



Review

# The Effect of Arbuscular Mycorrhizal Fungi on Photosystem II of the Host Plant Under Salt Stress: A Meta-Analysis

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**Abstract:** As important components of the photosynthetic apparatus, photosystems I (PS I) and II (PS II) are sensitive to salinity. Salt stress can destroy the PS II reaction center, disrupt electron transport from PS II to PS I, and ultimately lead to a decrease in the photosynthetic capacity of the plant. Arbuscular mycorrhizal fungi (AMF) can enhance the photosynthetic capacity of a host plant under salinity stress. However, this specific effect of AMF is not always predictable. Here, we conducted a meta-analysis including 436 independent observations to compare chlorophyll fluorescence parameters in response to AMF inoculation under salt stress. The results showed that AMF inoculation had a positive total impact on photosynthesis in the host plant. Subgroup analysis showed that annual host plants had better performance in terms of photosynthesis after inoculation. The mitigating effects of AMF on the photosynthetic rate (Pn), actual quantum yield of photochemical energy conversion in PS II ( $\phi$ PS II), and electron transfer rate (ETR) in C4 species were higher than those in C3 species. Moreover, the photosynthesis performance of monocotyledon species was better than that of dicotyledon species after AMF inoculation. The woody host plants had higher energy utilization by way of an enhanced electron transfer rate to reduce energy dissipation after AMF inoculation. Finally, the mitigating effect of AMF on plants under moderate salinity was stronger than that under high salinity. Among AMF species, *Funneliformis mosseae* was found to be the most effective in enhancing the photosynthesis performance of plants. For the analyzed dataset, AMF inoculation alleviated the detrimental effects of salinity on photosystem II of the host plant by improving the utilization of photons and photosynthetic electron transport, and also by reducing the susceptibility of photosystem II to photoinhibition.

**Keywords:** Arbuscular mycorrhizal fungi; meta-analysis; photosynthesis; photosystem II; salt stress

## 1. Introduction

Soil salinization and associated land degradation is becoming an increasingly severe environmental problem throughout the world, especially in arid and semi-arid regions [1]. It is estimated that more than 955 million ha of land across the world has salinity problems [2]. Excess salt in the soil affects the physiological processes of plants by inducing water deficiency, osmotic stress, nutritional imbalance, and ionic toxicity [3,4]. Photosynthesis, the key process of primary metabolism, is sensitive to salinity [5]. Salt stress can reduce the CO<sub>2</sub> availability by limiting diffusion through stomata and the mesophyll,

destroying the photosystems II (PS II) reaction center and disrupting electron transport from PS II to PS I [6–8]. These adverse effects lead to a decline in photosynthetic capacity and ultimately inhibit plant growth.

Arbuscular mycorrhizal fungi (AMF) are one of the most important types of soil microorganism and can form symbiotic relationships with more than 80% of all terrestrial plant species [9]. Additionally, this kind of microorganism can also be found in saline soils [10]. It has been demonstrated that colonization with AMF can enhance the ability of a plant to resist salt stress via several mechanisms, such as by facilitating water uptake, limiting ionic uptake, and accumulating compatible solutes [4].

Many studies have also used chlorophyll fluorescence analysis to evaluate the positive effect of AMF on the photosynthetic capacity of the host plant under salinity stress, including *Oryza sativa* [7], *Jatropha curcas* [11], and *Zea mays* [8]. Chlorophyll fluorescence is a rapid, non-destructive method to examine the stress features and photosynthetic performance of a plant [12]. These parameters can clearly reflect several aspects of photosynthesis, such as energy-utilizing strategies, the conditions in the PS II reaction center, photosynthetic electron transport, and photophosphorylation [13]. However, the effects of AMF on fluorescence parameters related to photosynthetic capacity are not always predictable. For example, AMF resulted in an increase of the non-photochemical quenching coefficient (NPQ) in the leaf of *Zea mays* [14], a decrease of the NPQ in *Cucumis melo* [15], and no effect on the NPQ in *Robinia pseudoacacia* [16]. Similar results were also found for other photosynthetic parameters, such as the photosynthetic rate (Pn), apparent quantum yield of PS II (Fv/Fm), and electron transfer rate (ETR) [17].

Meta-analysis is a numerical and synthetic approach which can be used to analyze experimental factors that cause variations among studies [18]. It has been widely used to discover new aspects or to gather support for broader trends among contradictory published data. Chandrasekaran et al. conducted a meta-analysis on the symbiotically efficient AMF species and found that salinity alleviation was due to the AMF-enhancing nutrient uptake and antioxidant enzyme activity in different plants [19]. Auge et al. performed a meta-analysis and reported that AMF inoculation could improve ion balance and osmotic adjustment to relieve salt stress [20]. In addition, a weighted meta-analysis was also conducted to explore the effects of AMF inoculation on gas exchange in C3 and C4 plants under salt stress [21]. Many studies came to the conclusion that AM symbiosis alters the photosynthetic capacity of host plants [1,7]. However, the effects of AMF inoculation on photosystem II of a host plant under salt stress have never been reported in a meta-analysis. We aimed to determine whether there is a general consensus across the published literature. Hence, a quantitative analysis of the literature using meta-analysis was used to synthesize an overall effect size of AMF inoculation on plant characteristics, AMF species, and growth conditions associated with photosynthetic capacity under salt stress.

The present study aimed, more specifically, to answer the following questions: (1) What are the overall effects of AMF inoculation on the photosynthetic capacity of host plants under salt stress? (2) What impact does AMF inoculation have on photosystem II (PS II)? (3) Does PS II of the host plant change with the identity of the AMF species and plant characteristics (C3 vs. C4 vs. CAM (Crassulacean Acid Metabolism); monocotyledon vs. dicotyledon; herbaceous vs. woody; annual vs. perennial vs. annual/perennial)? (4) Are salinity levels related to the response of PS II in host plants?

