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The Growth Promotion of Two Salt-Tolerant Plant Groups with PGPR Inoculation: A Meta-Analysis

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Abstract: Understanding the primary mechanisms for plant promotion under salt stress with plant growth promoting rhizobacteria (PGPR) inoculation of different salt-tolerant plant groups would be conducive to using PGPR efficiently. We conducted a meta-analysis to evaluate plant growth promotion and uncover its underlying mechanisms in salt-sensitive plants (SSP) and salt-tolerant plants (STP) with PGPR inoculation under salt stress. PGPR inoculation decreased proline, sodium ion (Na^+) and malondialdehyde but increased plant biomass, nutrient acquisition (nitrogen, phosphorus, potassium ion (K^+), calcium ion (Ca^{2+}), and magnesium ion (Mg^{2+})), ion homeostasis (K^+/Na^+ ratio, Ca^{2+}/Na^+ ratio, and Mg^{2+}/Na^+ ratio), osmolytes accumulation (soluble sugar and soluble protein), antioxidants (superoxide dismutase), and photosynthesis (chlorophyll, carotenoid, and photosynthetic rate) in both SSP and STP. The effect size of total biomass positively correlated with the effect sizes of nutrient acquisition and the homeostasis of K^+/Na^+, and negatively correlated with the effect size of malondialdehyde in both SSP and STP. The effect size of total biomass also positively correlated with the effect sizes of carotenoid and the homeostasis in Ca^{2+}/Na^+ and Mg^{2+}/Na^+ and negatively correlated with the effect size of Na^+ in SSP, but it only negatively correlated with the effect size of Ca^{2+} in STP. Our results suggest that the plant growth improvement depends on the nutrient acquisition enhancement in both SSP and STP, while ion homeostasis plays an important role and carotenoid may promote plant growth through protecting photosynthesis, reducing oxidative damage and promoting nutrient acquisition only in SSP after PGPR inoculation under salt stress.

Keywords: plant growth promoting rhizobacteria; saline stress; ionic homeostasis; osmoregulation; antioxidant system; photosynthetic capacity; meta-analysis

1. Introduction

Soil salinity severely challenges plant growth on more than 6% of land globally [1]. Salinization marginalizes arable land and could lead to the abandonment of one-third of irrigated land worldwide [2–4]. By 2050, soil salinization will threaten more than 50% of arable land owing to climate change, irrational irrigation practices, wrong fertilizer application, and poor drainage systems [5–8]. Soil salinity inhibits plant productivity via direct or indirect adverse effects. For instance, the salt-induced osmotic stress on the root surface can result in physiological drought via regulating the production of plant hormones and hindering water acquisition [4,9]; and toxic ionic

stress, such as the accumulation of sodium and chloride ions in cells, can lead to nutrient deficiency and the growth retardance [1,10]. These two direct stresses destroy the dynamic equilibrium of reactive oxygen species (ROS) in cell and indirectly result in plant oxidative stress [11–13]. In addition, soil salinity could limit plant growth indirectly by hampering activities of beneficial microbes residing in the rhizosphere and by decreasing organic matter accumulation [14].

Soil remediations, such as bioremediation, phytoremediation, physical remediation, and chemical remediation, are practiced to address the salinity-induced plant growth retardation [15]. Bioremediation, with plant growth promoting rhizobacteria (PGPR) [16], could provide a sustainable and cost-effective solution [17,18]. PGPR can help plants tolerate salinity by several synergistic mechanisms [19]. The first one is to overcome osmotic stress by inducing osmolyte accumulation and phytohormone signaling [3]. The second one is to alleviate ion stress and nutrient deficiency by achieving ion homeostasis and enhancing nutrient uptake [2]. The third one is to dampen the oxidative stress by increasing the antioxidant capacity and photosynthesis [2,20].

Plant growth response to PGPR inoculation may vary with the experimental conditions and settings [21], PGPR identity and diversity [22,23], plant functional groups [6], etc. Within cultivars, when barley [24,25] and maize [17,26] were inoculated with PGPR, the growth of salt-sensitive cultivars increased more than the salt-tolerant cultivars under saline conditions, while, when rice was inoculated with PGPR, different cultivars exhibited a similar response under salt stress [22]. The inconsistent results of the PGPR inoculation within cultivars suggest an uncertain response of different plant groups to PGPR inoculation.

Halophytes have advantages over glycophytes in salt exclusion and salt compartmentalization [27,28]. PGPR play a crucial role in promoting plant growth in halophytes and glycophytes under salt stress [29–32]. A clear understanding of responses of two salt-tolerant plant groups and the underlying mechanisms would expand the use of PGPR as bioremediation. Thus, our objective was to determine whether salt-sensitive plants (similar to glycophytes) and salt-tolerant plants (similar to halophytes) respond similarly to PGPR inoculation and the mechanisms that regulate their responses.

