



# Wetland plant species improve performance when inoculated with arbuscular mycorrhizal fungi: a meta-analysis of experimental pot studies

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## Abstract

The presence of arbuscular mycorrhizal fungi (AMF) in wetlands is widespread. Wetlands are transition ecosystems between aquatic and terrestrial systems, where shallow water stands or moves over the land surface. The presence of AMF in wetlands suggests that they are ecologically significant; however, their function is not yet clearly understood. With the aim of determining the overall magnitude and direction of AMF effect on wetland plants associated with them in pot assays, we conducted a meta-analysis of data extracted from 48 published studies. The AMF effect on their wetland hosts was estimated through different plant attributes reported in the studies including nutrient acquisition, photosynthetic activity, biomass production, and saline stress reduction. As the common metric, we calculated the standardized unbiased mean difference (Hedges' *d*) of wetland plant performance attributes in AMF-inoculated plants versus non-AMF-inoculated plants. Also, we examined a series of moderator variables regarding symbiont identity and experimental procedures that could influence the magnitude and direction of an AMF effect. Response patterns indicate that wetland plants significantly benefit from their association with AMF, even under flooded conditions. The beneficial AMF effect differed in magnitude depending on the plant attribute selected to estimate it in the published studies. The nature of these benefits depends on the identity of the host plant, phosphorus addition, and water availability in the soil where both symbionts develop. Our meta-analysis synthesizes the relationship of AMF with wetland plants in pot assays and suggests that AMF may be of comparable importance to wetland plants as to terrestrial plants.

**Keywords** Wetland · Arbuscular mycorrhizal fungi · Pot experiments · Plant responsiveness to arbuscular mycorrhiza

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## Introduction

Wetlands are ecosystems of transition between aquatic and terrestrial systems in which the ground water level is usually at the soil surface level or the soil is covered with shallow waters (Kent 2001). These ecosystems include different habitats such as marshland, swamps, and seasonal wetlands with intermittent ponds and streams that last long enough to influence plant development. They may or may not be subjected to tides; may present salt water or fresh water; and may be lotic or lentic systems, permanent or temporary, and consisting of herbaceous or woody species, or there may be no plants at all (Kent 2001). Wetlands are among the most important ecosystems on the planet in terms of biodiversity, productivity, and carbon export to adjacent ecosystems. Wetlands occupy approximately 6% of the earth's land surface and are systems in constant transformation (Moore 2006).

### Arbuscular mycorrhizal fungi in wetlands

The arbuscular mycorrhizal symbiosis is formed by the interaction of fungi from Mucoromycota subphylum Glomeromycotina (as recently proposed by Spatafora et al. 2016) and approximately two thirds of plant species (Helgason and Fitter 2009). Many species of wetland plants associate with arbuscular mycorrhizal fungi (AMF), in both natural (Stenlund and Charvat 1994; Muthukumar et al. 2004; Fraccaro de Marins et al. 2009) and experimental conditions (Wolfe et al. 2006; Stevens et al. 2011; Sarkar et al. 2016). Under natural conditions, AMF have been registered in all major wetland types such as lowland timber forests (Stevens et al. 2010), swamps (Torti et al. 1997; Tawaraya et al. 2003), marshlands and bogs (Bohrer et al. 2004; Radhika and Rodrigues 2007), fens (Turner et al. 2000), freshwater marshes (Cornwell et al. 2001; Šraj-Kržič et al. 2006), saltwater marshes (Brown and Bledsoe 1996; Carvalho et al. 2003), and mangroves (D'Souza 2016; Gupta et al. 2016). According to Xu et al.'s (2016) review, AMF show high occurrence and diversity in wetland habitats and their roles in the composition, succession, and diversity of wetland plant communities have been demonstrated in some assays. Aspects such as the dependence of wetland plants on their AMF companions for phosphorus (P) acquisition, however, as well as the factors influencing that and other mycorrhizal benefits obtained by wetland plants are still poorly understood.

AMF colonize the roots of plants, where they facilitate mineral nutrient uptake from the soil through extra-radical mycelium, in exchange for plant-assimilated carbon (Smith and Read 2008). The enhancement in nutrient (e.g., P, N, and K; Karagiannidis et al. 2007) and water intake (Marschner and Dell 1994; Clark and Zeto 2000; Smith and Read 2008) is in most cases reflected in an improvement of plant growth, stress adaptation, and fitness (i.e., the plant's ability to increase its

numbers proportionately to other species; Pedersen and Sylvia 1996). This improvement can be significant or limited depending on the identity of the symbionts and the environmental factors in which they develop (Johnson et al. 2006; Cuenca 2015; Rúa et al. 2016), moving the association on a continuum from mutualistic to parasitic (Johnson et al. 1997).

### Symbiont identity

Many plant-fungus combinations form in nature (or even can be produced experimentally), but not all combinations behave in the same way (Streitwolf-Engel et al. 1997; van der Heijden et al. 1998a). There is small or no specificity between plant and fungus species involved in arbuscular mycorrhizas (Smith and Read 2008), but usually, there are some AMF combinations that deliver larger benefit than others to different plant species (Öpik et al. 2006; Helgason and Fitter 2009; Horton and van der Heijden 2012). Also, plants preferentially may associate with AMF species that are complementary in function instead of functionally redundant (Koide 2000). In addition, the degree of benefit that a host obtains from the fungi can differ according to its mycorrhizal dependency (Hetrick 1991; Chandrasekaran et al. 2014; van der Heijden et al. 1998a).

Related to AMF identity is the origin of the fungus with which the plant associates. It has been found that indigenous AMF are better adapted to their native environment conditions and function better under the homegrown stressors (e.g., salinity, flooding, drought) in comparison with non-native species (Lambert and Baker 1980; Weinbaum et al. 1996; Rúa et al. 2016). Also, inoculant complexity can be a relevant factor influencing the benefit received by the host plant, because in complex inoculants (larger number of AMF species), there are more chances that the plant finds AMF species that complement its root functions (or finds a very effective isolate) than in a less complex inoculants (smaller number of AMF species) (van der Heijden et al. 1998b).

### Soil nutritional status

Physical and chemical soil factors (e.g., flooding, salinity, nutrient availability) exert beneficial or detrimental effects on each of the mycorrhiza symbionts and modify the ability to accomplish their symbiotic function (acquire and deliver nutrients and carbon). According to Johnson et al. (1997), soil nutritional status is the best studied soil factor that influences the association outcome and likely is the most relevant environmental mediator of growth responses to mycorrhizal associations. Nitrogen (N) is one of the most limiting nutrients that regulates productivity in land and aquatic systems, as well as in wetland ecosystems. Wetlands receive nutrients from the water flowing over and under the surface from inland areas, so we can find wetlands that are very poor in nutrients, particularly in phosphorus (P), while others receive an excessive

discharge of it because of the contaminants generated by anthropogenic activity inland (Reddy and DeLaune 2008).

While P uptake is the primary symbiotic benefit to the plant, it is recognized that as soil P availability increases, the growth of some plant species associated with AMF declines. According to Johnson's (2010) Exchange Balance Model, the function of the mycorrhizal symbiosis in terrestrial systems depends particularly upon available N and P stoichiometry in the soil. Thus, we can predict that the mutualist benefits are greater when N availability is large and P availability is low, because the improved N supply increases the photosynthetic rate of the host plant (Johnson 2010) and low P availability makes the arbuscular mycorrhiza an important strategy to acquire the required P. On the other hand, reduced benefits would be observed under high P availability and poor N availability because N will limit the photosynthetic rate and the plant would have enough P for self-supply. Mutualistic function is more likely in P-limited systems (because AMF can effectively trade surplus P for plant photosynthate), and commensalism or parasitism is more likely in N-limited systems (because AMF are unlikely to have surplus N for trade because they have higher N requirements than their host plants; Johnson et al. 2015). This issue is still poorly understood in wetland habitats.

