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A meta-analysis of arbuscular mycorrhizal effects on plants grown under salt stress

Murugesan Chandrasekaran · Sonia Boughattas · Shuijin Hu · Sang-Hyon Oh · Tongmin Sa

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Abstract Salt stress limits crop yield and sustainable agriculture in most arid and semiarid regions of the world. Arbuscular mycorrhizal fungi (AMF) are considered bioameliorators of soil salinity tolerance in plants. In evaluating AMF as significant predictors of mycorrhizal ecology, precise quantifiable changes in plant biomass and nutrient uptake under salt stress are crucial factors. Therefore, the objective of the present study was to analyze the magnitude of the effects of AMF inoculation on growth and nutrient uptake of plants under salt stress through meta-analyses. For this, data were compared in the context of mycorrhizal host plant species, plant family and functional group, herbaceous vs. woody plants, annual vs. perennial plants, and the level of salinity across 43 studies. Results indicate that, under saline conditions, AMF inoculation significantly increased total, shoot, and root biomass as well as phosphorous (P), nitrogen (N), and potassium (K) uptake. Activities of the antioxidant enzymes superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase also increased significantly in mycorrhizal compared to nonmycorrhizal plants growing under salt stress. In addition, sodium (Na) uptake decreased significantly in mycorrhizal plants, while changes in proline accumulation were not significant. Across most subsets of the data analysis, identities of AMF (*Glomus fasciculatum*) and host plants (*Acacia nilotica*, herbs, woody and perennial) were found to be essential in understanding plant responses to salinity stress. For the analyzed dataset, it is concluded that under salt stress, mycorrhizal plants have extensive root traits and mycorrhizal morphological traits which help the uptake of more P and K, together with the enhanced production of antioxidant enzymes resulting in salt stress alleviation and increased plant biomass.

Keywords Arbuscular mycorrhiza · Meta-analysis · Salt stress · Nutrient uptake · Plant growth · Antioxidant enzymes

Introduction

Soil salinity is one of the most important abiotic stresses that limit crop yield and agricultural sustainability in most of the arid and semiarid regions of the world (Chinnusamy et al. 2005; Rengasamy 2006; Munns and Tester 2008). Of the current 230 million ha of irrigated lands, 45 million ha, i.e., above 7 % of which occupy agriculture lands, are affected by either salinity or sodicity (Munns and Tester 2008). Salinization of arable lands is estimated to result in 30 % land loss within the next 25 years and up to 50 % within the next 35 years (Munns 2002, 2005; Rengasamy 2006; Munns and Tester 2008). Salinity of soils can be attributed to cations such as sodium (Na^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}), as well as anions such as chloride (Cl^-), sulfate (SO_4^{2-}), and bicarbonate (HCO_3^-) (Tester and Davenport 2003). In plants, salinity increases the concentrations of Na^+ and Cl^- ions and decreases K^+, Ca^{2+}, NO_3^- as well as inorganic phosphate (Pi) concentration, causing plants to be susceptible to osmotic and

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M. Chandrasekaran · S. Boughattas · T. Sa (✉)
Department of Environmental and Biological Chemistry, Chungbuk National University, Cheongju, Chungbuk, 361-763, Republic of Korea
e-mail: tomsa@chungbuk.ac.kr

S. Hu
Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695, USA

S.-H. Oh
Department of Animal Sciences, North Carolina Agricultural and Technical State University, Greensboro, NC 27411, USA

S. Boughattas
Parasitology Laboratory, Institute Pasteur Tunis, Tunis, Tunisia

specific ion injuries in addition to nutritional disorders (Bothe 2012). Biological remediation, such as the application of arbuscular mycorrhizal fungi (AMF) to saline soils, could alleviate salt stress in plants (Evelin et al. 2009; Dodd and Pérez-Alfocea 2012; Porcel et al. 2012). This may be the result of a more efficient mineral uptake (Evelin et al. 2012), ion balance (Giri et al. 2007), protection of enzymatic activities (Patel and Saraf 2013), increase in photosynthetic ability (Sheng et al. 2008; Borde et al. 2011), and/or facilitation of water uptake (Aroca et al. 2007).

Reduced Na^+ influx into the root may be a key strategy in controlling Na^+ accumulation in plants and, hence, in improving salt tolerance in plants (Zhang et al. 2010). Other strategies include immobilization of Na in the soil, removal of Na prior to interception with the plant, etc. If Na^+ influx is reduced, such other mechanisms for dealing with Na^+ excess may not be necessarily invoked. Under stress conditions, K^+ and Na^+ are major contributors of osmotic pressure and ionic strength. Accumulation of Na^+ and impairment of K^+ nutrition are major characteristics of salt-stressed plants, the mechanisms of which are only partially understood (Giri and Mukerji 2004; Evelin et al. 2009; Wu et al. 2013). It seems that higher K^+ accumulation by arbuscular mycorrhizal plants under salt stress conditions may help in maintaining a high K^+/Na^+ ratio, thus preventing the disruption of various enzymatic processes and inhibition of protein synthesis (Wu et al. 2010). Therefore, the selectivity of K^+ over Na^+ is essential in understanding the tolerance of mycorrhizal plants to salt stress (Wu et al. 2013). Proline helps to maintain osmotic balance under low water potential and protects enzymes in the presence of high cytoplasmic electrolyte concentrations (Szabados and Savouré 2010). Proline content has been reported to vary among mycorrhizal plants (Sannazzaro et al. 2007), and thus, it may serve as a parameter to evaluate the effects of AMF and salinity on plants. However, the significance of proline accumulation in osmotic adjustment is still debated and varies with plant species (Ketchum et al. 1991; Sharifi et al. 2007).

Plants can also avoid the damage brought about by salt stress through responses such as accumulating osmotic regulators and/or activating reactive oxygen species (ROS, Hajiboland et al. 2010; Dudhane et al. 2011). ROS can damage chloroplasts, reduce photosynthesis, inhibit photochemical processes, and disturb the homeostasis of Na^+ and Cl^- ions and essential mineral nutrients, as well as causing peroxidation of membrane lipids, denaturation of proteins, and damage to nucleic acids (Munns and Tester 2008). Plants possess antioxidant defense enzymes which protect cells from oxidative stress induced by ROS; these include superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APOX). The efficiency of the antioxidant defense systems is correlated with resistance to salt stress (Gosset et al. 1994; Abogadallah 2010), and several studies have suggested that the arbuscular mycorrhizal symbiosis helps plants to alleviate salt stress by enhancing the activities of antioxidant enzymes as compared to nonmycorrhizal plants (Evelin et al. 2009; Borde et al. 2010; Hajiboland et al. 2010; Wu et al. 2010; Dudhane et al. 2011). All these beneficial effects of AMF in alleviating salt stress to plants make them crucial for the sustainable functioning of terrestrial ecosystems with saline soils.

To evaluate the magnitude of these response variables in alleviation of salt stress, we have undertaken a quantitative analysis of the effects of AMF inoculation on a wide range of ecological predictor variables using a meta-analytical approach. Meta-analysis has been used to uncover new aspects or to gather support for broader trends among contradictory published data. In previous studies, meta-analysis has been used to unveil general trends in the effectiveness of AMF in plant-pathogen interactions (Borowicz 2001), assess mycorrhizal and plant responses under elevated atmospheric CO_2 (Alberton et al. 2005), compare relative importance of plants in mycorrhizal symbioses vs. other interactions (Morris et al. 2007), and find variations in the effects of arbuscular mycorrhiza on insect herbivores (Koricheva et al. 2009) as well as mycorrhizal effects on allometric portioning of host plant biomass under different types of stress (Veresoglou et al. 2012). In 2004, Treseder performed a meta-analysis of mycorrhizal plant response to nitrogen, phosphorus, and elevated CO_2 in the field. Lekberg and Koide (2005) conducted a meta-analysis using three-factor analyses of variance as a mixed model to compare the impacts of different agricultural management practices on AMF colonization and the resulting growth responses of the crop plants. Hoeksema et al. (2010) published a multifactor meta-analysis on plant response to inoculation with mycorrhizal fungi using both fixed- and mixed-effect models to describe the inoculation effects. Two recent meta-analyses have investigated the influence of AMF on the growth and reproductive response of plants under water stress (Jayne and Quigley 2014) and plant biomass responses to both AMF and endophytes under drought conditions (Worchel et al. 2013).