2. Materials and Methods

2.1. Literature Search and Selection Criteria

We used two approaches to select articles and build a database for this meta-analysis. The first one was to search for relevant articles by keywords in the Web of Science. The keywords used were "PGPR and salt stress/or under salinity stress", "rhizosphere bacteri* and salinity stress/or under salt stress", and "rhizobacteri* and salinity stress/or under salt stress". The Boolean truncation (*) character was used to ensure that word variations (such as bacteria, bacterium, rhizobacteria, and rhizobacterium) were also included in the search. The second one was to search articles in a "retrospective" way from references in review articles. English articles spanning 15 years (from 2003 to 2017) were retrieved subject to the following criteria:

(1) Plants had to be exposed to saline conditions or imposed to salt treatments through irrigation.
(2) A pair-wise experimental design with a control and a PGPR treatment was used.
(3) Only extracellular PGPR taxa were included in this meta-analysis. If articles reported any PGPR interaction with other microbes, such as mycorrhizal fungi or intracellular PGPR, data were exclusively collected for extracellular PGPR to avoid any interactions.
(4) Plants had to be grown in pots, and the growth substrate had to be soil or a mixture of soil and another substrate.

Results from different experiments in one article were considered independent studies and were not a violation of independence in this meta-analysis. For example, responses of the same host plant using different PGPRs under either different or identical salt stress conditions was compared in a

single article, or responses of different host plants using the same PGPR under either different or identical salt stresses were considered as independent results. In total, 561 experimental results were extracted from 102 articles (Files S1 and S2).

2.2. Data Category and Collection

The definition of halophytes is still somewhat blurred [33], and there also exists significant variation in salt tolerance among glycophytes [1,34]. Thus, to better define salt tolerance, the plants included in this meta-analysis were classified into salt-sensitive plants (SSP) and salt-tolerant plants (STP) according to the salt tolerance information in the original publications (File S2). We recorded 21 physiological indicators in this meta-analysis (Table 1). Plant fresh weight or dry weight was the most reported measures of plant biomass. We used dry weight as biomass when it was available and otherwise used fresh weight. When indicators were reported in root and shoot biomass, total biomass was calculated as the sum of them. *Chl* contents were calculated as the sum of *Chl a* and *Chl b* when total *Chl* was not reported. When data were only provided for leaves and not provided for shoots, leaf data were used as a proxy of the shoot.

Table 1. Rank correlation tests for publication bias and fail-safe numbers.

Physiological Indicators (Abbreviation)	Study Numbers (*S*)	Spearman's Rank Order Correlation		Fail-Safe Numbers
		R	P	
Total biomass	399	−0.131	0.008	947,614
Shoot biomass	254	0.018	0.774	481,795
Root biomass	199	−0.01	0.887	287,007
Proline (*Pro*)	164	−0.019	0.813	92,740
Soluble sugar (*SS*)	49	0.111	0.448	13,472
Soluble protein (*SP*)	74	0.031	0.796	29,444
Nitrogen (N)	102	0.088	0.380	12,706
Phosphorus (P)	50	−0.126	0.383	24,152
Potassium ion (K^+)	188	−0.094	0.199	80,527
Calcium ion (Ca^{2+})	101	−0.282	0.004	22,491
Magnesium ion (Mg^{2+})	46	−0.542	0.000	10,050
Sodium ion (Na^+)	187	0.203	0.005	170,335
K^+/Na^+ ratio	182	0.077	0.303	54,041
Ca^{2+}/Na^+ ratio	102	−0.373	0.000	12,049
Mg^{2+}/Na^+ ratio	50	−0.23	0.108	1008
Superoxide dismutase (SOD)	79	−0.047	0.681	22,015
Catalase (CAT)	77	−0.323	0.004	26,831
Malondialdehyde (MDA)	63	−0.266	0.035	89,408
Chlorophyll (*Chl*)	220	0.086	0.203	408,830
Carotenoid (*Car*)	52	0.233	0.097	5913
Photosynthetic rate (*Pn*)	32	0.143	0.436	580

Indicators were often reported in different units. However, we did not consider such unit difference given that response ratios are dimensionless. We had no prior expectation that certain PGPRs would differ from other species. Thus, PGPR species were not grouped into different classes for analysis. In addition, we assumed that authors made appropriate choices of PGPR strains that were likely naturally associated with host plants.

For each study, the meta-analysis database required the mean, standard deviation (SD), and replicate number/sample size (n) for the control as well as the PGPR inoculation treatment under salt stress condition. Only $n \geq 3$ were included in this meta-analysis. In articles where means and errors are presented graphically, the data were extracted from graphs or figures using the WebPlotDigitizer software. If standard errors (SE) were reported, all were transformed to SD according to the equation:

SE =SD ($n^{-1/2}$). If SD was not provided, it was estimated as the mean divided by the square root of the sample size [35].

2.3. Meta-Analysis

Our meta-analysis was conducted in MetaWin software version 2.1 [36], based on a random effects model, and we assumed that there were random variations in PGPR effects on plant growth among the studies [5,37]. The confidence intervals (CIs) were estimated through a bootstrap procedure that performed bias-correction using 4999 iterations (designated as 95% CI) [38]. We used effect size as a metric for the response of PGPR inoculation in plants under salt stress conditions. Effect size was calculated as the natural log of the response ratio (lnR) using Formula (1) [5,37]:

$$\ln R = \ln\left(\frac{\overline{X}_T}{\overline{X}_c}\right) = \ln\left(\overline{X}_T\right) - \ln\left(\overline{X}_C\right), \quad (1)$$

where R is the response ratio, and X_T and X_C are the means of indicators in PGPR inoculation treatments and the control, respectively. Variance estimations for each study are represented as V, using the following formula in their calculation [37]:

$$V = \frac{(S_T)^2}{N_T\left(\overline{X}_T\right)^2} + \frac{(S_C)^2}{N_C\left(\overline{X}_C\right)^2} \quad (2)$$

where S_T and S_C are the standard deviations of indicators in the PGPR treatment and the control, respectively. N_T and N_C are the replication numbers. If 95% CIs did not overlap the zero-line, inoculation effects were considered significant. Zero effect size means there is no difference between the experimental and control groups [39]. Positive value indicates an increase in indicators inoculated with PGPR and negative value indicates a decrease in indicators inoculated with PGPR. Significant differences between SSP and STP were tested by examining the $P_{between}$ and $Q_{between}$ statistics [40].

