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Application of *Trichoderma* species increases plant salinity resistance: a bibliometric analysis and a meta-analysis

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Abstract

Purpose Soil salinization has become increasingly serious recently, leading to a significant decline in crop yields. Application of *Trichoderma* species can enhance plant salinity resistance and thus achieve greater yields. However, there are few relevant studies. Here, we conducted a bibliometric analysis of relevant articles to reveal the current research status, and then carried out a meta-analysis to investigate the potential mechanisms.

Methods We analyzed the relevant databases using bibliometric analysis and meta-analysis.

Results The bibliometric analysis revealed that there are relatively few studies on the enhancement of plant salt resistance through *Trichoderma* species. The meta-analysis revealed that inoculation with *Trichoderma* under salt stress significantly changed morphological indicators, physiological indicators and enzyme activity in plants. Moreover, through subgroup analysis, we also found that when plants experienced moderate salinity (4–8 dS m^{-1}) and medium-term (2–4 weeks) salt stress, the application of *Trichoderma* species had the greatest promoting effects. Inoculation with *Trichoderma* was more effective on plants that were monocotyledons or C_4 plants. Among the various *Trichoderma* strains, *T. hamatum* had the best inoculation effect.

Conclusions *Trichoderma* species can promote plant growth under salt stress and improve plant salinity resistance through three main pathways: (1) promoting the development of the roots to absorb more nutrients and water, (2) increasing the activity of antioxidant enzymes to scavenge excess reactive oxygen species, and (3) enhancing the performance of Photosystem II to improve plant photosynthetic capacity. Moreover, through subgroup analysis, we also found that inoculation with *Trichoderma* species can be affected by various factors, such as salinity, duration of salinity, plant groups, photosynthetic type, and *Trichoderma* species.

Keywords Salinization · *Trichoderma* spp. · Plant · Salt resistance · Quantitative analysis

1 Introduction

Since the twenty-first century, the world's population has been increasing and, according to the forecasts, the world population will exceed 9 billion by 2050, which will require a 57% increase in food production (Gerbens-Leenes and Nonhebel 2002; FAO 2011). However, improper irrigation, poor water quality, and excessive use of chemical fertilizers and pesticides have led to the emergence of soil salinization, which has led to a continuous decrease in the area of arable land used for agriculture each year and a subsequent decrease in the land productivity (Meena et al. 2019; Sun et al. 2021). Therefore, ways to improve the salt resistance and increase the yield of crops in saline soils are popular research topics in the field of agricultural production at present.

In the past, the methods commonly used to enhance plant resistance to salt stress mainly involved using traditional breeding methods or advanced molecular techniques to develop tolerant plant varieties, but the former were time-consuming and the latter were expensive (Ikram et al. 2019). Therefore, researchers have tried to develop cheaper and

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faster alternative methods, one of which was to use inoculation with endophytic fungi to improve plant resistance to salt stress (Bilal et al. 2018; Ikram et al. 2018).

Endophytic fungi are more effective than other bacteria because of their fast growth rate, environmental adaptability and broader ecological niche in the soil (Bell et al. 1982). Among the numerous endophytic fungi, *Trichoderma* species have been more widely used because of their great potential to help host plants against biotic and abiotic stresses (Contreras-Cornejo et al. 2016; Nieto-Jacobo et al. 2017). Research has shown that the inoculation with *Trichoderma* species could alleviate the harmful effects of salinity on plant growth and improved the salt resistance of plants through various mechanisms. For example, *Trichoderma* inoculation could enhance plant absorption of nutrients and water (Hashem et al. 2014), maintain osmotic balance (Zhao and Zhang 2015), increase the activity of the antioxidant system to prevent reactive oxygen species (ROS) damage (Pehlivan et al. 2017), accelerate the photosynthetic rate (Ikram et al. 2019), and regulate hormone levels (Yusnawan et al. 2021). In fact, most of the studies were based on indoor experiments, and few field studies. Moreover, little was known about the quantitative analysis of the effect of inoculation with *Trichoderma* species on improving plant salinity resistance at the global scale, and previous studies have lacked a systematic understanding of the mechanisms by which *Trichoderma* improved plant salinity resistance. For this reason, this study collected and extracted the published literature and data on improvements in plant salt resistance produced by *Trichoderma*, and conducted a bibliometric analysis to elucidate the current status and development trends of the research into improving plant resistance to salt stress by the use of *Trichoderma* species. In addition, we also performed a meta-analysis to quantify the effect of *Trichoderma* inoculation on different pathways of plants under salt stress, while we further explained the effects of different factors on the effect of *Trichoderma* inoculation by subgroup analysis.

2 Materials and methods

2.1 Bibliometric analysis

2.1.1 Data sources

In this study, the Web of Science Core Collection was chosen as the data source and the time search spanned from 1996 to 2022. Our subject terms were *Trichoderma* AND plant growth or alleviate or resistan* or toleran* improve AND salt stress or NaCl stress or salinity or saline or salt or NaCl**.** The Boolean truncation ("$*$") was used to include variations of the words "resistant" and "tolerant", such as "resistance" and "tolerance".

2.1.2 Research method

Bibliometric analysis can be implemented by many software packages, such as Citespace, Vosviewer, Bibliometrix and Biblioshiny (Xie et al. 2020). In this study, Bibliometrix and Biblioshiny were chosen, and four functions in Bibliometrix and Biblioshiny were used for the analysis, namely descriptive features of the literature, annual scientific yield, country-level scientific production, and trending topics.

2.2 Meta-analysis

2.2.1 Data sources and literature screening

In order to perform the meta-analysis, we conducted a search of all Web of Science databases. Our subject terms were *Trichoderma* AND plant growth or alleviate or resistan* or toleran* improve AND salt stress or NaCl stress or salinity or saline or salt or NaCl**.** The Boolean truncation ("$*$") was used as described above. In total, 635 articles were obtained through the search, which was conducted for articles published from 1930 to May 2023 (Retrieved on May 4, 2023.). The 635 articles obtained through the initial search were further screened according to the following inclusion criteria:

1. The microbial inoculum used in the experiment could only contain *Trichoderma* species and could not be mixed with other microorganisms;
2. Both *Trichoderma* inoculated and non-inoculated plants were grown under salinity stress and non-stress conditions;
3. Some physiological parameters of the plants were measured, such as morphological index, photosynthetic index, antioxidant index, hormone content and ion content;
4. The experimental results showed the sample size, mean, standard deviation or standard error, and other relevant statistical information so that the results could be converted into a standardized measure of the effect size.

The articles obtained after screening were used for a comparative analysis of the effects of *Trichoderma* inoculation on plant physiological parameters under salt stress. Detailed information is provided in the supplementary information.