### Substrate salinity

Coastal wetlands (e.g., mangroves and marshes) are characterized by the influences of both flooding and salinity (up to 70 ppt; Hogarth 2010; Wu et al. 2008) upon their biota. High salinity concentrations in the soil are detrimental for most plants (Aggarwal et al. 2012) because of osmotic stress, ion toxicity, and nutritional imbalance (Tomlinson 1986; Shi et al. 2005; Aggarwal et al. 2012; Asghari 2004; Evelin et al. 2009). Salinity also has been reported to be detrimental for AMF (Kim and Weber 1985; Juniper and Abbott 1993; Krishna 2005), and it can delay symbiosis formation (Juniper and Abbott 2006). Plants that inhabit saline areas, nevertheless, possess adaptations that enable them to deal with salinity (e.g., exclusion, excretion, and tolerance to salts in their tissues) (Tomlinson 1986; Hogarth 2010; Parida and Jha 2010). Another strategy for plants may be the establishment of the mycorrhizal association, because some AMF also possess strategies to deal with salinity (e.g., exclusion and tolerance of salts in their cells) (Hammer et al. 2011; Solaiman et al. 2014; Carvalho et al. 2003), thereby reducing their host's saline stress (Sinclair et al. 2014; Xie et al. 2014). Reduction of saline stress may occur through (a) the improvement of plant mineral nutrition, (b) improvement in antioxidant enzyme activity, (c) promotion of production and accumulation of plant compatible solutes, (d) promotion of preferential absorption of K<sup>+</sup> over Na<sup>+</sup>, and (e) promotion of physiological changes such as an increase in photosynthetic efficiency, relative

membrane permeability, and a minor abscisic acid accumulation (Aggarwal et al. 2012; Evelin et al. 2009; Porcel et al. 2012; Chandrasekaran et al. 2014; Solaiman et al. 2014).

### Flooding

Flooding has been reported as a detrimental environmental factor for AMF (Kumar and Ghose 2008; Wang et al. 2011) because it reduces the quantity of oxygen available in the substrate (Evans 2003; Moore 2006) which affects AMF development (Le Tacon et al. 1983). Oxygen transport in a liquid medium is very slow because it is controlled by molecular diffusion. Consequently, the oxygen in a saturated soil diffuses 10<sup>4</sup> times more slowly than in a non-saturated soil (Stepniewski and Glinski 1988; Brune et al. 2000). This implies that even low levels of oxygen demand are sufficient to deplete oxygen completely in the substrate (except for the surface layers) and diffusion is not fast enough to replenish the oxygen entirely before it is consumed and depleted again by the biota (Jackson and Armstrong 1999; Armstrong et al. 1991; Van Breemen and Buurman 2003). Flooding also reduces the concentrations of phosphate and nitrate by dilution, leaching, and microbial denitrification (Evans 2003).

Flooding has been described as one of the main factors affecting AMF root colonization in wetlands (Ray and Inouye 2006). According to field research, it previously has been proposed that AMF are unlikely to reduce stress of their hosts because of the hypoxia to which they are subjected and that such fungi may behave as parasites when the soil is saturated for prolonged periods of time, although mutualistic function may be reestablished once the sites become seasonally dry (D'Souza 2016). This premise can be assessed through synthesizing pot assay results. If the proposed mechanism is true, we would expect that plants under flooding treatments in pot assays will not show benefits from mycorrhizal associations.

### Assessing AMF effect on host plants in pot experiments

The improvement in nutrient uptake that plants get from their associated AMF can be reflected in an elevated nutrient concentration in plant tissues (Khan 1988; Miller and Sharitz 2000). Also, plants can use water and nutrients to accomplish their photosynthetic process, so a series of photosynthetic attributes improve when a plant is benefited by AMF (e.g., higher photosynthetic pigment concentrations, higher photosynthetic rate; Dunham et al. 2003; Caravaca et al. 2004; Liu et al. 2014). Resulting from the photosynthetic enhancement, mycorrhizal plants usually show increased biomass generation that can be reflected in a large leaf area, weight, height, etc. (Dhillon 1992; Read 2002; Soti et al. 2014; Lingua et al. 2015). Also, the nutritional enhancement

enables the plant to elaborate compounds that reduce stress (e.g., compatible solute accumulations in tissues that reduce saline stress; Augé 2001; Evelin et al. 2009; Liu et al. 2013; Hajiboland et al. 2015). Relief of saline stress due to arbuscular mycorrhiza benefits often is reflected in water relation parameters as heightened water use efficiency (Reuss-Schmidt et al. 2015) and water content in tissues (Hajiboland et al. 2015).

As stated above, the effects of AMF on their host plants can be measured through any of several plant attributes. Nonetheless, not all mycorrhizal plant attributes always show significant improvement in comparison with the same attributes from non-inoculated plants (e.g., dry weight of plants inoculated with non-indigenous inocula [Dhillon 1992], height [Solaiman and Hirata 1996], electron transport rate in some arsenic treatments [de Andrade et al. 2015]), and this could depend on the symbiont species involved, the physico-chemical substrate characteristics, and even the duration of the pot assay. One way of synthesizing such variation of results is through quantitative syntheses or meta-analysis, which allow attaining generalizations based on previous results from different systems and case studies in the global literature (Koricheva et al. 2013; Rúa et al. 2016).

Making use of meta-analysis, the aim of this study was to determine the direction and magnitude of the AMF effect on wetland plants associated with them in pot experiments and to explore whether certain experimental factors may influence the direction and magnitude of those AMF effects. The effect of AMF on wetland plants was estimated based on the four plant attributes most frequently evaluated in pot experiments: mineral nutrient acquisition, photosynthetic activity, saline stress reduction, and biomass generation, all of which are expected to improve when arbuscular mycorrhizal symbiosis is established. As the common metric (or effect size), we calculated the standardized unbiased mean difference (Hedges'  $d$ ), which can be interpreted as the inverse-variance-weighted difference between the mean value of a given plant attribute with versus without AMF colonization in pot experiments, measured in units of standard deviations. Large differences between control (AMF absence) and treatment (AMF presence) effects and low variability generate the largest effect sizes (e.g., Gurevitch and Hedges 2001). Furthermore, to explore whether certain experimental conditions and symbiont characteristics and identities determine the relative magnitude of AMF effects, we included a series of moderator variables, such as plant and fungus identity (including plant wetland preference and growth habit), mycorrhizal inoculum origin and complexity, factors of nutrient addition, water availability and salinity in the soil, and also the time of the final harvest, and if an association establishment time is allowed before the application of other treatments (e.g., salt, fertilization). The assessment of these moderator variables will help us to reach a better understanding of the variation in the results of AMF

inoculation assays with wetland plants and may give us an idea of how the association with AMF can vary in wetlands, according to seasonal changes and the variation of soil nutrimental status, water availability, and other physical and chemical soil properties.

Plants evaluated in each pot study that we included in our meta-analysis have been reported to associate with AMF in natural conditions (Driver 1950; Stenlund and Charvat 1994; Johnson-Green et al. 1995; Reddell et al. 1997; Tsang and Maun 1999; Miller 2000; Carvalho et al. 2001; Cornwell et al. 2001; Dunham et al. 2003; Nielsen et al. 2004; Wang et al. 2004; de Battista 2005; Weishampel 2005; Wang and Qiu 2006; Wang et al. 2010; Abdelhalim et al. 2013; Seerangan and Thangavelu 2014; Soti et al. 2014; Xie et al. 2014; Zhang et al. 2014; Xu et al. 2016). Although we did not find such reports for *Phragmites japonica* and *Miscanthus sacchariflorus*, they belong to genera reported as mycotrophic in natural conditions (Öpik et al. 2006; An et al. 2008).