Generally, journals tend to publish studies with statistically significant information, which will lead to an overestimation of results and cause publication bias [36]. There is also a potential bias in our study because we used the n to estimate variance in comparisons, which can cause an overestimation of within-study variance [35]. For the reasons mentioned above, we tested for potential publication bias by conducting Spearman's rank correlation analysis and calculating Rosenthal's fail-safe number. The Spearman's rank correlation test was used to search for the relationships between the standardized effect size and sample size [36]. If they did not show correlation, metadata have no publication bias [40]. Otherwise, we needed to calculate Rosenthal's fail-safe number further to quantify the potential bias. If Rosenthal's fail-safe number was considerably greater than $5S + 10$ (where S is the study numbers of indicators), it meant that the existing publication bias would not negate the reported effect size [35,40].

2.4. Linear Regression Analyses

PGPR can facilitate the growth of many plants, but there are many indicators that directly or indirectly modify the growth response to PGPR inoculation. Linear regression models were used to test relationships between the effect size of total biomass and the effect sizes of osmotic balance indicators (*Pro*, *SS*, and *SP*), nutrient uptake and ion homeostasis indicators (N, P, K^+, Ca^{2+}, Mg^{2+}, Na^+, K^+/Na^+ ratio, Ca^{2+}/Na^+ ratio, and Mg^{2+}/Na^+ ratio), antioxidant indicators (SOD, CAT, and MDA), and photosynthetic indicators (*Chl*, *Car*, and *Pn*) in both SSP and STP, respectively. All linear regression analyses were conducted using SPSS software 17.0.

3. Results

3.1. PGPR Inoculation Effects on Plant Biomass

PGPR inoculation significantly increased total, shoot and root biomass across studies (Figure 1). Although the trends of inoculation about the biomass were consistent in both SSP and STP, the effect sizes of total biomass and shoot biomass were significantly higher in SSP than that in STP (Figure 2a,b).

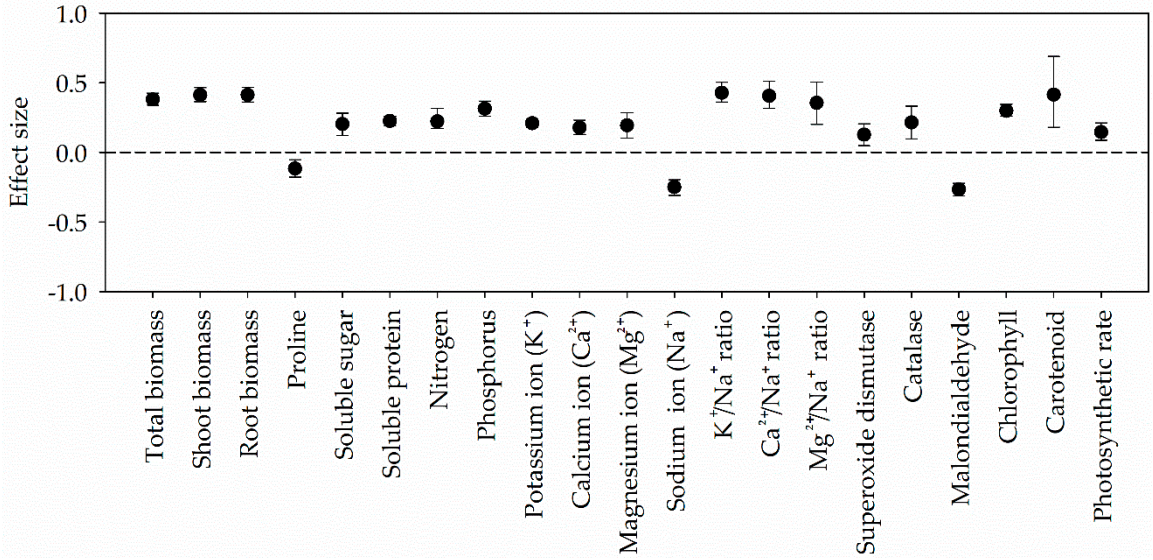

Figure 1. Responses of PGPR-inoculated plants to salt stress. Error bars represent 95% confidence intervals (CIs). The inoculation effects were considered significant if the 95% CIs did not overlap the zero line.

