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ORIGINAL PAPER

Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: a meta-analysis

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Abstract Stomata regulate rates of carbon assimilation and water loss. Arbuscular mycorrhizal (AM) symbioses often modify stomatal behavior and therefore play pivotal roles in plant productivity. The size of the AM effect on stomatal conductance to water vapor (g_s) has varied widely, has not always been apparent, and is unpredictable. We conducted a meta-analysis of 460 studies to determine the size of the AM effect under ample watering and drought and to examine how experimental conditions have influenced the AM effect. Across all host and symbiont combinations under all soil moisture conditions, AM plants have shown 24 % higher g_s than nonmycorrhizal (NM) controls. The promotion of g_s has been over twice as great during moderate drought than under amply watered conditions. The AM influence on g_s has been even more pronounced under severe drought, with over four times the promotion observed with ample water. Members of the Claroideoglomeraceae, Glomeraceae, and other AM families stimulated g_s by about the same average amount. Colonization by native AM fungi has produced the largest promotion. Among single-AM symbionts, *Glomus deserticola*, *Claroideoglomus etunicatum*, and *Funneliformis mosseae* have had the largest average effects on g_s across studies. Dicotyledonous hosts, especially legumes, have been slightly more responsive to AM symbiosis than monocotyledonous hosts, and C3 plants have shown over twice the AM-induced promotion of C4 plants. The extent of root colonization is important, with heavily colonized plants showing ×10 the g_s promotion of lightly colonized plants. AM promotion of g_s has been larger in growth chambers and in the field than in greenhouse studies, almost ×3 as large when plants were grown under high light than low light, and ×2.5 as large in purely mineral soils than in soils having an organic component. When AM plants have been compared with NM controls given NM pot culture, they have shown only half the promotion of g_s as NM plants not given anything at inoculation to control for associated soil organisms. The AM effect has been much greater when AM plants were larger or had more phosphorus than NM controls. These findings should assist in further investigations of predictions and mechanisms of the AM influence on host g_s.

Keywords Arbuscular mycorrhiza · Drought · Moderators · Meta-analysis · Phosphorus limitation · Root colonization · Stomatal conductance · Water relations

Introduction

Stomatal conductance to water vapor (g_s) is of critical agronomic and ecological importance because it determines rates at which CO_2 enters and water vapor exits leaves, exerting a controlling influence on photosynthesis, hydration and ultimately biomass accumulation, crop yield, and carbon sequestration. Altered g_s of the host plant is among the more highly investigated water relations characteristics affected by arbuscular mycorrhizal (AM) symbiosis (Ruiz-Lozano and Aroca 2010). AM and nonmycorrhizal (NM) plants often display different g_s (Gupta 1991; Koide 1993; Sánchez-Díaz

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and Honrubia 1994), yet several investigators have also reported no differences between AM and NM plants (Augé 2000). Reviewers have noted that despite a wealth of studies comparing g_s in AM plants and NM controls, the mechanism(s) of influence remains unclear and our ability to predict the frequency and extent of AM-induced changes in g_s is limited (e.g., Augé 2001; Smith et al. 2010).

We conducted a quantitative review using meta-analysis to compare results across the literature and synthesize an overall effect size of AM symbiosis on g_s. We included 19 moderator variables that we suspected may have influenced the size of the AM effect. Moderators—also termed factors (Schaeffer et al. 2013), categorical explanatory variables (Veresoglou et al. 2012), classificatory variables (Zvereva and Kozlov 2012), and descriptive characteristics (Kiær et al. 2013)—are often examined in meta-analyses to help understand how circumstances modify the treatment effect of interest. Moderators addressed identity or qualities of the symbionts as well as other experimental conditions. Reviewers have noted that g_s of some host taxa has been more sensitive to AM colonization than others (e.g., Augé 2001), but there have been so many studies on so many species with varying findings that a quantitative analysis is needed. The same is true of the fungal symbiont. Different AM fungi have been reported to differentially influence host g_s (e.g., Ruiz-Lozano et al. 1995; Gong et al. 2013). Stomatal conductance is very sensitive to abiotic and biotic variables and can change within seconds in response to changes in internal and external environment. Light and temperature can modify the extent of AM-induced changes in g_s (e.g., Augé et al. 2004). Light quality, such as sunlit greenhouses vs artificial light in growth chambers, can affect g_s (e.g., Sharkey and Raschke 1981). Woody plants tend to have lower g_s than herbaceous plants (Nobel 1991; Kelliher et al. 1995). Leaf phosphorus concentration and plant size, often markedly influenced by AM symbiosis, can affect stomatal behavior (e.g., Radin 1984).

We sought to answer the following four questions:

1. What is the overall extent of AM promotion of stomatal opening across studies?
2. Has the AM effect been more pronounced during drought?
3. Does the well-established influence of AM symbiosis on host P uptake and growth explain the AM effect on g_s?
4. Have particular experimental conditions or symbiont combinations led to especially large AM promotion of g_s?

Knowing which AM taxa affect g_s most markedly, which host taxa have been particularly sensitive to the symbiosis, and which environmental characteristics tend to favor or discourage AM modification of stomatal behavior can help investigators employ AM technology more successfully in cropping and conservation efforts.

Materials and methods

Data collection

Using *ISI Web of Science* and the bibliographies of the published work, we located 1,518 refereed publications, accessed through July 2013, that contained data on the water relations of mycorrhizal plants. Search terms are [vesicular-arbuscular* or arbuscular* or endomycorrhiz* or "AM fungi" or "AM symbiosis" or "VAM fungi" or "VAM symbiosis"] and [stomat* or transpira* or "water relations" or drought]. These articles were screened for measurements of g_s of AM and NM plants under amply watered and drought conditions. We identified 100 articles (Citations provided in Online Resource 1) that reported sample sizes and means for both AM treatment and NM control groups for g_s or stomatal resistance (r_s; inverse of conductance). Papers were in English, Spanish, and Chinese and spanned 31 years. Where r_s was reported, typical of earlier literature, we converted to g_s. Reports of whole-plant water conductances or resistances were not included. The g_s data for amply watered, nonsalinized controls of salinity stress articles were included. Studies with simulated drought via PEG or osmotic stress were included, e.g., Augé et al. (1992) and Benabdellah et al. (2011).

Treatment means and sample sizes were collected for each study. For publications reporting means for more than one NM control treatment in a nonfactorial experiment, we used the NM control that most closely approximated AM plants, e.g., plants given PO_4^{-3} in Ruiz-Lozano et al. (1995). We quantified sample size as experimental unit; for example, where authors may have indicated that $n=10$ (g_s measured on two leaves from each of five plants), we assigned $n=5$. Studies were not included if they did not report sample size or had a sample size of 1. If sample size was given as a range, we used the smallest value (e.g., Allen and Allen 1986, $n=3$ to 5). If data were provided in graphical form, means were extracted using WebPlotDigitizer (Rogatgi 2011).

Multiple treatments or host/symbiont combinations from one article were treated as independent studies and represented an individual unit in the meta-analysis. For example, Ruiz-Lozano et al. (1995) examined the effects of seven AM symbionts on the g_s of lettuce plants, which accounted for seven studies for the meta-analysis from that article. Newman and Davies (1988) reported g_s in AM and NM plants of three host taxa under four temperature treatments, which resulted in 12 studies. Although designating multiple studies from one publication has the disadvantage of increasing the dependence among studies that for the purposes of meta-analysis are assumed to be independent (Gurevitch and Hedges 1999), the greater number of studies increases statistical power (Lajuenesse and Forbes 2003). This approach has been used commonly in mycorrhizal and plant biology meta-analyses, e.g., Hoeksema et al. (2010), Holmgren et al. (2012),

Veresoglou et al. (2012), Mayerhofer et al. (2013), and McGrath and Lobell (2013). We derived 460 studies from the 100 articles.