We hypothesized that inoculated plants would show a greater enhancement of all attributes in comparison with those plants that were not inoculated with AMF. Furthermore, we expected that in the presence of nutrient (N and P) and salt addition and elevated water availability in the substrate, the mycorrhiza enhancement of plant attributes would be smaller than in the absence of nutrient and salt addition and with low water availability. We expected that the identity of the symbionts determined the magnitude of the benefits in the different assays. Finally, we expected that a multispecies inoculum would provide larger benefits than a monospecific one and that indigenous inoculum (comprising native AMF species) would provide greater benefits than a non-indigenous one (comprising non-native AMF species). Finally, we expected that a development time promoted before the application of other treatments would yield a stronger association (in comparison with the same time application of inoculation and other treatments), resulting in an elevated response by the plant and that this response would be weakest in short duration assays, in comparison with prolonged assays.

## Materials and methods

### Literature search

An extensive search of literature was performed using Web of Science, SCOPUS, Google, and Google Scholar with the following sequence of key words: (wetland\* OR swamp\* OR marsh\* OR bog\* OR fen\* OR “shallow water” OR “wet meadow” OR mangrove\* OR rice\* OR “aquatic plant” OR river\* OR lake\* OR lacus\* OR lagoon\* OR estuar\* OR delta\*) AND (arbusc\* OR mycorrhiza\* OR “AMF” OR “VAM”) AND (effect\* OR respon\* OR grow\* OR acqui\* OR biomass\* OR production\*). The literature search was made and

updated in May 2016–October 2017. The search included articles published between 1900 and 2017, which is the timespan over which most online multidisciplinary databases have available published studies. This search yielded 1354 articles that were subsequently examined for inclusion in the meta-analysis.

The first condition for meta-analysis inclusion was that the plant species used were from wetland habitats, which affiliation was determined in accordance with the wetland indicator status (WIS) of the USA (Lichvar et al. 2012) or, if no classification was found, by means of a search for records of habitat of the species under analysis (this information also was added to the database as a moderator variable; for a complete list of moderator variables, see Table 2). If the plant species had more than one WIS, the strictest was selected for the moderator variable to emphasize the belonging to wetland ecosystems (e.g., an obligate wetland plant is the strictest of all levels, because it implies that the plant is restricted to wetland habitat). The second inclusion condition was that a study had to present a treatment of AMF-inoculated plants (AMF inoculant added to pots or unsterilized field soil with AMF propagules in it) and a control without inoculation (sterile substrate without AMF addition). The response variables used to assess the effects of AMF on their hosts are shown in Table 1. A total of 48 studies (see Online Resource 1) were included, from which 543 entries were obtained (multiple data were obtained from most studies). From each article, operational variables were recorded and they were classified by the kind of plant's attribute response that they estimated (Table 1).

When provided, we also included information regarding fertility, salinity, and water availability treatments as moderator variables of AMF effects that were assessed within each study. Although ideally these moderators should be treated as continuous variables, information provided by the studies was quite heterogeneous, with either categorical approaches to these treatments or by the use of different scales for the moderator variable. As a result, we were unable to use a meta-regression approach, and instead, we assessed these moderator variables as categorical comparisons of nutrient addition (phosphorus and nitrogen addition vs no addition), salinity (application of salt vs non-application), and water saturation in the soil (different levels of water availability) (Table 2). In addition, from each article, we gathered information about symbiont identity, host plant and inoculant characteristics, and timing of experimental procedures. Because we expected these aspects to influence the overall AMF effect upon wetland hosts, we also included this information as moderator variables in our analysis (Table 2).

## Data analysis

With the numerical outcome of each study, a new standardized common metric was calculated (i.e., effect size). This common metric allowed us to estimate overall effects across all studies and to make comparisons among potential moderator variables. To calculate the effect size Hedges' *d*, each study had to provide, either within the text or in tables or figures: the mean values, sample sizes, and standard deviations of any

**Table 1** Response variables considered for the evaluation of the AMF effect on their hosts and the category to which they were assigned (column titles)

Nutrient acquisition	Photosynthesis	Saline stress reduction	Biomass
Phosphorus content and concentration <sup>T,S,R,s,l,g</sup>	Chlorophyll content <sup>T,a,b</sup>	K:Na <sup>S,R</sup>	Dry weight <sup>T,S,R,s,l</sup>
Nitrogen content and concentration <sup>T,S,R,s,l</sup>	Carotenoid content	Soluble sugars content <sup>S,R,l</sup>	Seed production
Potassium uptake and content <sup>T,S,R,s,l</sup>	CO <sub>2</sub> assimilation rate	Starch content <sup>S,R</sup>	Shoot and leaf number
	Transpiration rate	Proline content <sup>S,R</sup>	Bud number
	Stomatal conductance	Free amino acids content <sup>S,R</sup>	Leaf area
	PSII	Water-use efficiency	Root length, volume and area
	NPQ	Water content <sup>S,R,l</sup>	Height
	ETR		Carbon content or concentration <sup>T,S,R</sup>
	Internal CO <sub>2</sub> concentration		Diameter at ground level
			Relative growth rate

*PSII*, actual quantum yield of photosystem II; *NPQ*, non-photochemical quenching; *ETR*, electron transport rate

<sup>T</sup> Total content

<sup>S</sup> In shoot

<sup>R</sup> In root

<sup>s</sup> In stem

<sup>l</sup> In leaf

<sup>g</sup> In grain

<sup>a</sup> Chlorophyll a

<sup>b</sup> Chlorophyll b



**Table 2** Moderator variables selected for the evaluation of the AMF effect on their hosts. Next to each moderator variable name, in parenthesis, the number of articles supporting that variable is shown

Moderator variable	Definition
Plant identity (48)	Taxonomic identity of the plant at species level. Species nomenclatures were updated according to ITIS ( <a href="https://www.itis.gov/">https://www.itis.gov/</a> )
Plant growth habit (48)	Plant growth habit according to United States Department of Agriculture ( <a href="https://www.plants.usda.gov/">https://www.plants.usda.gov/</a> ): tree, forb, or graminoid
Wetland indicator status (41)	Plant species preference to wetland habitat. OBL (obligate = almost always occur in wetlands, 99% occurrence in wetlands), FACW (facultative wetland = usually occur in wetlands, but may occur in non-wetlands, 67–99% occurrence in wetlands), FAC (facultative = occur in wetlands and non-wetlands, 34–66% occurrence in wetlands), FACU (facultative upland = usually occur in non-wetlands, but may occur in wetlands, 1–33% occurrence in wetlands), UPL (upland = almost never occur in wetlands, 1% occurrence in wetlands). We did not obtain UPL data
Inoculum origin (48)	Native (inocula extracted from the natural habitat where study host plant develops). In this revision, in all analyzed articles, this kind of inocula also corresponded to “home” kind of inocula (inocula extracted from study host plant rhizosphere), non-native (inocula that have not developed in the native ecosystem of the study host plant). This could be extracted from a natural habitat or be a stock inocula produced by research laboratories or also a commercial inocula, produced by specialized companies
Inoculum complexity (48)	Multiple or single AMF species inocula
AMF identity (22)	Taxonomic identity of the AMF at species level. Species nomenclatures were updated according to index fungorum ( <a href="http://www.indexfungorum.org/names/names.asp">http://www.indexfungorum.org/names/names.asp</a> ). Taxonomic levels higher than species were registered as reported in the articles. This moderator variable was only analyzed for the monospecific inocula, but in the Online Resources, complete database is provided and there are listed also AMF species present in the multispecific inoculum
P addition (34)	If P was added to the soil or not
N addition (38)	If N was added to the soil or not
Salinity (47)	If salinity treatments were applied or not: salt applied or no salt applied
Water content in the soil (37)	Refers to how much water is contented in the soil pores (measured as soil saturation percentage): saturated (100%), field capacity (70–90%), below field capacity (< 70%), dry (< 25%), field capacity to dry (change in water regime from field capacity to dry during experiment = watering decrease), dry to field capacity (change in water regime from dry to field capacity during experiment = watering increase)
Mycorrhiza development time extended (48)	If an association establishment period was allowed or not, before other treatments (e.g., fertility, salinity, watering) were applied: development time extended (association establishment period was allowed, before other treatments were applied), no development time extended (mycorrhizal inoculation and other treatments were applied at the same time) or single treatment (mycorrhizal inoculation was the only treatment applied)
Final harvest (46)	Number of days between the planting and the final harvest of the plants