2.2.2 Data extraction and analysis

From these selected articles, we extracted relevant data about the plant growth parameters, photosynthetic parameters, enzyme parameters, ion parameters, hormone levels, and others. Each study provided the mean, sample size (replication) and standard deviation (SD). If standard errors (SE) were provided in the literature, we converted them to SD with the equation $SE = SD\ (n^{-1/2})$ (van Groenigen et al. 2011). In addition, the data in the results in the literature were often presented in graphs, so we used Getdata (Graph Digitizer software, http://getdata-graph-digitizer.com) to digitize the values. Finally, the obtained data were organized and a meta-analysis was performed using Meta-Win v2.1 software (Gu et al. 2022).

2.2.3 Effect size and deviation

Because of its statistical properties (an approximately normal distribution) and biological interpretation (Hedges et al. 1999; Wallace et al. 2009), the effect size in this study was calculated using the natural logarithm of the response ratio (LRR) as an indicator for evaluating the effect of *Trichoderma* inoculation under salt stress. These calculations were performed by Meta-Win v2.1 software (Gu et al. 2022).

$$\mathrm{LRR} = \ln\left(\frac{\overline{X}^{E}}{\overline{X}^{C}}\right) = \ln\left(\overline{X}^{E}\right) - \ln\left(\overline{X}^{C}\right) \tag{1}$$

$$\mathrm{V}_{\ln\mathrm{R}} = \frac{\left(\mathrm{S}^{\mathrm{E}}\right)^{2}}{\mathrm{N}^{\mathrm{E}}\left(\overline{X}^{\mathrm{E}}\right)^{2}} + \frac{\left(\mathrm{S}^{\mathrm{C}}\right)^{2}}{\mathrm{N}^{\mathrm{C}}\left(\overline{X}^{\mathrm{C}}\right)^{2}} \tag{2}$$

where LRR is the effect size, $\overline{X}^{\mathrm{C}}$ and $\overline{X}^{\mathrm{E}}$ are the means of the control groups (without *Trichoderma* inoculation under salt stress) and the treatment groups (with *Trichoderma* inoculation under salt stress); S^{C} and S^{E} are the SD of the control groups and the treatment groups; N^{C} and N^{E} are the numbers of experimental replicates or the sample size of the control groups and the treatment groups, respectively.

After processing by Meta-Win v2.1, if the confidence interval of the obtained results contained zero, this meant that *Trichoderma* inoculation had no significant effect on plant growth and physiological indexes. If the confidence interval was greater than zero or less than zero, this meant that *Trichoderma* inoculation had a significant positive or negative effect on plant growth and physiological indexes.

2.2.4 Subgroup analysis

The effect of different factors on the promotion effect of *Trichoderma* inoculation on plants under salt stress was investigated by subgroup analysis after considering the different factors mentioned below. The significance of between-group heterogeneity ($\mathrm{Q_b}$) indicates significant differences in the treatments between groups.

Salinity: There are three levels of soil salinity, namely low, medium, and high salinity. The different salinity levels in the literature were classified with reference to the relevant regulations of the USDA Natural Resources Conservation Service. Low salinity has an electrical conductivity (EC) of the soil saturation extract ≤ 4 dS $\mathrm{m^{-1}}$ or a salt concentration (C) ≤ 42.68 mM; medium salinity has EC of 4–8 dS $\mathrm{m^{-1}}$ or C of 42.68–85.37 mM while high salinity has EC ≥ 8 dS $\mathrm{m^{-1}}$ or C ≥ 85.37 mM.

Duration of salinity: There are also three levels of duration, namely short-term (< 2 weeks), medium-term (2–4 weeks), and long-term (> 4 weeks).

Plant groups: There are two plant groups, monocotyledons and dicotyledons.

Photosynthetic type: There are two photosynthetic types, $\mathrm{C_3}$ plants and $\mathrm{C_4}$ plants.

Trichoderma species: Five *Trichoderma* species were included in the analysis, such as *T. harziamum*, *T. longibrachiatum*, *T. atroviride*, *T. hamatum*, and *T. viride*. (Top five *Trichoderma* species used in the literatures.)

It is worth noting that some of the literature did not contain sufficient details for explicit subgroup analysis, so relevant data from these papers were rounded off. For example, some of the literature did not specify the salinity, duration of salinity, and *Trichoderma* species in the experiments.

3 Results and discussion

3.1 The current status of plant salinity resistance enhanced by *Trichoderma*

3.1.1 Descriptive features of the literature

By searching for relevant subject terms, this study extracted 253 articles from the Web of Science Core Collection, published from 1996 to 2022. These articles were from 163 journals and periodicals, with 1041 scholars involved in the publication of the articles. The average citation rate of each article was 28.85, which indicated the high academic level and the large influence of studies related to enhancing plant salinity resistance with *Trichoderma* species (Table 1).

3.1.2 Annual scientific yield

The annual scientific yield can reflect the level of concern and the "hotness" of related research in a scientific field, as well as the development speed and research prospects of the research field (Xie et al. 2020; Wang et al. 2022). During the 27 years from 1996 to 2022, there were 253 publications on the enhancement of plant salt resistance through *Trichoderma* species worldwide in the Web of Science Core Collection (Fig. 1). The number of relevant publications showed a fluctuating growth trend. Before 2010, the number of related studies grew very slowly and basically remained at about five articles per year. After 2010, the growth increased and reached the maximum number of articles in

Table 1 Basic information of the dataset (1996–2022)

Description	Results
Timespan	1996–2022
Sources (journals, books, etc.)	163
Documents	253
Average years since publication	6.35
Average citations per document	28.85
Average citations per year per document	3.741
References	12486
Keywords plus (ID)	1004
Authors' keywords (DE)	932
Authors	1041

2021, with a total of 38 articles. Overall, it seemed that there were relatively few studies on the enhancement of plant salt resistance through *Trichoderma* species. Although existing studies have shown the effectiveness of *Trichoderma* spp. in improving salt resistance in plants, their application has not been widespread. This is due to the fact that *Trichoderma* spp. were in most cases used as biocontrol fungi in agricultural production and researchers were more concerned their antagonistic effect on plant pathogens, while it was only through further investigation of *Trichoderma* spp. that their ability to desalinate, promote growth and improve plant salinity resistance was discovered (Woo et al. 2014). Therefore, researchers began to consider the use of *Trichoderma* spp. in saline soils, but the current research on *Trichoderma* spp. were still more concerned with their inhibitory effect on various pathogens.

