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Influence of arbuscular mycorrhiza on growth and reproductive response of plants under water deficit: a meta-analysis

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Abstract Despite a large body of literature that describes the effects of arbuscular mycorrhizal colonization on plant response to water deficit, reviews of these works have been mainly in narrative form, and it is therefore difficult to quantify the magnitude of the effect. We performed a meta-analysis to examine the effect of mycorrhizal colonization on growth and yield of plants exposed to water deficit stress. Data were compared in the context of annual vs. perennial plants, herbaceous vs. woody plants, field vs. greenhouse conditions, degree of stress, functional group, regions of plant growth, and mycorrhizal and host species. We found that, in terms of biomass measurements, mycorrhizal plants have better growth and reproductive response under water stress compared to non-mycorrhizal plants. When variables such as habit, life cycle, or water stress level are considered, differences in mycorrhizal effect on plant growth between variables are observed. While growth of both annual and perennial plants is improved by symbiosis, perennials respond more favorably to colonization than annuals. Overall, our meta-analysis reveals a quantifiable corroboration of the commonly held view that, under water-deficit conditions, plants colonized by mycorrhizal fungi have better growth and reproductive response than those that are not.

Keywords Meta-analysis · Plant growth · Symbiosis · Arbuscular mycorrhizal fungi · Water stress

Introduction

An estimated 80 % of terrestrial plants have arbuscular mycorrhizal associations during some or all of their life stages (Schussler et al. 2001). Thousands of studies have tested the physiological effect of mycorrhiza on plants, and many show a positive influence on plant function and fitness; symbiosis with arbuscular mycorrhizal fungi (AMF) is commonly considered to be highly beneficial for plants (Ruiz-Lozano et al. 1995; Clark and Zeto 2000). The mycorrhizal condition is shown to have wide-ranging effects on host plants, from improved nutrition (Marschner and Dell 1994) and stress tolerance (Marulanda et al. 2009) to herbivore defense (Gange and West 1994; Hempel et al. 2009) and disease resistance (Liu et al. 2007; Trotta et al. 1996). Fungal hyphae can even act as a means of resource sharing between two otherwise unconnected plants (Chiariello et al. 1982).

Interactions between microbial organisms and their host plants range from mutualism to parasitism. Most agronomically important fungal organisms are classified as disease-causing crop pests, parasites that kill or injure their hosts while consuming tissues or resources. In contrast, there are mutualistic microbes that improve host fitness or resource acquisition in exchange for other resources or habitat. Commensal relationships, in which one partner benefits while the other is left unimproved but unharmed, occupy the center of the range. AMF may span the continuum from weakly parasitic to mutualistic, depending upon environmental and biological conditions (Kogel et al. 2006). While the mycorrhizal symbiosis yields increased access to phosphorous (P), in high-P soil conditions mycorrhizal colonization may actually result in a carbon deficit to the plant, resulting in a negative growth response (Graham and Eissenstat 1998; Mortimer et al.

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2005). Although entirely non-mycorrhizal plants are rare in nature, certain soil disturbances, such as tillage, not only break up large water-stable aggregates (Beare et al. 1994) but can also reduce AMF abundance (Drijber et al. 2000). Urban and suburban development includes topsoil removal and compaction, depressing the local soil biota as well as altering soil structure. Manipulative studies can illustrate the benefits of inoculating AMF into disturbed and depleted soils.

Presence of AMF in soil has some influence on plant fitness beyond root colonization. Auge et al. (2001) showed that soil grown with mycorrhizal cowpea (*Vigna unguiculata*) for 7 months had more water-stable aggregates and extra-radical hyphal densities than soil with non-mycorrhizal cowpea, even when root mass, length, surface area, and density were similar. A later experiment (Auge 2004), in which wild-type and non-mycorrhizal mutant bean plants (*Phaseolus vulgaris*) were grown for 12 months in soil colonized with *Glomus intraradices* and *Gigaspora margarita* produced on sorghum (*Sorghum bicolor*), demonstrated that about half of the increase in stomatal conductance (g_s) was derived from soil colonization by AMF, illustrated by the increased g_s in non-mycorrhizal bean relative to the wild type. In other words, mycorrhizal soil affected non-mycorrhizal plants growing in that soil.

The aim of the present meta-analysis study was to establish a statistical quantification of the effect of mycorrhiza on water-stressed plants. It is not intended as an examination of the mechanistic or molecular means of AMF influence but rather the frequency and degree of that influence on plants. Collectively, the studies included 36 measures of plant growth of 43 host species in 41 plant genera and at least 18 species of AMF within five genera. The analysis was framed to address the question on whether symbiosis has a real effect on plant response to water deficit and, if so, what is the overall effect size. Although vote counting would indicate that mycorrhizal symbiosis does improve plant performance, reporting effect size is a better way to illustrate the magnitude of the effect. Other important questions can also be answered, depending upon the volume and quality of the collected data; for example:

