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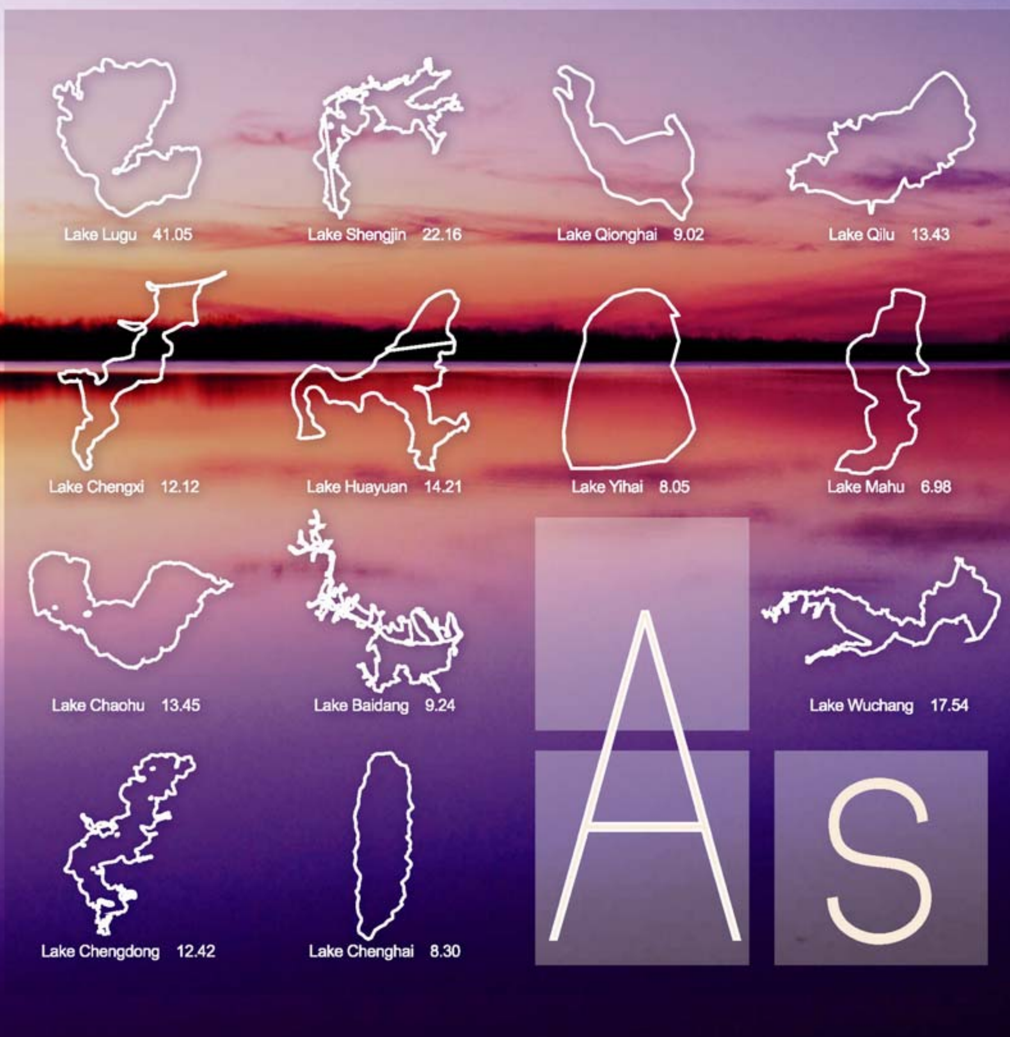

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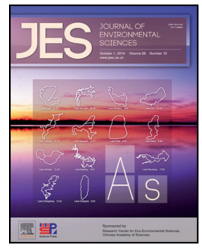

Arbuscular mycorrhizal fungal phylogenetic groups differ in affecting host plants along heavy metal levels