3.1.3 Country-level scientific production

The country-level scientific production can reflect the importance and influence of each country in the field of using *Trichoderma* species to improve salt resistance in plants to some extent (Xie et al. 2020). The top five countries in this field in terms of the number of publications were China, India, Egypt, Spain and Italy (Fig. 2). The number of articles published in China and India even exceeded the third country by two to three times, showing that agriculture-oriented countries paid more attention to the role of *Trichoderma* spp. in improving plant salinity resistance and enhancing crop yield. In addition, studies have also shown that Asia was the region most threatened by salinity globally, with a saline soil area of 7.14 Mkm^2, and China had the largest saline soil area among Asian countries (211.74 Mha), while Europe and the United States had less salinity problems and less saline soil area, which may be related to the implementation of mechanized production in Europe and the United States to reduce the risk of salinization of arable land (Hassani et al. 2020). Therefore, not much research has been conducted on improving the salt resistance of plants in Europe and the United States. Zin and Badaluddin (2020) also found, through their survey, that Asia was the region where *Trichoderma* products were widely used, followed by Europe, Central and South America, and North America.

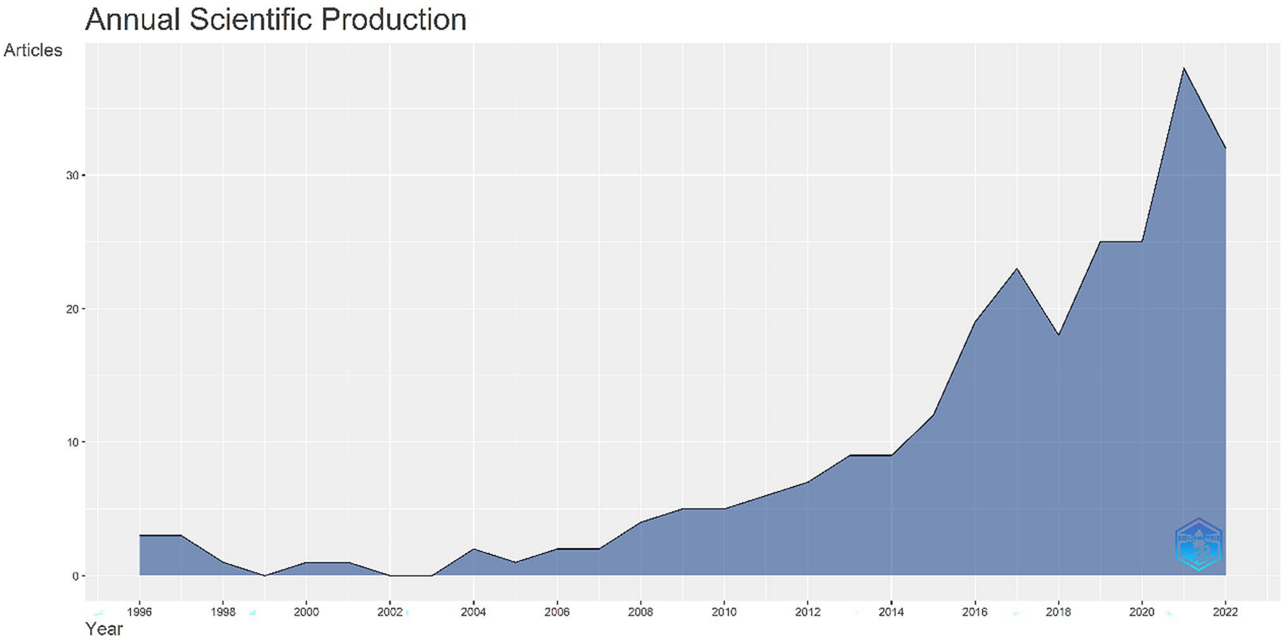

Fig. 1 Number of papers published annually in the field of the enhancement of plant salinity resistance with *Trichoderma* species

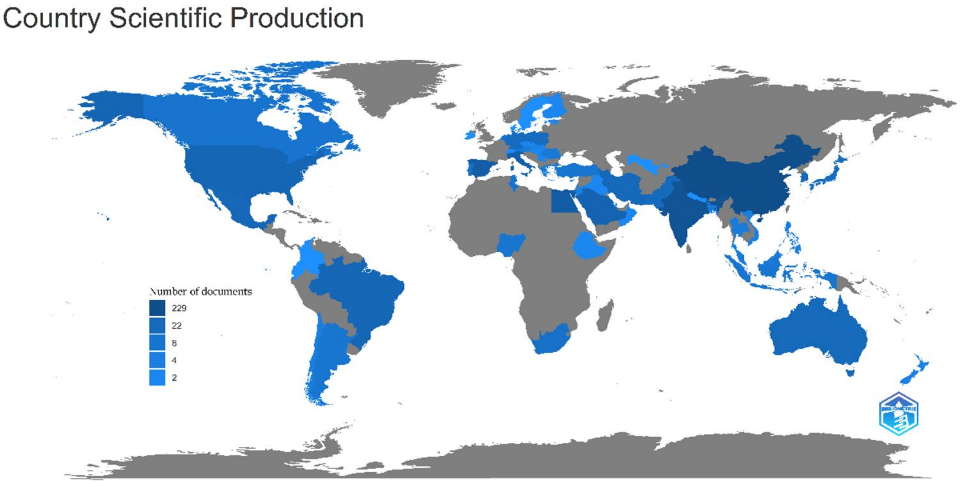

Fig. 2 The geographical distribution of scientific publications in the field of the enhancement of plant salinity resistance with *Trichoderma* species

3.1.4 Trending topics

Trending topics can reflect changes in research hotspots (Xie et al. 2020). Through the trends of keywords during the 27 years from 1996 to 2022, we could see that researches on *Trichoderma* species have mainly focused on their antagonistic effect on pathogenic fungi as the biocontrol agent before 2013. Since 2016, the research on the use of *Trichoderma* species to improve plant resistance to salt stress increased and studies began to focus on the changes in the morphological indicators, physiological indicators, enzyme activity, and gene expression levels of plants inoculated with *Trichoderma* species under salt stress, which ultimately improved plant resistance and promoted plant growth (Fig. 3). In fact, in early studies, *Trichoderma* species were often used as biopesticides to explore their effectiveness in controlling plant pathogens. However, in recent years, with increased in soil salinization, the use of microbial techniques to improve the salt resistance of plants has become a new research hotspot in China and abroad, so researchers have also paid more attention to the effect of *Trichoderma* species in improving salt resistance. In addition, although the total number of related studies was still low, some results have been achieved. Researchers have discussed the improvements in plant physiological and biochemical parameters achieved by inoculation with *Trichoderma* species under salt stress and the relevant mechanisms, which ranged from the individual level to the cellular level, from the molecular level to the genetic level, and so on. In the future, we can integrate multiple studies to systematically understand the mechanisms involved in the improvements in salt resistance in plants by the use of *Trichoderma* species.