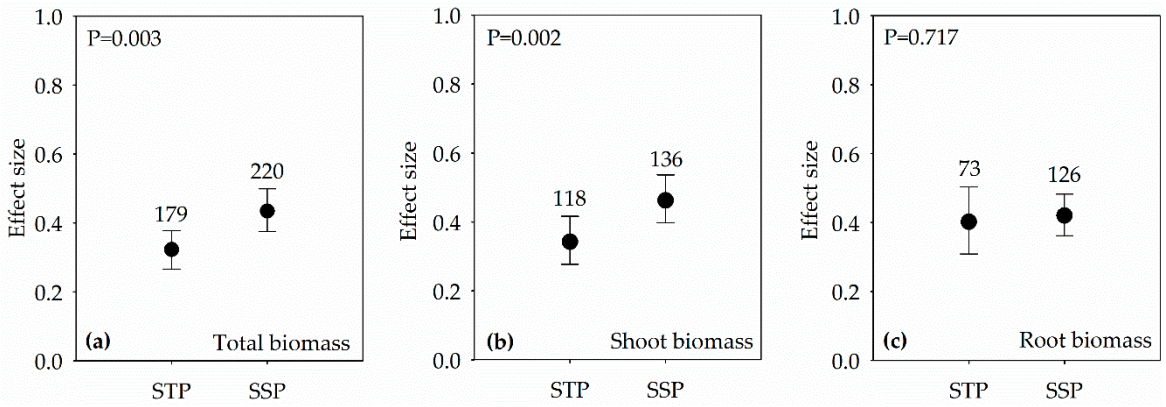

Figure 2. Effect sizes of PGPR in both salt-sensitive plants (SSP) and salt-tolerant plants (STP) under salt stress condition on: total biomass (**a**); shoot biomass (**b**); and root biomass (**c**). Error bars represent 95% confidence intervals (CIs). The inoculation effects were considered significant if the 95% CIs did not overlap the zero line. The numbers of studies are shown above the error bars. *p* values show the significant differences between SSP and STP.

3.2. PGPR Inoculation Effects on Osmolytes

Effect sizes of *Pro* accumulation were significantly negative for SSP and STP, and it had no difference between the two groups (Figure 3a). *SS* and *SP* accumulation were positively stimulated after PGPR inoculation in the STP, while they had no change in the SSP as the 95% CI overlapped zero (Figure 3b,c).

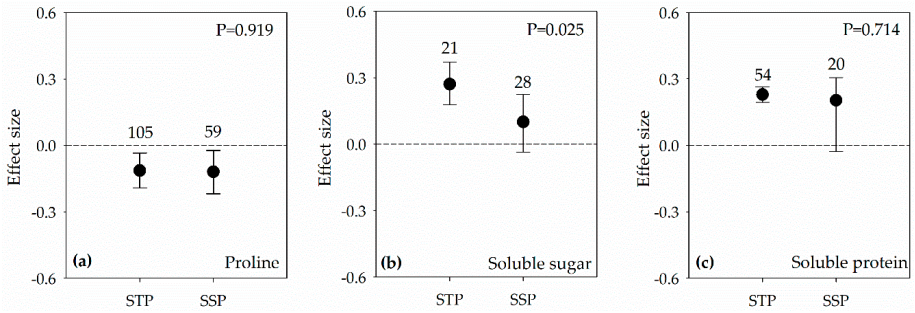

Figure 3. Effect sizes in both salt-sensitive plants (SSP) and salt-tolerant plants (STP) under salt stress condition of PGPR on: proline (**a**); soluble sugar (**b**); and soluble protein (**c**). Error bars represent 95% confidence intervals (CIs). The inoculation effects were considered significant if the 95% CIs did not overlap the zero line. The numbers of studies are shown above the error bars. *p* values show the significant differences between SSP and STP.

3.3. PGPR Inoculation Effects on Plant Nutrient Uptake and Ion Homeostasis

PGPR inoculation significantly increased N uptake, P uptake, K^+ uptake, Ca^{2+} uptake, Mg^{2+} uptake, K^+/Na^+ ratio, Ca^{2+}/Na^+ ratio, and Mg^{2+}/Na^+ ratio, while decreased Na^+ uptake across all studies (Figure 1). The effect sizes of these indicators had no difference between SSP and STP (Figure 4).