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A B S T R A C T

Arbuscular mycorrhizal fungi (AMF) are important components of soil microbial communities, and play important role in plant growth. However, the effects of AMF phylogenetic groups (Glomeraceae and non-Glomeraceae) on host plant under various heavy metal levels are not clear. Here we conducted a meta-analysis to compare symbiotic relationship between AMF phylogenetic groups (Glomeraceae and non-Glomeraceae) and host plant functional groups (herbs *vs.* trees, and non-legumes *vs.* legumes) at three heavy metal levels. In the meta-analysis, we calculate the effect size (ln(RR)) by taking the natural logarithm of the response ratio of inoculated to non-inoculated shoot biomass from each study. We found that the effect size of Glomeraceae increased, but the effect size of non-Glomeraceae decreased under high level of heavy metal compared to low level. According to the effect size, both Glomeraceae and non-Glomeraceae promoted host plant growth, but had different effects under various heavy metal levels. Glomeraceae provided more benefit to host plants than non-Glomeraceae did under heavy metal condition, while non-Glomeraceae provided more benefit to host plants than Glomeraceae did under no heavy metal. AMF phylogenetic groups also differed in promoting plant functional groups under various heavy metal levels. Interacting with Glomeraceae, herbs and legumes grew better than trees and non-legumes did under high heavy metal level, while trees and legumes grew better than herbs and non-legumes did under medium heavy metal level. Interacting with non-Glomeraceae, herbs and legumes grew better than trees and non-legumes did under no heavy metal. We suggested that the combination of legume with Glomeraceae could be a useful way in the remediation of heavy metal polluted environment.

Introduction

Soil contamination by heavy metals has deteriorated and become a serious environmental problem because of the increasing intensity of anthropic activities and industrialization (Nriagu and Pacyna, 1988; Arriagada et al., 2007). The primary sources of this pollution are the burning of fossil fuels, mining, industrial activities, municipal wastes and the application of fertilizers or pesticides (Moreira et al., 2011). The low molecular weight heavy metals (*e.g.*, Zn, Cu, Ni, Mn, Mo and Fe) are essential minerals for plant growth, while high molecular heavy metals (*e.g.*, Cr, Cd, Pb, As and Hg) have no biological function to plants (Prasad et al., 2011; Lin and Aarts, 2012). Excessive accumulation of heavy metals in soils will limit development and growth of plants (Wang et al., 2006; Pichtel and Salt, 1998; Shetty et al., 1995; Wong, 2003). Excessive heavy metals in soil could also pose a health hazard to humans and animals because heavy metals are not biodegradable and tend to accumulate in organisms (Miransari, 2011; Bhargava et al., 2012). Thus, it is necessary to take efficient soil cleanup techniques to restore the heavy metal pollution soil. Phytoremediation is an efficient and inexpensive method to

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clean up the soil polluted by heavy metal (Khade and Adholeya, 2008; Azcón et al., 2009). Some plants have evolved tolerant abilities to adapt to excessive heavy metal soil (Hall, 2002). One of these abilities in plants is to develop symbioses with soil microorganisms (*e.g.*, arbuscular mycorrhizal fungi, AMF) (Schloter et al., 2003; Shah and Mongkyrih, 2007; Garg and Singla, 2012; Orłowska et al., 2012).

Arbuscular mycorrhizal fungi (AMF) of the Glomeromycota are the most common soil microorganisms in natural and agricultural soils (Mohammad and Mittra, 2013). AMF can form symbiotic associations with many terrestrial plants (Smith and Read, 1997). The host plants provide AMF with carbon, and in return, AMF acquire nutrients (*i.e.* phosphorus and nitrogen) for their hosts (Smith and Read, 2008; Xu et al., 2012). Studies have demonstrated that AMF can help their host plants to resist heavy metal, and can increase metal uptake and translocation (Chen et al., 2005; Souza et al., 2011; Punamiya et al., 2010; Zhang et al., 2010). Several mechanisms explain why AMF can alleviate the stress of heavy metal. One of these mechanisms is that mycorrhizal plants have large biomass that can dilute the metal concentration (Göhre and Paszkowski, 2006). Experiments also found that the heavy metal was immobilized and compartmentalized in AMF hyphal cells (Göhre and Paszkowski, 2006; Andrade et al., 2010b). In addition, AMF can produce metal chelation of glomalin, fungal polyphosphates and metallothioneins that have high binding capacities for heavy metal (Kaldorf et al., 1999; Vodnik et al., 2008). AMF can also alter the gene express that relate to metal tolerance of host plant (Ouziad et al., 2005).