3.2 The mechanisms of plant salinity resistance enhanced by *Trichoderma* species

Salt stress is one of the most important factors that inhibits plant growth and reduces crop yield. It not only causes osmotic stress but also impacts the physiological and biochemical processes in plants. However, many studies in

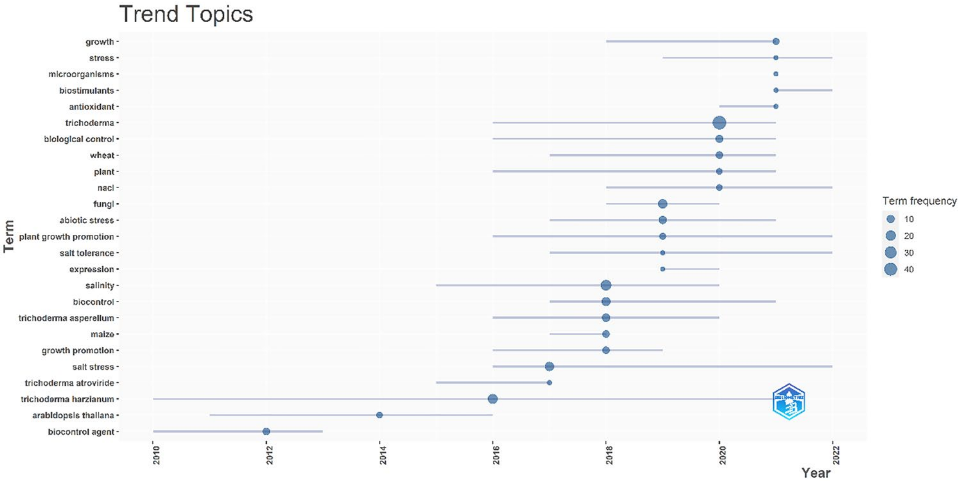

Fig. 3 Time and frequency of occurrence of topic words in the field of the enhancement of plant salinity resistance with *Trichoderma* species

recent years have shown that inoculation with *Trichoderma* species, a genus of endophytic fungi, could effectively enhance salt resistance in plants and promote the growth of plants under salt stress.

In general, growth parameters were significantly increased in plants inoculated with *Trichoderma* compared with uninoculated plants (Fig. 4). The plants inoculated with *Trichoderma* increased shoot fresh weight (SFW) by 29%, root fresh weight (RFW) by 31%, shoot dry weight (SDW) by 32%, root dry weight (RDW) by 31%, shoot length (SL) by 28%, and root length (RL) by 29%. Physiological and biochemical plant data showed that *Trichoderma* species could improve the salt resistance of plants through three main pathways as described below.

(1) Inoculation with *Trichoderma* promoted the development of the root system of the host plant, and thus the plant absorbed nutrients and water from the environment.

The root system, as a key link in the soils–plant–atmosphere–water continuum, is often the first to recognize changes in the soil environment and respond to external stresses. It has been shown that the root system promotes plant growth and allows plants to tolerate biotic and abiotic stresses such as salinity, acidity, and insect pests through mechanical support, nutrient transport, gas exchange, and symbiosis with beneficial microorganisms (DuanMu et al. 2015). Plant root length root surface area are important indicators of root function and growth. High salt concentrations inhibit root activity, limit root elongation, and decrease root growth (Karlova et al. 2021). However, the meta-analysis found that inoculation with *Trichoderma* under salt stress significantly increased the plant root growth as measured by the fresh and dry weights of roots (RFW, RDW) and root length (RL). This promoting effect of *Trichoderma* inoculation on root development might be related to its ability to stimulate the synthesis and secretion of phytohormones. It has been shown that some *Trichoderma* species could increase the concentrations of phytohormones such as cytokinin, gibberellin acid and zeatin in plants, which have beneficial effects on the growth of plant roots under salt stress (Harman 2000; Benitez et al. 2004; Iqbal and Ashraf 2013; Ahmad et al. 2015). This was also confirmed in the present study. The concentrations of auxin (IAA) and gibberellin acid (GA) increased by 6% and 23%, respectively, while the concentrations of abscisic acid (ABA) decreased by 26% and ethylene (ET) remained unchanged in inoculated plants compared to uninoculated plants. However, it was worth noting that observations of GA and ethylene were relatively few, and further experiments were needed to verify their functions for an accurate understanding (Fig. 5). Among these hormones, IAA promotes cell elongation and effectively promotes root growth, while ABA inhibits plant growth.

In addition, previous studies have shown that inoculation with *Trichoderma* species can induce changes in the root structure of the host plants, promote the formation of lateral roots and adventitious roots, increase the root absorption area, and facilitate plant uptake of nutrients and water from the external environment, thus likely enhancing the plant ability to cope with salinity stress. (Adrio and Demain 2003). Under saline stress conditions, a large amount of salt-damaging ions will enter and accumulate in the plant,

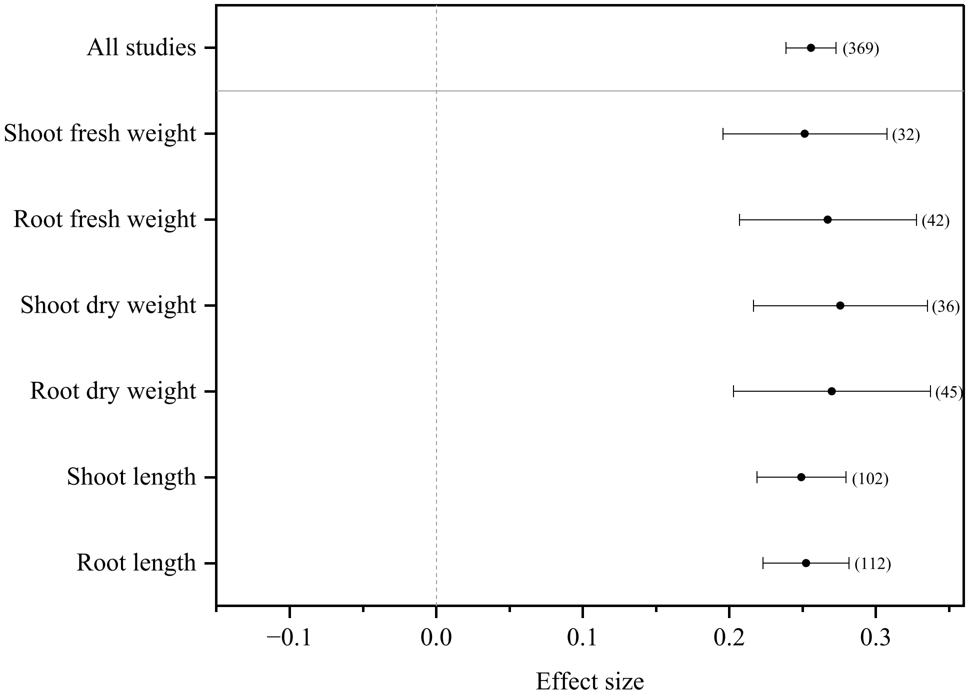

Fig. 4 Effects of *Trichoderma* inoculation on plant growth parameters under salt stress. Numbers in parentheses show the number of data observations. The vertical dotted lines at 0 indicate the effect of the control. Error bars are the mean effect size ± 95% bootstrapping (BS) confidence intervals (CIs). All studies, all the parameters