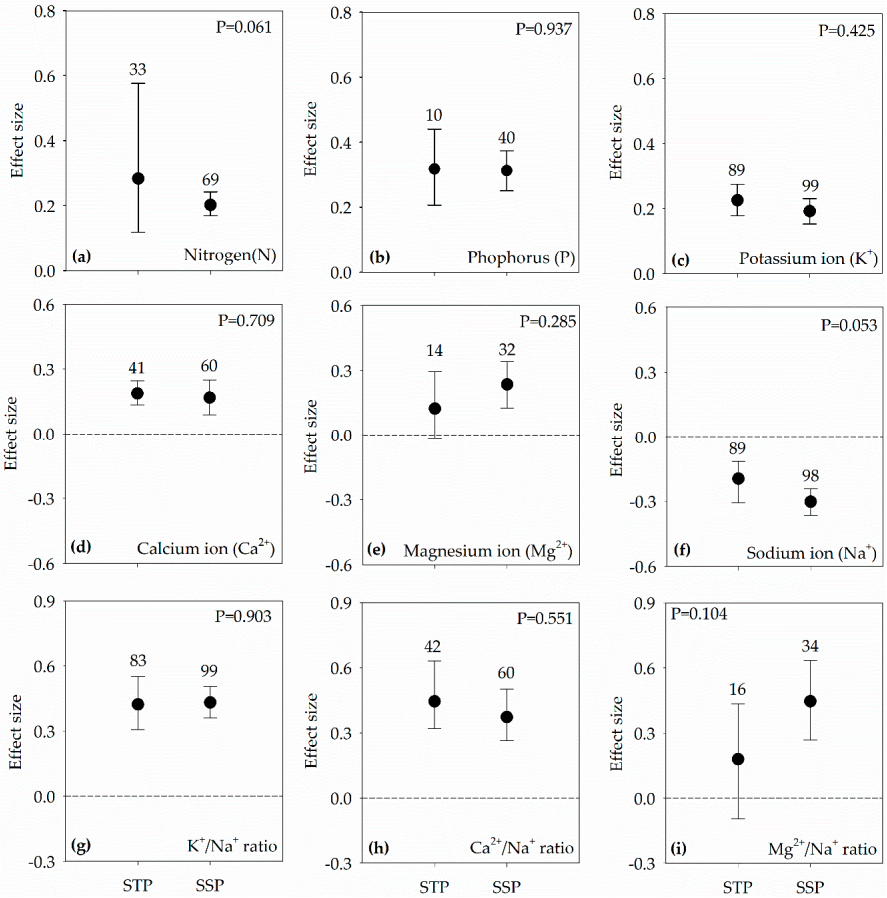

Figure 4. Effect sizes in both salt-sensitive plants (SSP) and salt-tolerant plants (STP) under salt stress condition of PGPR on: nitrogen (**a**); phosphorus (**b**); potassium ion (**c**); calcium ion (**d**); magnesium (**e**); sodium ion (**f**); K^+/Na^+ ratio (**g**); Ca^{2+}/Na^+ ratio (**h**); and Mg^{2+}/Na^+ ratio (**i**). Error bars represent 95% confidence intervals (CIs). The inoculation effects were considered significant if the 95% CIs did not overlap the zero line. The numbers of studies are shown above the error bars. *p* values show the significant differences between SSP and STP.

3.4. PGPR Inoculation Effects on Antioxidants, MDA and Photosynthesis

Although 95% CI overlapped zero in SSP, effect sizes of SOD activities increased in both SSP and STP, respectively (Figure 5a). The effect sizes of CAT activities were significantly different between the two groups, which decreased in STP but markedly increased in SSP (Figure 5b). Contrary to SOD and CAT, the effect sizes of MDA contents markedly decreased in both SSP and STP (Figure 5c). The effect sizes of *Chl*, *Car* and *Pn* were all positive, and they had no difference in the two groups (Figure 5d–f).

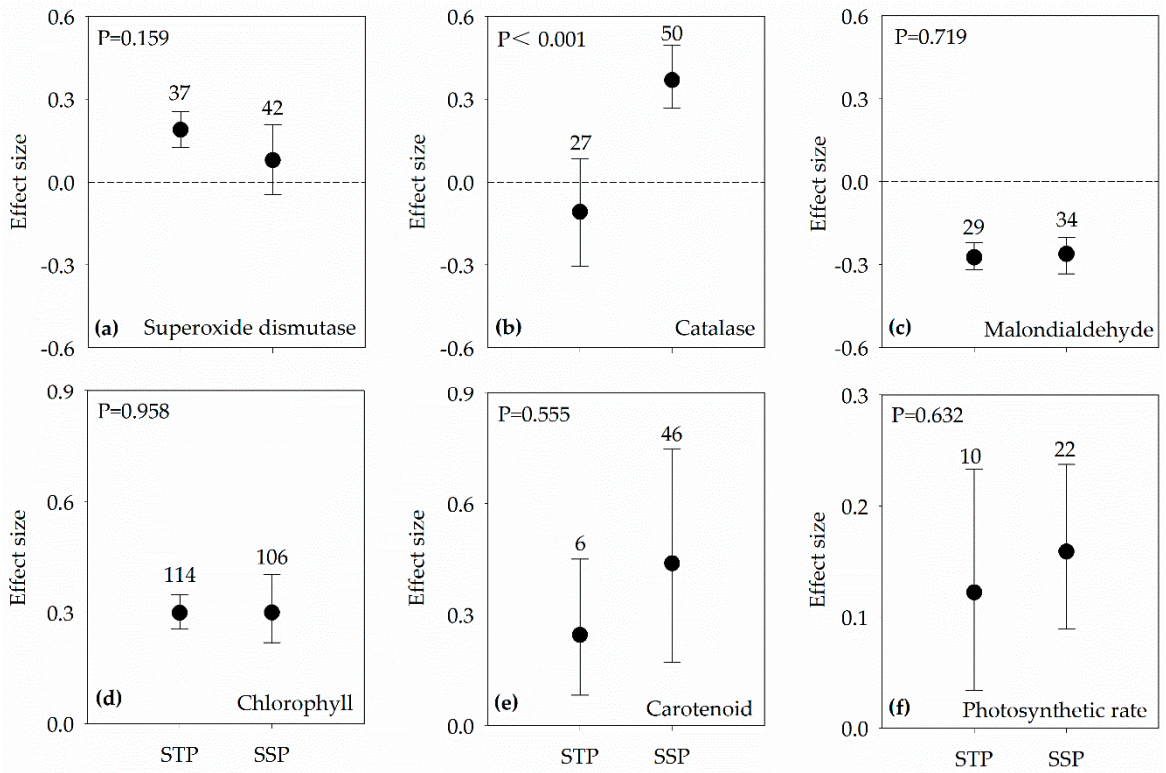

Figure 5. Effect sizes in both salt-sensitive plants (SSP) and salt-tolerant plants (STP) under salt stress condition of PGPR on: superoxide dismutase (**a**); catalase (**b**); malondialdehyde (**c**); chlorophyll (**d**); carotenoid (**e**); and photosynthetic rate (**f**). Error bars represent 95% confidence intervals (CIs). The inoculation effects were considered significant if the 95% CIs did not overlap the zero line. The numbers of studies are shown above the error bars. *p* values show the significant differences between SSP and STP.

