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Performance of halophytes in soil desalinization and its influencing factors: a meta-analysis

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Soil salinization threatening natural and agricultural production challenges global food security. Halophytes are of great interest in soil desalinization in recent years; yet, there is a lack of a comprehensive quantitative overview of biotic and abiotic factors for halophytes' desalinization performance across global scales. Here, a meta-analysis was conducted using 400 observations from 53 peer-reviewed studies to assess desalinization by halophytes in relation to 27 variables. Results showed that soil salinity was significantly decreased in halophytes field on average by 37.7% compared to control on a global scale ($p < 0.05$). Desalinization performance was better in cold and hot regions than in temperate regions, in dry regions than in wet regions, in alkaline saline soils than in neutral saline soils, and in conditions with low sand content than high sand content. Under aboveground harvest treatment, desalinization increased with the years of cultivation, while no trends were detected under no harvest treatment, indicating the importance of aboveground accumulation. Desalinization was not related to soil CaCO_3 content but was accompanied by soil structure improvement, nutrition enrichment, and microbe propagation, implying other root-microbe-soil interactions rather than CaCO_3 dissolution play important roles. Shoot biomass could be used as an indicator of the desalinization performance, and the performance would not be decreased due to the high uptake selectivity for K^+ over Na^+ . Notably, desalinization was similar in the pot experiments and field experiments, but pot experiments would magnify the contribution of aboveground salt accumulation to desalinization. Our findings can help to expand the applicability and efficiency of halophytes for sustainable agricultural development in saline soils.

KEYWORDS

saline soil, soil salinity, halophytic, desalination, phytoremediation, phytodesalination

Abbreviations: MAT, mean annual air temperature; MAP, mean annual precipitation; PET, potential evapotranspiration; AI, aridity index; BD, bulk density; SOC, soil organic carbon; TN, total nitrogen; AP, available phosphorus; AK, available potassium; MB, microbial biomass; LnRR, natural logarithm response ratio; LnRR++, weighted natural logarithm response ratio.

1 Introduction

The global population is expected to reach 9.7 billion by 2050, and it is estimated that agricultural production should increase by 70%–110% to meet global food demand (Tilman et al., 2011; FAO, 2021). Soil salinization, exacerbated by climate change and intensive land usage, impacts both natural and agricultural production and challenges global food security (Panta et al., 2014; Jesus et al., 2015; Eswar et al., 2021). It affects an area of more than 1 billion hectares in over 100 countries all over the world. Worse still, the amount of salt-affected land expanded continuously each year at a rate of approximately 1–2 million ha of land or even more (Qadir et al., 2014; Ivushkin et al., 2019; Hopmans et al., 2021), which means 50% of arable lands will be lost by the mid-21st century (Mahajan and Tuteja, 2005). Obviously, there is a contradiction between food security and accelerated soil salinization worldwide which puts an urgent of saline land utilization and remediation (Khanom, 2016; Litalien and Zeeb, 2020; Hopmans et al., 2021).

Owing to the limitation of fresh water resources, the improvement and utilization of saline soil gradually changed from conventional physical and chemical measures to comprehensive utilization of halophytes (Rozema and Flowers, 2008; Nouri et al., 2017; Litalien and Zeeb, 2020). Halophytes are naturally evolved salt-tolerant plants that are widely distributed in a variety of saline habitats, from coastal areas and salt marshes to drylands, providing a good perspective of saline agriculture (Rabhi et al., 2010a; Rozema and Schat, 2013; Panta et al., 2014; Nikalje et al., 2018; Barcia-Piedras et al., 2019). There has recently been an increased interest for halophytes in soil phyto-desalinization, particularly in developing countries, producing economic benefits while limiting soil erosion and environmental disturbance (Ravindran et al., 2007; Rabhi et al., 2010a; Barcia-Piedras et al., 2019). Halophytes are also considered to be an ideal alternative to glycophytes hyperaccumulators for phytoremediation of heavy metals pollution in contaminated saline soils, where most glycophytes cannot survive (Manousaki and Kalogerakis, 2011; Anjum et al., 2014; Wang et al., 2014).