In the present meta-analysis, random-effect models were used to estimate the relative importance and magnitude of the effects of predictor variables on plant responses to inoculation with AMF under salt stress. The aim was to, more specifically, answer the following questions: (1) Does inoculation of plants with AMF under salt stress modify plant uptake of minerals and enhance growth? (2) Do plant responses change with the identity of AMF, plant species, or plant functional groups? (3) Is Na uptake related to proline accumulation in arbuscular mycorrhizal plants? (4) Does plant uptake of K and Na differ between plants with and without arbuscular mycorrhiza?

Materials and methods

Literature search and data collection

To build a database, searches were conducted for articles published from 1993 to 2013 in electronic databases (Science, Nature, Elsevier, Science Direct, Springer, Wiley & Blackwell) and in Web of Science® and the references cited in the publications retrieved. The search combinations entered were mycorrhiza* inoculation and salt stress/or under salinity stress, Arbuscular Mycorrhiza* inoculation and salinity stress/or under salt stress, Mycorrhiza*/or Arbuscular Mycorrhiza* nutrient uptake under salt stress, and Mycorrhiza*/or Arbuscular Mycorrhiza* plant growth under salt stress. The use of the Boolean truncation ('*') character ensured that the variations of the word such as mycorrhizae, mycorrhizas, and mycorrhizal were also included.

These searches resulted in 575 published and unpublished online references, of which 250 were considered likely to contain significant information. However, articles had to meet a set of criteria which included information on (i) plant biomass, nutrient uptake, and antioxidant enzyme activities; (ii) crop plants (annual and/or perennial); (iii) a control for AMF inoculation; and (iv) the experiments had to be performed under a saline condition. Those studies that did not provide information on all of the above response variables and those that presented irrelevant data were excluded. Among the 250 references, 207 papers were rejected based on these criteria, and the list was refined to 43 studies. From these studies, we extracted 530 quantitative measures of variables identified as potentially meeting the selection criteria of presenting information on the effects of AMF inoculation under salinity stress. One major assumption of the meta-analysis is that the results of different individual studies, or observations within the database, are independent of one another. If particular publications reported data from more than one study system/group, those systems were considered as independent data points/observations (Hedges et al. 1999).

Selection criteria

For each publication, any information given on different fixed-factors was recorded; these included authors, taxonomy of AMF, taxonomy or growth of the host plant, experimental conditions, level of salinity, biomass, nutrient uptake and proline accumulation, as well as statistical data including sample size, mean effect, standard deviation/error, and response ratio with respect to salt stress (Supplementary information Table S1). For the purpose of the analysis, AMF were defined as being members of the phylum *Glomeromycota*. Twenty-five plant species were represented in the analysis, with data included for family members (11) of the Anacardiaceae, Asteraceae, Chenopodiaceae, Fabaceae, Lamiaceae, Liliaceae, Malvaceae, Poaceae, Rutaceae, Solanaceae, and Verbenaceae. Studies were coded to include the following variables: life style (herbaceous vs. woody), seven functional groups (forb/herb, shrub, herb, grass, tree, sub-shrub, or shrub/tree), life cycle (annual vs. perennial), study site (field vs. greenhouse), and sample size. Plant growth response variables included shoot dry weight, root dry weight, and total dry weight, expressed in terms of units such as grams, milligrams, milligrams per pot, grams per pot, milligrams per plant, and grams per plant. Total dry weights were either presented as such or calculated as the sum of shoot and root dry weight. Uptake of N, P, and K was expressed on a dry mass basis. Only the nutrient uptake data were included; articles that expressed data as nutrient concentrations were excluded. In some studies, similar measures were reported in different units. Nutrient uptake, for instance, was most often reported as milligrams per gram, milligrams per gram plant, milligrams per gram DW, milligrams per pot, grams per pot, millimolar per kilogram DW, grams per kilogram, and percent, whereas for proline accumulation, units reported were in grams per kilogram, milligrams per gram, nanomoles per gram, and micromoles per gram. Also, we chose to categorize all outdoor studies as field and all indoor experiments as greenhouse. The experiments had to be performed under saline conditions or at least an EC$\leq$4 dS/m and/or >40 mM NaCl. For each study, meta-analysis required the mean, standard deviation (SD), and sample size (n) for the control as well as for the treatment under salt stress. Sample size n was chosen based on the number of replicates in the original study. If standard errors (SE) were reported, these were calculated according to the equation: $SE = SD\ (n^{-1/2})$ using MetaWin 2.1 Statistical calculator. When means and errors were presented in a graph, the image was digitized, and Dexter (GAVO Data Center) software was used to estimate the values (http://dc.zah.uni-heidelberg.de/sdexter/).

Meta-analysis

Meta-analyses were conducted with the software MetaWin v2.1 (Hedges et al. 1999). The effect sizes were calculated as the *natural log of the response ratio* (further denoted as LRR/ln$R$) (Gurevitch and Hedges 1999). A random-effects model was used in the analyses because of the large number of diverse studies examined and the assumption that there are random variations among studies

in the effects of interest. All models were weighted by the inverse of variance in effect size (Hedges et al. 1999). LRR/ln$R$ calculations and statistical analysis were conducted using the following formula:

$$\ln R = ln\left(\frac{\bar{X}^{E}}{\bar{X}^{C}}\right) = ln\left(\bar{X}^{E}\right) - \ln\left(\bar{X}^{C}\right) \quad v\ln R = \frac{\left(S^{E}\right)^{2}}{N^{E}\left(\bar{X}^{E}\right)^{2}} + \frac{\left(S^{C}\right)^{2}}{N^{C}\left(\bar{X}^{C}\right)^{2}}$$

where R is the response ratio and X^{E} is the treatment mean (with AMF inoculation), X^{C} is the control mean (without AMF inoculation), S^{E} is the treatment standard deviation, S^{C} is the control standard deviation, N^{C} is the control replication number, and N^{E} is the treatment replication number (Rosenberg et al. 2000). The estimate of variance within each study was represented as $v_{\ln R}$, which is a function of means, standard deviations, and replicate numbers for controls and treatments (Gurevitch et al. 2001).

Testing for the significance of predictors was based on a randomization resampling procedure with 4,999 iterations. Confidence intervals (95 % CIs) were constructed according to the bootstrapping (BS) method integrated in MetaWin. The specific meta-analytical procedure does not make any assumption about data distribution (Hedges et al. 1999). According to Mayerhofer et al. (2013), when the homogeneity statistic Q, an estimate of the among-study variance, was found to be significant ($P<0.05$ when tested against a chi-square distribution), the data was considered to be heterogeneous and further analyzed by single factor categorical analyses. When conducting categorical analyses, three Q statistics were generated per factor: one for the variation within categories (Q_W), one for the variation among categories (or the variation of the model, Q_M or Q_B), and lastly for the total Q (Q_T), which is the sum of the previous two ($Q_T=Q_W+Q_B$). A significant Q_T value means that the variance among studies is greater than expected due to sampling error. According to Gurevitch and Hedges (1999), Q_B rather than Q_W may be of considerable scientific interest. An independent variable had a significant impact on the response ratio when Q_B was larger than the critical value. In the present meta-analysis, factors were considered as significant when Q_B was significant and described at least 10 % of the total variation ($Q_B/Q_T \geq 0.1$). A significant Q_B value indicates that a significant portion of the total heterogeneity can be explained by subdividing the studies into the group of interest (Rosenberg et al. 2000). AMF inoculation efficiency was estimated as a percentage change in inoculated plants relative to controls (%), using the equation (exp (LRR)−1)×100 %, where LRR is the weighted mean response ratio across studies. The inoculation effects were considered as significant if the 95 % BS CIs did not overlap. Statistical differences were considered as significant at $P<0.05$. A sensitivity analysis was conducted to test for any disproportional impact of single studies and their reproducibility (Copas and Shi 2000). Significant results were tested, and only robust or corrected results were presented in the "Results" section (for further information see Supplementary information).