3.5. Contributions of the Physiological Indicators to Biomass Promotion between SSP and STP

The effect size of total biomass correlated positively with that of *Pro*, N, P, K^+, and K^+/Na^+ ratio, while it had a significant negative correlation with that of MDA in both SSP and STP (Figure 6). The effect size of total biomass in SSP also positively correlated with that of Ca^{2+}, Ca^{2+}/Na^+ ratio, Mg^{2+}/Na^+ ratio, and *Car* and negatively correlated with that of Na^+. However, the effect size of total biomass in STP only negatively correlated with the effect size of Ca^{2+} (Figure 6).

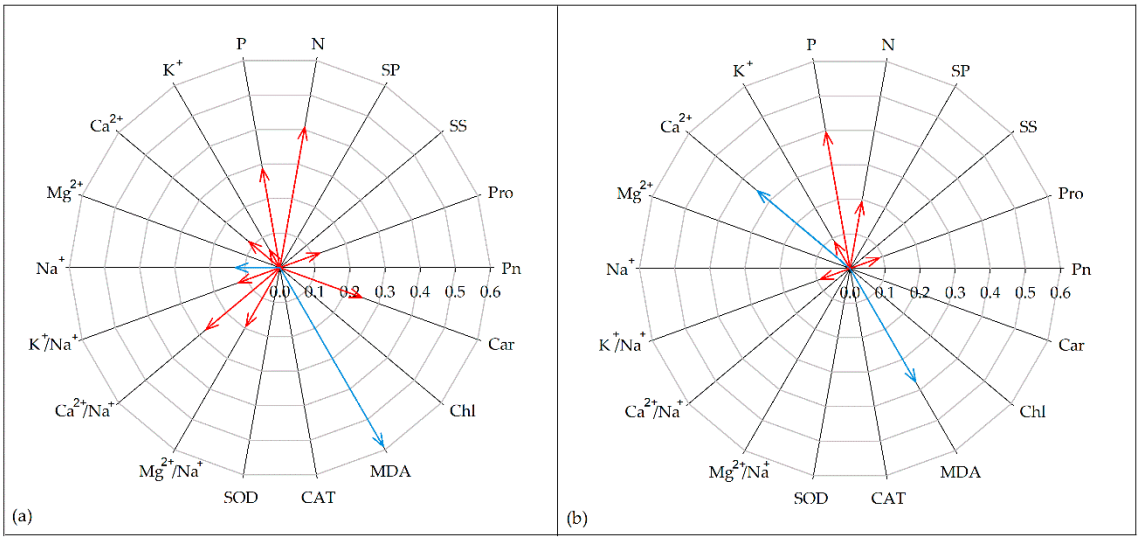

Figure 6. Relationships between the effect sizes of total biomass and the effect sizes of proline (*Pro*), soluble sugar (*SS*), soluble protein (*SP*), nitrogen (N), phosphorus (P), potassium ion (K^+), calcium ion (Ca^{2+}), magnesium ion (Mg^{2+}), sodium ion (Na^+), K^+/Na^+ ratio ($K^+/Na^{+)}$, Ca^{2+}/Na^+ ratio ($Ca^{2+}/Na^{+)}$, Mg^{2+}/Na^+ ratio (Mg^{2+}/Na^+), superoxide dismutase (SOD), catalase (CAT), malondialdehyde (MDA), chlorophyll (*Chl*), carotenoid (*Car*), and photosynthetic rate (*Pn*) under salt stress conditions for: salt-sensitive plants (**a**); and salt-tolerant plants (**b**). The significance of the relationships between the effect size of total biomass and other indicators is presented with an arrow. The length of the arrow indicates the size of R^2. Red arrows indicate positive relationships and blue arrows indicate negative relationships.

4. Discussion

4.1. Publication Bias Test

We examined the publication bias for the dataset of 21 indicators. The results of Spearman's rank correlation analysis showed that no significant correlation between effect size and sample size for most indicators except the total biomass (Spearman's $r = 0.131$, $p = 0.008$), Ca^{2+} (Spearman's $r = -0.282$, $p = 0.004$), Mg^{2+} (Spearman's $r = -0.542$, $p < 0.001$), Na^+ (Spearman's $r = 0.203$, $p = 0.005$), Ca^{2+}/Na^+ ratio (Spearman's $r = -0.373$, $p < 0.001$), CAT (Spearman's $r = -0.323$, $p = 0.004$), and MDA (Spearman's $r = -0.266$, $p = 0.035$). Statistics suggested that large effect size were more likely to be published than small effects and that publication bias existed for these indicators [36]. However, fail-safe numbers of the above indicators were much larger than $5S + 10$ (Table 1). These results indicate that slight publication bias exists for these indicators, but such existing publication bias would not change the overall results [40].