Studies have showed that AMF phylogenetic groups differed in morphology (Redecker and Raab, 2006). For example, Glomeraceae and Gigasporaceae differed in hyphal architecture and growth patterns (Redecker and Raab, 2006). Compared to the Glomeraceae, AMF in the Gigasporaceae lacked the ability to form extensive hyphal networks (de la Providencia et al., 2005; Voets et al., 2006). Gigasporaceae can only colonize roots from germinating spores, but do not form anastomoses (cross-links) among hyphae. Thus, if the hyphae are injured, only the main hyphae can be repaired (de la Providencia et al., 2005; Voets et al., 2006). However, Glomeraceae are able to colonize roots and extensive anastomoses in their mycelium. Glomeraceae can repair injured hyphae by forming a network of anastomoses instead of repairing the main hyphal axis (de la Providencia et al., 2005; Voets et al., 2006; Redecker and Raab, 2006).

Studies have also showed that AMF phylogenetic groups differed in affecting host plant growth. For example, Wang et al. (2006) found that the biomass of *Zea mays* was improved by *Glomus caledonium* of Glomeraceae, while was not affected significantly by the *Gigaspora margarita* of Gigasporaceae under heavy metal stress. Bai et al. (2008) showed that the indigenous consortia *Glomus* spp. and *Acaulospora* spp. could protect their host plants (*Z. mays*) from the toxicity of excessive As through activating P.

The plant–AMF symbiotic functions are affected not only by the host plants, the AMF types, but also by the abiotic or biotic environmental gradients (Hoeksema et al., 2010; Lehmann et al., 2012). For example, the host plant *Canavalia ensiformis* with AMF inoculation exhibited higher tolerance to Zn up to 300 mg/kg, but not when Zn reached up to 900 mg/kg (Andrade et al., 2009). The biomass of this host *C. ensiformis* was enhanced by *Glomus etunicatum* under highest Cu concentrations (450 mg/dm). AMF decreased Cu concentrations in plant organs and promoted biomass accumulation (Andrade et al., 2010a). Compared to without *Glomus intraradices* inoculation, *Z. mays* with *G. intraradices* decreased Pb concentrations in both shoots and roots at low Pb level (0.01 mmol/L), but only decreased Pb concentrations in roots at high Pb level (0.1 mmol/L) (Malcová et al., 2003).

There are a few articles to discuss how the AMF phylogenetic groups (Glomeraceae and non-Glomeraceae) affect the growth of host plants along heavy metal levels (no heavy metal addition, medium level, and high level) (Wang et al., 2006; Bai et al., 2008). Here we present a meta-analysis to analyze the effects of AMF phylogenetic groups on the growth of host plants under different heavy metal levels. We used host plant biomass as indicators of plant growth. Our meta-analysis focuses on two main questions. First, whether the AMF phylogenetic groups differ in affecting the growth of host plants under different heavy metal levels. Second, whether host plant functional groups differ in response to AMF phylogenetic groups under different heavy metal levels.

1. Materials and methods

1.1. Sources of data

Meta-analysis is a statistical tool that synthesizes and analyses the results of several independent studies to search for generalizations (Hedges and Olkin, 1985; Gurevitch and Hedges, 1999). It is employed here to explore whether the experience accumulated over the past few decades can be used to formulate specific results. We focused on published studies that examined plant–AMF symbioses under heavy metal (*e.g.* Pb, Cu, Cd, As, Zn, Cr, Al and Fe) gradients. Studies were located by searching keywords in Web of Science (http://apps.webofknowledge.com/) and Google Scholar (http://scholar.google.com.hk/) for terms combinations of (biomass) and (arbuscular mycorrhizal fungi, AMF) and (heavy metal) from 1970 to 2012. We found a total of forty-two articles that met the following criteria for our meta-analysis: (1) plant performance has pair-wise control (without AMF) and experimental treatments (with AMF); (2) plant performance at different heavy metal levels in greenhouse (three or more than three levels); (3) AMF identity and host plants should be exact, and mixed AMF species or plant species were excluded; (4) when the same host plant or the same AMF species were studied in different papers, each study was used as an independent data record; (5) when a single paper reported results for multiple AMF-plant species pairs at different heavy metal levels, each species pair was considered as an independent data record (Hoeksema et al., 2010); (6) when systems only differed in duration of experiment, only the last harvest was included in the dataset; (7) when the study reported AMF interacting with other microbes, such as rhizobia and P solubilizing bacteria, the data was only recorded for solely AMF without any interactions.