## 2. Materials and Methods

### 2.1. Literature Search and Data Collection

To build a database, extensive literature searches were performed using Web of Science (<http://apps.webofknowledge.com>) and the Chinese National Knowledge Infrastructure database (<http://www.cnki.net>) in 2018 with the following keyword search: (arbuscular mycorrhizal fungi or arbuscular mycorrhizal fungal or mycorrhiza or mycorrhizal or AM fungi or AM fungal or AMF) and (salt stress or salt resistance or salt tolerance or salinity stress). Initial screenings returned about 992 articles, which were checked for the following inclusion criteria: (i) photosynthetic rate (Pn), apparent quantum yield of

PS II (Fv/Fm), actual quantum yield of photochemical energy conversion in PS II ( $\phi$ PS II), photochemical quenching coefficient ( $q_p$ ), non-photochemical quenching coefficient (NPQ), and electron transfer rate (ETR); (ii) effect of AMF inoculation compared with a noninoculated group; (iii) Experiments performed under salt stress.

Among the 992 articles, 957 papers were excluded based on these criteria, and the list was refined to 35 studies (from 2007 to 2018). Detailed information is provided in Table S1. From these studies, 436 independent observations were identified for the comparative analysis of chlorophyll fluorescence parameters in response to AMF inoculation under salt stress (Table S2).

## 2.2. Data Acquisition

The information on different fixed factors for each publication was extracted, including authors, published year, taxonomy of the AMF and host plant, level of salinity, photosynthetic rate, apparent quantum yield of PS II, actual quantum yield of photochemical energy conversion in PS II, photochemical quenching coefficient, non-photochemical quenching coefficient, and electron transfer rate. In addition, the mean, standard deviation (SD) or standard error (SE), and sample size or replicate number (N) were also extracted for the control and the AMF inoculation under salt stress in each study. The SE was transformed to an SD via  $SE = SD(n^{-1/2})$  when studies only provided an SE value. If the SD or SE was missing, we used the method described by Groenigen et al. to estimate the SD or SE [22]. When means and errors were presented in a graph, GetData (Graph Digitizer software, <http://getdata-graph-digitizer.com>) was used to extract the values. For the purposes of the analysis, the categorical independent variables in each study were coded, including the photosynthetic types (C3, C4, and CAM), plant groups (monocotyledon and dicotyledon), plant types (herbaceous and woody), salinity stress levels (low:  $EC \leq 4 \text{ dS}\cdot\text{m}^{-1}$  or  $C \leq 42.68 \text{ mM}$ , moderate:  $4 \text{ dS}\cdot\text{m}^{-1} < EC < 8 \text{ dS}\cdot\text{m}^{-1}$  or  $42.68 \text{ mM} < C < 85.37 \text{ mM}$ , and high:  $EC \geq 8 \text{ dS}\cdot\text{m}^{-1}$  or  $C \geq 85.37 \text{ mM}$ ), and life cycles of plants (annual, perennial, and annual/perennial).

## 2.3. Statistical Analysis

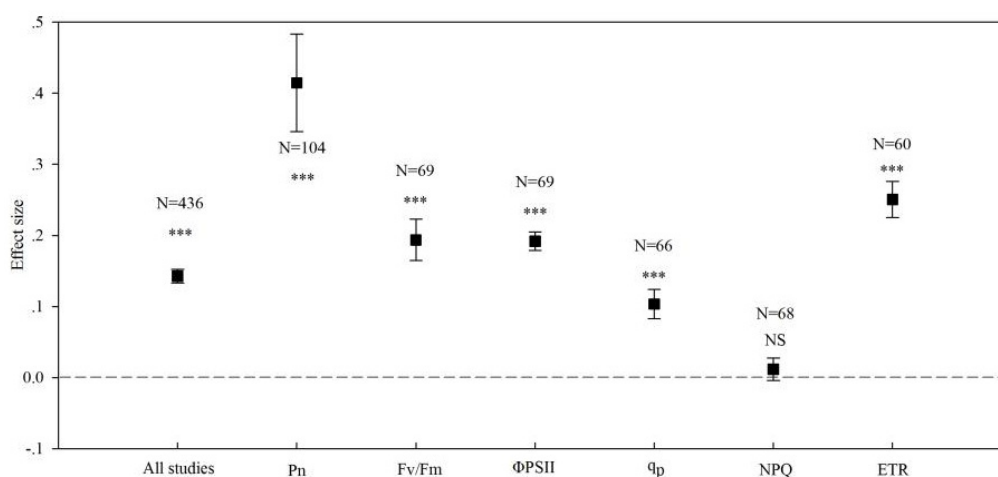
Random-effects model meta-analyses were conducted for each of the categorical independent variables to test the effect size of AMF inoculation on chlorophyll fluorescence under salt stress using MetaWin2.1 software [23], following the calculation method described by Chandrasekaran et al. [21]. Effect sizes were considered to be significant if their bias-corrected bootstrap 95% confidence intervals (CI) did not include zero. Heterogeneity in the effect sizes was calculated using Q statistics and compared against a chi-squared distribution [24]. We calculated the total heterogeneity ( $Q_T$ ) and the total heterogeneity between groups ( $Q_B$ ) and compared them against a chi-squared distribution. Studies were considered significant when the  $Q_B$  was significant ( $p < 0.05$ ) and described at least 10% of the total variation ( $Q_B/Q_T \geq 0.1$ ) [23]. Moreover, categorical independent variables were analyzed to find the reason for true heterogeneity. To this end, the significance level of the random-valued between-level difference in categorical moderators was investigated, and a significance level of 0.05 was considered to be statistically significant. In addition, Begg and Mazumdar rank (Kendall) correlations, represented graphically via funnel plots of effect sizes versus their standard errors, were used to assess potential publication bias [18,25].

