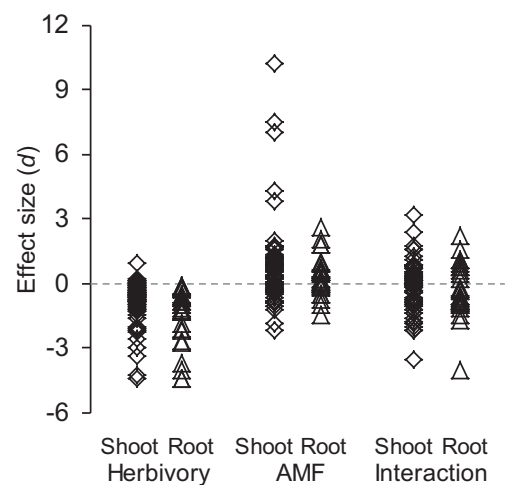

Fig. 1. Effect sizes of herbivory, AM fungi, and their interaction on shoot or total mass (diamonds) and root mass (triangles) from individual experiments in the full data set. $n = 59$ for shoots, $n = 28$ for roots.
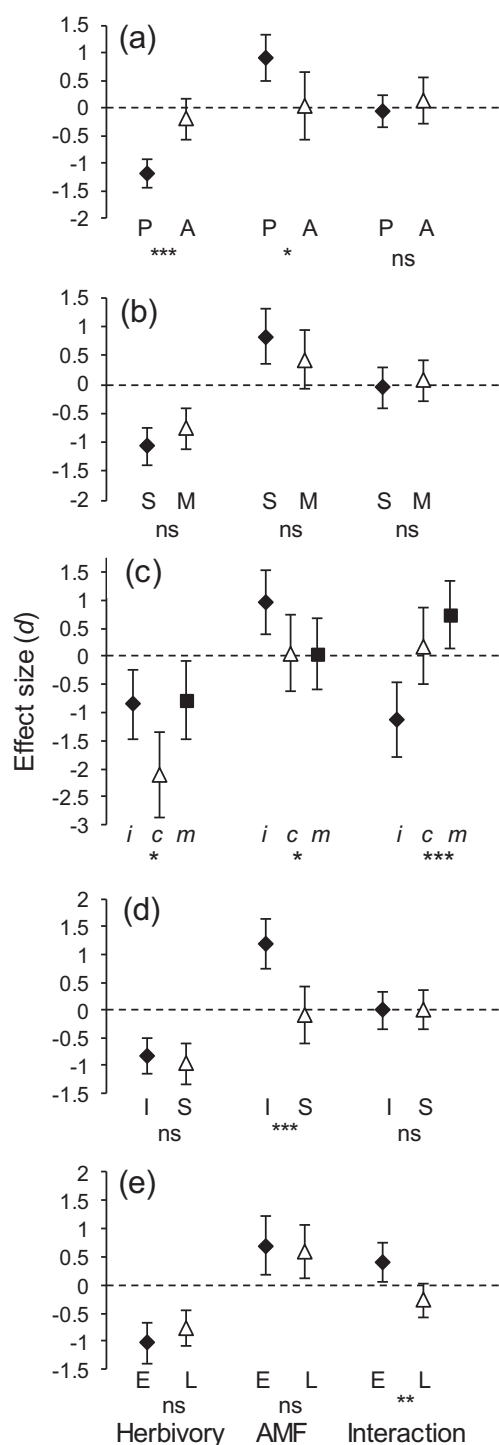
Fig. 2. Mean effect sizes ±95% confidence intervals for overall effect of herbivory, AM fungi, and the AMF × herbivory interaction on dry shoot or total mass. Panels present results from different ways of categorizing experiments in the full data set. (a) Life history: P = perennial ($n = 41$) vs. A = annual ($n = 18$). (b) Inoculum type: S = single species ($n = 30$) vs. M = multispecies ($n = 26$). (c) AM fungus species: $i = Glomus$ $intraradices$ ($n = 10$), $c = G.$ $clairodeum$ ($n = 6$), and $m = G.$ $mosseae$ ($n = 7$), (d) Agent of damage: I = insect ($n = 34$) vs. S = simulated ($n = 25$). (e) Publication date: E = early (papers published through 2005: $n = 32$) vs. L = later (papers published after 2005; $n = 27$). Significant homogeneity tests for differences between classes are indicated with asterisks below each panel. $* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$.