1. Is the size of the effect different between plant growth variables? In other words, do variables such as life cycle (annual vs. perennial) or lifestyle (herbaceous vs. woody) affect response to the symbiosis?
2. Is the effect of symbiosis different among study locations, such as field or nursery vs. greenhouse or growth chamber conditions? Interpretations of study site data vary. One meta-analysis has shown greenhouse plants to be more significantly improved by mycorrhiza than field plants (Lekberg and Koide 2005), while another called the effect “relatively unimportant” when other variables are controlled (Hoeksema et al. 2010).
3. Are certain plant functional groups more improved by AMF colonization? Response to the symbiosis varies among grasses (Hartnett et al. 1994), and there may not be a synergistic effect of co-inoculation of AMF and N-fixing bacteria associated with legumes despite improved access to different macronutrients (Larimer et al. 2010).
4. Does the effect correlate to the stress level experienced by the plant? Are more stressed plants improved to a greater degree than less stressed plants? AMF colonization can be prevented under non-limiting conditions, and the carbon costs of mycorrhiza can be classified as parasitic if plants can independently obtain sufficient resources.
5. Does effect size differ among treatments with AMF species? In our analysis, we examined single species of AMF, combinations of species, and consortia of AMF from different origins; however, the large majority (89.7 %) of previous experiments investigated the effects of treatments with species of *Glomus*. Are certain species of *Glomus* more effective at improving plant–water relations?
6. Are plant parts affected differently by mycorrhiza depending on the plant species and the variable being analyzed? If measures are grouped into categories that represent aboveground, belowground, reproductive, or whole plant growth, do we see improvements in some of these categories more than others either between or within a variable such as life cycle or study site?

The meta-analyses that we conducted to answer these questions included measures of all plant growth parameters using the log-transformed response ratio or log response ratio (LRR). LRR measures the proportionate change between treatment and control groups (Hedges et al. 1999), log-transformed to account for variability. In our analysis, this is mycorrhizal (M) to non-mycorrhizal (NM) plant growth, or $\ln(X_M/X_{NM})$, transformed due to the high variation in values of plant growth parameters collected from the literature.

Methods

Eligibility criteria for included studies

Data sources were found in studies through searches of Web of Science (Institute for Scientific Information), ProQuest Dissertations & Theses (PQDT), and references therein using the keywords *arbusc**, *mycorrhiz**, *water*, and *stress*. We used the Boolean truncation (*) to include variations of the primary terms of interest. These searches yielded 285 published and unpublished studies dating from 1983; however, works had to meet certain eligibility criteria to be included. For instance, the analysis had to be a manipulative study comparing water-stressed mycorrhizal and non-mycorrhizal plants. After reading the abstracts of the 285 articles, 221 papers were rejected based on these criteria and the list was refined to 64 eligible studies. Still more were excluded because data were only reported graphically and authors were unresponsive to requests for raw data, ultimately resulting in 54 eligible studies. For any study to be eligible, results had to be reported as tabular numerical data. We omitted research with data that were not a measure of morphological growth or yield (e.g., biomass) and defined growth as a change in size or numbers of observable plant parts between treatment and control groups after the study period. Parameters such as nutrient content, gene expression, photosynthetic rate, or other biochemical or metabolic effects were not included in the meta-analysis.

Study Coding

Information was collected from each of the 54 eligible studies (Supplementary material) on mycorrhizal classification, host plant classification, life cycle, habit, test site and growth measure, as well as statistical data including sample size, mean effect, and standard deviation/error. In some cases where a mix or consortium of inocula was used, we used collective terms when specific identification was not available. For example, a default label of "AMF" was used if fungal genera were mixed or not identified and "spp" if species were mixed or not identified to a genus. Additionally, we collected relevant notes that were important to the treatment or result, such as plant age, water content data, or stress period/severity (Supplementary material). Plant growth parameter labels had a broad range but followed a common motif, typically two to three words beginning with the plant part, tissue type, or collective term followed by the metric and units, such as *root dry weight* (*g*). A total of 36 different measures of plant growth were considered in the analysis. When it was clear that the authors used terms synonymously with common plant terms, for example, *foliar area* versus *leaf area*, we substituted the more common terminology. In some cases, similar measures were reported in different units; when this occurred, we converted the less commonly reported units to the most common. Shoot height, for instance, was most often reported in centimeters (cm), so if a study reported shoot height as 0.6 m, this was changed to 60 cm. While field and nursery experiments may sometimes yield different results and greenhouses and growth chambers have environmental controls of varying precision, we chose to categorize all outdoor studies as "field" and all indoor experiments as "greenhouse". Where the level of water stress was reported, typically in terms of percent soil moisture or mPa of soil water pressure, and more than one stress-level was tested, the data were placed into low, moderate, and high categories according to this value. Most of these variables were included in the selected studies or could be deduced from the information provided (i.e., lifestyle could be determined from the plant species); however, even studies with some information missing could be included in subset analyses of the variables they reported. Studies were coded to include the following variables: life cycle (annual or perennial), lifestyle (herbaceous or woody), study site (field or greenhouse), functional group (tree/shrub, forb, grass, or legume), water regime (water-stressed or well-watered), and water stress level (low, moderate, or severe).