## 3. Results

### 3.1. Overview

The meta-analysis included 436 independent observations which were extracted from 35 published studies about the effects of AMF inoculation on gas exchange and chlorophyll fluorescence in salt-stressed plants. In detail, there were 104 observations on Pn in 27 studies, 69 observations on Fv/Fm in 16 studies, 69 observations on  $\phi$ PS II in 15 studies, 66 observations on  $q_p$  in 9 studies, 68 observations on NPQ in 11 studies, and 60 observations on ETR in 7 studies (Figure 1 and Table S2). The effects

were examined among the plant group, life cycle, photosynthetic type, plant type, soil salinity level, and major AMF species. Most of the studies were focused on dicotyledon (86.70%) and perennial plants (65.37%). Most experiments were designed at high salinity (71.11%), followed by moderate (22.71%). The major AMF inoculant was *Funneliformis mosseae* (51.38%). In addition, most observations concentrated on herbaceous (63.72%) and C3 (46.10%) plants, followed by CAM (32.11%) species. Inoculation with AMF had significantly positive effects on the total effect size ( $df = 435$ ; log response ratio = 0.14; 95% confidence interval (CI), 0.133 to 0.152; Figure 1 and Table 1). Moreover, the funnel plot for total effect sizes was symmetrical in general, with spots of effect sizes centered at the top of the funnel plot (Figure S1). The results indicated that there was no significant publication bias and that the research accuracy was high.



**Figure 1.** Overall analysis of the effect of arbuscular mycorrhizal fungi (AMF) inoculation on photosystem II of host plants under salt stress. Error bars are the mean effect size  $\pm$  95% bootstrapping (BS) confidence intervals (CIs). If the BS CIs do not overlap the zero line, the effect size was considered significant at the 0.05 level. \*\*\*, and non-significant (NS) indicate significance at  $p < 0.001$ , and  $p > 0.05$ , respectively. The number of independent observations is presented above the bar. Pn: Photosynthetic rate; Fv/Fm: apparent quantum yield of PS II;  $\Phi$ PS II: actual quantum yield of photochemical energy conversion in PS II; qp: photochemical quenching coefficient; NPQ: non-photochemical quenching coefficient; ETR: electron transfer rate.

**Table 1.** The overall heterogeneity analysis among and within groups.

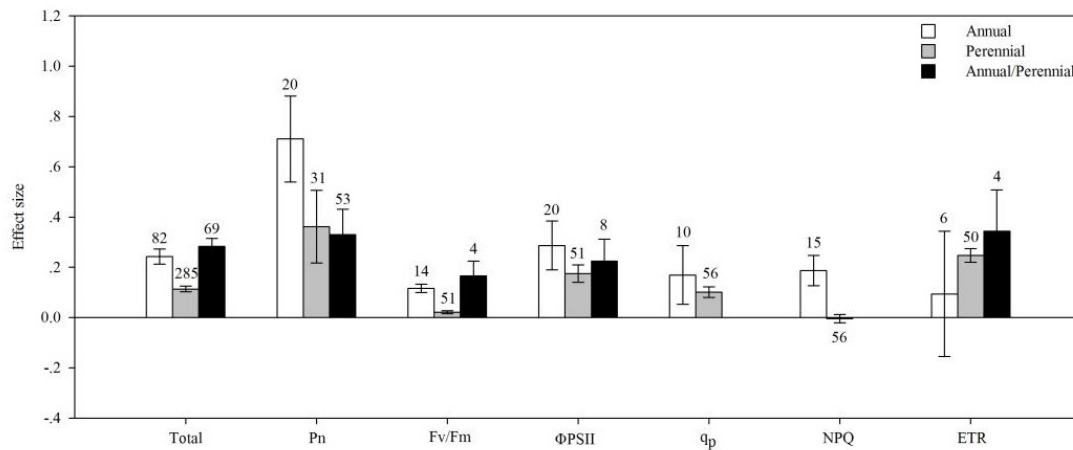
Noncategorical Predictor Variables	Effect Size	$df^a$	95% BS CIs	$Q_{Total}$	$P_{(chi-square)}$
All studies	0.143	435	0.133 to 0.152	2477.046	0
Pn	0.415	103	0.346 to 0.483	167.351	0
Fv/Fm	0.042	68	0.033 to 0.050	259.403	0
ΦPSII	0.192	68	0.165 to 0.223	182.492	0
qp	0.104	65	0.083 to 0.124	309.468	0
NPQ	0.012	67	-0.004 to 0.027	710.539	0
ETR	0.251	59	0.225 to 0.276	152.112	0

<sup>a</sup>:  $df = n - 1$  ( $n$  = number of observations). Pn: Photosynthetic rate; Fv/Fm: apparent quantum yield of PS II;  $\Phi$ PS II: actual quantum yield of photochemical energy conversion in PS II; qp: photochemical quenching coefficient; NPQ: non-photochemical quenching coefficient; ETR: electron transfer rate.

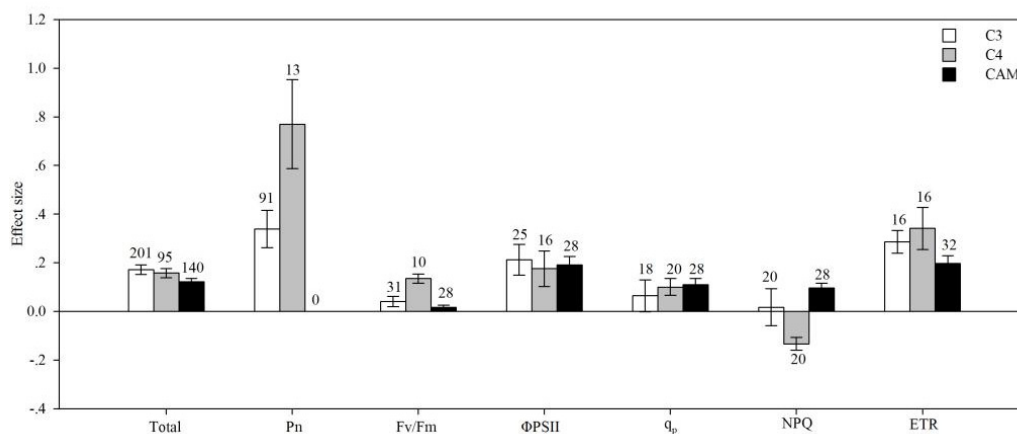
### 3.2. Effects of Arbuscular Mycorrhizal Fungi (AMF) Inoculation on the Photosynthetic Rate in Plants