Compared to herbivory, AM fungi produced a broader range of effect sizes (Fig. 1) but the average effect was more moderate in size and positive (Table S1). AM fungi reduced shoot growth in a number of experiments (Fig. 1). The only experiment conducted with a mix of plant species (Kula et al., 2005) had the largest effect of AM fungi but omitting this single experiment did not change the results qualitatively. A significant amount of variance was explained by life history and also agent of damage. Overall, perennials responded positively to AM fungi but annuals showed no consistent pattern (Table S1). The effect of AM fungi on shoot growth was very large and positive in studies with insect herbivory but nil or slightly negative when simulated damage was imposed (Table S1, Fig. 2d).

3.1.2. Root growth

Effects of herbivory on root growth were very large and negative across most ways of categorizing data, including distinguishing by damage imposed on the roots vs. shoots (Table S2). All individual experiments produced negative effect sizes but the average effect size for annuals was not significant (Table S2, Fig. 3a). The mean herbivory effect size was larger for experiments with crop plants but root growth in noncrop plants was still significantly reduced (Table S2; Fig. 3b).

AM fungi increased growth moderately across all analyses of root mass but the range of effect sizes was narrower than for the analysis of shoot growth (Fig. 1). The difference in range may not reflect a biological effect because the experiments that produced the largest effect sizes for shoot growth did not examine root growth. There was a tendency for multi-species inocula to produce a stronger positive effect than single-species inocula (Fig. 3c). Single species inocula produced a small increase in mass that was significant only in the full (nonindependent) data set using parametric confidence intervals as the determinant of significance (Table S2).

Heterogeneity in both the AM fungi and the herbivory effects emerged when the root growth data were organized by year of publication. The mean effect sizes were larger from the group of papers published through 2005; the mean AM fungi effect was not significant for the group of studies published after 2005 (Table S2; Fig. 3d).

3.2. Do AM fungi alter the effects of herbivory on plant growth?

3.2.1. Shoot and total growth

The interaction between herbivory and AM fungi, which indicates whether AM fungi alter the effects of herbivory, was generally very small and rarely significant (Fig. 2a). None of the overall effect sizes (i.e., averaged over categories) were significant suggesting little consistent effect of AM fungi on plant response to herbivory. Two ways of organizing the data accounted for significant heterogeneity in the interaction and produced a significant mean effect size, but only one of these was biologically meaningful. Considering only those experiments with single-species inocula, the response of plants to the joint effects of herbivory and AM fungi depended on the identity of the symbiont (Table S1; Fig. 2c). *G. intraradices* exacerbated the effects of herbivory (very large negative interaction) even though this species significantly increased plant growth overall. By contrast, *G. mosseae* ameliorated herbivory effects (moderate positive interaction) even though, overall, this species did not significantly affect plant growth.