As in prior meta-analyses (e.g., Mayerhofer et al. 2013), we did not consider measurements at multiple times as separate studies. For multiple time points, we computed the means of the time points and used the synthetic score as the unit of analysis as described for multiple time points by Borenstein et al. (2009). In the 33 articles reporting multiple time points, sample size did not differ between AM and NM treatments. Sample size rarely differed among time points within a study; where it did, we used the smaller sample size. With similar sample sizes within multiple time-point studies, mean weight (reciprocal of variance) was computed as (Borenstein et al. 2009):

$$1/((m \times (1/w) + m \times (m-1)/2 \times 2 \times r \times ((1/w)^{0.5})^2)/m^2)$$

where m is number of time points, w is weight of each time point (similar for time points with similar sample size), and r is the correlation coefficient that describes the extent to which effect sizes covary across time points. Correlation analysis was performed for each multiple time-point study to determine r for that study. We used mean r over all multiple time-point studies (r=0.51) as an estimate of r for studies with two time points. When multiple g_s time points involved different plants (different experimental units), these time points were considered one study (not multiple studies).

Effect size and moderator variables

We conducted an overall and several grouped meta-analyses on g_s, comparing studies via effect size. The effect size for each study was computed as ln R, the natural logarithm of the response ratio of mycorrhizal to NM g_s:

$$\ln R = \ln Y_{\mathrm{AM}}/Y_{\mathrm{NM}}$$

where Y_{AM} and Y_{NM} are means of AM treatments and NM controls, respectively (Rosenberg et al. 2000). These were used to measure the overall effect: the summary or cumulative AM/NM effect size across studies (Borenstein et al. 2009). It is common to use a response ratio in meta-analyses of plant and mycorrhizal behaviors (e.g., Lehmann et al. 2012; Mayerhofer et al. 2013; Worchel et al. 2013), as it gives a standardized expression of treatment-induced change and has direct biological significance. The log transformation is needed to properly balance positive and negative treatment effects across response ratios (to maintain symmetry in the analysis, Borenstein et al. 2009). For our analyses with response ratios, ln values above 0 indicate an AM-induced increase in g_s, values below 0 indicate an AM-induced decrease in g_s, and a value of 0 signifies a lack of mycorrhizal effect.

In addition to measures of g_s, we recorded information from each study on 19 moderator variables, characteristics that may modify g_s and potentially the degree of AM influence on g_s (Table 1). Each moderator had at least two categories (levels), and the data within each of these levels were from at least seven studies (moderator levels are detailed in Online Resource 1, and number of studies in each moderator level are shown in Figs. 1, 2, 3, 4, 5, and 6). These moderators were used as categorical explanatory variables in the meta-analyses. We chose some of these moderators to represent factors that have been shown to affect g_s and thereby have the potential to enhance or diminish AM effect on g_s. Other moderators were chosen to determine if an AM effect has been observed more often under some conditions than others, to guide design of future experiments to help better predict AM effect sizes involving g_s. We followed the taxonomic scheme of Schüßler and Walker (2010) and Redecker et al. (2013) for reclassifying taxa in AM family and AM species moderators, and grouped *Glomus fasciculatum* with *Glomus intraradices* into the new classification *Rhizophagus intraradices* (Morton 2014). Originally reported genus and species names are provided with their new names in Online Resource 1. AM species investigated most often (represented in more than 20 studies) were compared, with species occurring in fewer than 20

Table 1 The ratio of variation among levels of a moderator (Q_M) and amount of total variation (Q_T) for each categorical moderator analysis

Moderator	Q_M/Q_T	p
Soil water	*0.123*	*<0.001*
Drought pre-acclimation	0.001	0.520
AM family	0.008	0.715
AM species	0.005	0.935
Shoot size	*0.119*	*<0.001*
Leaf P concentration	*0.133*	*<0.001*
Root colonization	*0.055*	*0.001*
Host type	0.007	0.246
Lifestyle	<0.001	0.870
Photosynthetic pathway	*0.015*	*0.018*
Host propagation	0.007	0.116
Inoculum type	0.006	0.138
Inoculum host	0.002	0.385
Associated soil organisms	0.013	0.087
Substrate	0.009	0.074
Phosphorus fertilization	<0.001	0.994
Environment	*0.046*	*<0.001*
Light	*0.062*	*0.001*
Temperature	0.009	0.123

p value refers to probability that levels within a moderator differed. Moderators with $p \leq 0.05$ are shown in italic

studies grouped into an "other species" level of this moderator. AM families represented in more than 10 studies were compared, with families represented in fewer than 10 studies grouped into an "other family" level of the family moderator. "Native" AM fungi refer to unidentified species present in local, unsterile soil used as inoculum (e.g., Allen and Allen 1986).

Stomatal response to soil drying was a focal point of our analysis, with a principal objective being to determine if g_s is affected more by mycorrhizae when soils are dry than moist. We conducted one meta-analysis with two levels for the soil water moderator: unstressed vs drought-stressed plants. The extent of drought to which plants were exposed varied considerably across studies, and we wanted to take advantage of this, to fine-tune the analysis to attempt to discern if the mycorrhizal effect was more or less pronounced at different severities of water limitation. However, soil moisture at time of g_s measurements was quantified and reported in only a small minority of studies. Growth substrate also varied widely across studies, and so, measures of soil water content, when reported, could not be used to compare soil drought among studies. Soil water potential (Ψ)—which would allow comparisons of soil dryness among studies—was rarely reported. Drought can be assessed as external pressure applied (drought *stress*) or internal plant response (drought *strain*) (Levitt 1980). Because drought stress was applied and quantified in very diverse ways across the studies, it was difficult to apply a meaningful, consistent category of degree of drought stress. Drought strain afforded greater opportunity for consistency across studies.

We defined drought strain of treatment means in relation to controls, NM plants given ample water. Mild drought=g_s of droughted NM plants was above 50 % of amply watered NM control plants, moderate drought=g_s between 15 and 50 % of NM controls, and severe drought=g_s less than 15 % of NM controls. If an experiment did not include fully watered controls for each day of drought, the initial day of drought was considered amply watered and used as the basis to determine level of drought strain for subsequent days of drought. When a time series was associated with a drying period, we scored measurements at each time point as mild, moderate, or severe. Time points with the same drought strain designation were treated as one study and integrated as described above for multiple time points. Hence, an experiment that subjected plant treatments to drought by withholding water from pots for several days and involved measurement of g_s at several time points during the drying period may have resulted in multiple time points at mild, moderate, and/or severe drought. Split-pot experiments in which part of the root system was watered and part was dried (e.g., Ebel et al. 1996) were handled like single-pot drought experiments (where the situation may be similar: surface soil drying while deeper soil is still moist). Our scoring of drought severity is based on foliar response to the drought treatment, which can be evoked in pot and field situations by hydraulic signals, nonhydraulic signals, or a combination of the two (Wilkinson and Davies 2002).

Meta-analysis

We estimated the summary effect (mean effect size across studies) with Comprehensive Meta-Analysis (CMA) software (Biostat, Englewood, NJ, USA), generating 95 % confidence intervals (CIs), Q statistics, and p values using a bootstrapping randomization procedure. Q is a measure of weighted squared deviations, used to help separate observed variation and true variation (Borenstein et al. 2009). We examined both fixed-effects and random-effects models to test for differences in the summary effect among moderator groups, examining p values associated with the between-class heterogeneity (Q_m). Q_m represents the variation in effect size among levels within a moderator. The mean effect size of a moderator or level of a moderator was considered significant if its 95 % CI did not overlap zero and if the heterogeneity p value was <0.05. Total heterogeneity (Q_t), the sum of Q_m, and within-level variance (Q_w) was used to compare the importance of moderators, Q_m/Q_t (Table 1). I^2, a descriptive statistic computed as $((Q-df)/Q)\times 100$ %, estimates the ratio of true heterogeneity to total variance across the observed effect sizes (Borenstein et al. 2009). To avoid Simpson's Paradox, effect sizes were computed for each study and then combined: each study's effect size was based on the comparison of an AM group with its own NM control group (Borenstein et al. 2009).