Enhanced Pn was found in AMF-inoculated plants under salt stress, and significant variation was found among the studies ( $df = 103$ ; log response ratio = 0.415; 95% CI, 0.346 to 0.483;  $Q_T = 167.351$ ;  $p < 0.05$ ; Figure 1 and Table 1). Categorical analysis of Pn showed significant differences with respect to life cycle ( $Q_B = 16.620$ ;  $Q_B/Q_T = 0.111$ ;  $p = 0.011$ ; Figure 2, Table 2). AMF-inoculated annual plants

had a higher effect size ( $n = 20$ ; log response ratio = 0.711) than did perennial ( $n = 31$ ; log response ratio = 0.362) and annual/perennial plants ( $n = 53$ ; log response ratio = 0.330; Figure 2). Categorical analysis by photosynthetic type also showed significant differences ( $Q_B = 21.774$ ;  $Q_B/Q_T = 0.330$ ;  $p = 0.009$ ; Figure 3, Table 2). The AMF inoculation response of Pn in C4 plants ( $n = 13$ ; log response ratio = 0.330) was greater than that in C3 plants ( $n = 91$ ; log response ratio = 0.340; Figure 3).



**Figure 2.** Categorical analysis of life cycle with respect to the effect of AMF inoculation on photosystem II of host plants under salt stress. Error bars are the mean effect size  $\pm$  95% BS CIs. If the BS CIs did not overlap the zero line, the effect size was considered significant at the 0.05 level. The number of independent observations is presented above the bar. Pn: Photosynthetic rate; Fv/Fm: apparent quantum yield of PS II;  $\phi$ PS II: actual quantum yield of photochemical energy conversion in PS II; q<sub>p</sub>: photochemical quenching coefficient; NPQ: non-photochemical quenching coefficient; ETR: electron transfer rate.



**Figure 3.** Categorical analysis of photosynthetic type with respect to the effect of AMF inoculation on photosystem II of host plants under salt stress. Error bars are the mean effect size  $\pm$  95% BS CIs. If the BS CIs did not overlap the zero line, the effect size was considered significant at the 0.05 level. The number of independent observations is presented above the bar. Pn: Photosynthetic rate; Fv/Fm: apparent quantum yield of PS II;  $\phi$ PS II: actual quantum yield of photochemical energy conversion in PS II; q<sub>p</sub>: photochemical quenching coefficient; NPQ: non-photochemical quenching coefficient; ETR: electron transfer rate.

**Table 2.** The results of categorical analyses based on the significance of the variation among categories ( $Q_B$ ) and the amount of total variation ( $Q_T$ ) described by  $Q_B/Q_T$  under salt stress.

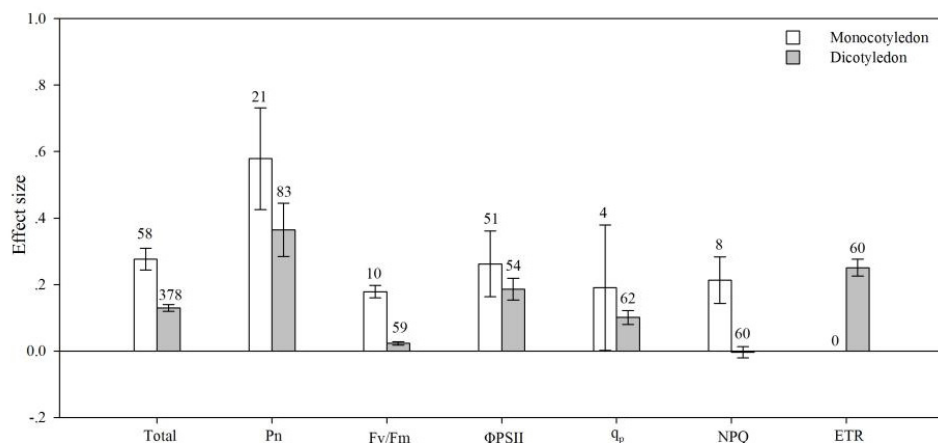
Non-Categorical Predictor Variable	Categorical Predictor Variable	$Q_B$	$Q_T$	$Q_B/Q_T$	$P_{(random)}$
Pn	AMF species	14.692	126.905	0.116	0.429
	plant group	6.558	160.387	0.041	0.068
	life cycle	16.623	149.681	0.111	0.011
	plant type	1.391	163.991	0.008	0.398
	photosynthetic type	21.774	163.697	0.133	0.009
Fv/Fm	soil salinity	0.702	141.474	0.005	0.828
	AMF species	33.038	257.847	0.128	0.232
	plant group	320.848	647.156	0.496	0.001
	life cycle	187.509	535.195	0.350	0.003
	plant type	1.213	257.056	0.005	0.589
$\Phi$ PS II	photosynthetic type	166.424	422.353	0.394	0.001
	soil salinity	54.171	320.944	0.169	0.023
	AMF species	16.530	209.559	0.079	0.406
	plant group	2.432	182.479	0.013	0.369
	life cycle	6.032	182.427	0.033	0.339
qp	plant type	5.485	209.639	0.026	0.158
	photosynthetic type	0.658	201.819	0.003	0.908
	soil salinity	7.365	209.721	0.035	0.267
	AMF species	12.761	368.440	0.035	0.625
	plant group	2.246	309.377	0.007	0.429
NPQ	life cycle	1.731	309.382	0.006	0.578
	pPlant type	2.058	368.368	0.006	0.573
	photosynthetic type	1.967	373.050	0.005	0.852
	soil salinity	213.493	503.059	0.424	0.001
	AMF species	417.222	840.666	0.496	0.001
ETR	plant group	49.912	716.181	0.070	0.051
	life cycle	44.551	715.785	0.062	0.068
	plant type	379.257	837.278	0.453	0.001
	photosynthetic type	210.668	789.315	0.267	0.001
	soil salinity	51.491	741.433	0.069	0.116
ETR	AMF species	35.317	158.558	0.223	0.003
	plant group	-	152.112	-	0.000
	life cycle	5.879	152.183	0.039	0.320
	plant type	25.296	162.155	0.156	0.003
	photosynthetic type	29.543	162.254	0.182	0.006
	soil salinity	11.037	158.732	0.070	0.118

Pn: Photosynthetic rate; Fv/Fm: apparent quantum yield of PS II;  $\Phi$ PS II: actual quantum yield of photochemical energy conversion in PS II; qp: photochemical quenching coefficient; NPQ: non-photochemical quenching coefficient; ETR: electron transfer rate.