We extracted data of host plant growth from the studies that met the above criteria. The host plant growth was measured as shoot biomass. If the shoot biomass was unavailable, we use total plant biomass data instead. We collected all data from tables or digitized from figures by using GetData software (http://getdata-graph-digitizer.com/). Then we recorded the means, sample sizes (N), standard deviation (SD) or standard error (SE). We also recorded AMF phylogenetic groups (Glomeraceae and non-Glomeraceae) and host plant functional groups (herbs *vs.* trees and legumes *vs.* non-legumes) in the pair-wise comparisons (treatments inoculated with AMF *vs.* noninoculated controls). SE was transformed to SD by Eq. (1):

$$SD = SE \times \sqrt{N}. \quad (1)$$

But if both the SE and SD were not provided by the original studies, we estimated SD with the method developed by van Groenigen et al. (2011). We calculate the averaged coefficient of variation (CV) of the whole dataset by Eq. (2):

$$\mathrm{CV} = \mathrm{SD}/\mathrm{mean}. \quad (2)$$

The missing SD was approximately estimated by multiplying the mean and the average CV.

Because the assignment of metal levels was arbitrary in some studies and did not have a unified standard, we computed a value to uniform the gradient by Eq. (3):

$$S = T_i/T_{i,\max} \tag{3}$$

where, S is the gradient value ($0 \le S \le 1$), T_i is the heavy metal treatment value in the original publication, and $T_{i,\max}$ is the maximal heavy metal treatment value in the original publication. According to the magnitude of gradient values, we designated heavy metal levels as "no heavy metal" (0), "medium level" ($0 < S < 1$), and "high level" ($S = 1$). If there were more than three heavy metal levels in the original publications, we have only chosen one group as medium level.

1.2. *Meta-analysis*

The meta-analysis included two steps by the MetaWin 2.0 software by random model (Rosenberg et al., 2000). First, the effect size was calculated by taking the natural logarithm of the response ratio (lnRR) of inoculated to non-inoculated plant shoot biomass from each study (Hoeksema et al., 2010; Lehmann et al., 2012). Second, effect sizes are statistically summarized to estimate a weighted average for the sample of studies (average effect size) and to test the hypothesis. To determine whether AMF phylogenetic groups differ in affecting the host plant functional groups along a heavy metal gradient, AMF were divided into two groups (Glomeraceae and non-Glomeraceae). Plants were also divided into two types of plant functional groups. Plant functional group1 included herbs and trees, and plant functional group2 included legumes and non-legumes. The meta-analysis was conducted separately for the hypothesis with a resampling of 9999 iterations. Positive lnRR values indicate that plant growth was facilitated by AMF. For the data sets, the Q statistic was used to examine homogeneity. Q_b was used to assess whether classes within each data set differed significantly. Q_w was used to test homogeneity within-class (Adams et al., 1997). We estimated 95% confidence intervals (CIs) of the means. If CIs of the two groups were non-overlapping, they were considered significantly different.

Meta-analysis may produce biased results because a published study often reported positive data, or because the original studies had different statistical methods (Koricheva et al., 2009). Therefore, it is necessary to test the publishing biases by examining the relationship between standardized effect sizes of raw data and sample size for all datasets using the method of the Spearman rank correlation tests. We found no publication biases for Glomeraceae and non-Glomeraceae ($Rs = -0.107$, $P = 0.14856$; $Rs = 0.074$, $P = 0.64325$) along a heavy metal gradient. The fail-safe numbers is a quick way to estimate whether publication bias is a problem for a specific study. If the fail-safe number is larger than 5 N + 10 (N means sample size), it was safe to conclude that results were robust regarding publication bias (Rosenberg, 2005; Rosenthal, 1979). In the current study, the fail-safe number and 5 N + 10 were 92,464,594 and 925 for Glomeraceae; 5805 and 220 for non-Glomeraceae, indicating that the results of our meta-analysis were not affected by publication bias.