Individual studies within the meta-analyses were weighted nonparametrically

$$W_{\ln R} = (n_{\mathrm{AM}} \times n_{\mathrm{NM}})/(n_{\mathrm{AM}} + n_{\mathrm{NM}})$$

where $W_{\ln R}$ is the weight (inverse of variance) of the natural log of the response ratio R and n_{AM} and n_{NM} are the sample sizes of the AM and NM treatments, respectively (Rosenberg et al. 2000). Several publications did not report standard errors or standard deviations nor was sufficient information given in many instances to estimate these from LSD or other mean separation test values. As has often been noted (e.g., Adams et al. 1997; Lehmann et al. 2012; Veresoglou et al. 2012; Mayerhofer et al. 2013), it is not uncommon for measures of dispersion to have been omitted from publications involving plants, which makes calculating weighting based solely on sample size (nonparametric weighting) a necessity. Excluding studies that report sample size but not some measure of dispersion would represent a substantial loss of data and diminish analytical power.

Meta-analysis can potentially be subject to the skewing effect of publication bias: greater likelihood of statistically

significant findings being published in the refereed literature over nonsignificant ones (Borenstein et al. 2009). We used graphical and statistical approaches to test for the possibility of publication bias. The funnel plot was examined to visualize if studies were distributed symmetrically about the mean effect size, whether studies with small effect sizes were missing from the distribution of effect sizes among our studies (Borenstein et al. 2009). A Begg and Mazumbar rank correlation was conducted in CMA to examine the relationship between effect size and sample size across studies (Begg et al. 1994; Borenstein et al. 2009). A significant correlation would suggest that larger effect sizes or significant AM effects were more likely to be published than small or insignificant sizes. Orwin's *Fail-safe N*, a variant of the often-used Rosenthal Fail-safe number (Rosenthal 1979), was calculated to determine the number of missing or unpublished studies reporting no AM effect that would have to be included in our meta-analysis to result in a biologically insignificant overall cumulative effect size in g_s (Orwin and Boruch 1982; Borenstein et al. 2009).

Results

Overall heterogeneity, Q_T, was 379.4 (df=459). I^2 was zero for the overall analysis, indicating that the fixed-effects model was the appropriate model for these data as true heterogeneity among effect sizes from the different studies was absent. Q_m, which represents the variation in effect size among levels within a moderator, was identical in the fixed-effects and random-effects models for each of the 19 moderators. Use of the fixed-effects model is further justified by inclusion of an extensive set of moderators (Cooper 2010).

Natural log of summary effect sizes is depicted in the forest plots (Figs. 1, 2, 3, 4, 5, and 6). To the right of the symbol showing the summary effects, we also provide the degree to which AM symbiosis increased g_s, as thinking in terms of raw percentage increase or promotion of a quantity is more intuitive. The raw summary AM/NM effect for the overall meta-analysis was 1.24 (p<0.001, CI 1.19–1.30); i.e., AM symbiosis increased g_s by an average of 24 % over all 460 studies. The ln AM/NM mean effect sizes for individual studies were below 0.95 for 82 studies, between 0.95 and 1.05 for 78 studies (negligible AM effect), and above 1.05 for 300 studies. Plant hosts were represented by 52 genera in 24 families. The analysis included 20 AM species in nine genera. The best studied woody host plant was citrus (*Citrus* spp., 44 studies). Among herbaceous plants, the most information was available for *Zea mays* (43 studies). *R. intraradices* was the most examined AM symbiont (167 studies), followed by *Funneliformis mosseae* (105 studies).

We did not see evidence of publication bias in the meta-analysis parameters. Visually, the funnel plot showed no

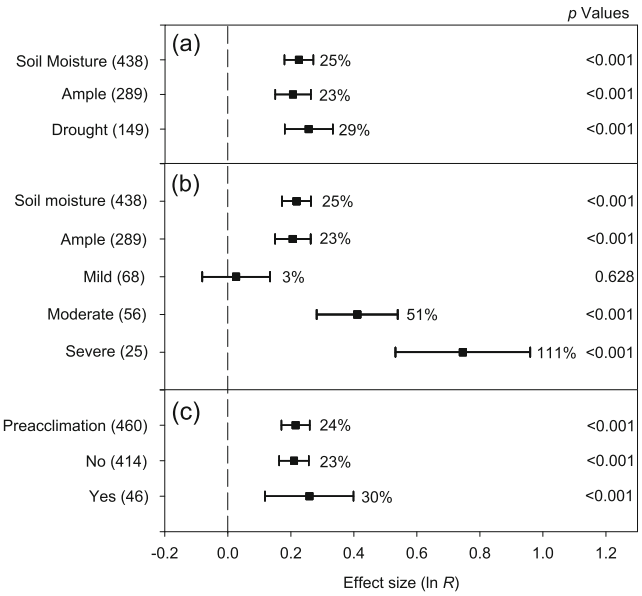

Fig. 1 Weighted summary effect sizes (ln R) and 95 % bootstrapped confidence intervals (CIs) for influence of soil water on AM promotion of stomatal conductance (g_s). Comparisons among **a** amply watered and droughted plants, **b** levels of drought, and **c** pre-acclimation to drought. Number of studies reporting data for each level of moderator is given in parentheses. Values to the right of the CI line for each moderator level are percent mycorrhizal promotion of g_s (ln R effect size transformed back to raw effect size). $p \leq 0.05$ indicates that the moderator level was significantly different than zero

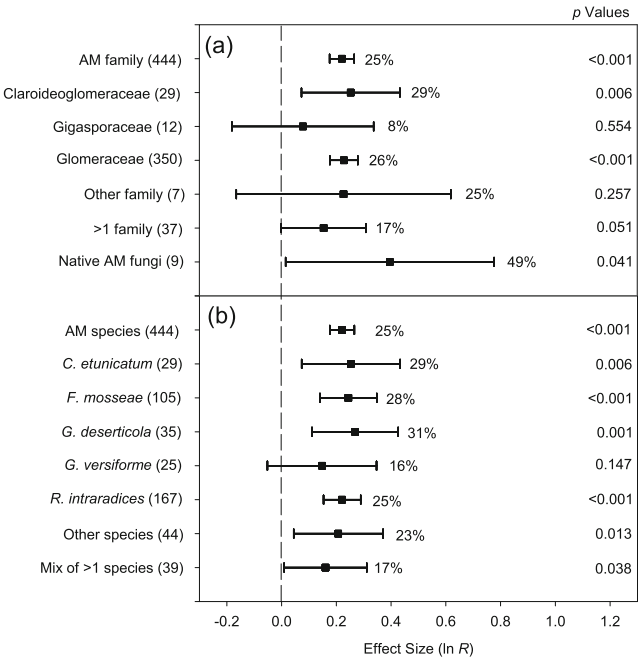

Fig. 2 Weighted summary effect sizes (ln R) and 95 % bootstrapped confidence intervals (CIs) for influence of AM taxa on promotion of stomatal conductance (g_s). Comparisons among levels of **a** AM family and **b** AM species. Number of studies reporting data for each level of moderator is given in parentheses. Values to the right of the CI line for each moderator level are percent mycorrhizal promotion of g_s (ln R effect size transformed back to raw effect size). $p \leq 0.05$ indicates that the moderator level was significantly different than zero