Calculating effect sizes

Each unique assemblage of variables was coded as a single observation for calculating effect size. For example, in a study examining the effect of *Glomus mosseae* on leaf area (cm^2), root dry weight (g), and flower count of pepper and cucumber, these variables yield six effect sizes in combination: one mycorrhizal treatment × two plant species × three growth parameters. Complex multi-factorial studies can, therefore, produce a large number of effect sizes.

Regrettably, only a few of our colleagues studying water relations of plant–mycorrhizal ecology reported data sufficient for all meta-analytical methods. Many excellent papers were rejected from consideration simply for presenting data exclusively in a graphical format. In most cases where tabular numerical data were reported, no measure of variation was included. Only 14 of the 54 experiments cited here provided adequate detail to calculate Hedges' d, a commonly reported effect size. A few studies even failed to explicitly indicate the sample size in their methods. One reason why many of these studies needed to be removed could be that their publication date, from the 1980s and 1990s, was before it was widely advocated to include effect size in published data. In graphically reported data, measures of variation are usually illustrated using error bars, and although it is possible to digitize graphs to determine means and variation (Borowicz 2001), we elected to exclude them from meta-analysis due to limitations in our study. To broaden the analysis to all studies that minimally included mean effect and sample size, the natural log-transformed response ratio or log response ratio was used. The effect size was calculated using Meta-Win (Sinauer Associates, Sunderland, MA, USA). Effect size values are positive if treatment yields an increase in the plant growth measure compared to untreated controls and negative if treatment is deleterious to plant growth.

Results analysis

Tests for significance were conducted in JMP version 9 (SAS Institute Inc., Cary, NC, USA) using one-way analysis of variance. Most tests were between binary variables such as annual vs. perennial or herbaceous vs. woody. Some tests, however, were on summary statistics of certain treatments or measures that included more than two factors. If a significant difference was discovered between three or more variables, post hoc tests using Tukey–Kramer HSD were adopted to determine which means were different. Statistical tests were conducted on effect size of water-stressed treatments unless otherwise indicated. We analyzed the overall effect of AMF colonization, the overall effect of colonization between two or more variables, the improvement of categorical regions of plant growth, i.e., aboveground (AG), belowground (BG), reproductive (RP), or whole plant (WP) between variables, and the improvement of categorical regions of plant growth within a variable.

Results

Overall effects

Under water deficit conditions, mycorrhizal plants outperform non-mycorrhizal plants in most measures of growth and yield. The overall log response ratio of 0.324±0.020 (Fig. 1) was determined from 602 effect size calculations of water-stressed plants. Only measures with an effect size $n>1$ were included in the calculations. The positive mean value indicates an overall growth-promoting effect of mycorrhiza in plants under water stress. Pod dry weight and grain head count ($n=20$ and $n=4$, respectively) were not significantly changed, while shoot/root ratio ($n=3$) and shoot growth ($n=2$) were negatively affected by AMF colonization. Total calculations for some of these parameters may be inadequate. Indeed grain head count, shoot/root ratio, and shoot growth were measured only in single studies. When growth measures are organized into categories that represent the primary region of plant growth, i.e., AG, BG, RP, or WP, mean effect sizes are all positive. A difference in the overall effect of AMF colonization is evident between regions of growth ($F_s=3.50$; df=3, 601; $P=0.015$). Whole plant measures showed the most improvement from mycorrhiza. Significant differences are between WP and BG ($P=0.013$) and AG and BG ($P=0.044$). There are no differences between any other groups (Fig. 2).

Effects of plant habit variables

In response to water stress, mycorrhizal annuals and perennials perform differently ($F_s=13.14$, df=1, 601; $P=0.0003$) (Fig. 3). Both respond favorably to the symbiosis; however, perennial species show more growth overall with a mean LRR of 0.272±0.024 for annuals and 0.426±0.036 for perennials. WP growth in perennial plants is higher than in annual plants ($F_s=17.52$; df=1, 139; $P<0.0001$) but AG, BG, and RP growth is the same. Mycorrhiza have no effect on annual plant shoot dry weight ($n=57$), pod dry weight ($n=16$), total dry weight ($n=26$), or shoot/root ratio ($n=3$). Among perennials, root/shoot ratio ($n=8$) is unaffected, and shoot growth ($n=2$) is negatively influenced.

There is also a difference between herbaceous and woody plant response to the mycorrhizal symbiosis ($F_s=9.07$; df=1,