4.2. PGPR Responsiveness on Biomass between SSP and STP

Salt tolerance is generally quantified as the plant biomass production [9]. The significant increases in the total, shoot and root biomass with the PGPR inoculation (Figure 1) align with previous findings [18,41,42]. The higher effect size of total biomass in SSP than that in STP (Figure 2a) is consistent with results of crop cultivars with contrasting salt tolerance [17,24,26]. The difference in total biomass accumulation between SSP and STP after PGPR inoculation can be ascribed to the changes of the physiological process such as osmoregulation, nutrient acquisition, ion homeostasis, antioxidant capacity, and photosynthesis, which would alleviate the salt stress [43,44]. Hence, the different responses of plant promotion in SSP and STP are discussed in terms of the physiological processes and indicators as follows.

4.3. Osmotic Adjustment Responding to PGPR Inoculation between SSP and STP

High salinity lowers soil osmotic potentials, which inhibits absorption of water by root [4,45]. Osmoregulation is an essential mechanism for a plant to tolerate the osmotic stress induced by soil salinity [46]. Plants often consume a substantial amount of energy to accumulate organic osmolytes (such as *Pro*, *SS*, and *SP*) for osmoregulation at the cost of biomass penalty [27,43,47,48].

Both *SS* and *SP* are typically non-injurious at a high cellular concentration and play a fundamental role in osmotic adjustment [39,44,47,49]. The positive changes of *SS* and *SP* in both SSP and STP indicate PGPR could biosynthesize osmolytes thus facilitate host plants to absorb more compatible solutes to maintain osmotic balance [3]. However, the 95% CIs of *SS* and *SP* overlapped zero in the SSP, but the effect sizes of them significantly increased in the STP (Figure 3b,c), which imply a relative weak improvement of the biosynthesis of *SS* and *SP* in SSP than in STP. However, no correlation between the effect size of total biomass with the effect sizes of *SS* and *SP* (Figure 6) suggest the indirect effect of *SS* and *SP* in biomass accumulation.

Pro is the most frequently examined organic osmolyte for plants under abiotic stress [39,44]. Some studies demonstrate that *Pro* accumulation signals injury caused by water deficiency under salt stress [50,51], while others report that *Pro* acts as a compatible solute for osmoregulation and an indicator of salt stress [12]. Both elevations and reductions in *Pro* have been ascribed to PGPR inoculation under salt stress [26,52,53]. Although the *Pro* decreased markedly in both SSP and STP after PGPR inoculation (Figure 3a), it is risky to conclude that the decrease in *Pro* indicates the remediation of osmotic stress because of the weak positive correlations between the effect sizes of *Pro* and total biomass in both SSP and STP (Figure 6).

4.4. Nutrient Acquisition and Ion Homeostasis Responding to PGPR Inoculation between SSP and STP

Soil salinity imposes ionic stress on plants, which leads to ion imbalance and nutrient deficiency [48]. Na^+ is the primary cause of ion stress for many plants, which not only competitively inhibits K^+, Ca^{2+}, and Mg^{2+} uptake thus disturbs the intracellular ion balance but also interferes with N and P acquisition and utilization [43,54,55]. The lower Na^+ uptake and higher N, P, K^+, Ca^{2+}, and Mg^{2+} uptake and consequently the higher K^+/Na^+ ratio, Ca^{2+}/Na^+ ratio, and Mg^{2+}/Na^+ ratio in the PGPR-inoculated plants than the control under salt stress in both SSP and STP (Figure 4) support the mechanism that PGPR could decrease toxic ions acquisition and maintain the intracellular ionic equilibrium and increase nutrients availability in plants [2,3].

The positive relationships between the effect size of total biomass and the effect sizes of N, P, and K^+ uptake in both SSP and STP support findings that PGPR can aid in the resumption of plant growth by retaining the nutrient acquisition of plants [3] (Figure 6) as PGPR could: (1) increase the nutrient availability by altering the root structure and root exudates and accelerating the nutrient cycling [56]; (2) promote the root nutrient absorption capacity by changing the root physiology; and (3) strengthen the capability of Na^+ detoxification [3], hence leading to the increase in the biomass.

The opposite changes in Na^+ uptake and other ions (Figure 4 and Figure S1) prove that PGPR could protect plants from the salt toxicity by maintaining ion homeostasis [3]. However, the specific ions that regulate the salt toxicity are different in SSP and STP. In the SSP, the effect size of total biomass correlated with that of Na^+ uptake, K^+/Na^+ ratio, Ca^{2+}/Na^+ ratio, and Mg^{2+}/Na^+ ratio, while in the STP, the effect size of total biomass only correlated with that of K^+/Na^+ ratio (Figure 6). The intrinsic salt tolerant mechanisms of different plant species might explain the difference. SSP cannot control or regulate Na^+ uptake and transportation and is thus "panic" into ionic damage in salinity condition [13,48]. Thus, the suppression of Na^+ uptake with PGPR inoculation can resume plant growth by protecting plants from toxic effects of salt ions and keeping the homeostasis of ions in the SSP [3]. However, STP can remain relatively "calm" when compared to SSP because the ionic damage is no longer a major cause of biomass penalty [13], thereby the increase in plant biomass has no direct correlation with the decrease in Na^+ (Figure 6). It is noteworthy that the correlation between the effect size of total biomass and that of Ca^+ uptake was positive in SSP but negative in STP (albeit effect size

of Ca^+ is positive). This suggests that, although the Ca^+ uptake can promote biomass accumulation, its promoting effect will be weakened and even inhibited when the Ca^{2+} concentration is too high.