Categorizing by year of publication also explained heterogeneity in the interaction. Those published through 2005 showed a significant, moderate, positive interaction between AM fungi and herbivory, indicating that AM fungi ameliorated the effect of herbivory in these studies, but this was significant only for the nonindependent data set (Table S1, Fig. 2e). The mean for those experiments published later showed a small, negative, nonsignificant effect (Table S1). The opposite signs for the
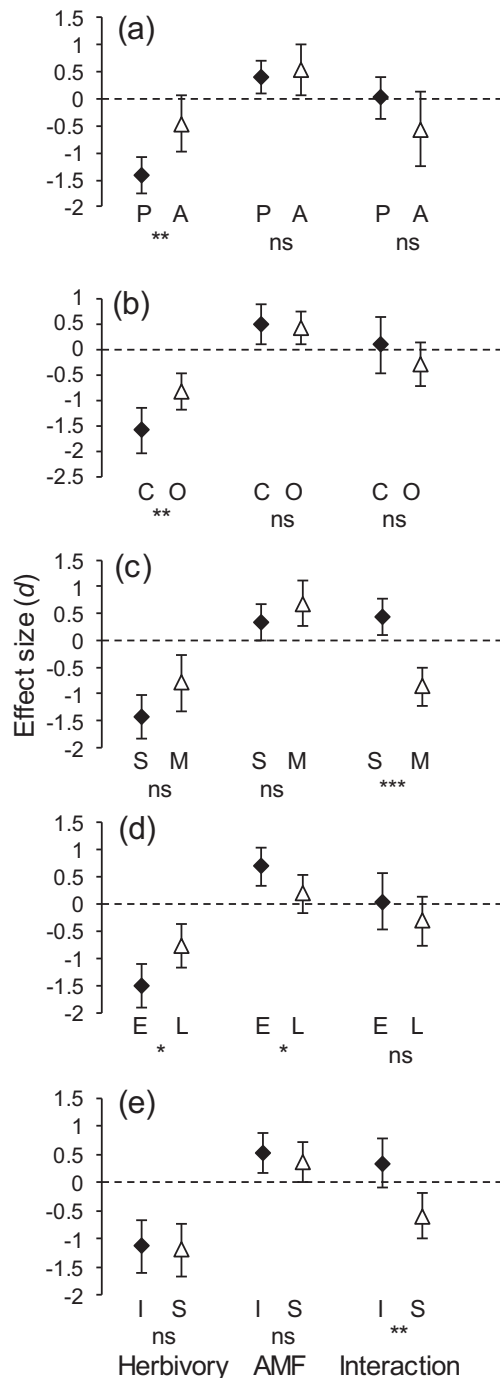
When plants were categorized by agricultural status there was a tendency for crops damaged by herbivory to grow better when colonized by AM fungi. However, the interaction of AM fungi and herbivory was limited to one independent data set (Table S1). Effect size for non-crops was small, negative, and not significant.

3.2.2. Root growth

Similar to analyses of shoot mass, none of the overall effect sizes for the interaction of AM fungi and herbivory were significant, again suggesting little consistent effect of AM fungi on plant response to herbivory (Table S2). Nonetheless, significant heterogeneity was evident for cause of damage and inoculum type. AM fungi tended to ameliorate the effects of herbivory on root growth when the agent of damage was an insect (Fig. 3e), but this interaction was significant in just one independent data set (Table S2). AM fungi tended to magnify negative effects when simulated herbivory was imposed but this effect was not significant when independent data sets were created (Table S2).

The greatest differences between categories emerged in the analysis of inoculum type. Single-species inocula significantly ameliorated effects of herbivory in the full data set and also in the independent data set that included the largest (most positive) effect size from among non-independent experiments. Inoculation with multiple species produced a large, negative effect size in all three data sets (Table S2). Thus, inoculation with a single species reduced the difference in root growth between damaged and undamaged plants whereas inoculation with two or more species magnified the effect of herbivory (Fig. 3c).

3.3. Is the impact of AM fungi on tolerance independent of an effect on resistance?

Twenty experiments that examined the effects of AM fungi on shoot mass also evaluated performance of the insect herbivore. Inoculation with AM fungi increased resistance (effect size >0) in 11 experiments and decreased resistance (effect size <0) in 9 experiments. Plotting effect sizes for insect resistance against the effect sizes for the AM fungi × herbivory interaction places all but four points in the upper right or the lower left quadrants (Fig. 4).

Fig. 3. Mean effect sizes ±95% confidence intervals for overall effect of herbivory, AM fungi, and the AMF × herbivory interaction on dry root mass. Panels present results from different ways of categorizing experiments in the full data set. (a) Life history: P = perennial ($n = 20$) vs. A = annual ($n = 8$). (b) Plant type: C = crop ($n = 12$) vs. O = other ($n = 16$). (c) Inoculum type: S = single species ($n = 16$) vs. M = multispecies ($n = 9$). (d) Publication date: E = early (papers published through 2005; $n = 16$) vs. L = later (papers published after 2005; $n = 12$). (e) Agent of damage: I = insect ($n = 14$) vs. S = simulated ($n = 14$). Significant homogeneity tests for differences between classes are indicated with asterisks below each panel. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