However, there are still many concerns about this technology, including its universality, the influence of cultivated practice, and the possible mechanisms of desalinization (Shabala, 2013; Jesus et al., 2015). The performance can be influenced by environmental conditions, which directly or indirectly result in different patterns of water-salt migration (Rajkumar et al., 2013; Jesus et al., 2015; Eswar et al., 2021), and the differences may consequently affect the performance of halophytes desalinization. For example, in arid areas with scarce precipitation but strong evaporation, soil salinization is mainly due to the upward force driving the salt accumulation on the soil surface, while in humid and coastal areas the driving force of salinization may be related to seawater movements (Ketabchi et al., 2016; Khanom, 2016; Pauw et al., 2017; Eswar et al., 2021). Cultivated practices are important for subsequent crop cultivation, of which the desalinization duration is of great concern because the progress may take longer than traditional desalinization techniques, for it depends on the rate of ion extraction of halophytes and the improvement in physical-water properties due to the presence of root systems (Rabhi et al., 2010a; Shabala, 2013; Jesus et al., 2018). Halophytes selection will affect the desalinated soil layer because of the root growth and distribution

within soil layers, which may also affect subsequent crop root development and yields (Barrett-Lennard, 2002; Rabhi et al., 2010a; Liang and Shi, 2021). In addition to the factors affecting the performance of halophytes mentioned above, the possible mechanisms of halophytes desalinization need clarifying (Shabala, 2013; Jesus et al., 2015; Jesus et al., 2018; Litalien and Zeeb, 2020). Debate on the main mechanism contributing to soil remediation has yet to be settled, including aboveground salt accumulation and root-microbe-soil interactions which improve soil properties leading to salt leaching (Qadir et al., 2000; Rabhi et al., 2009; Rasouli et al., 2013). The mechanisms are crucial to improve the phytoremediation-beneficial traits to enlarge the applicability and effectiveness of halophytes desalinization.

So far, there are several narrative reviews on the tolerance of halophytes and the theoretical frameworks of possible mechanisms of their soil desalinization (Kronzucker and Britto, 2011; Rabhi et al., 2015; Nikalje et al., 2018; Hopmans et al., 2021), while all of the above concerns about halophytes desalinization performance need further clarification. Meta-analysis is a statistical method for quantitatively synthesizing the findings of previous studies, compared with traditional narrative reviews, providing more objective conclusions (Hedges et al., 1999; Liao et al., 2012; Leifheit et al., 2014). Since it was introduced into ecology in the 1990s, it has become an important means for summarizing evidence across studies to reach general conclusions (Liao et al., 2012; Leifheit et al., 2014; Alvarez et al., 2017; Song et al., 2019; Beyene et al., 2022), to find the main reasons for the inconsistent results between studies (Liao et al., 2012; Wang et al., 2021; Beyene et al., 2022; Hu et al., 2023), to uncover the underlying mechanisms (Wang et al., 2021; Beyene et al., 2022; Feng et al., 2022), and to find the existing problems and research prospects in the field (Leifheit et al., 2014; Alvarez et al., 2017; Song et al., 2019; Hu et al., 2023). It can be well revealed by meta-analysis for the general rule of the effect of plant growth such as cultivation (Alvarez et al., 2017; Hu et al., 2023), plantation (Liao et al., 2012; Wang et al., 2021), and non-native plant invasion (Beyene et al., 2022) on soil properties and its influencing factors and underlying ecological mechanisms. Here, we use a meta-analysis aimed to assess halophytes desalinization performance on a global scale and its influencing biotic and abiotic factors, and the desalinization mechanisms. The following aspects were analyzed in detail: 1) the relationships between desalinization by halophytes and their growing environment including climate and soil physical and chemical properties; 2) cultivated practices that would influence subsequent crops cultivation such as duration of halophytes planting and lifeforms selection influencing desalinization within different soil layers; 3) the potential mechanism of aboveground and underground parts leading to desalinization. We expect these results would help to better understand and expand the applicability and efficiency of halophytes in ongoing saline agriculture.

2 Materials and methods

2.1 Data compilation

Peer-reviewed publications were collected from January 1990 to September 2022 by searching Web of Science [included 1) WoS Core