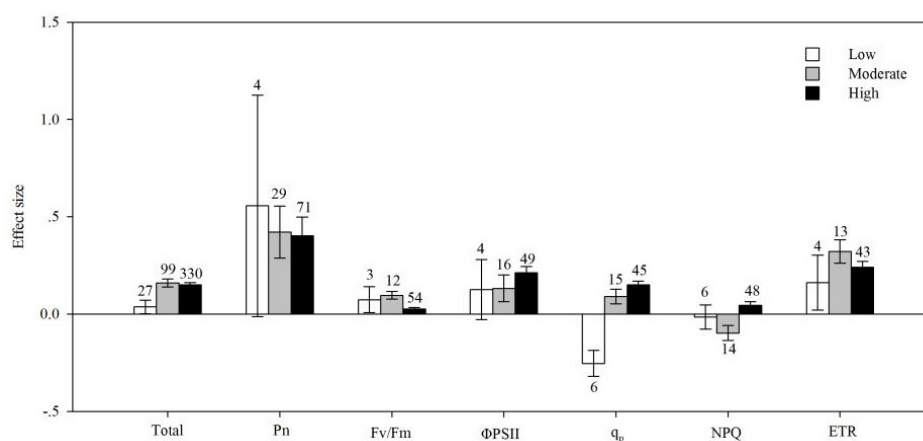
### 3.3. Effects of AMF Inoculation on the Apparent Quantum Yield of Photosystems II (PS II) in Plants

AMF inoculation significantly increased Fv/Fm under salt stress, and significant variations among the studies were observed ( $df = 68$ ; log response ratio = 0.042; 95% CI, 0.033 to 0.050;  $Q_T = 259.403$ ;  $p < 0.05$ ; Figure 1 and Table 1). Categorical analysis showed that the plant group ( $Q_B = 320.848$ ;  $Q_B/Q_T = 0.496$ ;  $p = 0.001$ ), life cycle ( $Q_B = 187.509$ ;  $Q_B/Q_T = 0.350$ ;  $p = 0.003$ ), photosynthetic type ( $Q_B = 166.424$ ;  $Q_B/Q_T = 0.394$ ;  $p = 0.001$ ), and soil salinity level ( $Q_B = 54.171$ ;  $Q_B/Q_T = 0.169$ ;  $p = 0.023$ ) significantly affected the Fv/Fm in AMF-inoculated plants under salt stress (Table 2). The Fv/Fm value in monocotyledon plants ( $n = 91$ ; log response ratio = 0.179) was significantly higher than that in dicotyledon plants ( $n = 59$ ; log response ratio = 0.023; Figure 4). When compared with respect to each life-cycle type, the Fv/Fm of annual/perennial plants ( $n = 4$ ; log response ratio = 0.166) was significantly higher than those of annual ( $n = 14$ ; log response ratio = 0.117) and perennial plants ( $n = 51$ ; log response ratio = 0.022; Figure 2). The response of the Fv/Fm in C4 plants to AMF inoculation ( $n = 10$ ; log response ratio = 0.135) was greater than those in C3 ( $n = 31$ ; log response ratio = 0.041) and CAM plants ( $n = 28$ ; log response ratio = 0.017). The Fv/Fm value of AMF-inoculated plants in moderate salinity ( $n = 12$ ; log response ratio = 0.094) was significantly greater than those of AMF-inoculated plants in low ( $n = 3$ , log response ratio = 0.074) and high salinity ( $n = 12$ , log response ratio = 0.025, Figure 5).





**Figure 4.** Categorical analysis of plant group with respect to the effect of AMF inoculation on photosystem II of host plants under salt stress. Error bars are the mean effect size  $\pm$  95% BS CIs. If the BS CIs did not overlap the zero line, the effect size was considered significant at the 0.05 level. The number of independent observations is presented above the bar. Pn: Photosynthetic rate; Fv/Fm: apparent quantum yield of PS II;  $\phi$ PS II: actual quantum yield of photochemical energy conversion in PS II; qp: photochemical quenching coefficient; NPQ: non-photochemical quenching coefficient; ETR: electron transfer rate;



**Figure 5.** Categorical analysis of soil salinity with respect to the effect of AMF inoculation on photosystem II of host plants under salt stress. Error bars are the mean effect size  $\pm$  95% BS CIs. If the BS CIs did not overlap the zero line, the effect size was considered significant at the 0.05 level. The number of independent observations is presented above the bar. Pn: Photosynthetic rate; Fv/Fm: apparent quantum yield of PS II;  $\phi$ PS II: actual quantum yield of photochemical energy conversion in PS II; qp: photochemical quenching coefficient; NPQ: non-photochemical quenching coefficient; ETR: electron transfer rate.

### 3.4. Effects of AMF Inoculation on the Actual Quantum Yield of Photochemical Energy Conversion in PS II

Enhanced  $\phi$ PS II was found in AMF-inoculated plants under salt stress in all the studies but showing significant variation ( $df = 68$ ; log response ratio = 0.192; 95% CI, 0.165 to 0.223;  $Q_T = 182.492$ ;  $p < 0.05$ ; Figure 1 and Table 1). However, no significant variation was found among the groups, indicating inconsistencies in the  $\phi$ PS II values of AMF-inoculated plants under salt stress (Table 2).