interactions noted above for *G. mosseae* vs. *G. intraradices* may explain this heterogeneity. The former was used in a greater proportion of experiments through 2005 whereas the latter was included in a greater proportion of experiments after 2005.
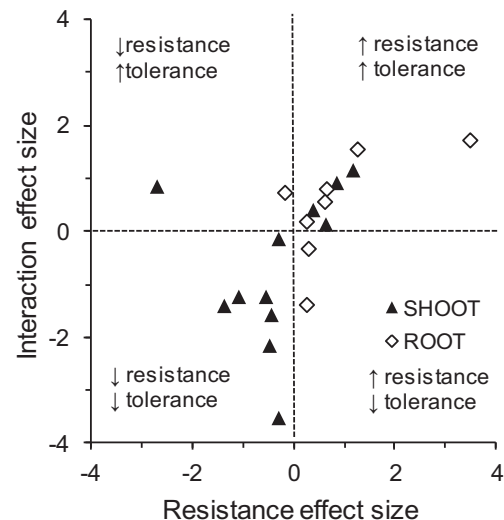

Fig. 4. Association between effects of AM fungi on plant resistance (insect performance) and tolerance to herbivory (interaction between AM fungi and herbivory) on shoot growth. Values are Hedges' d calculated from experiments that reported measures of both resistance and tolerance. Values are coded by part of plant damaged for illustrative purposes.

Thus the impact of AM fungi on insect performance was positively correlated with the impact of AM fungi on tolerance measured as shoot mass (Pearson product moment $r = 0.492$, $P = 0.031$, $n = 20$). Nonetheless, both tolerance and resistance declined in many cases. AM fungi increased resistance in seven of the eight experiments in which damage was imposed on roots (Fig. 4). Approximately one-third of the experiments used G. intraradices as the sole inoculum, and this AM fungus decreased both resistance and tolerance in six of these seven experiments. Only two experiments involved sap-feeders and these are the two values plotted in the upper right quadrant closest to the origin, indicating very small increases in resistance and tolerance. These were not independent values because effects on the plant were measured against a common control (Hempel et al., 2009).

4. Discussion

The main effects of herbivory and AM fungi on plant growth were clear and significant even though individual experiments deviated from overall trends: herbivory reduces plant growth and, under the conditions investigators usually conduct AM fungus studies, AM fungi generally increase plant growth. In contrast, the interaction effects were not significant overall and much more variable than either herbivory or AM fungi separately; no broad patterns in the effect of AM fungi on plant-herbivore relations were evident. Some ways of categorizing data indicate that AM fungi modify the impact of herbivory in more circumscribed systems, yielding patterns in AM fungi–plant-herbivore relations that are limited in scope. Although meta-analysis provides a quantitative summary of available data it is, like any review, subject to bias in what investigators have chosen to study (Gurevitch et al., 2000). Next, I review the results with respect to characteristics of the data to suggest which patterns are robust vs. which may be the product of research bias, and to suggest profitable directions for future study.

4.1. Responses to overall effects of herbivory and AM fungi

Life-history accounted for significant variation in root and shoot growth following herbivory, with perennials responding more strongly, and this agrees with a global assessment of herbivory (Díaz et al., 2007). However, the nonsignificant effect for annuals could be a product of sampling bias with respect to life history. Among functional groups, grasses tended to have larger effect sizes for aboveground growth and all grasses were perennials. In other meta-analyses, monocot herbs, or more specifically grasses, were more responsive to herbivory than dicot herbs (Bigger and Marvier, 1998; Hawkes and Sullivan, 2001; Zvereva and Kozlov, 2012). Consequently, the nonsignificant effect of herbivory for annuals could be biased by an absence of experiments with annual grasses.

The effect of herbivory on plant performance has been examined in a number of meta-analyses, yielding a range of values for the effect sizes. Morris et al. (2007) suggested that their herbivory effect was larger than that determined by Bigger and Marvier (1998) because the latter included more vertebrate studies, which generally had smaller herbivory effect sizes than did experiments with invertebrates. Yet, the effect size for experiments with insects in a subsequent analysis of root herbivory was intermediate to the other two meta-analyses (Zvereva and Kozlov, 2012). By contrast, Zvereva and Kozlov (2012) found the effects on aboveground growth were very large when root damage was applied artificially, which is a treatment that neither Bigger and Marvier (1998) nor Morris et al. (2007) included. Because effects of simulated herbivory may not parallel insect herbivory (Hjältén, 2004) investigators need to interpret results cautiously. Approximately 45% of the

experiments in the present meta-analysis of non-woody plants used simulated herbivory, however the main effect sizes for natural and simulated herbivory did not differ regardless of plant part measured. Nykänen and Koricheva (2004) also found no difference in their analysis of woody plants.