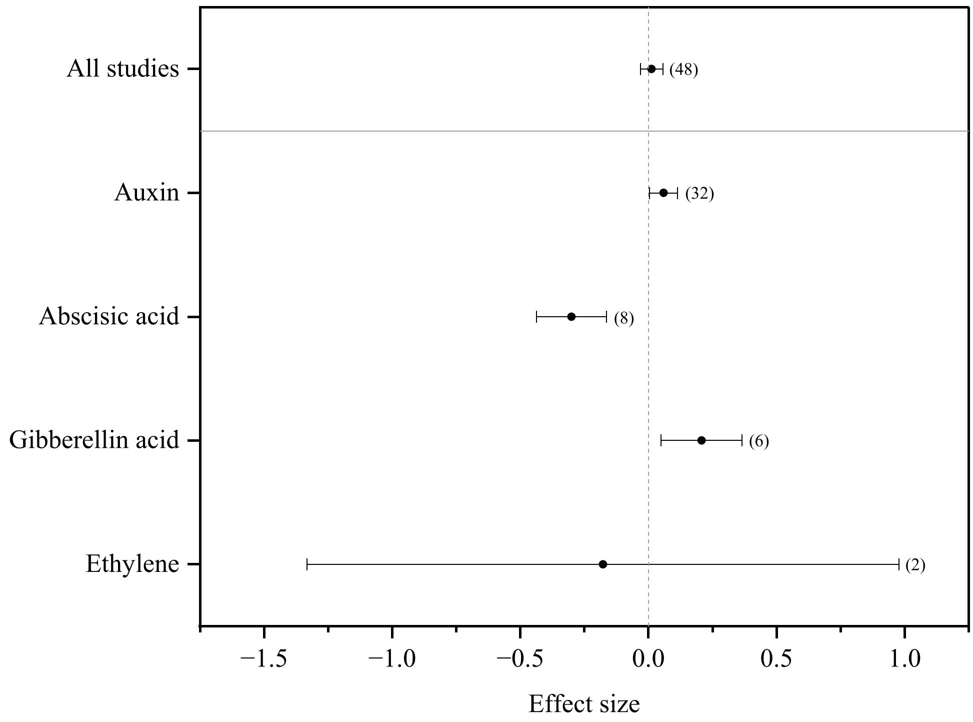

Fig. 5 Effect of *Trichoderma* inoculation on hormone levels in plants under salt stress. Numbers in parentheses show the number of data observations. The vertical dotted lines at 0 indicate the effect of the control. Error bars are the mean effect size ± 95% bootstrapping (BS) confidence intervals (CIs). All studies, all the parameters

and the water uptake and balance of cells in the plant suffered from damage, thus affecting the normal growth of the plant, while the root system of the plant increases the uptake of nutrients such as K^+ and Ca^{2+} and restricts the entry of Na^+, which can help Na^+ efflux and be compartmentalized, ensuring the ion balance in the plant and alleviating saline damage (Chinnusamy et al. 2005). Our meta-analysis showed that under salt stress conditions, when plants were inoculated with *Trichoderma*, the concentrations of K^+ and Ca^{2+} in the body would increase by 42% and 17%, respectively, while the concentrations of Na^+ would decrease by 28% and the concentrations of Mg^{2+} would not change significantly, which might be related to its fewer observations of only six (Fig. 6). Thus, it seemed that the application of *Trichoderma* spp. could significantly increase the concentrations of beneficial ions in plants, enhance the regulation with ionic balance, reduce ion toxicity, and thus enhance the salt resistance of plants. At the same time, the results of the meta-analysis also showed that the relative water content (RWC) of plants inoculated with *Trichoderma* increased significantly (Fig. S1). In fact, the high concentration of salts in the soil can increase the osmotic pressure of the soil, causing difficulties in water uptake by the plants and even leading to water extravasation from the plants, which can lead to dehydration, while the inoculation of *Trichoderma* can effectively solve this problem (Sahab et al. 2021). In addition to water and nutrients, *Trichoderma* inoculation also increased the concentrations of soluble sugars and soluble proteins in the plant (Fig. S1).

In conclusion, the inoculation with *Trichoderma* species under salt stress increased the levels of growth hormones in the host plant, promoted root development, and increased the uptake of nutrients and water.

(2) Inoculation with *Trichoderma* species enhanced the activity of antioxidant enzymes in plants, helping to scavenge excessive ROS.

After plants were inoculated with *Trichoderma* species, the content of H_2O_2 decreased by 28%, the content of malondialdehyde (MDA) decreased by 28%, and the membrane stability index (MSI) increased. Moreover, the activity of antioxidant enzymes changed, among which the activity of superoxide dismutase (SOD), glutathione reductase (GR), catalase (CAT), and ascorbate peroxidase (APX) increased by 29%, 26%, 13% and 36%. In contrast, the activities of peroxidase (POD) did not change significantly (Fig. 7). Salt stress triggers the production of large amounts of ROS in plants, and inoculation with *Trichoderma* species can accelerate the removal of ROS in host plants. Normally, the synthesis and decomposition of ROS in plants is in a dynamic balance, which is mainly dependent on the antioxidant system in plants. When plants are stressed, the antioxidant system in the body will be damaged, leading to the production of large amounts of ROS, which will react with phospholipids and membrane receptor proteins for lipid peroxidation, severely damaging the integrity and fluidity of the membrane system, leading to membrane damage and lipid peroxidation, and the loss of membrane stability. Thus the membrane stability index is also considered to be one