Results

Overview

The present meta-analysis was based on 530 independent observations extracted from 43 published scientific assessments that explored the effects of AMF inoculation on the growth and nutrient uptake of salt-stressed plants. It included 91 observations from 26 studies for shoot dry weight, 73 from 24 studies for root dry weight, 93 from 29 studies for total dry weight, 16 from 5 studies for N uptake, 38 from 10 studies for P uptake, 61 from 12 studies for K uptake, 79 from 14 studies for Na uptake, 79 observations from 11 studies for proline accumulation, and 194 observations from 9 studies for four antioxidant enzymes (CAT, SOD, POD, and APOX). After the exclusion of four observations by the meta-analysis software due to 0 effects, the remaining 530 observations were taken into consideration in the present study. The effects were examined between AMF species, plant species, level of stress, and study site (Supplementary information). *Glomus intraradices* (33.2 %) followed by *Glomus mosseae* (25.6 %) were the major AMF inoculants, and *Zea mays* (20.1 %) followed by *Lycopersicon esculentum* (14.1 %) constituted the major plant species. The majority of the experiments concerned herbaceous (72.4 %) and annual (55.4 %) plants followed by woody perennial species. Forbs/herb were tested most often (44.4 %) followed by grass (27.9 %). Tree and shrub species accounted for 19.5 % of the studies and 7.6 % for sub-shrub. Most experiments (87.4 %) took place in a greenhouse. The overall effect size of AMF inoculation under salinity stress was positive and significantly different from zero according to 95 % bootstrap CI ($df=529$; LRR=0.2656; 95 % BS CI, 0.2227 to 0.3081; Fig. 1). P values associated with the Q_T statistic showed that AMF inoculation under saline conditions significantly differed in effect ($Q_T=627.2138$; $P_{Chi\text{-}square}=0.00205$; Table 1), and significant publication bias was observed using Kendall's tau ($P=0.00001$) and Spearman rank correlation ($P=0.00000$).

AMF inoculation effects on plant biomass

AMF inoculation significantly increased total biomass ($df=92$; LRR=0.4225; $Q_T=45.9860$; 95 % BS CI, 0.3286 to 0.5236), and 95 % BS CI did not overlap with zero (Fig. 1, Table 1). There were differences in the inoculation responses between shoot ($df=90$; LRR=0.4225; $Q_T=221.4081$; 95 % BS CI, 0.3286 to 0.5236; $P<0.0001$) and root biomass

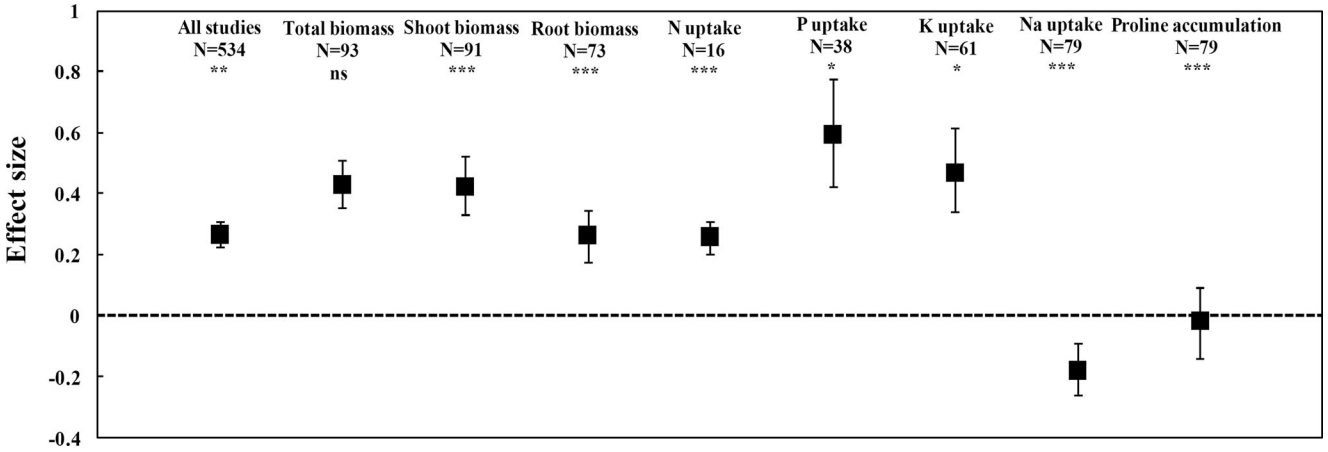

Fig. 1 Response of AMF-inoculated plants to salt stress. *Error bars* are means±95 % BS CIs. Where the BS CIs do not overlap the *horizontal dashed lines*, the effect size for a parameter is significant at $P<0.05$. All effect sizes differed significantly from zero (chi-square tests, ***$P<0.001$, **$P<0.01$, ns=$P>0.05$). *N*=number of studies included in the meta-analysis

(*df*=72; LRR=0.2629; Q_T=159.7027; 95 % BS CI, 0.1763 to 0.3457; $P<0.0001$) across studies (Fig. 1 and Fig. S1). AMF species categorical analysis showed the effects of the three most used species of *Glomus* inoculum among all studies. These are, in order of the most to the least often used, *G. mosseae* (*n*=82), *G. intraradices* (*n*=73), and *G. fasciculatum* (*n*=41). Significant difference was evident between these three AMF inoculum treatments on overall plant growth (Q_B/Q_T=0.2447; P=0.0002; Fig. 2, Table 2). Significant variations on the overall plant growth were also observed among plant species under salt stress condition (Q_B/Q_T=0.5736; P=0.0002, Fig. 2). These variations are, in order of the most to the least often used species, *Z. mays* (*n*=61), *L. esculentum* (*n*=18), *Cicer arietinum* (*n*=18), *Poncirus trifoliate* (*n*=18), *Gossypium arboretum* (*n*=18), *Cajanus cajan* (*n*=12), and *Lactuca sativa* (*n*=12). The AMF inoculation response of plant biomass in herbaceous plants (*n*=156; LRR=0.3998) was greater than that in woody plants (*n*=80; LRR=0.3800). Also, the responses to mycorrhizal inoculation of plant functional groups varied significantly under salt stress (Q_B/Q_T=0.2647; P=0.0002). For herbaceous plants, biomass of herbs (*n*=9; LRR=1.1349) and forbs/herbs (*n*=74; LRR=0.5088) was enhanced by 211.1 and 66.3 %, respectively, but the biomass of grass (*n*=73; LRR=0.2144) increased only by 23.9 %. For woody plants, both mycorrhizal shrubs and trees showed a significant increase in biomass under salt stress. Also, mycorrhizal enhancement of shrub biomass (*n*=11; LRR=0.6675) was higher than that of trees (*n*=30; LRR=0.4290). When compared within plant life cycle, the mycorrhizal responses of perennial plants (*n*=101; LRR=0.4705) were significantly greater than those of annual plants (*n*=135; LRR=0.3394) (Fig. S2). Comparisons within each AMF and plant functional group showed that the greatest inoculation-induced shoot biomass enhancement occurred with *G. fasciculatum* (75.6 %) for AMF species, in *L. sativa* (219.9 %) for plant species, Fabaceae (89.1 %) for plant family, herbaceous plants (53.8 %) for life style, and perennial plants (58.7 %) for life cycle. Greatest root stimulation occurred with *G. fasciculatum* (60.3 %) for AMF species, in *C. arietinum* (56.04 %) for plant species, Fabaceae (68.9 %) for plant family, herbaceous plants (34.2 %) for life style and perennial plants (46.5 %) for life cycle (Fig. S1).

Table 1 Statistical results of comparison among and within groups

Noncategorical predictor variables	Effect size	*df*[a]	95 % BS CIs	Q_{Total}	$P_{(Chi\text{-}square)}$
All studies	0.2656	529	0.2227 to 0.3081	627.2138	0.00205
Shoot biomass	0.4225	90	0.3286 to 0.5236	221.4081	0.00000
Root biomass	0.2629	72	0.1763 to 0.3457	159.7027	0.00000
Total biomass	0.4290	92	0.3547 to 0.5109	45.9860	0.99998
N uptake	0.2583	15	0.2033 to 0.3065	86.3950	0.00000
P uptake	0.5937	37	0.4237 to 0.7754	57.6395	0.01646
K uptake	0.4680	60	0.3388 to 0.6168	87.3675	0.01208
Na uptake	−0.1806	78	−0.2626 to −0.0916	155.9338	0.00000
Proline accumulation	−0.0181	78	−0.1435 to 0.0937	113.0768	0.00037

[a] *df*=*n*−1 (*n*=number of studies)