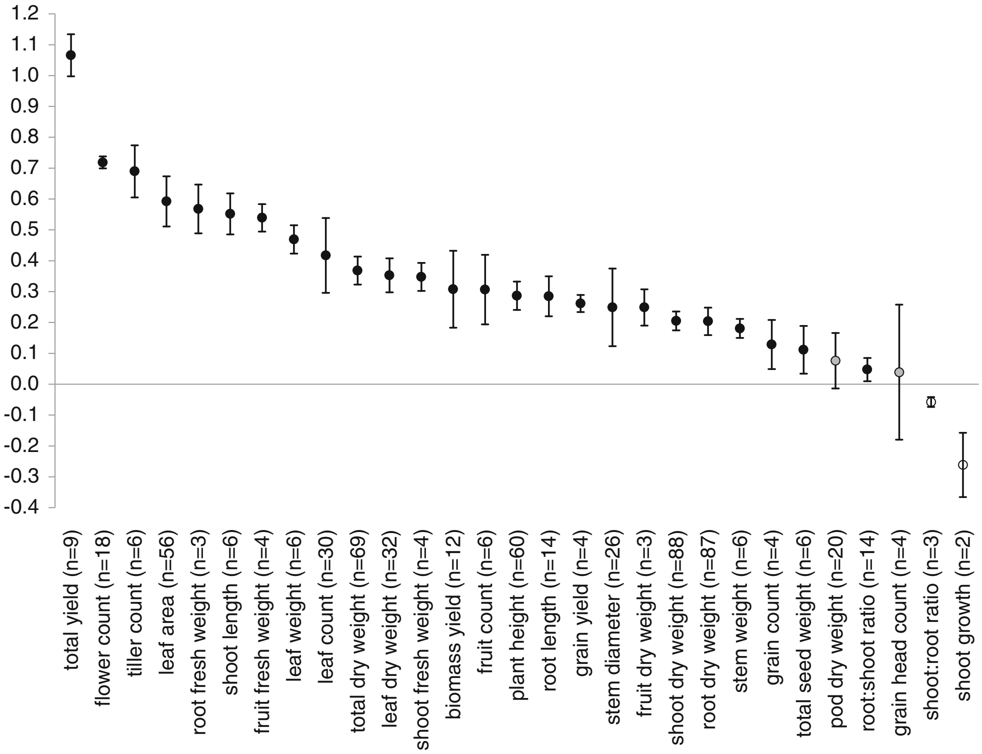

Fig. 1 Detail of log response ratios (LRR ± SE) of all plant growth responses to mycorrhizal symbiosis under water deficit. Positive values (*black-filled circles*) indicate an increase in plant growth parameter; negative values (*open circles*) indicate that the treatment is deleterious to plant growth. *Gray-filled* circles are values which are not significant. Measures with $n=1$ were excluded. Overall LRR = 0.324±0.020, indicating a positive effect of mycorrhizal symbiosis

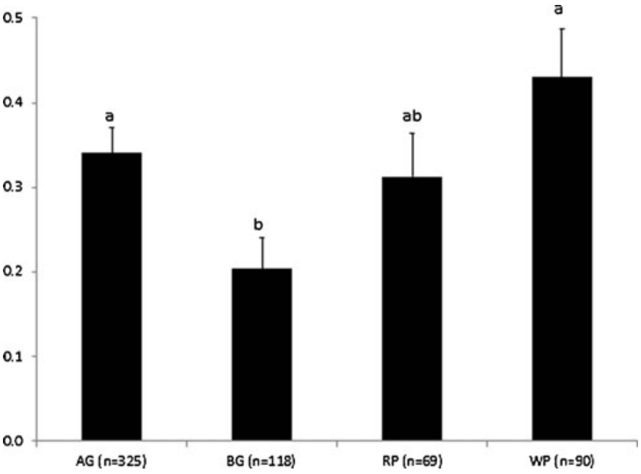

Fig. 2 Log response ratios (±SE) of plant growth response to mycorrhizal symbiosis related to growth category. Aboveground (*AG*) LRR = 0.341±0.029, belowground (*BG*) LRR = 0.204±0.036, reproductive (*RP*) LRR = 0.313±0.051, and whole plant (*WP*) LRR = 0.430±0.054. Plant growth response varied significantly between the categories stressed (F_s=3.50; df=3, 601; P=0.015). Values sharing the same *letter* do not differ significantly after Tukey's HSD

601; P=0.003) (Fig. 4). BG growth is much greater in woody plants than in herbaceous ones (F_s=6.47; df=1, 117; P=0.012), but AG and WP growth is the same between the types. Both WP and AG growth of herbaceous species is more than BG (P=0.028 and P=0.044, respectively). Pod dry weight (n=20), grain head count (n=4), and shoot/root ratio (n=3) of the herbaceous samples are not influenced. In woody species, root/shoot ratio (n=6) was unaffected and shoot growth (n=2) was reduced by AMF colonization. No growth region of woody plants was favored significantly more than another by AMF colonization, and no reproductive structures of woody species were measured for comparison.

Effects of study site

Field and greenhouse results from the meta-analysis are the same overall (F_s=0.98; df=1, 592; P=0.324) (Fig. 5). However, increase in RP biomass of greenhouse plants was greater than those in the field (F_s=4.80; df=1, 67; P=0.032), and large WP gains were observed in field-grown plants compared to greenhouse-grown ones (F_s=8.64; df=1, 135; P<0.0001). WP growth is strongly favored over BG (P=0.001), RP (P=0.0003), and AG (P<0.0002) within field plants. There was no particular growth benefit favored more than another among greenhouse-grown plants. Plant growth in greenhouse studies was generally positively affected by mycorrhiza save for pod dry weight (n=20), root/shoot ratio (n=14), and shoot/root ratio (n=3). In the field, grain head count (n=4) and root dry weight (n=7) were unchanged, while shoot growth (n=2) was weakened by AMF colonization.