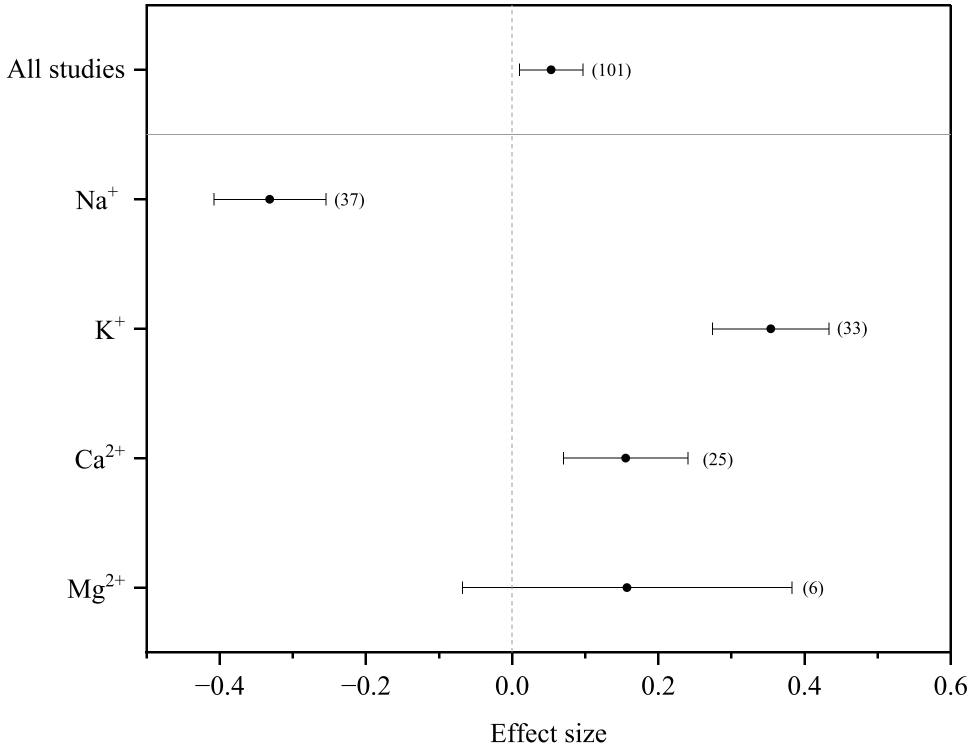

Fig. 6 Effect of *Trichoderma* inoculation on the ion concentrations of plants under salt stress. Numbers in parentheses show the number of data observations. The vertical dotted lines at 0 indicate the effect of the control. Error bars are the mean effect size ± 95% bootstrapping (BS) confidence intervals (CIs). All studies, all the parameters

of the important indicators to evaluate the salt resistance of plants (Farooq and Azam 2006). OH·, one of the ROS, can act directly on lipids to form hydroperoxides, which are broken down into highly toxic lipid peroxidation end-products such as MDA; therefore, the level of MDA is often used to characterize the degree of damage in plants exposed to stress. Under salt stress conditions, MDA and H_2O_2 levels in plants inoculated with *Trichoderma* species decreased significantly and their membrane stability increased, indicating that the oxidative stress caused by salt stress in these plants

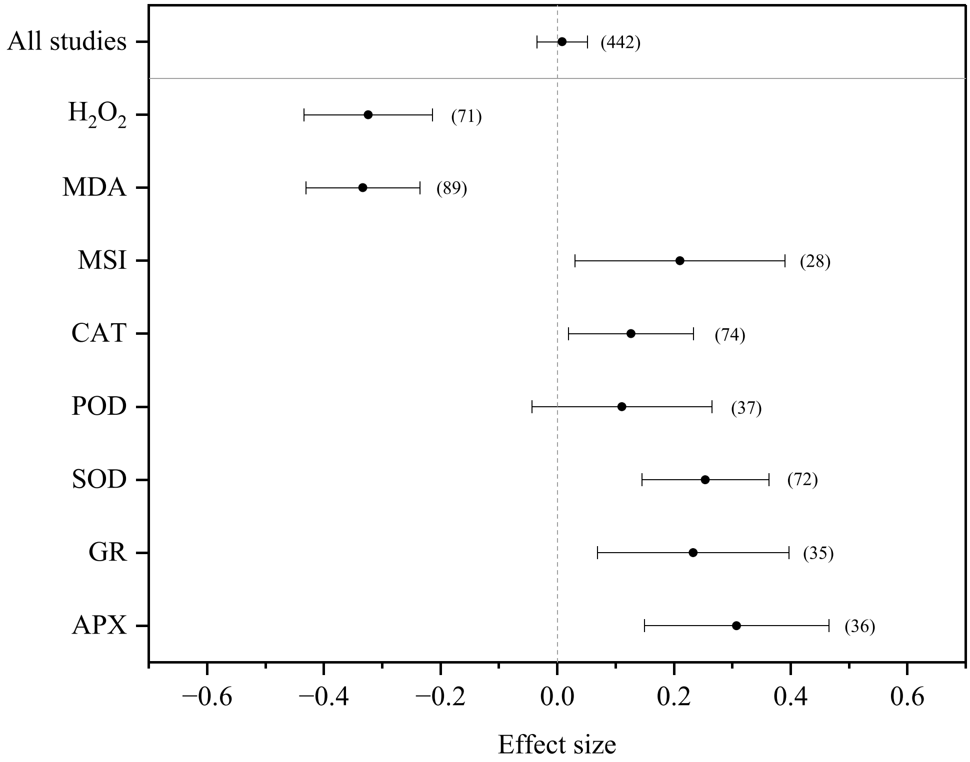

Fig. 7 Effect of *Trichoderma* inoculation on the antioxidant parameters of plants under salt stress. Numbers in parentheses show the number of data observations. The vertical dotted lines at 0 indicate the effect of the control. Error bars are the mean effect size ± 95% bootstrapping (BS) confidence intervals (CIs). MDA, malondialdehyde; MSI, membrane stability index; CAT, catalase; POD, peroxidase; SOD, superoxide dismutase; GR, glutathione reductase; APX, ascorbate peroxidases; All studies, all the parameters