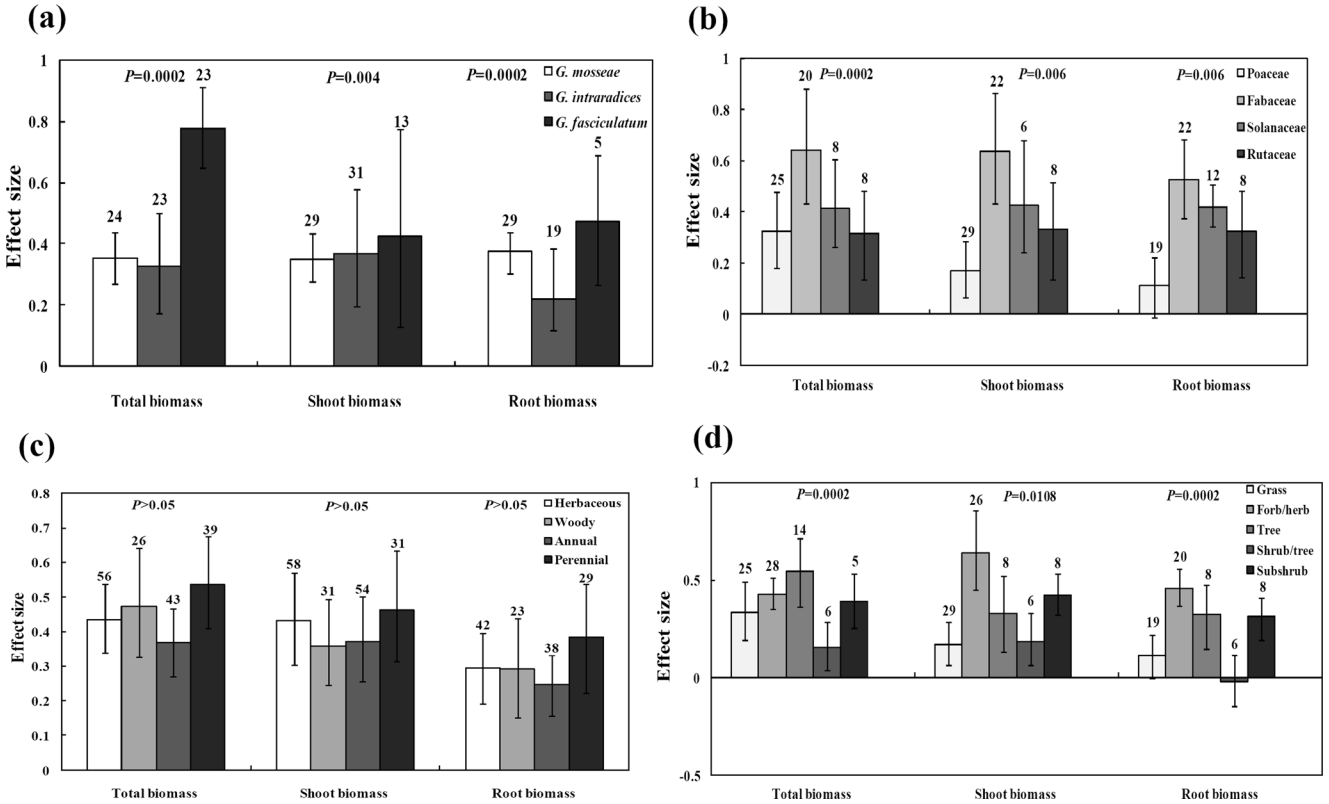

Fig. 2 Effect sizes of plant biomass as a function of salt stress. *Error bars* are means ±95 % BS CIs. Categorical analysis for response variables is grouped into **a** AMF species, **b** plant family, **c** life style vs. life cycle, and **d** plant functional groups. Where the BS CIs do not overlap the *horizontal dashed lines*, the effect size for a parameter is significant at $P<0.05$. Numbers of studies are shown above the *bars*

AMF inoculation effects on plant P uptake

Among all the studies included in the meta-analysis, P uptake associated with the presence of AMF in the roots was increased by 81.06 % under salt stress. Significant variations among studies were observed ($df=37$; LRR=0.5937; $Q_T=57.6395$; 95 % BS CI, 0.4237 to 0.7754; $P<0.05$; Fig. 1, Table 1). Categorical analysis of P uptake with AMF species ($Q_B=56.7369$; $Q_B/Q_T=0.5518$; $P=0.0030$) showed a significant positive effect under salt stress (Table 2). Among AMF species, *G. fasciculatum* ($n=9$; LRR=1.002) had a more positive effect than *G. intraradices* ($n=15$; LRR=0.2561) (Fig. 3a). Significant variations were found among plant species ($Q_B=117.1588$; $Q_B/Q_T=0.6552$; $P=0.0020$). Among the plant families ($Q_B=67.0409$; $Q_B/Q_T=0.6176$; $P=0.0036$), the Solanaceae ($n=16$; LRR=0.2516) showed greater P uptake under salt stress (Fig. 3b). P uptake responses to salt stress of AMF-inoculated woody plants ($n=10$; LRR=0.7726) were significantly greater than those of herbaceous plants ($n=28$; LRR=0.5294). The response of plant functional groups to mycorrhizal inoculation varied significantly under salt stress ($Q_B=37.9828$; $Q_B/Q_T=0.3999$; $P=0.0084$). Trees, herbs, and forb/herb showed significant increases in P uptake as compared to other functional groups (Fig. 3b). Mycorrhizal annual and perennial plants performed differently ($Q_B=24.7248$; $Q_B/Q_T=0.2981$; $P=0.0002$) under salt stress but both responded favorably to AMF inoculation. However, perennial species ($n=20$; LRR=0.8687) showed more P uptake than annuals ($n=18$; LRR=0.2642) (Fig. 3b).

AMF inoculation effects on plant N uptake

The number of observations was small (<20) for the study of AMF inoculation effects on N uptake. Across studies, plant N uptake (29.4 %) had positive log response ratio ($df=16$; LRR=0.2583; $Q_T=86.3950$; 95 % BS CI, 0.2033 to 0.3065; $P<0.0001$; Fig. 1, Table 1) in relation to AMF inoculation under salt stress. Significant publication bias was observed in Kendall's tau ($\tau=0.609$, $z=3.291$ with $P=0.001$) and Spearman rank correlation ($Rs=0.725$ with $P=0.0015$). However, variation among groups was not significant, indicating inconsistencies in mycorrhizal plant responses to N uptake under salt stress (Table 2). There were no significant differences among any other response variables.

AMF inoculation effects on plant K uptake

Increased K uptake (59.6 %) was significant in AMF-inoculated plants under saline condition and showed a

Table 2 Significance of factors analyzed in the categorical analyses based on the significance of the variation among categories (Q_B) and the amount of the total variation (Q_T) described by Q_B/Q_T under salt stress

Noncategorical predictor variables	Categorical predictor variables	Q_B	Q_B/Q_T	$P_{(random)}$
Shoot biomass	AMF species	87.5224	0.1192	0.0044
	Plant species	109.149	0.5514	0.0144
	Plant family	80.1554	0.3650	0.0060
	Herbaceous vs. woody plants	1.1666	0.0053	0.5394
	Plant functional groups	70.6320	0.3209	0.0108
	Annual vs. perennial plants	1.9028	0.0087	0.4328
Root biomass	AMF species	60.0928	0.2631	0.0002
	Plant species	74.5296	0.5347	0.0010
	Plant family	57.1625	0.3650	0.0060
	Herbaceous vs. woody plants	0.0036	2.1701	0.9656
	Plant functional groups	58.1842	0.4011	0.0002
	Annual vs. perennial plants	5.3284	0.038	0.1146
Total biomass	AMF species	100.1129	0.3529	0.0002
	Plant species	174.9210	0.6286	0.0002
	Plant family	65.9012	0.2271	0.0002
	Herbaceous vs. woody plants	0.3682	0.0022	0.4064
	Plant functional groups	51.7657	0.2818	0.0002
	Annual vs. perennial plants	8.0225	0.0428	0.0022
P uptake	AMF species	56.7369	0.5518	0.0030
	Plant family	67.0409	0.6176	0.0036
	Plant species	117.1588	0.6552	0.0020
	Herbaceous vs. woody plants	2.4416	0.0388	0.2154
	Plant functional groups	37.9828	0.3999	0.0084
	Annual vs. perennial plants	24.7248	0.2961	0.0002
N uptake	AMF species	26.3306	0.5098	0.1744
	Plant species	47.8662	0.6366	0.0884
	Plant family	47.8662	0.6366	0.0720
	Herbaceous vs. woody plants	0.2213	0.006	0.8062
	Plant functional groups	43.2867	0.5775	0.0802
	Annual vs. perennial plants	4.2723	0.1374	0.3290
K uptake	AMF species	132.1997	0.6445	0.0412
	Plant species	357.0684	0.8128	0.0084
	Plant family	88.9706	0.3747	0.0300
	Herbaceous vs. woody plants	3.8713	0.0162	0.1576
	Plant functional groups	95.7459	0.3949	0.0188
	Annual vs. perennial plants	19.8026	0.0859	0.0048
Na uptake	AMF species	28.9270	0.2017	0.0476
	Plant species	68.0993	0.3837	0.0036
	Plant family	30.3196	0.1868	0.0062
	Herbaceous vs. woody plants	5.2399	0.0337	0.1046
	Plant functional groups	14.6566	0.1011	0.1046
	Annual vs. perennial plants	0.1699	0.0011	0.7626
Proline accumulation	AMF species	21.3366	0.1901	0.0328
	Plant species	109.3472	0.5571	0.0002
	Plant family	21.2895	0.1696	0.0246
	Herbaceous vs. woody plants	0.5984	0.0053	0.5512
	Plant functional groups	8.8791	0.0762	0.2336
	Annual vs. perennial plants	0.0302	0.0002	0.9008