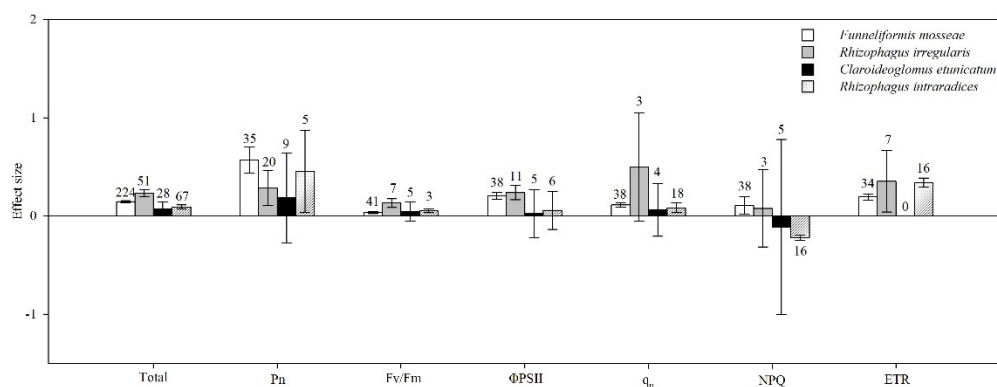
### 3.5. Effects of AMF Inoculation on the Photochemical Quenching Coefficient in Plants

Enhanced  $q_p$  values were found in AMF-inoculated plants under salt stress, with significant variation among the studies ( $df = 65$ ; log response ratio = 0.104; 95% CI, 0.083 to 0.124;  $Q_T = 309.468$ ;  $p < 0.05$ ; Figure 1 and Table 1). Categorical analysis of  $q_p$  showed significant differences with regard to

soil salinity level ( $Q_B = 213.493$ ;  $Q_B/Q_T = 0.424$ ;  $p = 0.001$ ; Figure 5, Table 2). The plants under high salinity had a higher positive effect size with AMF inoculation ( $n = 45$ ; log response ratio = 0.151) than did those under moderate salinity ( $n = 15$ ; log response ratio = 0.090). In addition, we found that the effect size under low salinity was negative with AMF inoculation ( $n = 6$ ; log response ratio = 0.254).

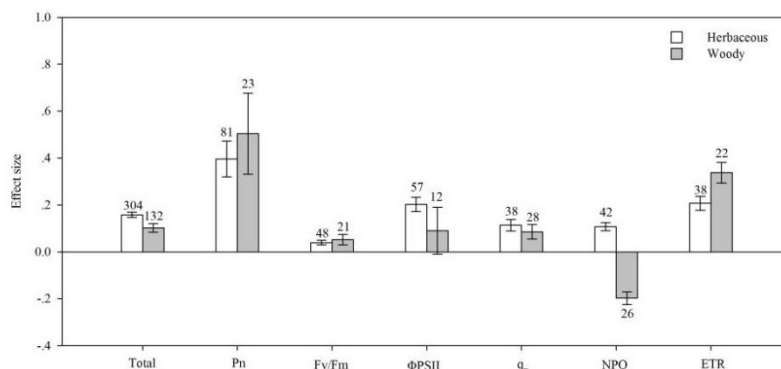
### 3.6. Effects of AMF Inoculation on the Non-Photochemical Quenching Coefficient in Plants

AMF inoculation increased the NPQ under salt stress, but the 95% CI ( $-0.004$  to  $0.027$ ) contained zero. Hence, the effect size was not significant ( $df = 67$ ; log response ratio = 0.012;  $p < 0.05$ ; Figure 1 and Table 1). However, categorical analysis of NPQ showed significant differences between AMF species ( $Q_B = 417.222$ ;  $Q_B/Q_T = 0.496$ ;  $p = 0.001$ ; Figure 6, Table 2). *Funneliformis mosseae* induced a significant enhancement of NPQ in plants under salt stress ( $n = 38$ ; log response ratio = 0.108), while the opposite result was found in *Rhizophagus intraradices* inoculation ( $n = 16$ ; log response ratio =  $-0.221$ ). When compared across each plant group, AMF inoculation only increased the NPQ in monocotyledon plants under salt stress ( $n = 8$ ; log response ratio = 0.213). Significant variations were found among plant types ( $Q_B = 379.257$ ;  $Q_B/Q_T = 0.453$ ;  $p = 0.001$ ; Figure 7, Table 2). AMF induced a significant enhancement in the NPQ in herbaceous plants ( $n = 42$ ; log response ratio = 0.107) and decreased the NPQ in woody plants ( $n = 26$ ; log response ratio =  $-0.198$ ). Categorical analysis with respect to the photosynthetic type also showed significant differences ( $Q_B = 210.668$ ;  $Q_B/Q_T = 0.267$ ;  $p = 0.001$ ; Table 2). AMF inoculation decreased the NPQ in C4 plants ( $n = 20$ ; log response ratio =  $-0.134$ ) and increased that in CAM plants ( $n = 28$ ; log response ratio = 0.096; Figure 3).



**Figure 6.** Categorical analysis of AMF species with respect to the effect of AMF inoculation on photosystem II of host plants under salt stress. Error bars are the mean effect size  $\pm$  95% BS CIs. If the BS CIs did not overlap the zero line, the effect size was considered significant at the 0.05 level. The number of independent observations is presented above the bar. Pn: Photosynthetic rate; Fv/Fm: apparent quantum yield of PS II;  $\phi$ PS II: actual quantum yield of photochemical energy conversion in PS II; qp: photochemical quenching coefficient; NPQ: non-photochemical quenching coefficient; ETR: electron transfer rate.





**Figure 7.** Categorical analysis of plant type with respect to the effect of AMF inoculation on photosystem II of host plants under salt stress. Error bars are the mean effect size  $\pm$  95% BS CIs. If the BS CIs did not overlap the zero line, the effect size was considered significant at the 0.05 level. The number of independent observations is presented above the bar. Pn: Photosynthetic rate; Fv/Fm: apparent quantum yield of PS II;  $\phi$ PS II: actual quantum yield of photochemical energy conversion in PS II; qp: photochemical quenching coefficient; NPQ: non-photochemical quenching coefficient; ETR: electron transfer rate.