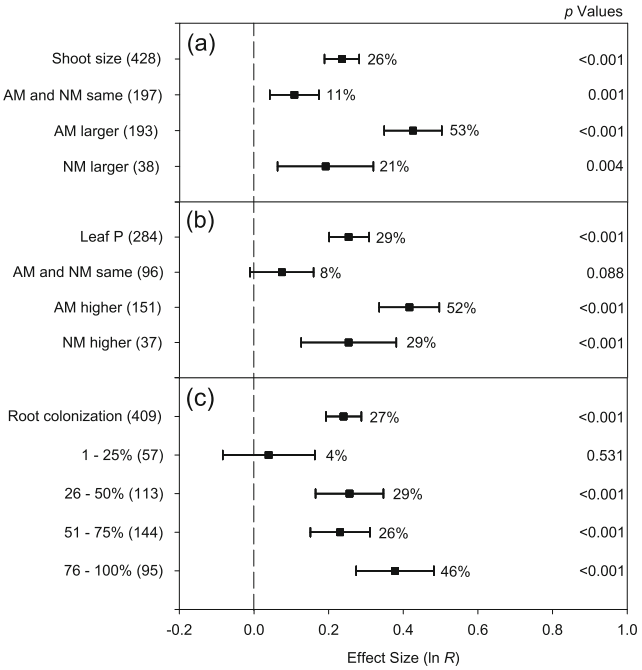

Fig. 3 Weighted summary effect sizes (ln *R*) and 95 % bootstrapped confidence intervals (CIs) for fungal influences on the host and how these influence AM promotion of stomatal conductance (g_s). Comparisons among levels of **a** shoot size, **b** leaf P concentration, and **c** root colonization by AM fungi. Number of studies reporting data for each level of moderator is given in parentheses. Values to the right of the CI line for each moderator level are percent mycorrhizal promotion of g_s (ln *R* effect size transformed back to raw effect size). $p \leq 0.05$ indicates that the moderator level was significantly different than zero

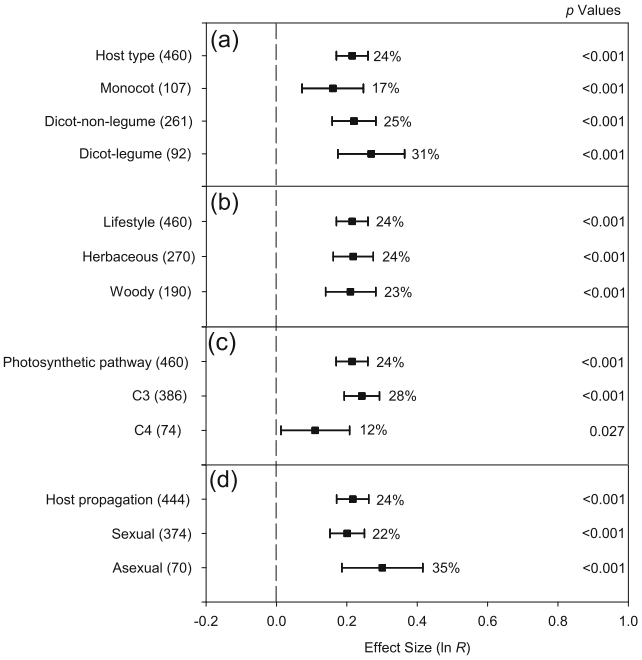

Fig. 4 Weighted summary effect sizes (ln *R*) and 95 % bootstrapped confidence intervals (CIs) for influence of host characteristics on AM promotion of stomatal conductance (g_s). Comparisons among levels of **a** host types, **b** lifestyle, **c** photosynthetic pathway of the host, and **d** propagation asexually or by seed. Number of studies reporting data for each level of moderator is given in parentheses. Values to the right of the CI line for each moderator level are percent mycorrhizal promotion of g_s (ln *R* effect size transformed back to raw effect size). $p \leq 0.05$ indicates that the moderator level was significantly different than zero

pattern that would reflect bias. Selecting an AM promotion of 5 % as the smallest effect likely to be of biological importance, the Orwin *Fail-safe N* for the overall meta-analysis was 1,560, the number of missing or unpublished studies with an AM treatment effect of zero that would have to be added to the meta-analysis to reduce the summary effect to 5 %. The Begg and Mazumdar rank correlation indicated little to no publication bias (tau=0.089).

Soil water

In separate analyses of nondrought and drought data, a meta-analysis of g_s under amply watered conditions (289 studies) yielded a mean effect size of 23 % and a meta-analysis of g_s under drought (any extent of drought, 149 studies) an effect size of 29 % (Fig. 1a). These summary effect sizes were similar; CIs overlapped considerably. Partitioning drought into three levels of severity revealed that the AM effect on g_s was much more pronounced as drought strain increased (Fig. 1b). In the meta-analysis of the 438 studies that reported g_s data for amply watered and drought conditions, there was no effect of AM symbiosis on g_s during mild drought, whereas AM symbiosis promoted g_s by 51 % under moderate drought and by 111 % under severe drought. *p* values for the

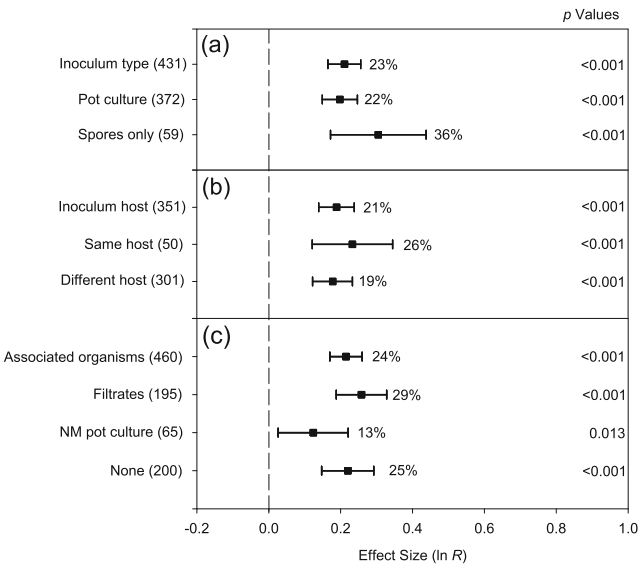

Fig. 5 Weighted summary effect sizes (ln *R*) and 95 % bootstrapped confidence intervals (CIs) for influence of inoculum characteristics on AM promotion of stomatal conductance (g_s). Comparisons among levels of **a** inoculum type, **b** inoculum host, and **c** associated organisms. Number of studies reporting data for each level of moderator is given in parentheses. Values to the right of the CI line for each moderator level are percent mycorrhizal promotion of g_s (ln *R* effect size transformed back to raw effect size). $p \leq 0.05$ indicates that the moderator level was significantly different than zero

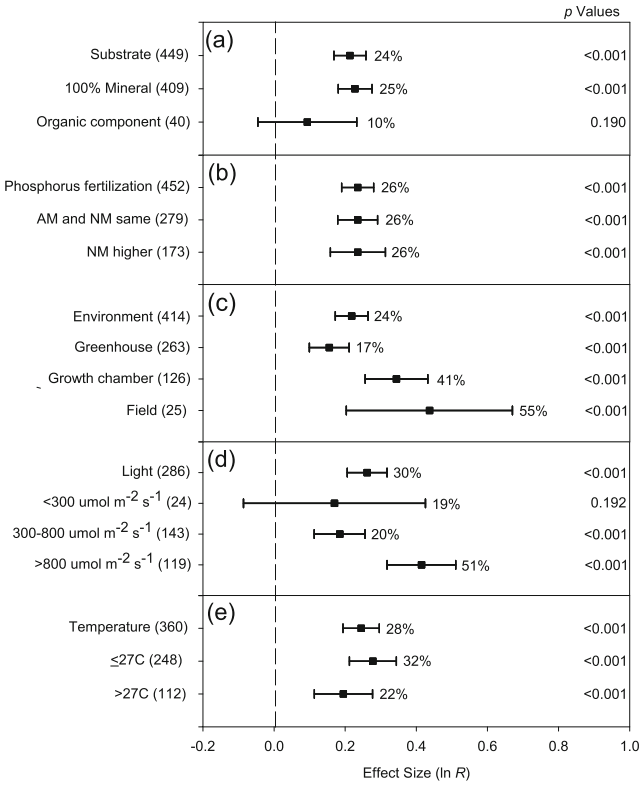

Fig. 6 Weighted summary effect sizes (ln *R*) and 95 % bootstrapped confidence intervals (CIs) for influence of experimental conditions on AM promotion of stomatal conductance (g_s). Comparisons among levels of **a** substrate components, **b** P fertilization, **c** growth/measurement environment, **d** light, and **e** temperature. Number of studies reporting data for each level of moderator is given in parentheses. Values to the right of the CI line for each moderator level are percent mycorrhizal promotion of g_s (ln *R* effect size transformed back to raw effect size). $p \leq 0.05$ indicates that the moderator level was significantly different than zero

unstressed (amply watered), moderately droughted, and severely droughted levels of soil water were each <0.001, and the heterogeneity *p* for the soil water moderator (<0.001) indicated that groups within this moderator differed significantly. Pre-acclimation to drought did not modify the extent of the AM-induced influence on g_s (Fig. 1c).