Effects of functional group

The response to mycorrhiza of four functional groups varied significantly under water stress (F_s=14.08; df=3, 601; P<0.0001) (Fig. 6). Trees and shrubs benefit most overall from AMF colonization. Post hoc tests revealed differences between all functional groups except grasses and legumes. AG growth of trees and shrubs is higher than of legumes (P=0.002) but not forbs or grasses. The tree/shrub group also has the highest BG growth, significantly higher than legumes (P=0.0009). No reproductive structures were measured on

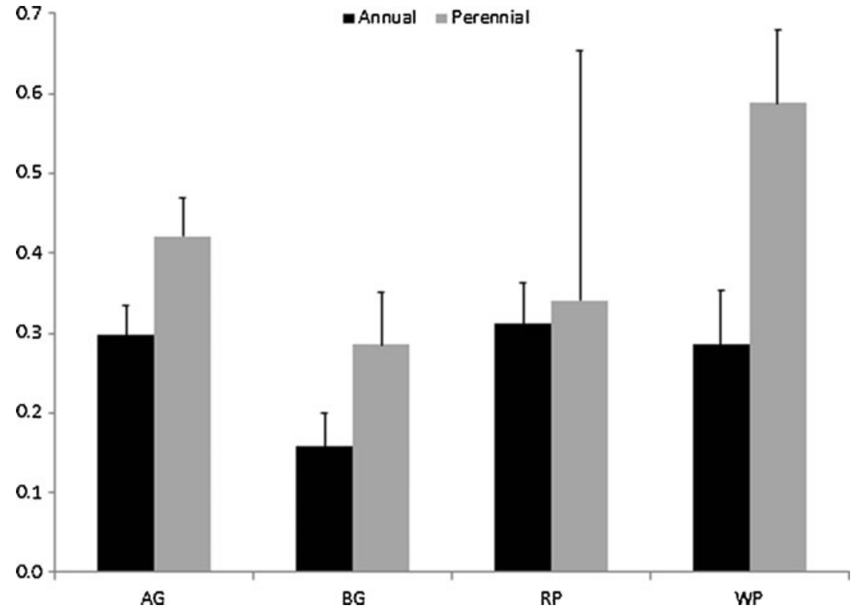

Fig. 3 Log response ratios (±SE) of plant growth response to mycorrhizal symbiosis related to life cycle. Annuals overall LRR=0.272±0.024, perennials overall LRR=0.426±0.036. Overall, drought-stressed perennials responded significantly better to AMF colonization. WP growth is significantly greater in perennials (F_s=8.74; df=1, 92; P=0.004). Low sample size (n=4) for perennial reproductive measures contributed to a high SE. *AG* aboveground, *BG* belowground, *RP* reproductive, *WP* whole plant

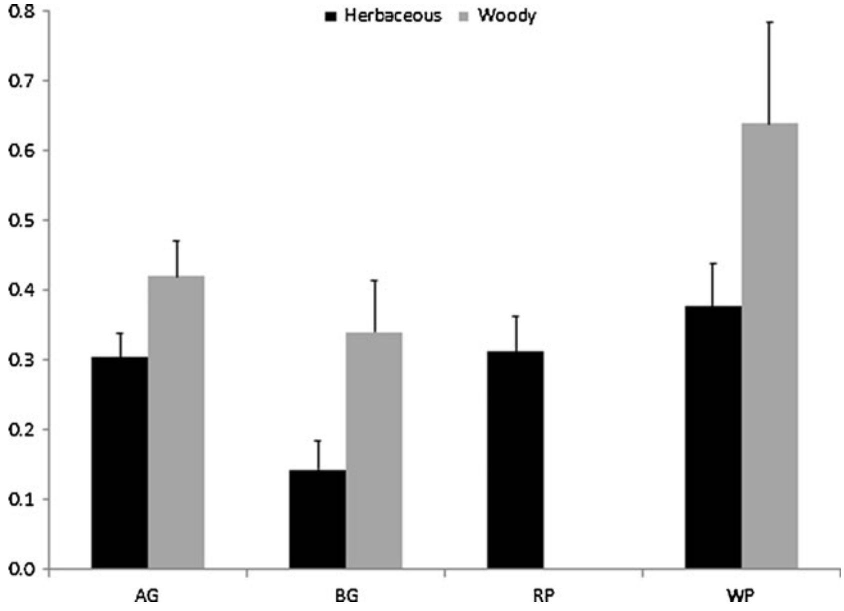

Fig. 4 Log response ratios (±SE) of plant growth response to mycorrhizal symbiosis related to lifestyle. Herbaceous overall LRR=0.288±0.023, woody overall LRR=0.324±0.020. Plant growth response varied significantly between herbaceous and woody plants. BG growth is much greater in woody species than herbaceous plants (F_s=6.47; df=1, 117; P=0.012). *AG* aboveground, *BG* belowground, *RP* reproductive, *WP* whole plant