Table 2 (continued)

Noncategorical predictor variables	Categorical predictor variables	Q_B	Q_B/Q_T	$P_{(random)}$
Antioxidant enzymes	AMF species	4,553.7447	0.1071	0.1140
	Plant species	14,614.4171	0.3435	0.0040
	Plant family	14,574.9575	0.3425	0.0038
	Herbaceous vs. woody plants	4,185.0231	0.0314	0.0314
	Plant functional groups	14,556.0480	0.3421	0.0022
	Annual vs. perennial plants	8,121.9372	0.1909	0.0024

significant variation among studies (df=60; LRR=0.4680; Q_T=87.3675; 95 % BS CI, 0.3388 to 0.6168; P<0.05; Fig. 1, Table 1). Categorical analyses showed significant differences between AMF species (Q_B=132.1997; Q_B/Q_T=0.6445; P=0.0412; Fig. 4a, Table 2). *G. fasciculatum* (n=7; LRR=1.5971; 95 % BS CI, 1.1047 to 1.9464) promoted greater increased K uptake than *G. intraradices* (n=27; LRR=0.2975). A significant variation was found among plant species (Q_B=357.0684; Q_B/Q_T=0.8128; P=0.0084; Table 2). Mycorrhizal increased uptake of K was observed in *L. esculentum* (n=14; LRR=0.4187) and *Z. mays* (n=16; LRR=0.2609; Fig. 4a). K uptake of herbaceous plants (n=48; LRR=0.4981) was significantly greater than that of woody plants (n=13; LRR=0.3318). When compared within each plant functional group (Q_B=95.7459; Q_B/Q_T=0.3949; P=0.0188), K uptake of herbs (n=10; LRR=1.1831) was significantly greater than that of trees (n=11; LRR=0.3365). In addition, mycorrhizal enhancement of K uptake by perennial plants (n=27; LRR=0.6343) was significantly higher than that of annual plants (n=34; LRR=0.31817) under salt stress (Fig. 4b, Table 2).

AMF inoculation effects on plant Na uptake

In contrast to N, P, and K uptake, mycorrhizal plants consistently and strongly decreased Na uptake by an average of 16.5 % across all studies (Fig. 1, Table 1). However, variation among studies was significant (df=78; LRR=−0.1806; Q_T=155.9338; 95 % BS CI, −0.2626 to −0.0916; P<0.05; Fig. 1, Table 1) indicating inconsistency among groups in mycorrhizal responses to salt stress. Categorical analysis indicated that AMF species (Q_B=28.9270; P=0.0476), plant species (Q_B=68.0993; P=0.0036), and plant family (Q_B=30.3196; P=0.0062) contributed significantly to Na uptake, whereas plant functional groups (P>0.05) were not statistically significant (Fig. 5, Table 2). Among AMF species, *G. mosseae* (n=23; LRR=−0.2584; 95 % BS CI, −0.3154 to −0.2029) had a significant decrease in Na uptake compared to other species (Fig. 5a). The host plant species *Z. mays* (n=16; LRR=−0.3409; 95 % BS CI, −0.4859 to −0.2064) had a

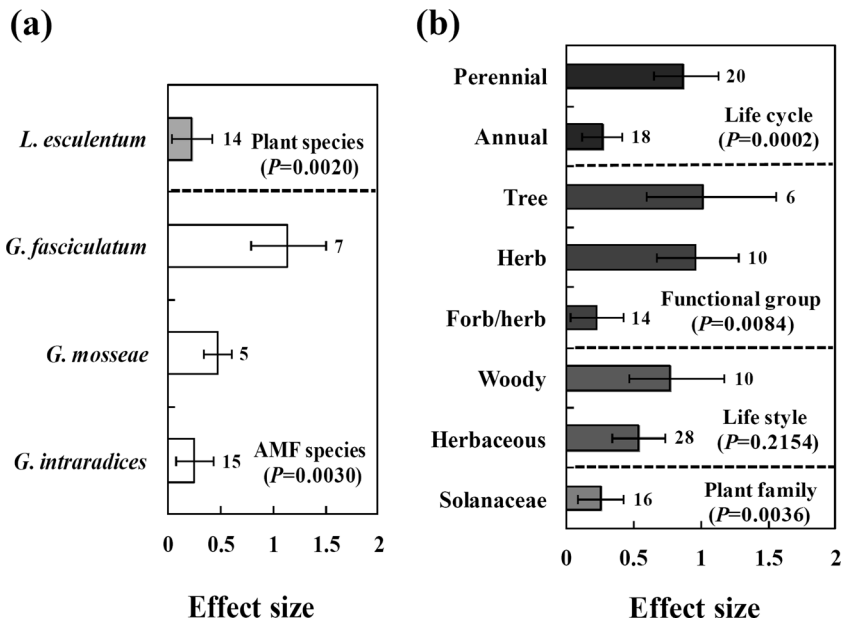

Fig. 3 Effect sizes of P uptake categorical analysis as a function of salt stress. *Error bars* are means±95 % BS CIs. Categorical analysis for response variables is grouped into **a** AMF species and plant species and **b** trials grouped according to the plant family, life style, plant functional groups, and life cycle. Where the BS CIs do not overlap with zero, the effect size for a parameter is significant at P<0.05. Numbers of studies are shown *above the bars*

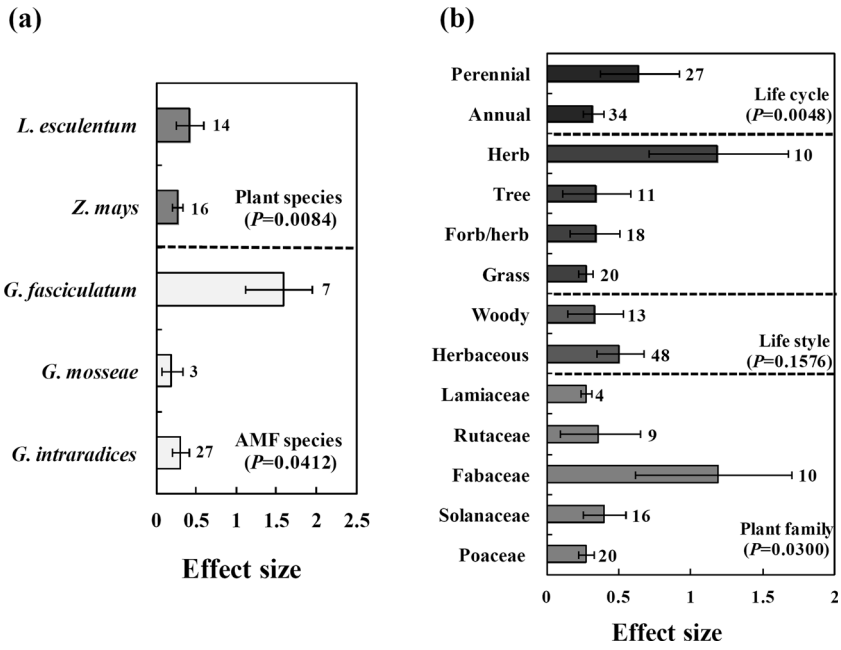

Fig. 4 Effect sizes of K uptake categorical analysis as a function of salt stress. *Error bars* are means±95 % BS CIs. Categorical analysis for response variables is grouped into **a** AMF species and plant species and **b** trials grouped according to the plant family, life style, plant functional groups, and life cycle. Where the BS CIs do not overlap with zero, the effect size for a parameter is significant at $P<0.05$. Numbers of studies are shown *above the bars*

significant decrease in Na uptake with AMF inoculation under salt stress (Fig. 5a). Na uptake of herbaceous plants ($n=64$; LRR=−0.213; 95 % BS CI, −0.2990 to −0.1239) was significantly greater than that of woody plants ($n=15$; LRR=−0.0225; 95 % BS CI, −0.2547 to 0.2730), whose 95 % BS CI overlapped with zero. AMF-inoculated annual plants ($n=50$; LRR=−0.1902; 95 % BS CI, −0.2752 to −0.1036) had significantly decreased Na uptake, while mycorrhizal perennial species ($n=29$; LRR=−0.1630; 95 % BS CI, −0.3403 to 0.0339) showed no significant decrease (Fig. 5b).