AM symbionts

Stomatal conductance was not increased by members of the Gigasporaceae nor by colonization by fungi from more than one AM family (Fig. 2a). Members of the Claroideoglomeraceae, Glomeraceae, and other families stimulated g_s by about the same average amount. Colonization by native AM fungi exhibited the largest promotion, an average increase in g_s of 49 %. Average summary effect sizes for the most-studied AM species varied from 16 to 31 % (Fig. 2b), with *Glomus deserticola*, *Claroideoglomus etunicatum*, and *F. mosseae* having the largest average effects on g_s across studies. The heterogeneity *p* for the AM family and AM species moderators (0.715 and 0.997, respectively) indicated that groups within these moderators did not differ significantly; CIs overlapped considerably.

Fungal effects on host

Three host characteristics affected by AM symbiosis each contributed importantly to AM influence on g_s (Fig. 3). In studies where AM and NM plants were similar in shoot size, an AM effect was less apparent at just 11 % (Fig. 3a). The AM effect was about five times greater, 53 %, when AM plants were larger than NM plants. Across studies where NM plants were larger than AM plants, the AM effect was similar to the summary effect over all studies, at 21 %. A similar trend occurred in the leaf phosphorus concentration moderator (Fig. 3b). When AM and NM plants were similar in leaf P, no AM effect occurred (average of 8 %, lower CI overlapped zero). When AM symbiosis increased P concentration in leaves, AM promotion of g_s was dramatic at 52 % higher than NM controls. Higher rates of AM root colonization were associated with greater AM treatment effects (Fig. 3c). With low colonization, in the 1–25 % range, AM symbiosis did not affect g_s. Very high colonization, above 75 %, led to quite marked AM-induced increases in g_s, averaging 46 % across those 95 studies. The summary effect in studies with moderate colonization, 26–75 % of root length colonized, gave AM promotion similar to the overall summary effect, around 27 % increase in g_s.

Host characteristics

Some host characteristics appeared to be linked to AM-induced increases in g_s while others did not (Fig. 4). Stomatal conductance was increased by AM symbiosis in monocots by an average of 17 % and in legumes by an average of 31 % (Fig. 4a). AM-induced promotion of g_s was essentially identical in woody hosts and herbaceous hosts (Fig. 4b). Whether the host was a C3 or C4 plant has affected how much the symbiosis increased g_s; the AM promotion was less than half as large in C4 than in C3 plants (Fig. 4c). How the experimental host plant was propagated may also have been an important determinant of extent of AM promotion, 13 % greater in asexually produced hosts than in those grown from seed (Fig. 4d).

Inoculum characteristics

We examined some characteristics of the inocula used to produce AM plants, to gain a sense of whether other soil organisms associated with AM fungi and roots of experimental plants may have impacted how much the symbiosis affected g_s. I.e., treatment effects of inoculum are attributed to AM fungi, but if inoculum contained other organisms or attributes

not applied to NM control plants, it is possible that those organisms or attributes accounted for some of the treatment effect. Inoculation by spores alone has given a higher average promotion, 36 %, than inoculation by live pot cultures, 22 % (Fig. 5a). We also looked at whether pot cultures were produced on the same plant or on a different genus and species than experimental plants on which g_s was measured. This had a small effect on the magnitude of the AM promotion, 19 vs 26 % (Fig. 5b). Effect size varied within the associated organism's moderator, with roots receiving no filtrate and no NM pot culture showing twice the effect size as that of roots receiving NM pot culture (Fig. 5c).

Experimental conditions

When plants were grown in a substrate containing an organic component—bark, peat moss, or manure—little AM effect on g_s was observed (Fig. 6a; lower CI overlapped 0). Whether or not NM plants were supplemented with additional P did not affect the size of the AM promotion of g_s (Fig. 6b). The growing environment used in experiments had a sizeable influence. The AM-induced effect on g_s more than doubled from the 17 % summary effect observed in greenhouses to 41 % in growth chamber experiments, and it increased even more markedly to 55 % in field sites (Fig. 6c). The greenhouse/glasshouse has been by far the most used environment for mycorrhizal g_s experiments (263 studies), and substantially less AM effect was observed there. Size of the AM promotion on g_s also relied on the maximum amount of light that plants received during the experiment (Fig. 6d). At irradiances below 300 μmol m^{-2} s^{-1}, the AM effect was much lower than over studies in which plants were grown or measured at irradiances above 800 μmol m^{-2} s^{-1}. The g_s of plants grown or measured below 27 °C tended to be slightly more affected by AM symbiosis (32 % AM promotion) than those grown at air temperatures that exceeded 27 °C during the study (22 % AM promotion) (Fig. 6e).

Discussion

The literature published over the past several decades substantiates that AM symbiosis affects stomatal opening of the plant. Yet the many dozens of studies in varying experimental conditions has left us unable to predict when AM symbiosis is most likely to affect g_s. Without a quantitative synthesis, we have also been unable to develop a good sense of the overall size of the mycorrhizal effect. This meta-analysis over all studies that provided g_s data for amply watered or drought conditions reveals that the g_s of AM plants has been on average 24 % higher than NM plants. This answers our first question.

Our second question addresses whether the overall AM effect has been larger during drought than under well-watered conditions. In comparing amply watered studies with all drought studies, the answer is no; the summary effect size is only slightly larger under drought, 29 % AM promotion of g_s vs 23 % AM promotion in well-watered controls, with CIs overlapping substantially. However, in considering all drought studies as a whole, the lack of an AM effect during slight or incipient drought obscures quite marked AM effects during more severe drought. Because drought treatments have been administered in many different ways and degree and duration of drying treatments have varied widely across studies, we attempted to fine-tune the analysis to reveal AM effects at different levels of drought. Under mild drought strain, when stomata have not yet been appreciably affected by the drying treatment (g_s still above 50 % of controls), AM symbiosis had little effect on g_s. Yet, when the drying treatment became extensive enough that stomata closed to the point that g_s declined below 50 % of amply watered NM controls, the AM effect was much greater. In moderately drought-strained plants, the AM promotion was twice that of the overall 24 % AM promotion seen across all studies. As soils dried further, causing greater drought strain, the AM effect became even more pronounced; the more soils dried, the greater the difference in g_s between AM and NM treatments. The AM-induced promotion of g_s was over twice as large in severely strained plants as in moderately strained plants and over four times as large as amply watered plants. Greater AM effects on g_s under moderate and severe drought is consistent with a meta-analysis of grass growth, where the AM influence was found to be greater under drought conditions (Worchel et al. 2013). These findings support the contention that arbuscular mycorrhizae may have special significance in arid environments (e.g., Smith et al. 2010).