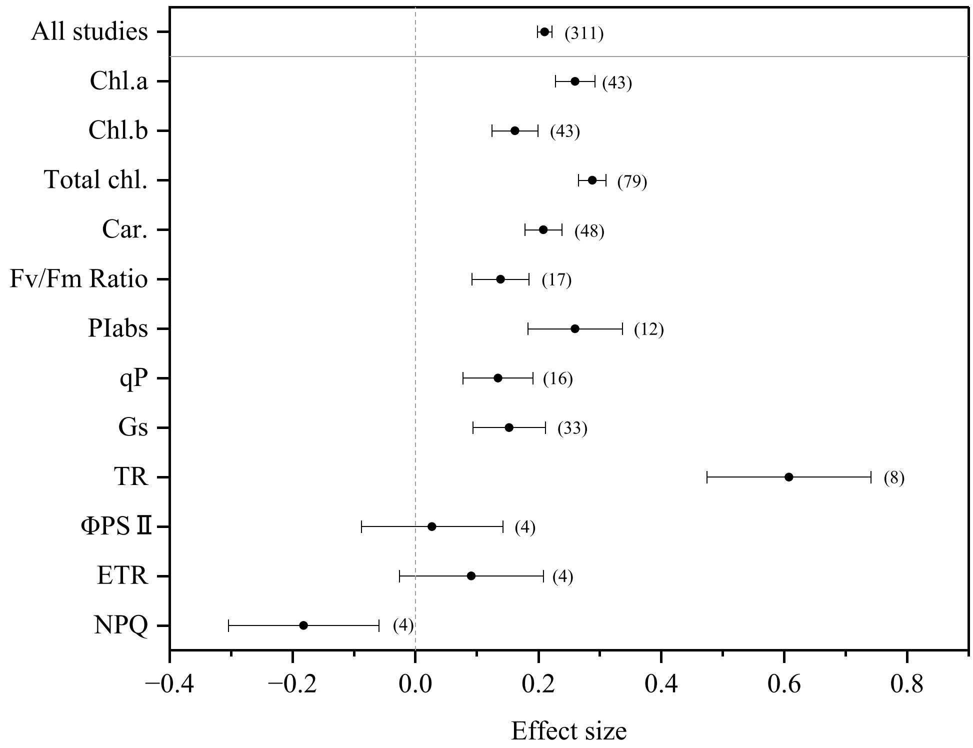

Fig. 8 Effect of *Trichoderma* inoculation on the photosynthetic parameters of plants under salt stress. Numbers in parentheses show the number of data observations. The vertical dotted lines at 0 indicate the effect of the control. Error bars are the mean effect size ± 95% bootstrapping (BS) confidence intervals (CIs). Chl. a, chlorophyll a; Chl. b, chlorophyll b; Total chl., total chlorophyll a; car., carotenoids; F_v/F_m ratio, dark-adapted quantum yield; PIabs, performance index; qP, photochemical quenching; SC, stomatal conductance; TR, transpiration rate; ΦPSII, the quantum yield of PSII's photochemistry; ETR, electron transport rate; NPQ, nonphotochemical quenching; All studies, all the parameters

was reduced compared with that in plants without *Trichoderma* inoculation. However, previous studies have shown that the activity of antioxidant enzymes (SOD, POD, CAT, and so on) and the content of some non-enzymatic antioxidant molecules (e.g., glutathione, carotenoids, isoflavones) in plants inoculated with *Trichoderma* species increased significantly when the plants were exposed to stress. This suggests that *Trichoderma* species can enhance plant resistance by inducing the host plant to activate its antioxidant system and produce more antioxidant enzymes and molecules (Ahmad et al. 2015; Durmus et al. 2017; Zhang et al. 2019).

(3) Inoculation with *Trichoderma* species promoted photosynthetic pigment synthesis and enhanced the performance of Photosystem II (PSII) in plants, ultimately improving photosynthetic capacity.

Inoculation with *Trichoderma* species significantly increased the content of photosynthetic pigments in plants, with 33% increase in total chlorophyll and 23% increase in carotenoids (Fig. 8). At the same time, the dark-adapted quantum yield (F_v/F_m ratio), photosynthetic performance index, photochemical quenching, stomatal conductance, and transpiration rate increased in inoculated plants compared with uninoculated plants, but the quantum yield of PSII's photochemistry and the electron transport rate of the photosystem did not change significantly, whereas the nonphotochemical quenching decreased (Fig. 8). It is worth noting that the quantum yield of PSII's photochemistry, electron transport rate, and nonphotochemical quenching had fewer observations and their results might not be fully representative.

Table 2 Analysis of the significant differences between groups in the heterogeneity (Q_b) of the effect of different factors on treatment with *Trichoderma*

Response variables	Categorical variables	DF_b	Heterogeneity between groups (Q_b)	*P*-value
Shoot length	Salinity level	2	0.358	0.837
	Salinity duration	2	18.601	**< 0.001**
	Plant group	1	14.307	**< 0.05**
	Photosynthetic type	1	26.876	**< 0.001**
	Trichoderma species	4	11.489	0.330
Root length	Salinity level	2	7.435	**< 0.05**
	Salinity duration	2	7.264	**< 0.05**
	Plant group	1	18.982	**< 0.001**
	Photosynthetic type	1	2.257	0.133
	Trichoderma species	4	13.102	**< 0.05**

Salt stress can damage the photosynthetic apparatus of plants, and inoculation with *Trichoderma* species can effectively alleviate this damage and promote photosynthesis. The content of photosynthetic pigments (e.g., chlorophyll a, chlorophyll b, and carotenoids) is usually reduced in plants in a high-salt environment (Sairam et al. 2002; Parida and Das 2005). Salt stress adversely affects the chloroplasts by increasing the activity of chlorophyll-degrading enzymes, which leads to a decrease in chlorophyll synthesis in plants. The decrease in carotenoid content may be caused by the decreased synthesis of β-carotene and zeaxanthin in plants under salt stress (Sultana et al. 1999). *Trichoderma harzianum* (*T. harzianum*) has been reported to promote chlorophyllase synthesis in plants under different stress conditions (Rawat et al. 2011; Zhang et al. 2013; Hashem et al. 2014). Moreover, Mishra and Salokhe (2011) found that inoculation with *Trichoderma* species can enhance PSII's performance under salt stress conditions. Previous studies found that when plants were exposed to salt stress, their PSII was also affected and the maximum the dark-adapted quantum yield (F_v/F_m), photochemical quenching, photosynthetic performance index, and stomatal conductance of PSII decrease with increasing salinity, but these parameters all increased when *Trichoderma* species are applied (Yasmeen and Siddiqui 2017).