AMF inoculation effects on plant proline accumulation

AMF inoculation decreased (1.7 %) proline accumulation under salt stress, but its effect was not statistically significant ($df=78$; LRR=−0.0056; $Q_T=114.6946$; 95 % BS CI, −0.1230 to 0.1042; Fig. 1, Table 1) where 95 % BS CI overlapped with zero. However, categorical model analysis of AMF species ($Q_B=21.3366$; $Q_B/Q_T=0.1807$; $P=0.0306$; Fig. 6a, Table 2) indicated that *G. fasciculatum* ($n=36$; LRR=0.1605) and *G. mosseae* ($n=13$; LRR=0.1733) induced significantly increased proline accumulation in plants under salt stress,

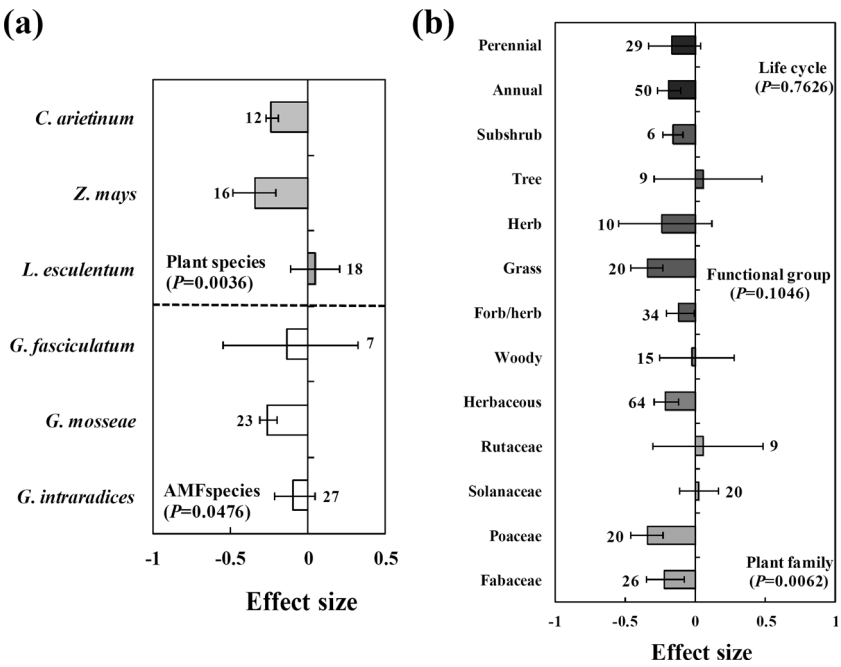

Fig. 5 Effect sizes of Na uptake categorical analysis as a function of salt stress. *Error bars* are means±95 % BS CIs. Categorical analysis for response variables is grouped into **a** AMF species and plant species and **b** trials grouped according to the plant family, life style, plant functional groups, and life cycle. Where the BS CIs do not overlap with zero, the effect size for a parameter is significant at $P<0.05$. Numbers of studies are shown *above the bars*

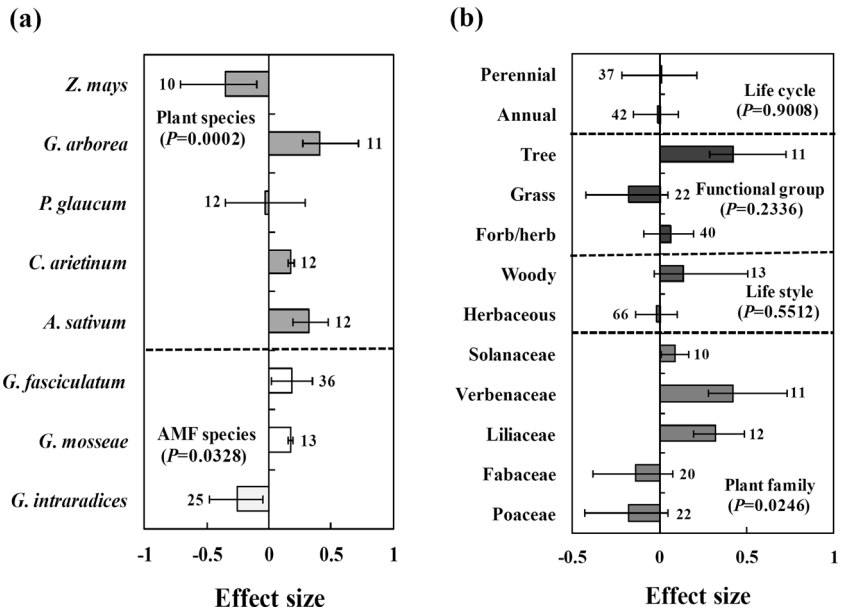

Fig. 6 Effect sizes of proline accumulation categorical analysis as a function of salt stress. *Error bars* are means±95 % BS CIs. Categorical analysis for response variables is grouped into **a** AMF species and plant species and **b** trials grouped according to the plant family, life style, plant functional group, and life cycle. Where the BS CIs do not overlap with zero, the effect size for a parameter is significant at $P<0.05$. Numbers of studies are shown *above the bars*

whereas *G. intraradices* ($n=25$; LRR=−0.2538) had significantly negative effects on proline accumulation. Among plant species ($Q_B=109.3472$; $Q_B/Q_T=0.5571$; $P=0.0002$; Fig. 6a, Table 2), *G. melina arborea* ($n=11$; LRR=0.4041), followed by *Allium sativum* ($n=12$; LRR=0.321), and *C. arietinum* ($n=12$; LRR=0.1728) showed significantly positive mycorrhiza-related effects on proline accumulation, whereas *Z. mays* ($n=10$; LRR=−0.3502) showed significantly negative responses in proline accumulation. When compared within each plant functional groups, proline accumulation in mycorrhizal trees ($n=11$; LRR=0.4237; 95 % BS CI, 0.2816 to 0.7242) was significantly more positive than that of herbs ($n=4$; LRR= 0.2197; 95 % BS CI, 0.0588 to 0.4011), >whereas all other functional groups were not statistically significant (Fig. 6b).

AMF inoculation effects on plant antioxidant enzymes

AMF inoculation increased the antioxidant enzyme activities of plants under saline conditions. Significant variations in antioxidant enzyme activities ($n=194$; LRR=0.3858; $Q_T=38676.667$; BS CI, 0.2673 to 0.5205; $P=0.0000$; Fig. 7) were found across studies. There were differences in the inoculation responses between CAT ($n=66$; LRR=0.2620; BS CI, 0.1310 to 0.4051), SOD ($n=66$; LRR=0.5519; BS CI, 0.3000 to 0.8116), POD ($n=46$; LRR=0.2858; BS CI, 0.1773 to 0.3971), and APOX ($n=16$; LRR=0.2895; BS CI, 0.2639 to 0.4150). Categorical analysis of AMF species ($Q_B=4,553.7447$; $Q_B/Q_T=0.1071$; $P=0.1140$; Table 2) showed that *G. fasciculatum* had a greater positive effect than *G. intraradices* and *G. mosseae*. Categorical analyses of antioxidant enzyme activities with inoculated plant species ($Q_B=14,614.4171$; $Q_B/Q_T=0.3435$; $P=0.0040$; Table 2) and plant family ($Q_B=14,574.9575$; $Q_B/Q_T=0.3425$; $P=0.0038$) were found to have significant positive effects under salt stress. Significantly positive effects on the production of antioxidant enzymes among AMF inoculated plant species were found in *G. arborea* ($n=36$; LRR=0.7899) followed by *Z. mays*, *L. esculentum*, *P. glaucum*, *T. aestivum*, and *A. sativum*. Moreover, plant functional group ($Q_B/Q_T=0.3421$; $P=0.0022$), life style ($Q_B/Q_T=0.1081$; $P=0.0314$), and life cycle ($Q_B/Q_T=0.1909$; $P=0.0024$) contributed significantly to antioxidant enzyme activity under salt stress in AMF-inoculated plants as compared to nonmycorrhizal plants (Fig. 7, Table 2).