We use the term "severe" for drought strain in the context of stomatal opening, defined as g_s between 0 and 15 % of amply watered controls. The amount of soil drying that led to g_s of 0–15 % probably did not constitute severe soil drying in terms of survival. Plants close their stomata to conserve water and survive periods of limited soil moisture, and under the varying stages of truly severe drought, for many species, g_s would likely have been zero or near zero for some time. There is often a substantial range of soil Ψ decline between the point at which stomata close fully and tissue death. Species differ in the sensitivity of their stomata to soil drying (Ludlow 1989), which may have affected the sensitivity of our approach to defining drought severity in terms of plant response. We would have liked to compare drought avoiders, species whose stomata close at relatively high soil Ψ (e.g., *Vigna unguiculata*), with drought tolerators, species that maintain relatively high or normal g_s for some time as soil dries and leaf Ψ declines (e.g., *Sorghum bicolor*), but these physiological characterizations were not available for most of the host species.

What might explain the ability of AM plants to maintain stomatal opening longer than NM plants as soils dry? Hyphae penetrate pores that are inaccessible to roots, and they spread beyond the root zone, effectively increasing the available volume of soil solution (Smith and Read 2008). Dakessian et al. (1986), Bethlenfalvay et al. (1988) and Franson et al. (1991) provided evidence that AM root systems can better exploit bound water in drying soils, in some cases providing access to soil water below the permanent wilting Ψ of NM plants. These and other authors (e.g., Reid 1979) have suggested that AM-mediated uptake of soil water of low Ψ is analogous to the uptake of P, where tapping supplies not available to the NM plant results in a positive response. One explanation for higher g_s in AM plants may be that, across studies in the meta-analysis, AM plants may have been generally less stressed than their NM counterparts, maintaining higher water status and hence more open stomata. The higher g_s of AM plants has been associated with higher leaf Ψ or higher leaf water content as well as with greater osmotic adjustment and higher turgor at similar Ψ (Augé 2001). AM promotion of g_s might also be related to the influence of the symbiosis on the carbon dynamics of host leaves. As much as 20 % of all carbon assimilated by the AM host plant is eventually moved into fungal structures and exudates (e.g., Pang and Paul 1980; Wang et al. 1989). AM fungi, by requiring carbon assimilates and thus increasing the sink strength of root systems (e.g., Wright et al. 1998; Kaschuk et al. 2009), may increase net movement of carbon out of leaves, lowering carbon concentrations in leaf mesophyll. Stomatal opening is stimulated by lowered internal CO_2 concentrations and/or pools of carbon-fixing substrates (Mansfield et al. 1990; Jarvis and Davies 1998).

The third question we posed was how much the AM effect on g_s was linked to AM promotion of plant size and/or leaf P concentration. The notion that AM effects on plant water relations were mainly nutritional in nature was prevalent in the early literature on this subject: the behavior of AM and NM plants differed because plants differed in size or tissue P concentrations (Augé 1989, 2001). Phosphorus concentration of leaves can affect their g_s (Radin 1984), and AM symbiosis often dramatically modifies P acquisition and tissue P contents. Better nutrition is accompanied by quicker growth. Other things being equal, more water usually moves through large plants than small plants per unit time. When AM plants have different g_s or soil drying rates than smaller NM plants, this may be similar to NM plants having different g_s or soil drying rates than smaller NM plants. AM-induced changes in total plant size probably affect stomatal behavior and plant water relations mostly through effects on tissue hydration: how quickly tissues lose water and how quickly they can replace it. The meta-analysis revealed that the shoot size and leaf P moderators do account for mycorrhizal influence, confirming the supposition of the earlier work. In the absence of growth promotion, the AM-induced increase in g_s is still significant, but at 11 %, it is much smaller than the overall 24 % AM promotion. However, across studies in which NM plants were larger or higher in leaf P than AM plants, the significant positive effect of AM symbiosis on g_s was still observed. Thus, the meta-analysis also confirmed that the AM effect can occur independently of effects on shoot size and leaf P.

The analysis provides some clear answers to our fourth question, whether particular experimental conditions or symbiont characteristics have led to especially large AM promotion of g_s. Sometimes, investigators have observed significant correlations between a water relations parameter and extent of root colonization. For example, Bethlenfalvay et al. (1988) demonstrated that the soil moisture content at permanent wilting of individual plants was closely inversely correlated with the extent of root colonization. However, in water relations and other physiological areas of mycorrhizal investigation, AM effects have often not been well correlated with root colonization levels (e.g., Dakessian et al. 1986; Ruiz-Lozano et al. 1995; Fitter and Merryweather 1992). Over the 409 studies that reported g_s and colonization data, the meta-analysis did find that root colonization has been a significant moderator variable. When roots of plants in an AM treatment were heavily colonized, the percentage increase in AM effect size was a dramatic ×10 greater than the negligible percentage increase observed when roots were relatively sparsely colonized. Greater colonization is likely related to both enhanced P acquisition and enhanced water absorption. The degree of mycorrhization of the soil itself has also been linked to the regulation of stomatal behavior of host plants (Augé et al. 2007).

Environmental variables have considerable influence on g_s (Salisbury and Ross 1985). Soil environmental variables such as soil water content, salinity, and fertility have been studied often in mycorrhizal work, but mycorrhizal impact on g_s has rarely been examined directly as a function of atmospheric environmental variables such as temperature, light, or humidity. In one study comparing AM promotion of g_s at six levels of irradiance, the AM promotion was greatest at irradiances between 300 and 1,000 μmol m^{-2} s^{-1} and relatively low at levels below 100 and above 1,000 μmol m^{-2} s^{-1} (Augé et al. 2004). This finding under low light is consistent with the meta-analysis. Conclusions about light levels must be drawn with caution from this analysis, as the available light data in the studies often summarized the range of conditions during the experiment but not the irradiance at which measurements were made. Irradiance on the leaf lamina at time of g_s measurement exerts a controlling influence on g_s, and interpreting experimental findings would be assisted if these data were provided in publications. Augé et al. (2004) observed a similar trend with air temperatures: not much AM promotion of g_s at the lowest temperatures (below 20 °C), the

most promotion at intermediate temperatures (20–26 °C), and not much promotion above 28 °C. This trend was seen with the meta-analysis, with AM promotion 10 % higher when air temperatures were kept at or below 27 °C relative to those that at least sometimes exceeded 27 °C.

Experiments in growth chambers are typically conducted under artificial light and those in greenhouses wholly or mostly under natural light. In these two controlled environments, AM promotion of g_s differed markedly. We may not have predicted this, as light levels are also generally lower in chambers than in greenhouses. Among the three growth sites, light levels would generally be highest in the field, where AM promotion of g_s has been relatively high. A biotic factor that increases g_s in the field by an average of 59 %, especially one like AM symbiosis that develops long term relationships with its host, can be expected to have very substantive impacts on plant productivity as well as soil structure and carbon sequestration (e.g., Wilson et al. 2009).

We included the three inoculum moderators in the meta-analysis as indirect ways of gauging the effects of soil organisms associated with AM fungi. When pot culture consisting of soil, live roots, and hyphae are used as an inoculant, organisms other than glomalean fungi are applied to the AM treatment. If these other organisms are not also applied to NM plants, an observed treatment effect due to one or more of these other organisms cannot be ruled out. Attempts are often made to control for these associated soil organisms, by applying water filtrates of inoculum or by inoculating NM controls with live NM pot culture produced on the same host species in the same location as AM pot culture. These are not perfect controls—filtrates, for instance, only contain propagules smaller than whatever fine mesh is used for filtering—but they have been considered to provide better controls than not making any attempt to standardize soil flora and fauna across treatments. If NM soil organisms and the propagules of these organisms move fairly freely within the experimental growth chamber, greenhouse, or field site, then NM pot culture may be the best method of controlling for their potential influence on host stomatal behavior (even better, NM pot culture+filtrates). Across the 200 studies lacking a filtrate or NM pot culture control, the AM effect was twice that observed across the 65 studies that did employ NM pot culture as a means of controlling for associated soil organisms. This suggests that caution is warranted in attributing AM treatment effects solely to AM fungi. By introducing to NM controls only those organisms having tiny propagule sizes, the same may be true for water filtrate controls.