trees and shrubs, but there are RP growth differences between the other functional groups (F_s=14.43; df=2, 68; $P<0.0001$). Forbs have the largest increase in biomass of RP parts and grew much more than legumes ($P<0.0001$) and grasses (P=0.0005). RP growth of grasses and legumes is not different. Even more differences existed in WP growth measures (F_s=6.18; df=3, 92; P=0.0007). Tree and shrub growth was again the most improved, being significantly better than grasses (P=0.002). Forbs also grew better than grasses in response to mycorrhiza (P=0.007). Forbs showed the most improvement in RP growth, significantly better than BG growth (P=0.034). WP growth of forbs also benefits from AMF colonization and significantly more than BG measures (P=0.050). WP growth of legumes is increased more than BG growth (P=0.009) and RP structures (P=0.039). Individual growth regions of grasses and tree/shrubs are not improved more than any other.

Effects of water regime and water stress level

The overall difference between well-watered and water-stressed plants that were both treated with mycorrhiza is not significant (F_s=3.74; df=1, 869; P=0.053) (Fig. 7). AG, BG, RP, and WP growth were all statistically similar whether plants were well-watered or water-stressed. Furthermore, the mycorrhizal association had no effect on response to low, medium, or high levels of stress experienced by plants (F_s=0.07; df=2, 601; P=0.932) (data not shown). Mycorrhiza had no effect on any particular

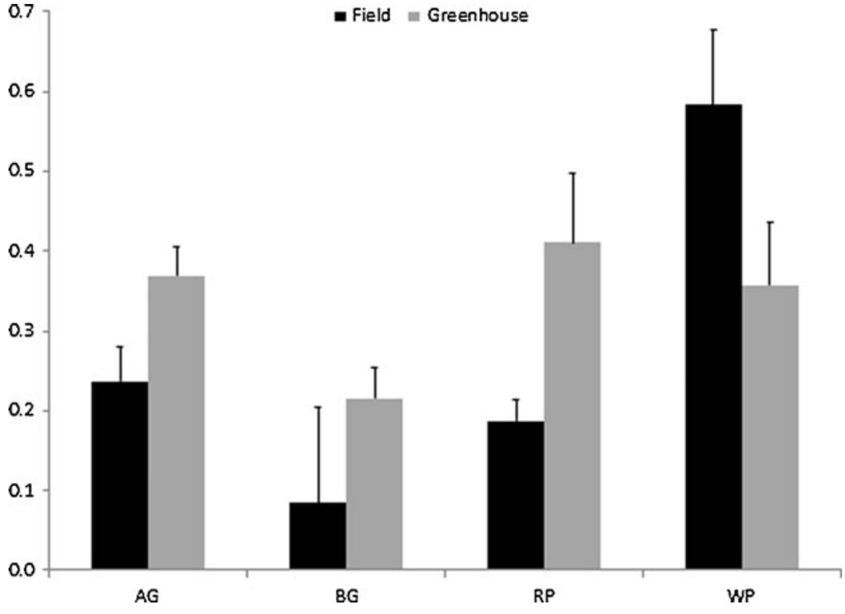

Fig. 5 Log response ratios (±SE) of plant growth response to mycorrhizal symbiosis related to study site. Field overall LRR=0.287±0.033, greenhouse overall LRR=0.335±0.025. Overall, there is no difference between study sites. Low sample size (n=10) for field belowground measures contributed to the high SE. *AG* aboveground, *BG* belowground, *RP* reproductive, *WP* whole plant

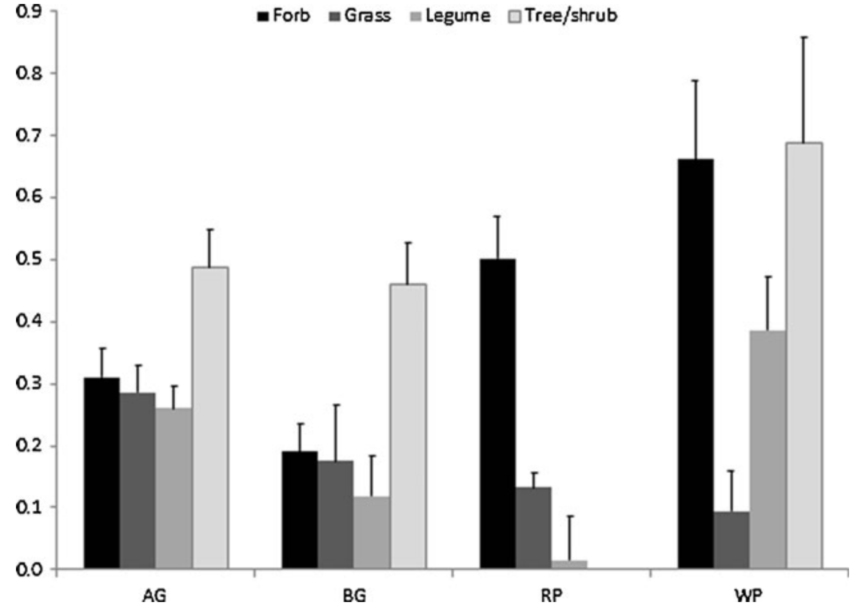

Fig. 6 Log response ratios (±SE) of plant growth response to mycorrhizal symbiosis related to functional group. Forb overall LRR=0.385±0.039, grass overall LRR=0.221±0.033, legume overall LRR=0.213±0.032, and tree/shrub overall LRR=0.578±0.057. Plant growth response varied significantly between functional groups (F_s=14.08; df=3, 601; P<0.0001). *AG* aboveground, *BG* belowground, *RP* reproductive, *WP* whole plant