Discussion

Meta-analysis involves consolidation of data from independent studies to estimate the magnitude of effects across similar studies and checks potentially contributing variations among them (Gurevitch and Hedges 1999). Several mycorrhizal ecologists have made use of meta-analyses studies to unveil general trends in the effects of AMF inoculation (Treseder 2004; Lekberg and Koide 2005; Hoeksema et al. 2010; Veresoglou et al. 2012; Treseder 2013). In the present meta-analysis study, resolute evidence is provided that AMF inoculation causes a significant impact on the ecological predictor variables plant biomass, nutrient uptake, proline accumulation, and antioxidant enzyme activities under salinity stress.

It has been reported that when plants are inoculated with AMF, the extent of growth suppression due to salinity stress decreases and AMF-inoculated plants have greater dry weights than noninoculated plants (e.g., Sannazzaro et al. 2007; Estrada et al. 2013). The present study across published

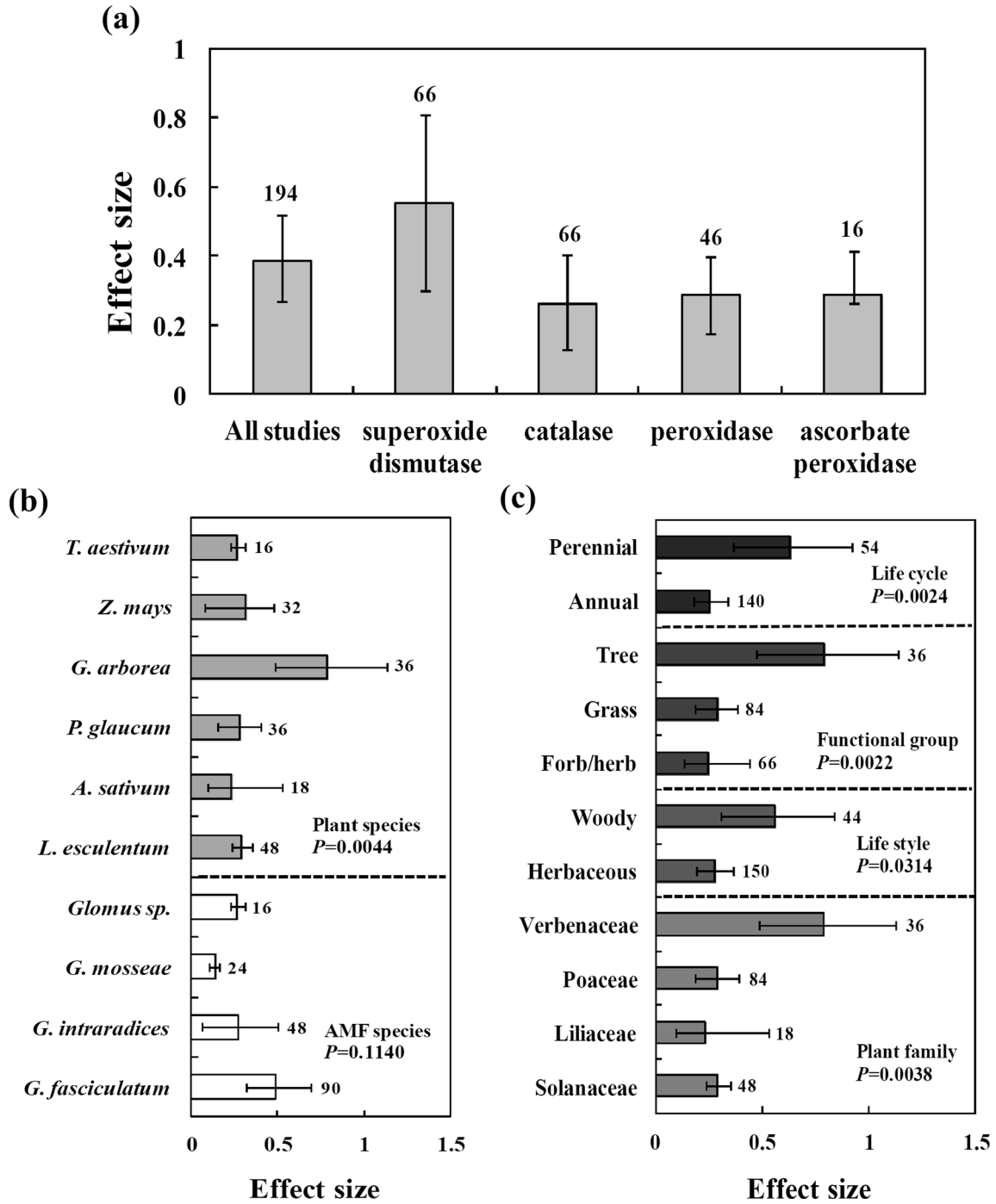

Fig. 7 Effect sizes of antioxidant enzyme analysis as a function of salt stress. *Error bars* are means±95 % BS CIs. Categorical analysis for response variables is grouped into **a** antioxidant enzymes, **b** categorical analysis of AMF species and plant species, and **c** trials grouped according to the plant family, life style, plant functional group, and life cycle. Where the BS CIs do not overlap with zero, the effect size for a parameter is significant at $P<0.05$. Numbers of studies are shown *above the bars*

work confirmed that AMF have a positive overall impact on plant biomass under saline conditions, with both shoot and root dry weights being significantly greater in mycorrhizal than in nonmycorrhizal plants. The results of this study agree with previous data (e.g., Tian et al. 2004; Garg and Manchanda 2009; Kaya et al. 2009). Shoot biomass of mycorrhizal plants increased more than root biomass (52.5 and 30.1 %, respectively) under salt stress. Ranking of the increased response in shoot biomass to the three most studied AMF species is *G. fasciculatum* (75.6 %)>*G. intraradices* (44.6 %)>*G. mosseae* (41.8 %) and *G. fasciculatum* (60.3 %)> *G. mosseae* (45.6 %)>*G. intraradices* (24.3 %) for root

biomass. Jahromi et al. (2008) suggested that if salinity persists, there can be reduction in mycorrhiza by reducing the ability of inoculum (i.e., spores) to colonize roots. An increase in salinity will reduce spore germination and extraradical hyphal length which will reduce root colonization and symbiotic capability of AMF (Juniper and Abbott 2006; Evelin et al. 2009). Although salinity could affect negatively mycorrhizal colonization, many reports show improved growth and productivity of mycorrhizal plants under saline conditions by exhibiting considerable degree of dependence on AMF species (Giri and Mukerji 2004; Daei et al. 2009; Evelin et al. 2012; Hajiboland et al. 2010; Jahromi et al. 2008; Talaat and Shawky 2014). The effectiveness of inoculation of *G. fasciculatum* in alleviating salt stress and promoting plant growth in comparison to *G. intraradices* and *G. mosseae* may be ascribed to variation in efficacy of stress tolerance among the fungal species (Daei et al. 2009). Variation in plant growth stimulation by AMF has also been frequently reported under nonstressed conditions among isolates belonging to different species, as well as among isolates of the same species (e.g., van der Heijiden et al. 1998; Munkvold et al. 2004; Jansa et al. 2008). In terms of plant species, mycorrhizal *L. sativa* (Kohler et al. 2010) had the highest increase in plant biomass under salt stress compared to the other studied plants. Despite overall positive effects of AMF inoculation, the present meta-analysis concords with others that biomass responses in plants are strongly dependent upon plant functional groups (Treseder 2013; Jayne and Quigley 2014). Herbaceous plants were more favored by AMF than woody plants under salt stress, with herbs benefiting the most among the six functional groups of herbaceous and woody plants. Some herb/forbs tend to develop an extensive rooting system that allows access to a greater soil volume giving an edge over woody plants. Results confirmed that overall plant growth was significantly improved by mycorrhizal inoculation in perennial plants as compared to that of annual plants under salt stress conditions.