The ratio of variation among levels within moderators to total variance, Q_m/Q_t, gives an indication of the relative importance of each environmental and symbiont moderator in affecting the size of the AM modification of g_s (Table 1). Stomatal conductance data often contain a great deal of inherent biological variability because stomata are very sensitive to numerous internal and most external variables (Meidner and Mansfield 1968; Fitter and Hay 1987; Nobel 1991). These variables change, sometimes quickly, during the day and from day to day: e.g., leaf-to-air gradients in water vapor pressure and CO_2 concentration, light quantity and quality, temperature, wind, and leaf water and hormonal status. Consequently, measures like g_s within a population of similar individuals, and even within one individual, can vary considerably from day to day and even from minute to minute. Stomatal conductance can also vary with leaf age and with position on lamina. This variability may be compounded by the effects of measurement procedures on stomata: shading and compression of lamina, atmosphere changes by cuvettes, and moving plants prior to making measurements (mechanical stress). For these reasons, g_s has much more potential to fluctuate than more stable measures such as biomass or P accumulation, whose values can generally be expected to remain similar from one hour to the next. Consequently, one-time measurements of g_s may not be reliable indicators of AM treatment effects; multiple time-point measurements are usually needed to give confidence in an effect or lack thereof. The majority of AM studies in this meta-analysis (314 studies) reported g_s at just one time, adding to the inherently noisy aspect of the g_s data. We believe this contributed to the relatively low Q_m/Q_t ratios.

The meta-analysis does not identify causal relationships. It establishes how different moderator variables have influenced the magnitude of the AM effect sizes, which can assist our understanding about when AM effects on g_s have occurred and situations that have promoted the AM effect. The moderator analysis should be useful in planning future experiments to clarify mechanisms. As it appears important to assure a high degree of root colonization, early tests that indicate relatively low colonization may cause investigators to wait until roots are more thoroughly colonized before measuring g_s. Characterizing mycorrhizal influence on stomatal opening may be more fruitful under adequate irradiance. When controlling for plant size and or leaf P concentrations—producing AM and NM plants that are similar in these regards—researchers can expect to see less mycorrhizal effect on g_s than when experiments are conducted in P-deficient soils and without fertilization. The results of the meta-analysis indicate the importance of quantifying the severity of the drought treatment; measures of soil water status at time of g_s measurement are important. Most articles did not detail inoculum source or environmental origin of fungal isolates. Providing this information, if known, would assist future quantitative literature reviews, e.g., comparisons of xeric vs mesic isolates.

An overall AM promotion in g_s of above 20 % is remarkable. Any variable causing an increase in g_s of this magnitude, viewed over a wide diversity of taxa and experimental conditions, can be expected to have important fundamental and practical consequences. Stomata are the guardians of gas exchange in higher plants (Meidner and Mansfield 1968;

Weyers and Meidner 1990), providing paths for CO_2 uptake while governing the unavoidable efflux of water vapor under widely and continually changing conditions. Stomata may operate to minimize rates of evaporation at particular average rates of assimilation (Cowan 1977), maximizing water use efficiency. They may prevent drought injury through the avoidance of xylem cavitations and possible consequent runaway embolism (Jones and Sutherland 1991). Stomatal regulation of transpiration is thought to act to maintain optimal leaf temperature (Mahan and Upchurch 1988). By altering stomatal behavior, AM symbiosis can modify these processes, with broad ecological and agricultural impacts.

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References

Adams DC, Gurevitch J, Rosenberg MS (1997) Resampling tests for meta-analysis of ecological data. Ecology 75:1277–1283

Allen EB, Allen MF (1986) Water relations of xeric grasses in the field: interactions of mycorrhizas and competition. New Phytol 104: 559–571

Augé RM (1989) Do VA mycorrhizae enhance transpiration by affecting host phosphorus content? J Plant Nutr 12:743–753

Augé RM (2000) Stomatal behavior of arbuscular mycorrhizal plants. In: Kapulnik Y, Douds DD (eds) Arbuscular mycorrhizas: physiology and function. Kluwer Academic Publishers, Dordrecht, pp 201–237

Augé RM (2001) Water relations, drought and VA mycorrhizal symbiosis. Mycorrhiza 11:3–42

Augé RM, Stodola AJ, Brown MS, Bethlenfalvay GJ (1992) Stomatal response of mycorrhizal cowpea and soybean to short-term osmotic stress. New Phytol 120:117–125

Augé RM, Moore JL, Sylvia DM, Cho K (2004) Mycorrhizal promotion of host stomatal conductance in relation to irradiance and temperature. Mycorrhiza 14:85–92

Augé RM, Toler HD, Moore JL, Cho K, Saxton AM (2007) Comparing contributions of soil versus root colonization to variations in stomatal behavior and soil drying in mycorrhizal *Sorghum bicolor* and *Cucurbita pepo*. J Plant Physiol 164:1289–1299

Begg CB, Mazumdar MM (1994) Operating characteristics of a rank correlation test for publication bias. Biometrics 50:1088–1101

Benabdellah K, Abbas Y, Abourouh M, Aroca R, Azcon R (2011) Influence of two bacterial isolates from degraded and non-degraded soils and arbuscular mycorrhizae fungi isolated from semi-arid zone on the growth of Trifolium repens under drought conditions: Mechanisms related to bacterial effectiveness. Eur J Soil Biol 47:303–309

Bethlenfalvay GJ, Thomas RS, Dakessian S, Brown MS, Ames RN, Whitehead EE (1988) Mycorrhizae in stressed environments: effects on plant growth, endophyte development, soil stability and soil water. In: Hutchinson CF, Timmermann BN (eds) Arid lands: today and tomorrow. Westview, Boulder, pp 1015–1029

Borenstein M, Hedges L, Higgins J, Rothstein J (2009) Introduction to meta-analysis. Wiley, West Sussex

Cooper H (2010) Research synthesis and meta-analysis: a step-by-step approach, 4th edn. SAGE Publications Inc, London

Cowan IR (1977) Stomatal behavior and environment. Adv Bot Res 4: 117–228

Dakessian S, Brown MS, Bethlenfalvay GJ (1986) Relationship of mycorrhizal growth enhancement and plant growth with soil water and texture. Plant Soil 94:439–444

Ebel RC, Welbaum GE, Gunatilaka M, Nelson T, Augé RM (1996) Arbuscular mycorrhizal symbiosis and nonhydraulic signaling of soil drying in *Vigna unguiculata* (L.) Walp. Mycorrhiza 6: 119–127

Fitter AH, Hay RKM (1987) Environmental physiology of plants. Academic, New York

Fitter AH, Merryweather RW (1992) Why are some plants more mycorrhizal than others? An ecological inquiry. In: Read DJ, Lewis DH, Fitter AH, Alexander I (eds) Mycorrhizas in ecosystems. CAB International, Wallingord, UK, pp 26–36

Franson RL, Milford SB, Bethlenfalvay GJ (1991) The Glycine-Glomus-Bradyrhizobium symbiosis. XI. Nodule gas exchange and efficiency as a function of soil and root water status in mycorrhizal soybean. Physiol Plant 83:476–482

Gong M, Tang M, Chen H, Zhang Q, Xinxin F (2013) Effects of two Glomus species on the growth and physiological performance of Sophora davidii seedlings under water stress. New For 44:399–408

Gupta RK (1991) Drought response in fungi and mycorrhizal plants. Handbook Appl Mycol 1:55–75

Gurevitch J, Hedges LV (1999) Statistical issues in ecological meta-analyses. Ecology 80:1142–1149

Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC, Wilson GWT, Klironomos JN, Umbanhowar J (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol Lett 13:394–407

Holmgren M, Gómez-Aparicio L, Quero JL, Valladares F (2012) Non-linear effects of drought under shade—reconciling physiological and ecological models in plant communities. Oecologia 169:293–305

Jarvis AJ, Davies WJ (1998) The coupled response of stomatal conductance to photosynthesis and transpiration. J Exp Bot 49:399–406

Jones HG, Sutherland RA (1991) Stomatal control of xylem embolism. Plant Cell Environ 6:607–612

Kaschuk G, Kuyper TW, Leffelaar PA, Hungria M, Giller KE (2009) Are the rates of photosynthesis stimulated by the carbon sink strength of rhizobial and arbuscular mycorrhizal symbioses? Soil Biol Biochem 41:1233–1244

Kelliher FM, Leuning R, Raupach MR, Schulze E-D (1995) Maximum conductances for evaporation from global vegetation types. Agric For Meteor 73:1–16

Kiær LP, Weisbach AN, Weiner J (2013) Root and shoot competition: a meta-analysis. J Ecol 101:1298–1312

Koide R (1993) Physiology of the mycorrhizal plant. Adv Plant Pathol 9: 33–54

Lehmann A, Barto EK, Powell JR, Rillig MC (2012) Mycorrhizal responsiveness trends in annual crop plants and their wild relatives—a meta-analysis on studies from 1981 to 2010. Plant Soil 355:231–250

Levitt J (1980) Responses of plants to environmental stresses. II. Water, radiation, salt, and other stresses. Academic Press, New York

Ludlow MM (1989) Strategies in response to water stress. In: Kreeb HK, Richter H, Hinckley TM (eds) Structural and functional responses to environmental stresses: water shortage. SPB Academic Press, The Hague, pp 269–281

Mahan JR, Upchurch DR (1988) Maintenance of constant leaf temperature by plants. I. Hypothesis—limited homeothermy. Env Exp Bot 28:351–357

Mansfield TA, Hetherington AM, Atkinson CJ (1990) Some current aspects of stomatal physiology. Annu Rev Plant Physiol Plant Mol Biol 41:55–75

Mayerhofer MS, Kernaghan G, Harper KA (2013) The effects of fungal root endophytes on plant growth. Mycorrhiza 23:119–128

McGrath JM, Lobell DB (2013) Reduction of transpiration and altered nutrient allocation contribute to nutrient decline of crops grown in elevated CO2 concentrations. Plant Cell Environ 36:697–705

Meidner H, Mansfield TA (1968) Physiology of stomata. McGraw Hill, New York

Morton J (2014) International culture collection of (vesicular) arbuscular mycorrhizal fungi. *Rhizophagus fasciculatus* (Voucher specimens). http://invam.wvu.edu/the-fungi/classification/glomaceae/rhizophagus/fasciculatum. Accessed 6 March 2014

Newman SE, Davies FT Jr (1988) High root-zone temperatures, mycorrhizal fungi, water relations, and root hydraulic conductivity of container-grown woody plants. J Am Soc Hortic Sci 113:138–146

Nobel PS (1991) Physicochemical and environmental plant physiology. Academic, New York

Orwin RG, Boruch RF (1982) RRT meets RDD: statistical strategies for assuring response privacy in telephone surveys. Public Opinion Quarterly 46:560–571

Pang PC, Paul EA (1980) Effects of vesicular-arbuscular mycorrhizal on ^{14}C and ^{15}N distribution in nodulated faba beans. Can J Soil Sci 60:241–250

Radin JW (1984) Stomatal responses to water stress and to abscisic acid in phosphorus-deficient cotton plants. Plant Physiol 76:392–394

Redecker D, SchüßlerA SH, Stürmer SL, Morton JB, Walker C (2013) An evidence-based consensus for the classification of arbuscular mycorrhizal fungi (Glomeromycota). Mycorrhiza 23:515–531

Reid CPP (1979) Mycorrhizae and water stress. In: Reidacher A, Gagnaire-Michard G (eds) Root physiology and symbiosis. IUFRO Proc, Nancy, France, pp 392–408

Rogatgi A (2011) WebPlotDigitizer, http://arohatgi.info/WebPlotDigitizer/app/. Accessed August-November 2013

Rosenberg MS, Adams DC, Gurevitch J (2000) MetaWin: statistical software for meta-analysis, version 2. Sinauer Associates, Sunderland

Rosenthal R (1979) The "file drawer problem" and tolerance for null results. Psychol Bull 86:638–641

Ruiz-Lozano JM, Aroca R (2010) Host response to osmotic stresses: stomatal behavior and water use efficiency or arbuscular mycorrhizal plants. In: Koltai H, Kapulnik Y (eds) Arbuscular mycorrhiza: physiology and function. Springer, Dordrecht, pp 239–256

Ruiz-Lozano JM, Azcón R, Gómez M (1995) Effects of arbuscular-mycorrhizal Glomus species on drought tolerance: physiological and nutritional plant responses. Appl Environ Microbiol 61: 456–460

Salisbury FB, Ross CW (1985) Plant physiology. Wadsworth Pub. Co., Belmont, CA

Sánchez-Díaz M, Honrubia M (1994) Water relations and alleviation of drought stress in mycorrhizal plants. In: Gianinazzi S, Schüepp H (eds) Impact of arbuscular mycorrhizas on sustainable agriculture and natural ecosystems. Birkhäuser, Boston, pp 167–178

Schaeffer RN, Manson JS, Irwin RE (2013) Effects of abiotic factors and species interactions on estimates of male plant function—a meta analysis. Ecol Lett 16:399–408

Schüßler A, Walker C (2010) The Glomeromycota: a species list with new families. Arthur Schüßler & Christopher Walker, Gloucester. Published in December 2010 in libraries at The Royal Botanic Garden Edinburgh, The Royal Botanic Garden Kew, Botanische Staatssammlung Munich, and Oregon State University. Printed copy available under ISBN-13: 978-1466388048, ISBN-10: 1466388048. Available at http://www.amf-phylogeny.com/

Sharkey TD, Raschke K (1981) Effect of light quality on stomatal opening in leaves of *Xanthium strumarium* L. Plant Physiol 68: 1170–1174

Smith SE, Read D (2008) Mycorrhizal symbiosis. Elsevier Ltd, Amsterdam

Smith SE, Facelli E, Pope S, Smith FA (2010) Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas. Plant Soil 326:3–20

Veresoglou SD, Menexes G, Rillig MC (2012) Do arbuscular mycorrhizal fungi affect the allometric partition of host plant biomass to shoots and roots? A meta-analysis of studies from 1990 to 2010. Mycorrhiza 22:227–235

Wang GM, Coleman DC, Freckman DW, Dyer MI, McNaughton SJ, Acra MA, Goeschl JD (1989) Carbon partitioning patterns of mycorrhizal versus non-mycorrhizal plants: real time dynamic measurements using $^{11}CO_2$. New Phytol 112:489–493

Weyers JDB, Meidner H (1990) Methods in stomatal research. Longman Scientific and Technical, Essex

Wilkinson S, Davies WJ (2002) ABA-baased chemical signaling: the coordination of responses to stress in plants. Plant Cell Environ 25: 195–210

Wilson GWT, Rice CW, Rillig MC, Springer A, Hartnett DC (2009) Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. Ecol Lett 12:452–461

Worchel ER, Glauque HE, Kivlin SN (2013) Fungal symbionts alter plant drought response. Microb Ecol 65:671–678

Wright DP, Read DJ, Scholes JD (1998) Mycorrhizal sink strength influences whole plant carbon balance of *Trifolium repens* L. Plant Cell Environ 21:881–891

Zvereva EL, Kozlov MV (2012) Sources of variation in plant responses to belowground insect herbivory: a meta-analysis. Oecologia 169: 441–452