growth region in well-watered plants. Water-stressed samples, however, did show differences in the effect on growth region (F_s=3.50; df=3, 601; P=0.015). When water-stressed, BG growth was least improved. Both WP (P=0.013) and AG (P=0.044) benefited more from AMF colonization than BG growth.

Some levels of water stress do influence which growth region is improved. Low stress (F_s=3.86; df=3, 64; P=0.014) favored WP over AG growth (P=0.047), and moderate stress (F_s=2.91; df=3, 492; P=0.034) improved AG growth more than BG (P=0.036). Severe stress did not change the effect on a growth region (F_s=2.69; df=3, 43; P=0.059).

Effects of *Glomus* species

Species analysis (Fig. 8) examined the effects of the seven most used species of *Glomus* inoculum among all studies. These are, in order of the most to the least often used, *G. mosseae* (n=133), *G. intraradices* (n=127), *G. fasciculatum* (n=59), *G. versiforme* (n=53), *G. deserticola* (n=49), mixtures of two or more *Glomus* species (n=39), and *G. etunicatum* (n=35). No difference was evident between any of these seven inoculum treatments on overall plant improvement (F_s=1.92; df=6, 490; P=0.076). Some AMF species were more beneficial to some regions of plant growth than others. Mixed inoculum improved RP growth more than all

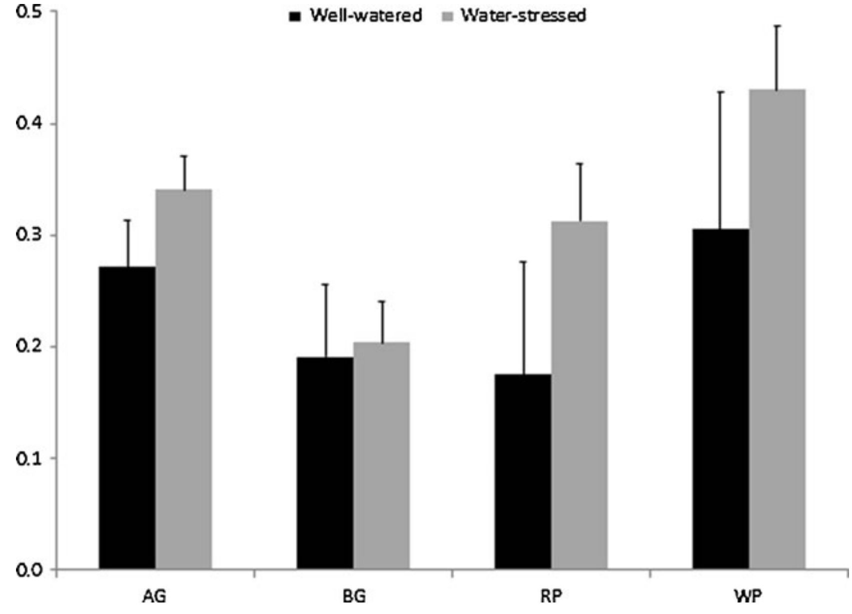

Fig. 7 Log response ratios (±SE) of plant growth response to mycorrhizal symbiosis related to water regime (well-watered, water-stressed) not accounting for the degree of water stress. Well-watered overall LRR = 0.250±0.034, water-stressed overall LRR =0.324±0.020. There is no overall difference in plant growth between water regimes. *AG* aboveground, *BG* belowground, *RP* reproductive, *WP* whole plant