plant performance response variable from each of the two contrasting effect categories: the control (without AMF inoculation) and the treatment (with AMF inoculation) (see Gurevitch and Hedges 2001 for detailed calculations and equations). When values only were provided in figures, we obtained the exact data using the software Datathief II (B. Tummers, <http://www.datathief.org>). Positive Hedges’ *d* values imply positive AMF effects on the performance of their host plant, whereas negative Hedges’ *d* values imply the opposite, a negative effect of arbuscular mycorrhizal inoculation on host performance.

We used mixed-effects models with fixed (see moderators in Table 2) and random effects to account for differences across studies, assuming they do not share a common mean effect, but recognizing that there is random variation among studies in addition to within-study sampling variation (Borenstein et al. 2009). Because most studies provided more than one output measure of host response to the presence or

absence of AMF, we performed hierarchical mixed-effects meta-analyses (Rossetti et al. 2017). These models incorporate the hierarchical structure of the data that results from including multiple observations (i.e., effect sizes) from the same study which violates the assumption that effect sizes are independent. Thus, we included a publication-level random effect as a nesting factor to consider this dependency of multiple outcomes within a study (Tuck et al. 2014; Rossetti et al. 2017).

Heterogeneity of effect sizes was assessed with *Q* statistics, which are weighted sums of squares tested against a chi-square distribution (Borenstein et al. 2009). Specifically, we examined the *p* values of *Q*<sub>Total</sub>, which describe the overall heterogeneity among all effect sizes included in the review, without any categorization, and also the *p* values of *Q*<sub>M</sub> statistics that describe the variation in effect sizes that can be attributed to differences among categories of each predictor variable (i.e., fixed effects) in the model (Table 2). Effect sizes were considered significantly different from zero if their bias-corrected bootstrap at 95%

confidence intervals (CI) did not include zero (Borenstein et al. 2009). All analyses were conducted in the R environment using the metafor package (Viechtbauer 2010; R Core Team 2015).

An intrinsic problem in any systematic quantitative review is the possibility of publication bias, i.e., studies showing significant results have a higher probability of being published. Evidence of potential publication bias in our dataset was explored with Kendall's rank correlations of effect size and standard error across the studies (Begg 1994). Significant  $p$  values indicate potential publication bias, whereby studies with small sample size (large standard errors) are only published if they show large effect sizes. Also, we calculated Rosenthal's fail-safe number, which estimates the number of non-significant, unpublished studies that need to be added to a meta-analysis to change its overall results from significant to non-significant. If the fail-safe number is larger than  $5n + 10$ , where  $n$  is the original number of effects included in the meta-analysis (Rothstein et al. 2005), then the overall results are robust, regardless of the presence of publication bias.

## Results

### Overview

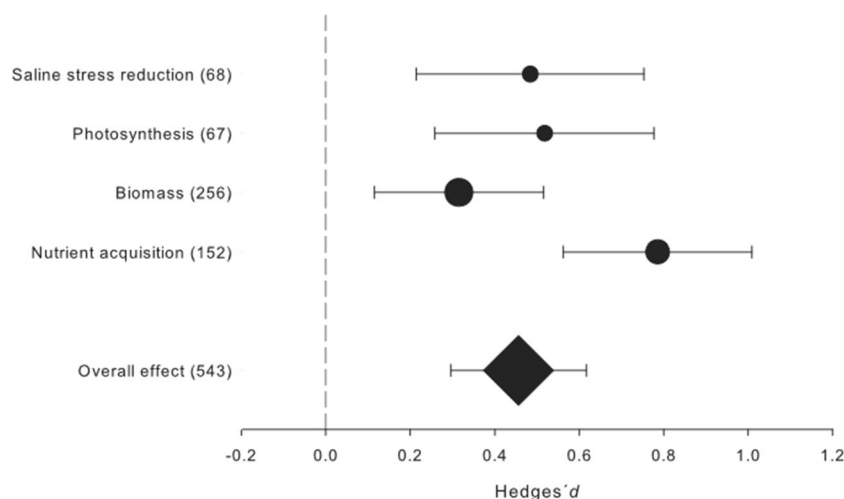
The overall effect of AMF on wetland plants was positive and significantly different from zero in accordance with the 95% CI ( $df = 542$ ; Hedges'  $d = 0.4556$ ; 95% BC CI, 0.2634 to 0.6479; Fig. 1). This result implies that the presence of AMF, on average, increases the overall performance of wetland plants in pot experiments. There was, however, significant heterogeneity among effect sizes across the studies ( $Q_{\text{Total}} = 2220.71$ ;  $df = 542$ ;  $p < 0.0001$ ), implying differential responses of wetland plants to

AMF inoculation. Therefore, we subsequently assessed the relative effects of the kind of plant attribute with which the AMF effect was estimated, on the direction and magnitude of this effect. After that, we assessed the relative effects of certain moderator variables of interest.

The rank correlation test between effect sizes and standard error was significant (Kendall's tau = 0.144;  $p < 0.01$ ), implying the potential of publication bias in our database. That is, the studies we incorporated into our meta-analysis may be a biased sample of the entire research on this subject and might represent only research that had significant results and thereby was likely to be published. Nevertheless, the calculated fail-safe number (74006) was much larger than  $5n + 10$  ( $5 \times 543 + 10 = 2725$ ), which supports that our results are robust and conclusive, despite the presence of publication bias in the dataset (Rothstein et al. 2005).

### The effect of AMF reflected in different kinds of plant attributes

Of the data included in the meta-analysis, 47.2% originates from biomass production attributes, 28% from nutrient acquisition, 12.5% from saline stress reduction, and 12.3% from photosynthetic activity attributes. The effect of the AMF on their hosts differs depending on the kind of plant attribute used to evaluate it. Differences were observed among the different kinds of plant attributes analyzed in the present study ( $Q_M = 40.16$ ;  $df = 3$ ;  $p < 0.0001$ ). The variables that showed the greatest effects of AMF on their hosts were those grouped in nutrient acquisition, followed by the photosynthetic activity, saline stress reduction, and finally biomass production attributes (Fig. 1).