### 3.7. Effects of AMF Inoculation on the Electron Transfer Rate in Plants

AMF inoculation significantly increased the ETR under salt stress, and significant variations among the studies were observed ( $p < 0.05$ ; Figure 1 and Table 1). Categorical analysis showed that AMF species ( $Q_B = 35.317$ ;  $Q_B/Q_T = 0.223$ ;  $p = 0.003$ ), plant family ( $Q_B = 36.618$ ;  $Q_B/Q_T = 0.231$ ;  $p = 0.009$ ), plant type ( $Q_B = 25.296$ ;  $Q_B/Q_T = 0.156$ ;  $p = 0.003$ ), and photosynthetic type ( $Q_B = 29.543$ ;  $Q_B/Q_T = 0.182$ ;  $p = 0.006$ ) significantly affected the ETR in AMF-inoculated plants under salt stress (Table 2). Plants inoculated with *Rhizophagus irregularis* showed the highest ETR values under salt stress ( $n = 7$ ; log response ratio = 0.353), followed by *Rhizophagus intraradices* ( $n = 16$ ; log response ratio = 0.341) and *Funneliformis mosseae* ( $n = 34$ ; log response ratio = 0.194, Figure 6). Among the plant types, the response of the ETR to AMF inoculation in woody plants ( $n = 22$ ; log response ratio = 0.338) was greater than that in herbaceous plants ( $n = 38$ ; log response ratio = 0.207; Figure 7). The ETR response to AMF inoculation in C4 plants ( $n = 16$ ; log response ratio = 0.341) was greater than those in C3 ( $n = 16$ ; log response ratio = 0.286) and CAM plants ( $n = 28$ ; log response ratio = 0.192; Figure 3).

## 4. Discussion

Meta-analysis is an effective way to merge data from independent studies, which can be used to estimate the effect sizes and find potentially contributing variations across similar studies [26]. Previous studies have used meta-analysis to unveil the effects of AMF inoculation on host plants under salt stress, including AMF's ability to increase P and K assimilation, antioxidant enzyme activities, gas exchange, and ionic adjustment by changing the root and mycorrhizal morphological traits [19–21]. In the present meta-analysis study, we provided sufficient evidence to confirm that AMF inoculation has a significant impact on the performance of PSII in host plants under salt stress.

### 4.1. Total Effects

It is widely accepted that AMF-inoculated plants exhibit better photosynthesis performance under salt stress, and the host plants have a higher photosynthetic rate than do non-inoculated plants [27,28]. In the present study, we confirmed that AMF inoculation has a positive total impact on the photosynthetic rate of a host plant under salt stress, as found by independent published works (Figure 1). Chlorophyll fluorescence is a rapid, non-destructive method to determine changes in photosystem II and is used in many fields [29]. The Fv/Fm value can reflect the photo-inhibition level of PS II by estimating the maximum quantum yield of primary acceptor (QA) reduction [12]. A positive total impact on the Fv/Fm values of host plants under salt stress was confirmed in the present

study, showing that AMF inoculation could alleviate photo-damage to PS II caused by stress [13]. The  $\phi$ PS II value reflects the utilization of photons absorbed by PS II antennae and is estimated from the quantum efficiency of photochemical energy dissipation [30]. Photochemical quenching ( $q_p$ ) is used to assess PS II susceptibility to photo-inhibition and reflects the oxidation reduction state of the primary acceptor (QA) for PS II [1]. In the present meta-analysis research, we were also able to confirm that AMF inoculation has a positive total impact on the  $\phi$ PS II and  $q_p$  values of host plants under salt stress, indicating that AMF inoculation can improve the utilization of photons and reduce PS II susceptibility to photo-inhibition. A previous study reported that an increase in NPQ is thought to be an energy dissipation mechanism that protects the photosynthetic apparatus against excess light under salt stress [31]. Many studies reported an observed increase in NPQ in AMF-inoculated plants under salt stress [12,14]. These results indicate that AMF inoculation could improve the energy dissipation ability of a plant, which protects the photosynthetic apparatus against excess light under salt stress [15,32]. Unlike these studies, we did not find a significant total impact on the NPQ of host plants under salt stress in this meta-analysis. However, subgroup analysis revealed different changes relative to the categorical predictor variables (AMF species, plant group, plant family, plant type, and photosynthetic type). We will discuss this part in the following sections. Salt stress not only directly leads to photosynthetic machinery injury but also affects photosynthetic electron transport [33]. In this study, we confirmed that AMF inoculation has a positive total impact on the ETR of host plants under salt stress, showing that AMF inoculation can alleviate the inhibition of photosynthetic electron transport caused by salt stress.

#### 4.2. Life Cycle

Subgroup analysis showed that the annual and annual/perennial species had a higher total increased response to AMF inoculation in terms of photosynthesis performance than did perennial species under salt stress. Moreover, the photosynthetic rate and Fv/Fm value examined by life cycle type showed significant variation, and the mediated effects of AMF on the photosynthetic rate and Fv/Fm of annual species were higher than those for perennial plants under salt stress. In addition, the effect size of Fv/Fm in annual/perennial species was also higher than that in perennial species. However, it should be noted that these are results from a small sample (Table 2 and Figure 2). These results indicate that annual host plant species had better photosynthesis performance and a lower PS II photo-inhibition level under salt stress after AMF inoculation. Previous studies have shown that annual species are characterized by root traits maximizing belowground resource acquisition, while perennials are characterized by root traits associated with resource conservation and root persistence. Under salt stress, AMF colonization is always reduced or inhibited, and the annual species with high specific root length and rapid nutrient acquisition might thus show a stronger advantage than perennial species [34,35]. This could explain why AMF inoculation has a higher effect size on the photosynthetic rate in annual host plant species.