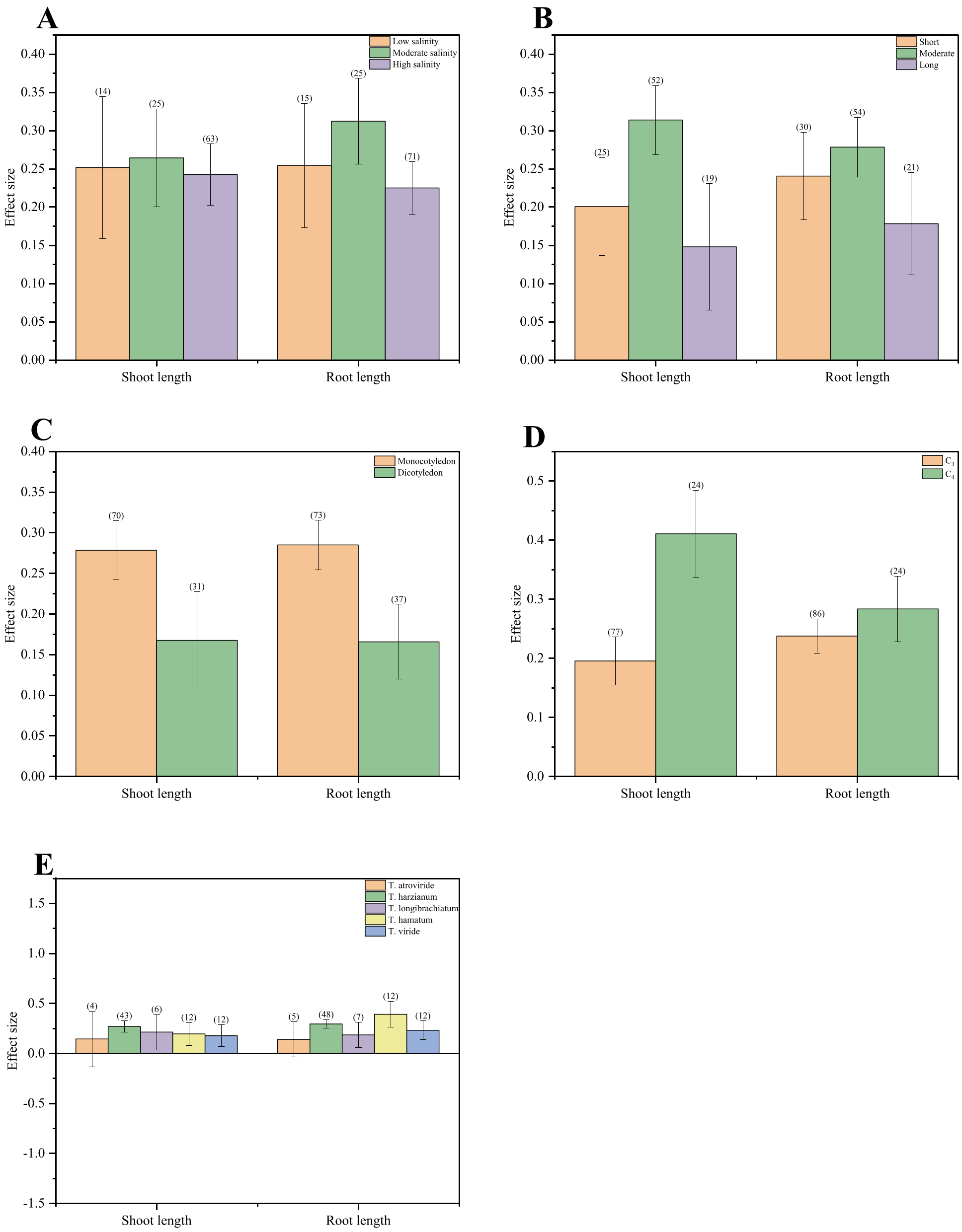

Fig. 9 Effects of different factors on the effect of *Trichoderma* inoculation: **A**, salinity; **B**, duration of salinity; **C**, plant groups; **D**, photosynthetic type; **E**, *Trichoderma* species. Numbers in parentheses show the number of data observations. Error bars are the mean effect size ± 95% bootstrapping (BS) confidence intervals (CIs)

3.3 Influence of different factors on the effect of *Trichoderma* inoculation: subgroup analysis

The promotion of plant growth by *Trichoderma* species under salt stress is often influenced by several factors. In this study, two indicators, shoot length (SL) and root length (RL), which had high numbers of observations, were selected as representatives. The effects of salinity, duration, plant group, photosynthetic type, and *Trichoderma* species on the effects of *Trichoderma* inoculation were investigated in a subgroup analysis (Table 2; Fig. 9). When plants experienced moderate salinity (4–8 dS m^{-1}), in the medium-term (2–4 weeks), the inoculation of *Trichoderma* species benefited most. Inoculation with *Trichoderma* species was more effective in monocotyledons or C_4 plants than dicotyledons or C_3 plants. Among the various *Trichoderma* strains reported, *T. hamatum* had the best inoculation effect (Fig. 9). However, it was worth noting that the strain used for inoculation was *T. harzianum* in most of the studies. This is because that *T. harzianum* is the dominant species of *Trichoderma* among many and has a worldwide distribution. (Chaverri et al. 2003; Druzhinina et al. 2010; Blaszczyk et al. 2011).

Several studies have shown that the effectiveness of microbial inoculation can be influenced by various factors. Fu et al. (2018) showed that the promotion effect of *T. asperellum* on plants under salt stress was greatly enhanced as the dose of inoculum was increased. It has also been reported that environmental factors such as temperature and pH could affect the growth-promoting effect by affecting the survival rate of microorganisms (Roy et al. 2021). In addition to these factors, the characteristics of the plants and *Trichoderma* spp. can also have an impact on the effectiveness of *Trichoderma* inoculation. For example, plants with well-developed root systems tend to respond better in terms of growth because they have more space for colonization. And *Trichoderma* spp. with faster growth rates and greater resistance to biotic or abiotic stresses are more effective in their application. Jiang (2016) reported that the inter-roots of graminaceous and leguminous plants were more suitable for colonization by *Trichoderma* species. This was because these crops were usually grown with long cropping cycles, fewer agricultural operations, and reduced amounts of pesticide and fertilizer, and thus their inter-root environment was more favorable for the growth and colonization of *Trichoderma* species (Jiang 2016). Therefore, we need to consider a variety of factors in the subsequent application to make the best effect of the inoculation of *Trichoderma* spp.

4 Conclusion and prospectives

Salinization has become an increasingly serious problem. With the increasing area of salinized arable land, ways to improve the salt resistance of crops and eventually increase their yields have become one of the important topics in the field of agriculture. As endophytic fungi, *Trichoderma* species have been shown to be effective in improving the salt resistance of plants, but the bibliometric analysis showed that relevant studies were limited. Subsequently, the meta-analysis of this study revealed that *Trichoderma* species could improve the salt resistance of plants through three main pathways: (1) promoting root development to absorb more nutrients and water, (2) enhancing the activity of antioxidant enzymes in plants to scavenge excessive ROS, and (3) increasing photosynthetic pigment synthesis and enhancing PSII's performance to improve the photosynthetic capacity of plants. Meanwhile, through our subgroup analysis showed that the effectiveness of *Trichoderma* inoculation was affected by various factors, such as salinity, duration of salinity, plant groups, photosynthetic type, and *Trichoderma* species.

Although *Trichoderma* species have achieved some effects and progress in improving plant salt resistance, it is worth noting that the current research on the mechanism of salt resistance enhanced by *Trichoderma* species has mainly focused on plant phenotypes. The mechanism of salt resistance has been elucidated by the dynamic changes in some physiological and biochemical indicators, and research on the genetic level is still relatively sparse. In addition, because of the complexity of the actual soil environment, the effectiveness of applying *Trichoderma* inoculation is often not as stable as in indoor experiments. Such applications face two main problems. First, *Trichoderma* species can differ greatly in their reproduction, survival, and competition in different soil types. Second, the survival of the inoculated *Trichoderma* strains is difficult to ensure, and multiple inoculations are often required. In respect of this, we propose the following directions for future research.

1. In-depth investigations of the genes related to the ability of *Trichoderma* species to induce resistance in plants should be carried out at the genetic level, using gene editing techniques to breed plant species with salt resistance.
2. The effects of the application of *Trichoderma* metabolites should be explored to produce more stable *Trichoderma*-based products.
3. Through microbial compounding, *Trichoderma* species could be mixed with other microbial strains to help them adapt to the complex soil environment and improve the salt resistance of plants.

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Declarations

Competing interests The authors declare no competing interests.

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