**Fig. 1** Weighted mean effect sizes and 95% bias-corrected confidence intervals for the overall effect (black diamond,  $N = 543$ ) and weighted mean effect sizes of the four different plant attributes used to estimate the overall effect of the AMF on their hosts. Sample sizes for each category are shown in parentheses. The size of each dot representing each

mean effect size is proportional to its weight or contribution to the overall mean calculation. Dotted line shows Hedges'  $d = 0$ . When confidence intervals overlap zero, the effect sizes are not significantly different from zero. Non-overlapping confidence intervals among plant attributes' effect sizes imply significant differences among them

## Host plant characteristics

A total of 32 plant species are included in this meta-analysis. Of the published data included, 36% originates from experiments with species of agricultural interest (27.6% of rice, *Oryza sativa*, and 8.28% of sorghum, *Sorghum bicolor*) and the remaining from wild species: 5.3% of the data corresponds to tree species, 21.6% to herbaceous plants, and 73.1% to graminoid plants. With respect to the preference of the plant species used in the experiments for the wetland habitat (represented by Wetland Indicator Status), 38.9% were cataloged as obligate, 16.4% as facultative wetland plants, 6.1% as facultative, and 13.8% as facultative upland, and for the remaining percentage, no classification was found, or it did not apply because the plant was identified only at genus level.

Significant differences were observed among the plant response magnitudes to AMF inoculation according to the host taxonomic identity ( $Q_M = 73.0764$ ;  $df = 31$ ;  $p < 0.0001$ ). This means that certain plant species had strong and positive performance responses when inoculated with AMF (e.g., *Leersia hexandra*, *Strophostyles helvola*, *Oryza sativa*), while others did not show significant changes (e.g., *Tripolium*, *Panicum*, *Sonneratia apetala*) (Fig. 2). The complete list of hosts species is given in Online Resource 2. Host preference for wetland habitat also determines the response of the species to inoculation with AMF ( $Q_M = 14.0503$ ;  $df = 3$ ;  $p = 0.0028$ ; Fig. 2), with the greatest effect of the fungi being observed in the facultative wetland species, followed by the facultative upland and, to a lesser degree, the obligate species. In contrast, the host plants with facultative status showed no significant effects. Regarding the host growth habit, graminoid plants showed a significant effect of AMF, but there are no significant differences between the three

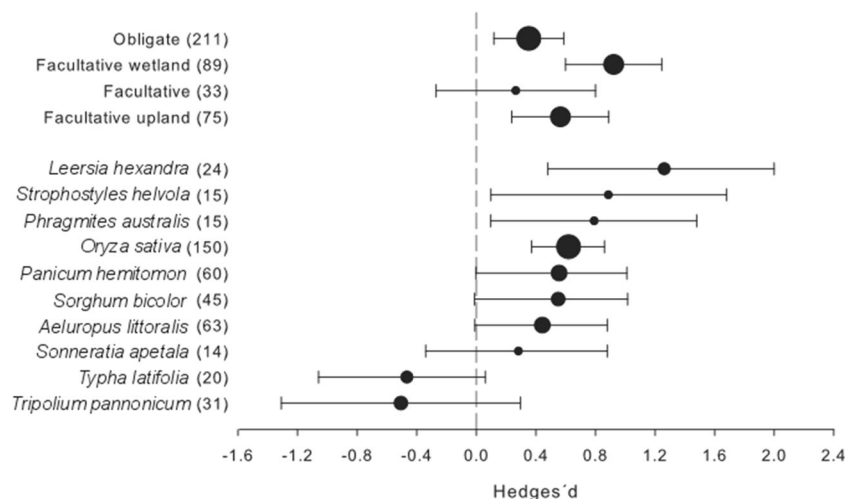
groups ( $Q_M = 5$ ;  $df = 2$ ;  $p = 0.0821$ ; figure provided in Online Resource 3).

## Origin and complexity of AMF inoculant and AMF identity

Of the data included in the meta-analysis, 52.7% originates from experiments in which the inoculation was carried out with a consortium of AMF species and the remaining percentage with only one species (monospecific inoculum). A total of 44% of the data were obtained from native inoculant and the remaining from non-native inoculant. To learn whether the AMF taxonomic identity influences their effect on the plants associated with them, we analyzed the monospecific inoculant. Results indicate that plants did not show different performance responses depending on the identity of their associated fungi ( $Q_M = 12.65$ ;  $df = 7$ ;  $P = 0.0812$ ) (Fig. 3). No differences were observed in the magnitude of the effects with respect to the complexity of the inoculum, i.e., using one species versus a consortium of AMF species to inoculate the plants ( $Q_M = 1.89$ ;  $df = 1$ ;  $p = 0.1628$ ). Regardless of the complexity of the inoculant, the overall effect on hosts was positive and significant (Fig. 4). There were no differences in relation to the origin of the inoculum ( $Q_M = 1.77$ ,  $df = 1$ ,  $p = 0.1828$ ); regardless of the origin of the inoculant, the overall effect on the host is positive and significant (Fig. 4).

## Nutrient addition

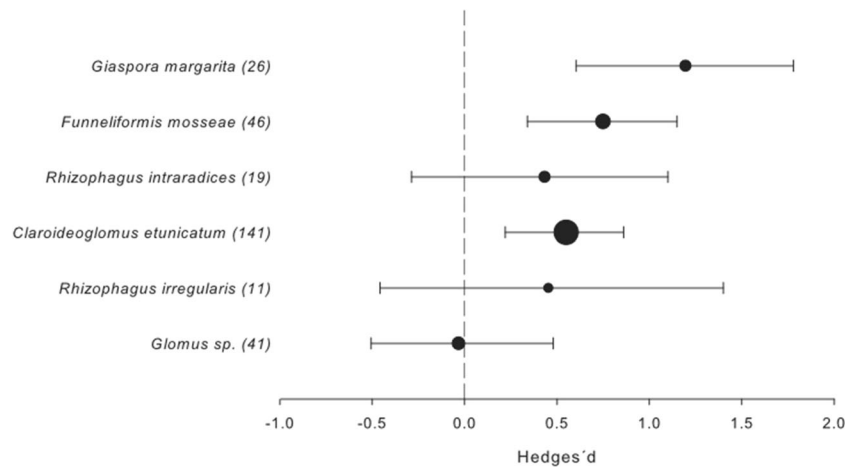
More than a half of the information corresponded to experiments that included nutrient addition to the substrate (61.1% with N and 54.3% with P). Significant differences were observed in the



**Fig. 2** Weighted mean effect sizes and 95% bias-corrected confidence intervals of the different included hosts and their wetland indicator status (WIS; obligate, facultative wetland, facultative, and facultative upland). Sample sizes for each category are shown in parentheses. Figure only shows host plant species with sample sizes > 10. The size of each dot representing each mean effect size is proportional to its weight or

contribution to the overall mean calculation. Dotted line shows Hedges'  $d = 0$ . When confidence intervals overlap zero, the effect sizes are not significantly different from zero. Non-overlapping confidence intervals among host plants' and WIS' effect sizes imply significant differences among them





**Fig. 3** Weighted mean effect sizes and 95% bias-corrected confidence intervals of different AMF species used in monospecific inoculum. Sample sizes for each category are shown in parentheses. Figure only shows AMF species with sample sizes > 10. The size of each dot

representing each mean effect size is proportional to its weight or contribution to the overall mean calculation. Dotted line shows Hedges'  $d = 0$ . When confidence intervals overlap zero, the effect sizes are not significantly different from zero

effects of AMF depending on whether P was added or not in the experiments ( $Q_M = 22.24$ ;  $df = 1$ ;  $p < 0.0001$ ). When P was not added, the effect of the AMF on their hosts was much greater than in experiments that added P (Fig. 5), but regardless of the condition (addition or non-addition), the overall effect on the host is positive and significant. A similar situation can be observed for the addition of N: when it is not added, the effects of the AMF on the performance of the plant tend to be greater than with the addition of N, but these differences were not significant ( $Q_M = 0.5186$ ;  $df = 1$ ;  $p = 0.4714$ ; Fig. 5).