The present meta-analysis confirmed that, at all salinity levels, AMF significantly increase P uptake (81.06 %) in plants. Both the type of the plant and AMF appeared to have a significant effect on P uptake. AMF facilitate host P uptake through the extensive extraradical hyphal network that allows mycorrhizal plants to explore more soil volume than nonmycorrhizal plants (e.g., Bonfante and Genre 2010; Fitter et al. 2011). Ability to acquire P is known to differ among AMF species, and similar results are expected for other functions as well (Smith et al. 2000; Jansa et al. 2005; Hoeksema et al. 2010; Treseder 2013). Commonly used AMF species in experiments under saline conditions were *Glomus* spp., of which *G. fasciculatum* appeared the most efficient in terms of plant performance and attenuation of detrimental effects posed by salinity. These findings are consistent with previous reports of AMF responses under saline conditions (Schellenbaum et al. 1991; Giri et al. 2007). Of the different host plants retained in the meta-analysis, mycorrhizal *L. esculentum* showed a significant increase in P uptake over control plants under salt stress. Plants with poorly developed root hairs may tend to be obligate mycotrophs in P-deficient soils (Sharma et al. 1996). Moreover, mycorrhizal root colonization promotes the formation of high order lateral roots by inducing more fine roots and less coarse roots, thereby enhancing root functioning to explore more water and nutrients under salt stress (Aroca et al. 2007; Wu et al. 2010; Fusconi 2013; Treseder 2013). It was observed across the analyzed studies that mycorrhizal perennial and woody plants have a greater increase in P uptake efficiency compared to annual or herbaceous plants. It is unclear whether different AMF species vary in their effect on root morphology of the host plants (Wu et al. 2010; Chatzistathis et al. 2013). This variation is in accord with many previous studies showing that mycorrhizal benefits are strongly dependent on the plant-fungus association and soil properties (e.g., Smith et al. 2004; Jansa et al. 2008). Mycorrhizal inoculation can also affect the physiological status of salt-stressed host plants.

Based on our meta-analysis data, it would appear that improved growth of mycorrhizal plants in saline conditions is primarily related to mycorrhiza-mediated enhancement of host plant P nutrition. However, enhanced P uptake by mycorrhizal plants under saline conditions may reduce the negative effects of Na^+ as well as Cl^- ions by maintaining vacuolar membrane integrity, which facilitates compartmentalization within the vacuoles and selective ion intake (Rinaldelli and Mancuso 1996), thereby preventing ions from interfering in metabolic pathways of growth (Borde et al. 2011; Wu et al. 2013). As a toxic monovalent cation, Na^+ not only causes plant cell injury but also degrades soil structures; in contrast, K^+ is essential to plant cells as a major inorganic nutrient and an osmotic regulator. Both Na^+ and K^+ have similar physicochemical structure, and Na^+ can compete with K^+ at transport sites in the symplast or at K^+ binding sites in the cytoplasm (Serrano and Rodriguez-Navarro 2001). Therefore, NaCl stress often triggers K^+ reduction in plant tissues, leading to an imbalance of K^+/Na^+ (Zhang et al. 2010). In the present study, data clearly evidenced a significant increase in plant K uptake (59.6 %) following AMF inoculation and a significant decrease in Na uptake (−16.5 %) compared to the nonmycorrhizal plants. Growth enhancement in mycorrhizal plants under saline conditions has been partly related to mycorrhiza-mediated decreased uptake of Na linked to a dilution effect due to growth enhancement (Giri and Mukerji 2004; Giri et al. 2007; Garg and Manchanda 2008, 2009; Hajiboland et al. 2010; Wu et al. 2013). Furthermore, Giri et al. (2007) reported a higher concentration of K^+ in root and shoot tissues in *A. nilotica* plants colonized by *G. fasciculatum* at all studied salinity levels. Likewise, AMF inoculation of citrus plants induced significantly higher K uptake and significantly lower Na uptake than in control plants, indicating a

preferential uptake of K against Na into the root xylem of stressed mycorrhizal plants (Wu et al. 2010, 2013). Together with similar results from the present meta-analysis, this suggests that inoculation with AMF increases K^+/Na^+ ratios which are beneficial in maintaining ionic homeostasis in the cytoplasm or Na^+ efflux from plants. Enhanced accumulation of K^+ in AM plants is vital for cytosolic enzyme activities and for maintaining an appropriate osmotic pressure and membrane potential, thereby benefiting the mycorrhizal plants in tolerating salt stress (Hajiboland et al. 2010; Wu et al. 2010, 2013).

Salinity also interferes with nitrogen acquisition and utilization, by influencing the different stages of N metabolism such as NO_3^- uptake and transformation in protein synthesis (Frechill et al. 2001). Some researchers have reported that the application of AMF may improve nitrogen assimilation by host plants (Garg and Manchanda 2008, 2009; Garg and Chandel 2011). For example, Giri and Mukerji (2004) recorded higher accumulation of N in the shoots of mycorrhizal *Sesbania grandiflora* and *Sesbania aegyptiaca* than nonmycorrhizal control plants. Improved N uptake may help to reduce the toxic effects of Na^+ ions by regulating its uptake and indirectly help to maintain chlorophyll content of the plant (Garg and Chandel 2011). However, in the present study, variation in N accumulation among groups was not significant, indicating inconsistencies among plants in mycorrhizal responses to N uptake under salt stress.

There are a number of publications supporting the view that proline accumulation in response to salt stress is a positive indicator of higher stress perception (Colmer et al. 1995; Vaidyanathan et al. 2003; Maiale et al. 2004). Investigations on osmoregulation by the arbuscular mycorrhizal symbiosis are relatively few and results are, to some extent, paradoxical. Some studies demonstrate that AMF inoculation significantly decreases proline accumulation (Sannazzaro et al. 2007; Jahromi et al. 2008; Borde et al. 2011), while others indicate an increase (Garg and Chandel 2012), little, or no effect on proline accumulation (Hajiboland et al. 2010). In the present study, inoculation with *G. mosseae* or *G. fasciculatum* increased proline accumulation, while decreased proline accumulation was observed following inoculation with *G. intraradices*. Also, among plant species, *G. arborea*, followed by *A. sativum*, *M. arvensis*, *C. arietinum*, and *L. esculentum*, showed a significant increase in proline accumulation, whereas *Z. mays* had a significant decrease in proline accumulation under salt stress, which may hint that *Z. mays* is under less stress than the other plant species. A nonsignificant relationship was observed between decreased proline accumulation (−1.7 %) and Na uptake (−16.5 %).

Production of ROS can occur in salt-stressed plants, and thus, plants have evolved specific protective mechanisms involving synthesis and activity of antioxidant enzymes protecting their cells against oxidants (Abogadallah 2010; Gill and Tuteja 2010; Sharma et al. 2012; Choudhury et al. 2013). Of these, SOD detoxifies superoxide to hydrogen peroxide, CAT and POD are implicated in the removal of H_2O_2 (Talaat and Shawky 2013), and ascorbate scavenges the most dangerous forms of ROS through the action of APOX. Meta-analysis results showed that salt stress increased SOD, CAT, POD, and APOX activities in AMF-inoculated plants, which suggests that activation of an antioxidant defense may be in response or not to increased ROS production. Moreover, these enzyme activities were significantly increased in mycorrhizal as compared to nonmycorrhizal plants under salt stress. The magnitude of the increased antioxidant enzyme activities was greatest in *G. fasciculatum*-inoculated plants followed by *G. intraradices* and *G. mosseae*. These results confirm those of Hajiboland et al. (2010), Wu et al. (2010), Dudhane et al. (2011), and Talaat and Shawky (2013). Although the plants possessed overall higher antioxidant enzyme activities as a result of mycorrhizal colonization, the response of the individual enzymes varied with respect to the host plant and the fungal species. This variation may also depend on micronutrient availability as some of the enzymes, for example CAT, APOX, and SOD, are metalloenzymes (Mittler 2002; Gill and Tuteja 2010; Alguacil et al. 2003; Sharma et al. 2012). Alguacil et al. (2003) found that arbuscular mycorrhiza enhance nutrient uptake under saline conditions, which may play a role in controlling the expression of antioxidant enzymes. Thus, arbuscular mycorrhiza facilitate the maintenance of a higher electrolyte concentration in plants growing under saline condition, by improving integrity and stability of cell membranes due to increased P and K uptake and antioxidant enzyme activities (Kaya et al. 2009; Wu et al. 2010).

In conclusion, the results from the present meta-analysis consolidate evidence for the potential of arbuscular mycorrhiza to protect host plants against salt stress and may pave the way for the exploitation of the symbiosis in sustainable agriculture in saline soils. AMF inoculation alleviates the detrimental effects of salinity on plant growth by improving plant mineral nutrition and increasing activity of antioxidant enzymes and reduces the impacts of salinity on plant physiology. Across the examined studies, the identity of AMF and of host plants was found to be much more important in predicting plant responses to salt stress than other predictor variables. AMF inoculation induced significantly higher K uptake and lower Na uptake than in control plants under salt stress, suggesting a preferential absorption of K^+ rather than of Na^+ into the root xylem of the salt-stressed mycorrhizal plants and a higher K^+/Na^+ ratio than in nonmycorrhizal plants. Thus, future research should address the AMF-mediated selectivity of K^+ over Na^+ as this will be essential to understanding tolerance mechanisms of mycorrhizal plants to salinity stress.

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