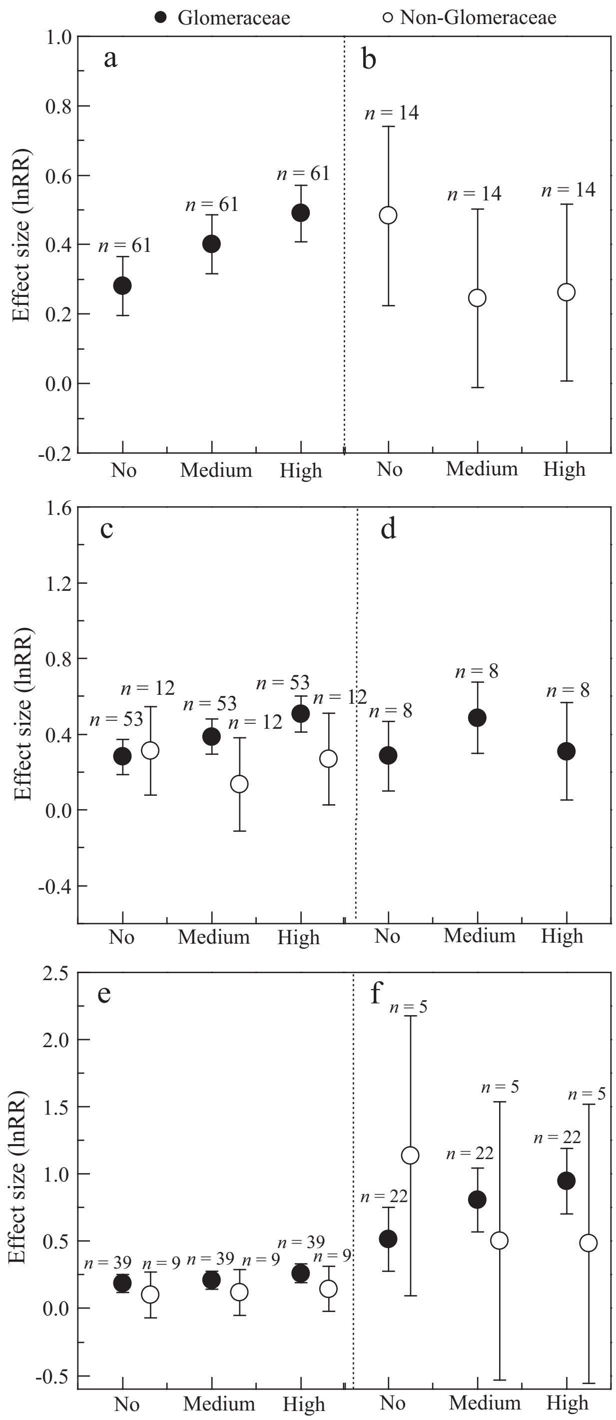

Fig. 1 – Mean effect sizes by categorical grouping variable for plant growth along heavy metal gradients. Effect size refers to the mean (95% CI) of the ln response ratio (lnRR) of the AMF-treated plants to the non-treated control plants. The "*n*" refers to the number of experiments. (a) Glomeraceae, (b) non-Glomeraceae; (c) Glomeraceae–herb and non-Glomeraceae–herb combination, (d) Glomeraceae–tree combination, not enough data were available to calculate an effect size for shrubs and non-Glomeraceae–tree; (e) Glomeraceae–non-legume and non-Glomeraceae–non-legume combination, (f) Glomeraceae–legume and non-Glomeraceae–legume.

2. Results

Positive effect of AMF on plant growth was detected when the full dataset was used, but this effect varied greatly among heavy metal levels (Fig. 1a and b; Table 1). For Glomeraceae, there was significant difference of effect size among heavy metal levels (Q_b = 11.8909, P = 0.00262). The effect size was significantly higher under high heavy metal level than that under no heavy metal (Fig. 1a; Table 1). For Non-Glomeraceae, there was no significant difference of the effect size among the heavy metal levels (Q_b = 2.4723, P = 0.29050). Under medium and high heavy metal levels, Glomeraceae provided more benefit to plants than non-Glomeraceae did, but under no heavy metal, non-Glomeraceae provided more benefit to plants than Glomeraceae did (Fig. 1a and b).

The presence of AMF generally had a positive effect on the growth of plants, but the magnitude of this effect depended on the specific combination of AMF and host plants (Fig. 1c–f). For the interaction between herbs and Glomeraceae, effect sizes were significantly affected by heavy metal levels (Q_b = 11.8508, P = 0.00267). Glomeraceae provided more benefit to herbs under high heavy metal condition compared to no heavy metal (Fig. 1c; Table 1). For the interaction between herbs and non-Glomeraceae, there were no significant difference of effect size among three heavy metal levels (Q_b = 1.3843, P = 0.50049). Under medium and high levels, the effect of Glomeraceae on herbs was higher than that of non-Glomeraceae. Under no heavy metal, however, the effect on herbs was similar between Glomeraceae and non-Glomeraceae (Fig. 1c).