The difference between natural and simulated herbivory was evident for the main effect of AM fungi on shoot growth, where experiments employing live insects produced a very large and positive effect size for AM fungi, but the effect size from experiments employing simulated herbivory was nil. Indeed, AM fungi were functionally parasitic in more than half of the individual experiments with simulated herbivory. The herbivory effect size was similar across levels of AM fungi indicating that the response to AM fungi was probably unrelated to the type of damage that was imposed; colonized plants simply grew more, regardless of herbivory, in experiments that involved live herbivores. The strength of response was probably determined by the type of inocula investigators chose to use in those experiments.

71% of the experiments with insects used single-species inocula, including all 10 of the experiments with G. intraradices, compared to 24% of experiments imposing simulated damage. Although not significantly different from multi-species inocula, individual AM fungi species tended to promote greater shoot growth, largely due to experiments with G. intraradices. These results underscore calls for caution regarding interpretation of effects from single AM fungi species or non-native combinations of AM fungi and host (Klironomos, 2003; Klironomos et al., 2004; Bennett and Bever, 2009; Koricheva et al., 2009; Baoming et al., 2010).

Contrary to Hoeksema et al. (2010), categorizing data by functional group did not reveal any consistent trends. Their analysis partitioned grasses into C_3 vs. C_4 species, where C_4 grasses tended to exhibit larger positive responses to AM fungi than did C_3 grasses, a response that has been linked to root structure (Hetrick et al., 1988, 1991; Miller et al., 1997). Investigators have not examined the interactive effects of AM fungi and herbivory on C_4 grasses and so I could not make this distinction. The generally weak effect of AM fungi on growth of the C_3 grasses included here agrees with other reports (Wilson and Hartnett, 1998; Hoeksema et al., 2010).

4.2. Responses to combined effects of herbivory and AM fungi

Although individual experiments have demonstrated that AM fungi ameliorate the effects of herbivory, this review produced strikingly little support for the hypothesis that AM fungi generally do so. An effect of AM fungi on the impact of herbivory was most clearly expressed when experiments were classified by inoculum type. Although single species inocula tended to diminish the negative effects of herbivory on root mass, multispecies inocula, arguably the more natural state, magnified the effects of herbivory. This was true even though, as a main effect, AM fungi promoted root growth. Furthermore, AM fungi as partners are not interchangeable, as evident from the shoot growth of plants in response to herbivory when partnered with G. intraradices, (exacerbated the effect of damage) compared with G. mosseae (moderated effects of damage). Interestingly, G. intraradices tends to reduce performance of chewing insects, opposite of the effect of G. mosseae and other species (Koricheva et al., 2009). In future experiments it would be interesting to determine whether reduced performance of insects, i.e., increased resistance, is due to reduced quality of the plant as food and whether this translates into increased consumption.

Meta-analysis of herbivory and resource supply (Hawkes and Sullivan, 2001) suggests that high resource concentration reduces effects of herbivory for graminoids but increases effects for dicot herbs and woody plants. If plants respond to addition of AM fungi as they do to increased nutrient supply, the interaction in the

present study should be positive for grasses and negative for legumes and other forbs. No such trend was observed which may underscore the biological differences between acquiring resources directly from the soil via roots vs. uptake facilitated by symbionts, which can demand significant investment by the host (Douds et al., 1987; Johnson et al., 1997).

In many species, shoot herbivory leads to reduced allocation to roots as the plant invests relatively more in replacement of lost photosynthetic tissue (Bloom et al., 1985). Carbon limitation may also explain reduced mycorrhizal colonization following herbivory (Gehring and Whitham, 2002) although analysis of a broad scope of studies revealed no significant pattern of mycorrhizal colonization and herbivory (Barto and Rillig, 2010). If AM fungi are more costly when the shoot is damaged, the benefit would be reduced in the presence of herbivory, i.e., a negative interaction. The interaction effect was negative when the shoot was damaged regardless of how the data set was constructed, but it was also always small and never significant.