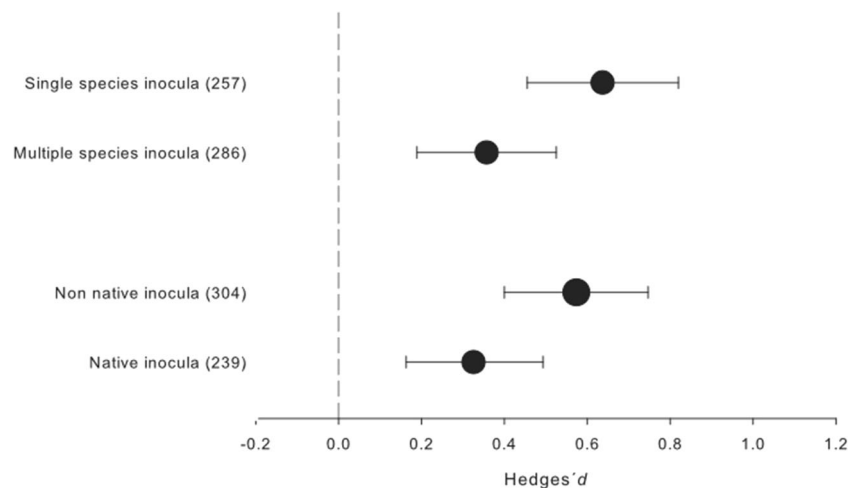
### Water availability and salinity in the substrate

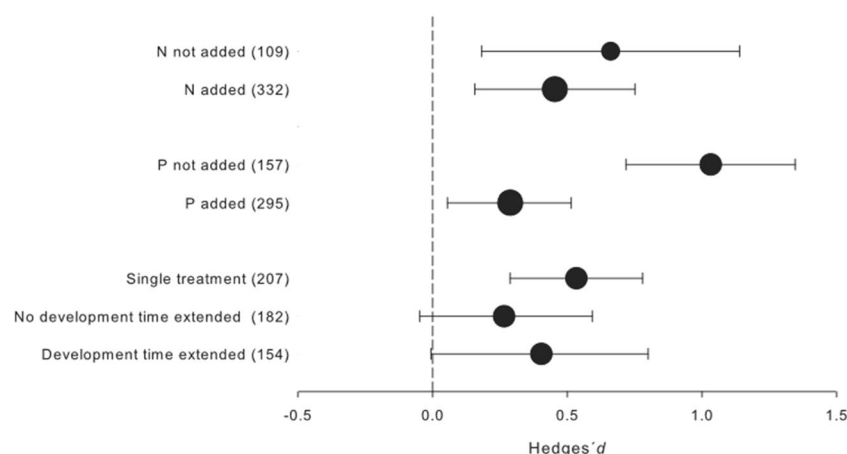
From the analyzed data, 18.9% of the data corresponded to salt addition treatments and 78.5% to absence of salt addition. Regarding water availability in the soil, 11% corresponded to flood treatments, 36.2% to field capacity, 35.7% to irrigation

below field capacity, 2.3% to a dry treatment, and a total of 4% to change of field capacity to dry and from dry to field capacity.

Regarding salinity treatments, we found that AMF, either with or without salt application to pots, exert positive and significant effects on their hosts. No significant differences were observed between salt application or non-application conditions ( $Q_M = 0.1428$ ;  $df = 1$ ;  $p = 0.7055$ ; Fig. 6). The levels of water availability in the substrate differentially influenced the effect of AMF on their plant hosts ( $Q_M = 57.35$ ;  $df = 5$ ;  $p < 0.0001$ ; Fig. 6). The treatments that positively and significantly influenced the effect of AMF on their hosts were flooding (100% saturation), irrigation below field capacity (69–25% saturation), and the change of field capacity to dry (change of 70–90% to < 25% saturation). The highest mean AMF effect on their hosts was related to below field capacity water availability, followed by the treatments of “change from field capacity to dry” and finally saturated (Fig. 6).

**Fig. 4** Weighted mean effect sizes and 95% bias-corrected confidence intervals of different inoculum origins (native and non-native) and complexities (multiple or single species). Sample sizes for each category are shown in parentheses. The size of each dot representing each mean effect size is proportional to its weight or contribution to the overall mean calculation. Dotted line shows Hedges'  $d = 0$ . When confidence intervals overlap zero, the effect sizes are not significantly different from zero





**Fig. 5** Weighted mean effect sizes and 95% bias-corrected confidence intervals of different fertilization treatments (P and N added and not added) and promotion of inoculation period (promoted, not promoted, or single treatment). Sample sizes for each category are shown in parentheses. The size of each dot representing each mean effect size is

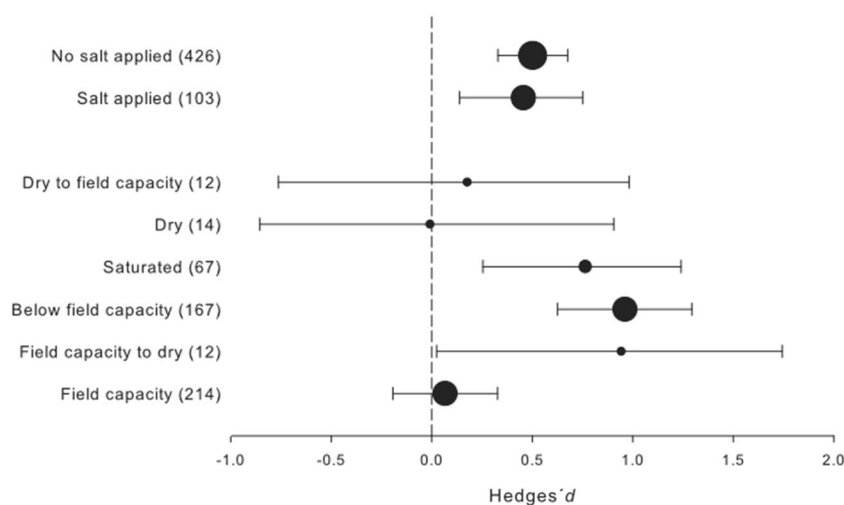
proportional to its weight or contribution to the overall mean calculation. Dotted line shows Hedges'  $d=0$ . When confidence intervals overlap zero, the effect sizes are not significantly different from zero. Similarly, non-overlapping confidence intervals among pot experiments manipulating P' effect sizes imply significant differences among them

### Mycorrhiza development time extended and time of final harvest

A total of 61.9% of the data originated from studies that included additional treatments besides inoculation with AMF, and the remainder originated from studies where AMF inoculation was the only treatment applied. 28.4% of the data were obtained from experiments in which an inoculation time was provided prior to the application of other treatments and 33.5% from experiments where the inoculation was applied at the same time as the other treatments. Duration of each of the different experiments registered in the literature differed considerably, ranging from 7 to 504 days ( $109.1 \pm 22.43$ ),

with 84 days being the most recurrent experiment duration used in 6 articles of the total 48 analyzed.

Regarding the inclusion of an inoculation period prior to the application of the other treatments (e.g., fertility, flooding, or salinity), significant effects were found only for AMF inoculation as the single treatment applied (Fig. 5), but the effects were not significantly different between the three levels of this category ( $Q_M = 1.29$ ;  $df = 2$ ;  $p = 0.5237$ ) (Fig. 5). The results of the meta-regression with log-transformed time of final harvest as the independent variable indicated that no significant relationship exists between the harvest time and the effect of AMF on their wetland hosts ( $Q_M = 0.0265$ ;  $df = 1$ ;  $p = 0.9706$ ; Online Resource 3).