Glomeraceae had a significant effect on trees as the 95% CI did not cross zero (Fig. 1d), but there were no significant difference of effect size among the three heavy metal levels (Q_b = 3.5271, P = 0.17143). For the interaction between trees and non-Glomeraceae, we did not report the results here because there were not enough available cases to calculate an effect (Fig. 1d).

There was no significant difference of effect size among the three heavy metal levels for both “interaction between non-legume and Glomeraceae” (Q_b = 2.6456, P = 0.26639) and “interaction between non-legume and non-Glomeraceae” (Q_b = 0.1626, P = 0.92194). Glomeraceae and non-Glomeraceae did not have a significant effect on non-legumes (Table 1).

For the interaction between legume and Glomeraceae, effect sizes were significantly affected by the different heavy metal levels (Q_b = 7.2577, P = 0.02655). Glomeraceae promoted the growth of legumes under high level, but did not under no heavy metal (Fig. 1f; Table 1). Glomeraceae had a significant effect on legumes (Table 1), and effect size was increasing with the heavy metal (Fig. 1f). For the interaction between legumes and non-Glomeraceae, there was no significant difference among the three heavy metal levels (Q_b = 1.9737, P = 0.37276).

Table 1 – Effects of arbuscular mycorrhizal fungi phylogenetic groups (Glomeraceae and non-Glomeraceae) on host plant functional groups (herbs *vs.* trees and non-legumes *vs.* legumes) at three levels of heavy metal: metal-analysis.

Comparison	Classification	Stress level group	Numbers of experiments	Effect size	95% CI	Q_b	P value
All	All-G	No addition	61	0.2810	0.1967–0.3654	11.8909	0.00262
		Medium	61	0.4011	0.3160–0.4861		
		High	61	0.4899	0.4018–0.5780		
	All-NG	No addition	14	0.4830	0.2248–0.7412	2.4723	0.29050
		Medium	14	0.2460	−0.0115–0.5034		
		High	14	0.2615	0.0065–0.5166		
Plant functional group1	Herb-G	No addition	53	0.2799	0.1873–0.3726	11.8508	0.00267
		Medium	53	0.3875	0.2942–0.4808		
		High	53	0.5066	0.4123–0.6008		
	Herb-NG	No addition	12	0.3120	0.0644–0.5596	1.3843	0.50049
		Medium	12	0.1337	−0.1117–0.3791		
		High	12	0.2685	0.0252–0.5118		
	Tree-G	No addition	8	0.2893	0.1058–0.4727	3.5271	0.17143
		Medium	8	0.4861	0.2979–0.6743		
		High	8	0.3088	0.0512–0.5665		
	Tree-NG	No addition	2	–	–	–	–
		Medium	2	–	–		
		High	2	–	–		
Plant functional group2	Non-legume-G	No addition	39	0.1844	0.1181–0.2507	2.6456	0.26639
		Medium	39	0.2091	0.1418–0.2765		
		High	39	0.2609	0.1906–0.3312		
	Non-legume-NG	No addition	9	0.1028	−0.0674–0.2729	0.1626	0.92194
		Medium	9	0.1181	−0.0503–0.2865		
		High	9	0.1441	−0.0242–0.3123		
	Legume-G	No addition	22	0.5151	0.2771–0.7531	7.2577	0.02655
		Medium	22	0.8047	0.5665–1.0429		
		High	22	0.9459	0.7032–1.1885		
	Legume-NG	No addition	5	1.1352	0.0956–2.1748	1.9737	0.37276
		Medium	5	0.5016	−0.5336–1.5369		
		High	5	0.4822	−0.5547–1.5190		

G: Glomeraceae; NG: non-Glomeraceae. CI: confidence interval; –: there are not enough available cases to calculate an effect size.

3. Discussion

The meta-meta-analysis showed that AMF had significantly effects on the growth of host plants among heavy metal levels. Many studies have showed AMF can affect uptake and translocation of heavy metal (*e.g.*, Cd, Zn, Pb, Cu and Al) in host plants (Chen et al., 2005; Heggo et al., 1990; Khan et al., 2000). Experiments also reported that AMF can improve the growth of host plants by enhancing host plant tolerance to heavy metal (Trotta et al., 2006; Dong et al., 2008), For example, Huang et al. (2002) found that the accumulations of Cu, Zn and Pb in mycorrhizal plants of maize were 10%, 18% and 29% lower than that in non-mycorrhizal ones respectively. Hildebrandt et al. (1999) reported that mycorrhizae improved the plants of *Viola calaminaria* tolerance to metal Zn and Pb stress in the polluted soils. Recent studies also showed plant species and AMF phylogenetic groups affected the effects of AMF in helping host plants to resist heavy metal (Hu et al., 2013; Lehmann et al., 2012; Hart and Reader, 2002). Our meta-analysis represented the accumulated experiences to learn how AMF phylogenetic groups and plant functional groups interact under different heavy metal levels. All the studies in our meta-analysis recorded AMF phylogenetic groups and plant functional groups.