Despite calls for more attention to root herbivory (Brown and Gange, 1990; Blossey and Hunt-Joshi, 2003; Van der Putten, 2003) relatively few experiments imposed belowground damage. Nonetheless, root herbivory significantly impairs root and especially shoot growth and many plants are less tolerant of belowground damage (Zvereva and Kozlov, 2012). By facilitating nutrient uptake, AM fungi might be especially valuable partners when root herbivory diminishes the plant's own infrastructure for acquiring nutrients. If AM fungi compensate for lost root functioning, they may effectively blunt the negative effect of root herbivory, and this should result in a positive interaction for shoot growth when roots are damaged. But AM fungi did not significantly increase shoot or total growth of plants stressed by root herbivory. The benefit to plants from mycorrhizal fungi is likely to vary nonlinearly with colonization level (Gange and Ayres, 1999) and nutrient availability. Factorial experiments may fail to capture the full range of AM fungus effects on responses to herbivory where damage varies quantitatively. Experiments that vary the intensity of damage to roots may better evaluate this hypothesis regarding the importance of AM fungi in augmenting root function.

Assuming that mechanisms of resistance and tolerance compete for plant resources, trade-offs between resistance and tolerance would be manifest as a negative correlation between post-herbivory plant growth and insect performance. Leimu and Koricheva (2006) failed to detect a significant relationship overall, suggesting that these two strategies are not mutually exclusive. The analysis presented here asks a different question, i.e., do AM fungi alter resistance and tolerance in the same direction? The answer is yes. The positive correlation between effect of AM fungi on insect performance (resistance) and effect of AM fungi on plant tolerance of herbivory (interaction) suggests that mycorrhizal fungi increase the resource base for plants to draw upon. Bennett et al. (2006) envisioned a phase plane formed by trade-offs among resistance, tolerance, and growth. Assuming that plants benefit nutritionally from AM fungi, Bennett et al. (2006) hypothesized that AM fungi free the host from these constraints and allow the plant to "step off" the phase plane. However, AM fungi may be functionally parasitic if the host plant's growth is not limited by nutrients. By taxing its host's ability to amass photosynthates, AM fungi may move the plant down the phase plane toward the origin. This effect describes the coupling of decreased tolerance with decreased resistance in roughly half of the experiments (Fig. 4).

Alternatively, the positive correlation between effects of AM fungi on tolerance and resistance would be predicted if poorer insect performance results in lower consumption, as expected if AM fungi boost or induce chemical or morphological defenses that result in suppressed feeding ("modification of defense" model of

Bennett et al., 2006). Colonization by AM fungi is associated with induction of a number of secondary chemicals (reviewed in Bi et al., 2007; Pozo and Azcón-Aguilar, 2007) but induction can vary with species of AM fungi (Bennett and Bever, 2007). Further, AM fungi may prime systemic defense against subsequent challenge by herbivores during the process of establishing a functioning symbiosis (Jung et al., 2012) as well as determine subsequent resistance following initial herbivory (Kempel et al., 2010). Despite these effects of AM fungi on plant chemistry, colonization by mycorrhizal fungi tends to increase consumption of plants by chewing insects (Koricheva et al., 2009; Barber, 2012).

4.3. Gaps in the data and other caveats

Taking a global perspective of response to grazing, Díaz et al. (2007) suggest that predictions regarding plant traits and herbivory should take into account regional climate and herbivory history. These factors are almost totally ignored in experiments of AM fungi and herbivory. In the present study, all 25 simulated defoliation and all but 6 of the 32 insect experiments were conducted with potted plants in greenhouses. Further, many experiments used agricultural species or commercially-prepared inocula, likely divorcing the interacting species from their joint ecological and evolutionary histories. In other meta-analyses the interaction between mutualists and enemies of plants was significant in the greenhouse but not field (Morris et al., 2007), and the effects of root damage were significant in agricultural but not natural systems and larger in the greenhouse setting (Zvereva and Kozlov, 2012). These lines of inquiry suggest that context is not trivial. Manipulation of AM fungi is more difficult in the field and results more variable, but placing these interactions in the context of the environments we wish to draw conclusions about is nonetheless important (Gehring and Bennett, 2009; Reidinger et al., 2012). More experiments that manipulate AM fungi in situ (e.g., Gange et al., 2005) or compare results from the greenhouse to those from the field (e.g., Pringle and Bever, 2008) are needed to determine whether the patterns observed in the highly reductionist setting of the greenhouse emerge when placed in the context of communities. It is nonetheless encouraging that Koricheva et al.'s (2009) analysis of impact of AM fungi on resistance to insects found no significant difference in performance of insect herbivores in field vs. laboratory experiments or in experiments controlling AM fungi with fungicide vs. inoculation.