**Fig. 6** Weighted mean effect sizes and 95% bias-corrected confidence intervals of different salinity treatments (salt added and not added) and water availability in the substrate resulting from irrigation treatments (dry, saturated, field capacity, below field capacity, dry to field capacity, and field capacity to dry). Sample sizes for each category are shown in parentheses. The size of each dot representing each mean effect size is

proportional to its weight or contribution to the overall mean calculation. Dotted line shows Hedges'  $d=0$ . When confidence intervals overlap zero, the effect sizes are not significantly different from zero. Similarly, non-overlapping confidence intervals among pot experiments manipulating salinity's and irrigation treatments' effect sizes imply significant differences among them

## Discussion

Wetland habitat is unlike any land habitat, given that the organisms that develop there are exposed to specific environmental problems deriving from water saturation of the substrate (Moore 2006). This saturation may be permanent or periodic, with the soil full of water in the wet season but dry in the dry season (Tiner 1991). Fluctuation in water levels implies that wetland organisms must be able to deal with both dry and wet conditions (Moore 2006). The presence of spores, extra-radical mycelium, and root colonization by AMF in wetland plants has been reported on numerous occasions (Ipsilantis and Sylvia 2007; Radhika and Rodrigues 2007; Harner et al. 2011; Wang et al. 2015). The results of our meta-analysis of pot assays suggest that AMF are not only capable of surviving in wetland conditions, but they also are functional and beneficial symbionts for the plants that establish in these ecosystems.

According to this meta-analysis, the benefit delivered by AMF to their wetland hosts can be observed in tissue nutrient content, biomass production, photosynthesis, and saline stress relief attributes, and it reflects differentially depending on the kind of attribute selected to evaluate it. According to the analyzed data, nutrient content could be the most reliable attribute for evaluating the response of plants to mycorrhizal inoculation; ultimately, nutrient acquisition is the core benefit that plants receive from associating with AMF (Smith and Read 2008). In experiment chambers, it has been observed that AMF can deliver up to 80% of P and 42% of N in the plant (Marschner and Dell 1994; Cuenca 2015). According to our results, the overall degree of benefit provided by AMF to their wetland hosts in pot assays depends on the identity of the host plant, the P addition, and water availability in the soil where both symbionts develop.

### Identity of the symbionts

As it has been registered for upland plants (Jun and Allen 1991), the identity of the wetland host plant in pot studies determines the degree of benefit that can be observed in the inoculated plants. Different plant and AMF species differ in their capacity to acquire and deliver nutrients and carbon to their symbiotic partner (Johnson 2010). This, along with aspects like root structure (e.g., suberin molecules that impede fungal colonization or root volume occupied by aerenchyma that could reduce cortex spaces for AMF establishment but which on the other hand, under flooding could deliver more oxygen to the rhizosphere) or mycorrhizal dependency, makes plant response to AMF inoculation be host identity dependent. This differential effect apparently is not dependent on plant growth habit but is dependent on their preference for wetland habitat.

Wetland plants are classified according to their frequency of occurrence in wetland conditions, which has been reported to be influenced by soil redox potential and the ability of these species to maintain an oxygenated root environment (Reddy and DeLaune 2008). Regarding the preference of different plant species for the wetland environment, among the indicators influencing the AMF effect, the highest significant effect was registered for the facultative wetland species and the facultative upland, while the lowest was for the obligate species. This could suggest a difference regarding the mycorrhizal dependency or precisely the flood conditions they must withstand and under which they are found with greatest frequency. For example, if facultative species (which receive the greatest positive effect of AMF) tolerate flooding to a lesser degree than a wetland obligate plant, these are found less frequently in permanently flooded soils, which also are more adverse for the AMF than soils flooded with less frequency. These relationships require further examination because it has been noted that the categories of the wetland indicator status fail in their correlation with the taxonomy of the plants (Lichvar et al. 2012). Nevertheless, these categories which are useful for multiple purposes (such as delimitation, evaluation, mitigation, and restoration of habitats), besides helping us to delimit this study, allow us to emphasize that the plant species restricted to the wetland environment (obligate wetland) are benefited consistently by establishing the arbuscular mycorrhizal association. This highlights the potential importance of the mycorrhizal association for plants establishing in the strictest wetlands.

As different plant species differ in their capacity to acquire and deliver their symbiotic fee (Johnson 2010) AMF also differ in that capacity and in their competitive ability for colonizing roots (Jansa et al. 2008). Thus, the effect that plants receive from AMF can be fungus identity dependent. Unexpectedly, AMF identity of the monospecific inoculant did not show a significant influence on the magnitude of the mycorrhiza effect and neither were differences in the effect observed depending on the origin of the inoculant. This also was contrary to what was expected, considering that different species of plants and AMF have adapted to their environment and are thus optimized for working together (Rúa et al. 2016). This lack of taxonomic identity and origin influence in our meta-analysis may indicate the plasticity of the fungi to adapt to different environmental conditions. Nonetheless, we must keep in mind that the AMF identity moderator variable only accounted for 48% of the total data information (monospecific inoculant), so it is possible that this result could change with a greater number of observations or under field conditions.

Regarding functional complementarity, there exists a greater possibility of complementing root functions or having a wider capacity for resource exploitation with a consortium of AMF species, rather than with only one species (Koide 2000). The results of the present meta-analysis, however,

show that there is no difference in the AMF effect, whether it is generated by one species or by a consortium of AMF. It is feasible that plants have not shown the differential benefit of having more than one AMF species (with different survival and nutrient and water acquisition/delivery strategies) in their rhizosphere, because most analyzed pot studies (except water availability levels in Miller and Sharitz 2000) maintained their treatments at relatively constant levels from the beginning to the end of the assay (e.g., salinity or flooding). Thus, there likely were no different niches to occupy in the restricted pot environment. This does not mean that inoculum complexity is not important in natural wetland systems; it probably is the opposite situation because wetlands are very dynamic ecosystems (Moore 2006). Associating with fungi that possess different hypoxia, drought, or salinity tolerance capacities is likely the best strategy to maintain the benefits of the association functioning in seasonally fluctuating soil conditions (Abbott and Gazey 1994; Pringle and Bever 2002), representing a strategy for buffering against change (Jansa et al. 2008). As will be discussed further, AMF are capable of tolerating and delivering benefits to their wetland host under varying stressful soil conditions that are common in wetland ecosystems.

Pot assays that aim to find optimal AMF for wetland reforestation and remediation should take this experimental issue into account. Our results show that in pot assays, the overall effects of AMF on their wetland host do not depend on the identity, origin, or complexity of the inoculant, but that could be because of the controlled conditions of pot experiments that do not necessarily mimic the conditions under which the symbionts develop in nature (Allen 1996) and do not allow us to observe a differential effect regarding the origin or the complexity of the mycorrhizal inoculum.