4.5. Antioxidant System Responding to PGPR Inoculation between SSP and STP

Salt stress can destroy the dynamic equilibrium of ROS and cause oxidative damage in plants [11]. Oxidative stress can destabilize membranes, increase MDA content and inhibit photosynthesis [17,57,58]. Synthesizing and balancing the ROS scavenging enzymes, by increasing SOD and CAT, can protect cells from oxidative damage induced by ROS [59]. The higher SOD and CAT activities in PGPR-inoculated plants under salt stress across all studies (Figure 1) could reflect expression of genes that encode for ROS scavenging enzymes [60]. The different responses of SOD and CAT to the PGPR inoculation between the SSP and STP and no correlation between the effect sizes of antioxidant enzymes and total biomass in both SSP and STP let us speculate that changes in activation of antioxidant enzymes may not be the mechanism to regulate the biomass increase under PGPR inoculation.

Higher salt tolerance leads to lower MDA content in plants [61]. The non-significant difference in the reduction of MDA content and the negative relationships between the effect sizes of MDA and that of total biomass in both SSP and STP (Figures 5c and 6) suggest that PGPR inoculation can promote biomass accumulation by alleviating or eliminating salt-induced oxidative damage (measured by MDA). Higher antioxidant activities lower MDA content, which in turn inhibits membrane damage of ROS, thus enhancing plant salt tolerance [61]. However, the decrease in MDA had no correlation with the increase of antioxidant enzymes but had a positive correlation with the decrease in Na^+ uptake in our study (Figure S2 and Figure S3). It suggests that PGPR helps host plants to alleviate oxidative stress mainly through reducing the generation of ROS formed on the onset of ionic stress not via scavenging ROS by accumulating antioxidant enzymes in host plants [27].

Generally, the oxidative stress induced by salinity reduces the photosynthetic capacity via changing photosynthetic pigments and reducing the photosynthetic rate [62–64]. An improvement in the antioxidative capacity, in turn, will contribute to the promotion of *Chl* and *Car* content, and *Pn* [3,59]. The significant increase in *Chl* and *Car* contents, and *Pn* in both SSP and STP under salt stress indicate that plants inoculated with PGPR can increase photosynthetic pigments, elevate photosynthetic capacity and prevent oxidative damage to photosystem [12,65] (Figure 5d–f).

The positive relationship between the effect size of N uptake and that of *Chl* content and the negative relationship between the effect size of Na^+ uptake and that of *Chl* content (Figure S4) suggest the N uptake and Na^+ exclusion might elevate *Chl* concentration in PGPR-inoculated plants. However, there is no correlation between the effect size of total biomass and that of *Pn* and *Chl* content in both SSP and STP (Figure 6). However, cause–effect relationship between photosynthesis and growth is difficult to disentangle [1]. Thus, it is risky to deny the contribution of *Chl* and *Pn* in salt tolerance of plants after PGPR inoculation. *Car* has multiple roles in the protection of photosynthesis, reduction of oxidative damage and reinforcement of plant nutritional quality [59,64]. The increase in *Car* content had a positive effect on the promotion of total biomass in SSP but not in STP. This difference may depend on the antioxidant capacity associated with salt tolerance in different plant species [59]. Future research is required to identify the underlying mechanisms of photosynthesis with PGPR inoculation.

5. Conclusions

Meta-analysis of 561 studies suggests that PGPR inoculation generally induces plant growth and changes plant metabolism, such as increasing partial osmolytes accumulation (*SS* and *SP*), nutrient acquisition (N, P, K^+, Ca^{2+}, and Mg^{2+}), Na^+ exclusion, ion homeostasis (K^+/Na^+ ratio, Ca^{2+}/Na^+ ratio, and Mg^{2+}/Na^+ ratio), SOD activity, and photosynthetic capacity (*Chl*, *Car*, and *Pn*) but decreasing *Pro* accumulation and MDA content in SSP and STP. However, the biomass improvement in SSP was higher than that in STP after PGPR inoculation under salt stress, and mechanisms regulating the growth promotion share some consistency but SSP and STP have their unique mechanisms. The nutrient acquisition enhancement is the common mechanism to improve the plant growth in both SSP

and STP, while ion homeostasis plays an important role and carotenoid may promote plant growth through protecting the photosynthesis, reducing the oxidative damage and promoting the nutrient acquisition only in SSP after PGPR inoculation under salt stress.

Supplementary Materials: The following are available online at http://www.mdpi.com/2071-1050/11/2/378/s1, File S1: References included in the meta-analysis, File S2: the salt tolerance information in the original publications, Figure S1: Relationships between effect size of Na^+ content in plants after PGPR inoculation under salt stress conditions and effect sizes of: K^+ content (a); Ca^{2+} content (b); and Mg^{2+} content(c)., Figure S2: Relationships between effect size of MDA content and effect size of Na^+ content in plants after PGPR inoculation under salt stress conditions., Figure S3: Relationships between effect size of MDA content in plants after PGPR inoculation under salt stress conditions and effect sizes of: SOD (a); and CAT content (b)., Figure S4 Relationships between effect size of chlorophyll content in plants after PGPR inoculation under salt stress conditions and effect sizes of: N content (a); and Na^+ content (b).

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