#### 4.3. Photosynthetic Type

Based on our subgroup analysis data, the Pn,  $\phi$ PS II, ETR, and NPQ values showed significant variations by photosynthetic type, and the mediated effects of AMF on Pn,  $\phi$ PS II, and ETR in C4 species were higher than those in C3 and CAM species under salt stress. In addition, we also found that AMF inoculation decreased the NPQ in C4 species and increased the NPQ in CAM species but did not induce changes in C3 species (Table 2 and Figure 3). A previous study reported that a decreased NPQ value indicates a reduction in heat dissipation ability, which is caused by chloroplast damage [31]. Unlike in this previous study, the NPQ in C4 species decreased after AMF inoculation due to the increased utilization of photons and reduced PS II susceptibility to photo-inhibition under salt stress (combined with the enhancement of Pn,  $\phi$ PS II, and ETR). Many studies have reported that AMF inoculation could reduce stomatal limitations in salt-stressed leaves by alleviating the osmotic stress and ionic imbalance caused by salt stress [16,36]. However, the stomatal limitations could be alleviated,

but not eliminated. The operation of a CO<sub>2</sub>-concentrating mechanism in C4 species could maintain higher photosynthetic capacity than C3 species under this condition [37]. The higher photosynthetic performance in C4 species than in C3 species after AMF inoculation and under salt stress can be explained in this way.

#### 4.4. Plant Group

The subgroup analysis showed that monocotyledon species had a higher total increased response to AMF inoculation in terms of photosynthesis performance than did dicotyledon species under salt stress. Moreover, the mediated effects of AMF on the Fv/Fm values of monocotyledon species were higher than those for dicotyledon species under salt stress, indicating that monocotyledon host plant species had lower photo-inhibition levels of PS II under salt stress after AMF inoculation (Table 2 and Figure 4). Rahim et al. reported that monocotyledon host plant species usually have a fibrous root system, which can provide a better association with mycorrhiza than dicotyledon species with a tap root system [38]. In addition, dicotyledonous plants have stronger mycorrhizal dependence than monocotyledon plants. When the growth of AM is inhibited under salt stress, the efficiency of mycorrhizal symbiosis with dicotyledon host plants is lower than that with monocotyledon host plant species [39]. This may be the reason why the photosynthesis response to AMF inoculation in monocotyledon host plant species was higher than that in dicotyledonous host plant species under salt stress.

#### 4.5. Plant Type

Subgroup analysis revealed that the NPQ and ETR showed significant variations by plant type, and the positive mediated effect of AMF on the ETR of woody species was higher than that for herbaceous plants under salt stress. In addition, we also found that AMF inoculation decreased the NPQ in woody species and increased the NPQ in herbaceous species (Table 2 and Figure 7). The result showed that woody host plant species gained higher energy utilization by enhancing the electron transfer rate to reduce energy dissipation as heat under salt stress after AMF inoculation. Tang et al. reported that woody plant species have higher photosynthetic capacity than herbaceous species due to their higher electron transfer ability and Rubisco carboxylation [40]. When AMF inoculation alleviated the limitations imposed by salt stress, the better photosynthesis characteristics of woody species than herbaceous species resulted in a better photosynthetic capacity.

#### 4.6. Soil Salinity

Based on our subgroup analysis data, the total mediated effects of AMF under moderate and high salinity levels were higher than that under low salinity. In addition, the mediated effect of AMF on Fv/Fm under moderate salinity was higher than that under higher salinity (Table 2 and Figure 5). In general, the soil salinity affects not only the host plant but also the AMF. A previous study reported that the colonization rate declines with increasing salinity, indicating that salinity suppresses the symbiotic effect of AMF [4]. In addition, high salinity also causes an ion imbalance in the host plant and finally disrupts normal cellular functions in the host plant. These can explain why high salinity decreased the positive effect of AMF inoculation on the photo-inhibition level of PS II. In addition, we also found that AMF inoculation had a negative effect on  $q_p$  under low salinity, unlike under moderate and high-salinity levels. There were only six observations for  $q_p$  in low salinity, and the sample size was also very low. Hence, the results need to be explored in further research.

#### 4.7. AMF Species

From the subgroup analysis, the ranking of the four most studied AMF species in terms of the total improvement in photosynthesis performance is *Rhizophagus irregularis* > *Funneliformis mosseae* > *Rhizophagus intraradices* > *Claroideoglossum etunicatum*. *Funneliformis mosseae* is an AMF species commonly used in studies under salt stress, and *Rhizophagus irregularis* is the most efficient species

in terms of the enhancement of photosynthesis performance under salt stress (Table 2 and Figure 6). These results are consistent with previous studies on the efficiency of AMF inoculation under salt stress [41,42]. Different AMF species differ in their capacity to acquire and deliver nutrients and carbon to host plants [43]. Under salt stress, *Rhizophagus irregularis* has higher capacity to provide nutrients to host plants than other AMF species, which could alleviate the decrease in photosynthetic capacity caused by nutrient deficiency. In addition, the results of the present meta-analysis show that most studies focused on the effect of a sample AMF on photosynthesis performance under salt stress but neglected the combined effect of a consortium of AMF species. Regarding functional complementarity, there may be a greater capacity for resource exploitation with a consortium of AMF species, and this should be investigated in future study.

## 5. Conclusions

The results from the present meta-analysis provide sufficient evidence of the positive effect of arbuscular mycorrhizae on the performance of PS II in host plants under salt stress. AMF inoculation alleviates the detrimental effects of salinity on photosystem II of a host plant by improving the utilization of photons and photosynthetic electron transport and reducing PS II susceptibility to photo-inhibition. Among the AMF species, *Rhizophagus irregularis* was found to be the most efficient species in terms of photosynthesis performance enhancement under salt stress. High salinity decreased the positive effect of AMF inoculation on PS II. After AMF inoculation and under salt stress, the C4 species had better photosynthesis performance when compared to C3 species. In addition, the mediated effects of AMF on photosystem II in annual, monocotyledon, and woody species under salt stress were much higher than those for other plant life cycles, groups, and types. Therefore, choosing the appropriate host plant and AMF species is important for using plant–AMF symbionts to improve salt-affected soil in practical applications.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/2073-4395/9/12/806/s1>: Figure S1 A funnel plot of total effect sizes of AMF inoculation on photosystem II of host plants under salt stress. Table S1 A list of references included in the meta-analysis. Table S2 Raw data in Excel format used in the meta-analysis.

**Author Contributions:** Wrote the manuscript, Y.W.; collect the references and analyzed the data, J.W.; give many good suggestions on this manuscript during revision process, X.Y.; make some figures in this manuscript, S.S.; designed and revised the manuscript, J.L.

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