Differential effects of single-species inocula raise the potential of crafting inocula commercially to match the needs of growers (Vannette and Hunter, 2009). However the results for G. intraradices and G. mosseae suggest that a grower's motivation for using AM inoculum should be considered carefully. Overall growth benefits are not necessarily coupled to positive effects on tolerance. Although they have management implications, results from experiments with monospecific inocula provide little insight into natural settings where individual plants host a community of fungi that differ between co-occurring plant species and over time (Vandenkoornhuyse et al., 2002). Further, environmental effects may alter AM fungus community composition in some host species but not in other species in the same community (Vandenkoornhuyse et al., 2003) and the host community itself affects the composition of AM fungi in a target species (Johnson et al., 2004). Studies that examine the interactive effects of herbivory and entire communities of AM fungi are likely to find the conclusion that mixed species inocula reduce tolerance is too simplistic a view.

AM fungi are only one of several types of symbiotic fungi colonizing roots of terrestrial plants but this group has received the most attention. A number of interesting studies have examined

aspects of indirect interactions between ectomycorrhizal fungi and herbivores (e.g., Del Vecchio et al., 1993; Gehring et al., 1997; Rieske, 2001; Nerg et al., 2008; Sthultz et al., 2009; also see reviews by Gehring and Bennett, 2009; Barto and Rillig, 2010) but effective factorial experiments evaluating tolerance are few. Given that ericoid mycorrhizal fungi are important for nitrogen relations of the host (Read and Stribley, 1973; Read and Bajwa, 1985) and that nitrogen supply affects insect performance (Kerslake et al., 1998; Ritchie, 2000) and infection by ericoid fungi (Hartley and Amos, 1999), it is surprising that ericoid mycorrhizal fungi have not received attention. Similarly, combined effects of herbivory and mycorrhizal fungi on orchids remains unexplored despite the economic significance and conservation issues for this largest of plant families (Dearnaley, 2007).

Effect of AM fungi on resistance to insect herbivory appears to be associated with the mode of feeding where sapsuckers benefit and leaf chewers do worse with AM fungi (Koricheva et al., 2009). AM fungi may prime systemic defense by stimulating production of jasmonic acid which is especially effective against chewers (Conrath et al., 2006; Pozo and Azcón-Aguilar, 2007; Jung et al., 2012). If AM fungi increase the plant's investment in ineffective defenses and promote herbivory by increasing quality of food for herbivores, colonization may reduce the plant's ability to compensate for herbivory (Vannette and Hunter, 2009). It would be interesting to know whether mode of feeding is related to impact of AM fungi on tolerance but only two experiments in this meta-analysis were identified as sapsuckers and the great majority was leaf chewers. Thus there is a dearth of studies with sapsuckers in general and complete absence of xylem-feeders, which may impose a particularly large burden on plants (Meyer and Root, 1993). Experiments that integrate mode of herbivory, demands of AM fungi, and the chemical basis of defense in the host plant are needed to elucidate mechanism underlying patterns.

This examination of AM fungi—plant-herbivore systems demonstrated some patterns that may come into sharper focus with additional study. However it is important to not overextend what this and other analyses thus far say. Meta-analysis allows comparison of studies that differ in the original metric by synthesizing an effect size, but studies included in meta-analyses typically differ in many factors. Stage of plant development, timing and intensity of herbivory, recovery period, plant species, AM fungi communities, and abiotic conditions are specific to individual studies and these are all factors that affect tolerance (Strauss and Agrawal, 1999). Categorization by one factor doesn't resolve other sources of heterogeneity that may obscure, or magnify subtle differences between categories. Finding — or failing to find — a significant effect of herbivory, AM fungi, or an interaction in itself is no longer news. Nonetheless, demonstrating the context that would produce consistent effects and the universe for which that context applies requires many more experiments conducted across a range of species and environmental conditions. Disentangling the interactive effects of above- and below-ground communities continues to be a complex yet enlightening endeavor.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2013.06.004.

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