## Nutrient addition

Growth depression of hosts has been reported as result of high P in the substrate, which may arise from the demand for carbon compounds exceeding nutrient delivery by AMF (Janos 2007). Plants growing in wetlands are considered efficient with respect to their use of nutrients, given that these are not very abundant in a natural form (e.g., Small 1972; Rejmánková 2005). Our results show, however, that even when wetland plants receive P fertilization, they continue receiving significant benefits from their associated AMF. Nevertheless, as with land plants, the benefit is greatest without the addition of P. This result, although requiring detailed examination (e.g., mycorrhizal dependency assays), highlights the relevance of arbuscular mycorrhizas for wetland plants. In the case of N, contrary to expectation, the addition (if sufficient N is available, photosynthesis is not restricted nor is the carbon delivery to AMF; Johnson 2010; Johnson et al. 2015) or non-addition of this element (low N could restrict mycorrhizal benefits; Johnson 2010; Johnson et al. 2015) does

not appear to determine its effect. In other words, the effect is positive, regardless of the addition of N. Nitrogen addition effects could be obscured by the driving force of P, the main benefit of AM symbiosis, because despite added N, P availability would determine if symbiosis tended to be parasitic (high P) or mutualistic (low P), or if N was not added, P availability would determine if the symbiosis tended to be commensal (high P) or a limited mutualism (low P). Our moderator variable addition versus non-addition of N and P is not sensitive enough to determine with certainty if the lack of N influence is a consequence of P and N stoichiometry.

## Water availability and salinity in the substrate

Water saturation of the substrate is the most determinant force for biological communities inhabiting wetlands (Cowardin et al. 1979), and arbuscular mycorrhizal association provides no exception. Regarding the water availability levels examined in the present study, the largest effect of AMF on their hosts was observed in below field capacity water availability. Even for the 100% saturation (equivalent to flooding), however, significant benefits were found. In the same way that plants established in wetlands have adapted to survive under flooded conditions, AMF must possess strategies that allow them to establish and develop in these environments. In plant species, such adaptations include the use of two kind of strategies: (i) anatomical: the risk of suffocation is minimized by internal routes of impediment-free transport consisting of a continuous plant tissue (aerenchyma) which contains enlarged spaces of gas (Evans 2003); (ii) metabolic: under severe conditions of oxygen deficiency, some plants are capable of respiration through anaerobic fermentation (Evans 2003; Reddy and DeLaune 2008).

In the case of AMF, they might be able to use three types of adaptations. First, they may have low oxygen requirements (Helgason and Fitter 2009; Le Tacon et al. 1983). Second, they may have a capacity to remain quiescent in the absence of oxygen and to recover their activity once the environment is oxygenated. Germination and hyphal growth are affected by flooding, but these effects may be reversible (Le Tacon et al. 1983). In this sense, the fluctuation of flooding in some wetlands could also be crucial for the survival of susceptible AMF species in such environments. If so, the spores with greatest probability of germinating and colonizing plants are those that are produced in the low tide seasons when there is the most oxygen in the substrate. Third, AMF may be able to cluster in the oxygenated rhizosphere of their hosts. The presence of aerenchyma in plant tissues has a secondary effect that involves leakage of oxygen from roots into the surrounding substrate, a process called “oxygen radial loss” (Armstrong et al. 1991; Brune et al. 2000). Oxygen radial loss can become the main source of oxygen supply in flooded soils (Stepniowski and Glinski 1988). The leaked oxygen from

the roots of wetland plants allows aerobic organisms to prosper in this particular environment, at least temporarily, by providing them with an oxygenated space in the rhizosphere (Brune et al. 2000; Evans 2003; Lai et al. 2012). It has been proposed that the radial loss of oxygen also favors the development of AMF around roots (Brown and Bledsoe 1996). In addition to the three types of adaptations listed, one aspect that has been poorly explored is the acquisition of oxygen directly from the aerenchyma of hosts. The presence of structures pertaining to AMF has been reported in the aerenchyma of salt marsh plants (Brown and Bledsoe 1996).

Stevens et al. (2011) support that flooding of the soil can inhibit the development of AMF in some emergent wetland species under certain conditions, but this is not always the case and arbuscular mycorrhizal associations can establish in flooded soils. The results of our meta-analysis support to that conclusion and allow us to assert that, in general, AMF deliver benefits to their hosts even under flooded conditions. Thus, although there may be species of AMF that tend to act as parasites during flooding, they generally function as mutualists. The premise that AMF act as parasites in wetlands arises from the inverse relationship between root colonization and spore density in field soils with the level or permanence of flooding (Anderson et al. 1984; D'Souza 2016). It is important to emphasize, however, that a low level of root colonization does not necessarily imply low functionality, and similarly for AMF spore density (Mosse 1981). Most mutualisms are vulnerable to cheating by some of the symbionts, and some symbionts will be ineffective in carrying out their function (Helgason and Fitter 2009) which may lead to parasitism on some occasions, but the experimental tests that have been carried out to date show that the association with AMF is of benefit to wetland plants under different conditions of flooding, P fertility, and salinity.

Coastal wetlands are highly variable systems not only with respect to oxygen availability, but also to salinity. Unfortunately, we were not able to obtain enough suitable quantitative data on substrate salinity to examine its influence on the overall effect of AMF on their hosts. Different studies that applied salt treatments were conducted under dissimilar experimental conditions, making salinity a very heterogeneous variable to analyze without a larger number of observations. Nonetheless, our results show that AMF overall effect is positive and significant, either under non-saline conditions or under saline conditions. On the other hand, we found that AMF do significantly alleviate saline stress in their wetland hosts, as has been found for upland plants (Chandrasekaran et al. 2014). Little is known of the combined effect of this variable with flooding because its relationship is complex, depending on the levels of both variables and on texture and filtration in the substrate (Lugo and Snedaker 1974; Odum et al. 1985; Feller and Sitnik 1996; Pennings et al. 2005; Moreno-Casasola et al. 2006), but it likely is a relevant factor affecting the symbiosis, and it needs further exploration.

## Timing of experimental procedures

Regarding the timing of experimental procedures, contrary to expectations, an extended mycorrhiza development time and extended time of the final harvest did not show significant influences on the overall effect of AMF upon wetland hosts in pot assays. Nevertheless, we did observe that positive effects were consistently obtained when inoculation was the only treatment. This suggests that in the pot assays without further pot environment variability, arbuscular mycorrhizal association is free of impediments to functioning, but when other treatments are applied, the effect that AMF exert on their hosts can vary and even diminish. Our results suggest that in pot studies, it is irrelevant if association already was established or if it must establish under complex environmental conditions. Ultimately, in natural conditions, the mycorrhizal association must establish under many soil conditions, stressful or not for the fungi (Brundrett 1991). This result also suggests that allowing a mycorrhiza development time before application of experimental treatments is unnecessary, which could help to shorten experiments.

## Conclusion

This meta-analysis not only synthesizes the relationship of AMF with plant species found in wetlands in pot assays, but also highlights the importance of arbuscular mycorrhizas for the plants that establish in these ecosystems. AMF are able to benefit their hosts under diverse conditions of water availability, nitrogen and phosphorus fertility, and salinity. They deliver improvements in nutrient acquisition, photosynthetic activity, biomass generation, and saline stress reduction with the magnitude of effects depending upon host identity as well as phosphorus addition and water availability (the defining wetland condition). Previously, it had been established that AMF represent an integral part of wetland ecosystems (Khan 2004), and now, we know by synthesizing the results of the pot studies carried out to date that AMF actually may be of comparable importance to wetland plants as they are to terrestrial plants.

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To the projects:

Enseñanza de las metodologías para establecer las bases ecológicas de la restauración y conservación de humedales costeros PAPIME-DGAPA (Programa de Apoyo a Proyectos para la Innovación y Mejoramiento de la enseñanza), PE204012.

Diversidad vegetal y fúngica del sistema lagunar de la Carbonera, Reserva Estatal de Ciénagas y Manglares de la costa norte de Yucatán



CONABIO (Comisión Nacional para el Conocimiento y uso de la Biodiversidad), JF078.

Bases metodológicas para la restauración ecológica de ecosistemas costeros: de las dunas a los humedales PAPIME-DGAPA (Programa de Apoyo a Proyectos para la Innovación y Mejoramiento de la enseñanza), PE207216.

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