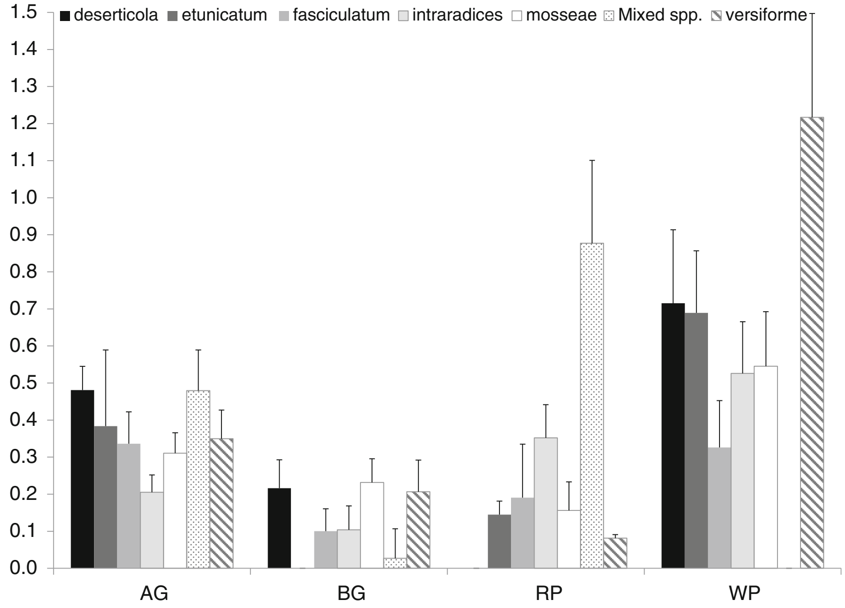

Fig. 8 Log response ratios (±SE) of plant growth response to mycorrhizal symbiosis related to the seven most often used species of *Glomus* inoculum. There is no overall difference between species. *AG* aboveground, *BG* belowground, *RP* reproductive, *WP* whole plant

other species, and *G. versiforme* increased WP growth more than *G. fasciculatum* ($P=0.023$). *G. intraradices* increased WP growth more than BG ($P=0.006$) and AG ($P=0.008$). *G. versiforme* promoted WP growth more than RP ($P=0.029$), BG ($P=0.001$), and AG ($P=0.008$). Mixed species of *Glomus* augment RP biomass better than BG growth ($P=0.021$). However, most of the species (*G. deserticola*, *G. etunicatum*, *G. fasciculatum*, and *G. mosseae*) did not benefit any particular growth region over another.

Discussion

The present meta-analysis was based on data from 54 published articles that explored the effects of AMF on the growth of water-stressed plants. The experiments included 19 species of AMF in five genera, 41 different host plant species, 36 plant growth measurements, and four water stress treatments (high, medium, or low stress and well-watered). Effects were examined between life cycle, habit, study site, functional group, water regime and level of stress, and AMF species treatment. The majority of experiments (55.6 %) concerned herbaceous annuals, followed by woody perennials including tree species (32.7 %), and herbaceous perennials (11.7 %). Most experiments (79 %) took place in greenhouses or growth chambers. Field studies investigated either large woody species or traditional field crops such as maize, wheat, and sorghum. Forbs were tested most often (31.5 %), followed closely by legumes (29.6 %). Tree and shrub experiments accounted for 20.4 % and grasses 18.5 % of the research. Eight studies (14.8 %) compared varying levels of water stress on plant growth, but most examined only a single-level stress treatment.

Results confirmed that overall plant growth is strongly improved by mycorrhizal colonization, with perennial plants responding more positively under water stress conditions than annual species. This may be due to a greater investment in persistent roots and recurring shoots; however, perennial growth improvements were only observed in the whole plant measures of total dry weight even though root dry weight, root length, and root/shoot were recorded for perennial plants. Contrary to our expectations, growth of reproductive structures was not improved by AMF colonization of annual plants. Semelparous species would seem to benefit most from developing reproductive tissues that increase the chance of continuing their genetic presence. Mean log response ratio of reproductive growth was the highest of all categories in annual plants, but it was not statistically significant. Responses to mycorrhiza observed between plants of different lifestyles were not the same, with woody plants being more improved than herbaceous species. Since woody species are all perennial by definition, the never fully dormant roots of such plants require year-round nutrition and water. It may be because of this that belowground growth was significantly enhanced in woody species colonized by AMF. We found no difference in the outcomes between plants grown under greenhouse or field conditions; in a recent meta-analysis, Hoeksema et al. (2010) suggested that site location had only a small effect on plant response to mycorrhizal symbiosis.

Water shortage is likely to have an effect on mycorrhizal development (Bolgiano et al. 1983), and it is also among the factors most limiting plant growth. Faber et al. (1991) demonstrated the improved transport of water by mycorrhizal hyphae. However, we found that the effect of mycorrhiza on well-watered plants was not different from that on water-stressed plants, showing that water-stressed plants grow as well as those that are watered adequately when both are mycorrhizal. Plant responses to varying levels of water stress are likewise equally improved by AMF. It is likely that certain plant–mycorrhiza relationships express more synergy than other combinations, although our meta-analysis indicated that, among the most studied species of *Glomus*, there were no differences in their effect on water-stressed plants.

There is no dearth of studies investigating the physiological improvement of plants by mycorrhizal symbiosis, and earlier meta-analyses have been conducted on the effects and interactions of some of these factors (Borowicz 2001; Morris et al. 2007; Koricheva et al. 2009). However, the present meta-analysis is the first to quantitatively affirm the view that the arbuscular mycorrhizal symbiosis benefits plants in terms of morphological growth when exposed to low-water conditions and reveal variations in those effects within differing contexts. AMF can provide a range of benefits to their hosts, and it is worth noting that other factors, such as improved P uptake, may have interacting effects on plant growth when less water is available.

In conclusion, meta-analysis of published data and findings supports the assertion that mycorrhizal plants show better growth and reproductive response to water deficit than non-mycorrhizal plants do. Most measures of growth are augmented by the symbiosis when plants are subjected to water stress; however, aboveground biomass such as leaf area, plant height, and stem diameters are significantly more improved than belowground measures such as root length or root dry weight.

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