The two AMF phylogenetic groups (Glomeraceae and non-Glomeraceae) in our meta-analysis can generally promote plant growth and nutrient acquisition at all heavy metal levels (Fig. 1). These two AMF phylogenetic groups also showed difference in affecting host plants, and in responding to heavy metal. Redecker and Raab (2006) have reported that Glomeraceae and Gigasporaceae differ in hyphal architecture and growth patterns, which may affect their functions. For example, Glomeraceae possibly play main roles in transporting nutrients to hosts, while non-Glomeraceae might be in charge with other functioning, *i.e.*, improving phenotypic plasticity, tolerating to salt and pathogens, *etc.* (Maherali and Klironomos, 2007). *G. caledonium* of Glomeraceae can improve the biomass of *Z. mays*, while *G. margarita* of Gigasporaceae did not under heavy metal stress (Wang et al., 2006). In our study, Glomeraceae have more positive effect on host plants under high heavy metal level, but non-Glomeraceae have more positive effect under no heavy metal. Under medium and high heavy metal levels, Glomeraceae promoted plant growth greater than non-Glomeraceae did. The possible reason for this phenomenon could be that Glomeraceae can colonize roots rapidly and can acquire and transport more nutrients and water to plants (Jansa et al., 2008; de la Providencia et al., 2005; Voets et al., 2006). As non-Glomeraceae can only colonize roots from germinating spores, only the main hypha can be repaired if their hyphae are injured under heavy metal stress, (de la Providencia et al., 2005; Voets et al., 2006).

Host plant functional groups also differ in responding to AMF phylogenetic groups. van der Heijden et al. (2004) reported that non-Glomeraceae in C_3 plants was much higher than Glomeraceae; while no difference was found between both phylogenetic types in C_4 plants. Different combinations of AMF-host plants affecting plant growth were also found under different heavy metal levels (Wang et al., 2006; Bai et al., 2008). In our study, we found that functional groups (herbs *vs.* trees and non-legume *vs.* legume) were affected differently by Glomeraceae and non-Glomeraceae. We also found that the effects of Glomeraceae and non-Glomeraceae on plant growth depended on heavy metal levels. For example, Glomeraceae promoted the growth of herbs and legumes under high heavy metal level; while Glomeraceae promoted the growth of trees and legumes under medium heavy metal level (Fig. 1c–f). Herbs and legumes were promoted by non-Glomeraceae only under no heavy metal treatment (Fig. 1c–f). Our results also showed that legumes had a higher response to Glomeraceae than non-legumes did under high heavy metal level. This could be due to the fact that Glomeraceae may promote plant photosynthetic efficiency and nutrient uptake (Humphreys et al., 2010) as legumes could form a tripartite symbiosis with nitrogen-fixing rhizobium bacteria and phosphorus-acquiring AMF (Scheublin et al., 2004).

The results from meta-analysis provide new evidence that AMF may not always have positive effects on their host plants. AMF phylogenetic groups, plant functional groups and heavy metal stress can affect the role of AMF. This evidence will enhance our understanding on how to use AMF effectively in agriculture and in the remediation of degraded land. In this study, we showed that the combination of Glomeraceae and legumes performed best in the heavy metal stress condition. It implies that we can apply this combination of Glomeraceae and legume to the remediation of heavy metal polluted soil.

4. Conclusions

Our results showed that both Glomeraceae and non-Glomeraceae promoted host plant growth. These effects of magnitudes depended on heavy metal levels and plant functional groups. Glomeraceae had stronger effects on host plants than non-Glomeraceae did under heavy metal condition, while non-Glomeraceae had stronger effects on host plants than Glomeraceae under no heavy metal condition. Legumes had the highest response to Glomeraceae among the plant functional groups under high heavy metal level, implying that legumes and Glomeraceae are better partners under heavy metal polluted condition. These results enhance our understanding on how AMF phylogenetic groups affect the host plants, and how we can use AMF phylogenetic groups in the remediation of heavy metal polluted environment.

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