Collection, 2) BIOSIS Previews, 3) Inspec, 4) Chinese Science Citation Database, 5) Derwent Innovations Index, 6) KCI-Korean Journal Database, 7) MEDLINE and 8) SciELO Citation Index] with a search of (*halophyt*) AND (*desalin* OR *restorat* OR *remediat* OR *reclasm* OR *ameliorat* OR salt remov* OR “soil propert*” OR “electrical conductivity” OR soil salt content OR “soil salinity” OR “total dissolved solids”) (topic). A total of 2,885 publications were collected and we excluded those titles that showed reviews or meta-analysis or conducted in aquatic ecosystems. Then articles were screened by the following criteria: 1) studies needed to have a control, including bare land with no halophytes or pre-soil salinity condition, but excluding that used bulk soil as a control for rhizosphere soil; 2) studies needed to report indicators that can reflect soil salinity. With the criteria mentioned above, we found that studies on soil salinity measurements are relatively rare compared with aboveground measurements. Plus 4 pieces of literature obtained from the review, this analysis finally included 53 studies. A total of 400 trials were obtained by the following criteria: 1) different species studied within each publication were treated as parallel experiments that generated different trials; 2) multiple trials within each publication obtained from different chosen factors were treated as independent (Lajeunesse, 2011; Leifheit et al., 2014); 3) additional treatments such as straw mulching, chemical amendments addition during the experiment share a same control with halophytes field were not independent and thus excluded; 4) multiple trials were not independent when they were measured in time sequence and shared a same before planted control, and thus the measures of the last time sequence were selected (Lajeunesse, 2011; Chen et al., 2013; Leifheit et al., 2014).

Apart from soil salinity data (salt content, electrical conductivity, total dissolved solids), soluble Na^+ , K^+ , Ca^{2+} , Mg^{2+} , Cl^- , SO_4^{2-} and HCO_3^- content, concentrations of Zn, Cu, Cd, and Pb, climatic data (mean annual air temperature, MAT, aridity index, AI, mean annual precipitation, MAP, potential evapotranspiration, PET), soil properties (bulk density, BD, sand content, CaCO_3 content, pH value, soil organic carbon, SOC, total nitrogen, TN, available phosphorus, AP, and available potassium, AK, soil microbial biomass, MB), plant growth (biomass, shoot Na^+ , K^+ , and Cl^- content and the amount of Na^+ and Cl^- removed by shoot), duration and setting of experiment, harvest or not, soil layers, and lifeforms (annual and perennial) were collected. If the author did not record climate data, then they were obtained from the studies at the same site, otherwise, MAT, MAP, and PET were obtained from the CRU TS database produced by the National Centre for Atmospheric Science (NCAS) (version 4.06, <https://crudata.uea.ac.uk/cru/data/hrg/>), and AI was calculated by the formula PET/MAP . The missing soil data were collected from studies at the same site but not from the database, because they were generally far from control and treated treatments in studies and the dataset was a little outdated. Because of the lack of plant root measurements and plant total salt content, only shoot Na^+ and Cl^- content was used here, for NaCl typically dominates saline soils at elevated concentrations (Kronzucker and Britto, 2011). To clarify the contribution of shoot accumulation to soil remediation, trials without harvest were excluded. With missing “harvest” data, trials of natural conditions were assigned as no-harvest while those of pot experiments were assigned as harvest. Trials of pot experiments

were not included in the analysis of the effects between soil layers, and trials of natural experiments were excluded from the analysis of the relationships between desalination and experiment duration.

2.2 Data analysis

Meta-analysis was conducted in the statistical software MetaWin v. 2.1. The effects of halophytes cultivation on desalination and other soil properties were evaluated through natural logarithm response ratio (LnRR), which allows combining different units of a variable and is commonly employed in ecology (Hedges et al., 1999; Alvarez et al., 2017; Beyene et al., 2022). For each observation, the LnRR was calculated as (Hedges et al., 1999):

$$\text{LnRR} = \ln\left(\frac{X_t}{X_c}\right) = \ln X_t - \ln X_c \quad (1)$$

with a variation (v) of:

$$v = \frac{s_t^2}{n_t X_t^2} + \frac{s_c^2}{n_c X_c^2} \quad (2)$$

where X_t and X_c are the mean values of soil properties in the halophytes planted group and in control, respectively. s_t and s_c are the standard deviations (SD), and n_t and n_c represent the number of samples. Standard error (SE) of the variables was transformed to SD by the formula $\text{SE} \times \sqrt{n}$, where n is sample size. For each research study, the weighting factor (W) was measured as the inverse of the variance ($1/v$).

We assumed that a random effect model would fit our data set better based on the hypothesis that effect sizes did not share the same true value across all studies (Gurevitch and Hedges, 1999; Hedges et al., 1999). Then between-experiment variance (τ^2) was calculated (Hedges et al., 1999):

$$\tau^2 = \frac{\left(\sum_i W_i (\text{LnRR}_i)^2 - \frac{\left(\sum_i W_i \text{LnRR}_i \right)^2}{\sum_i W_i} \right)}{\sum_i W_i - \frac{\sum_i W_i^2}{\sum_i W_i}} - (n-1) \quad (3)$$

then the weighting factor for each LnRR datapoint was recalculated as:

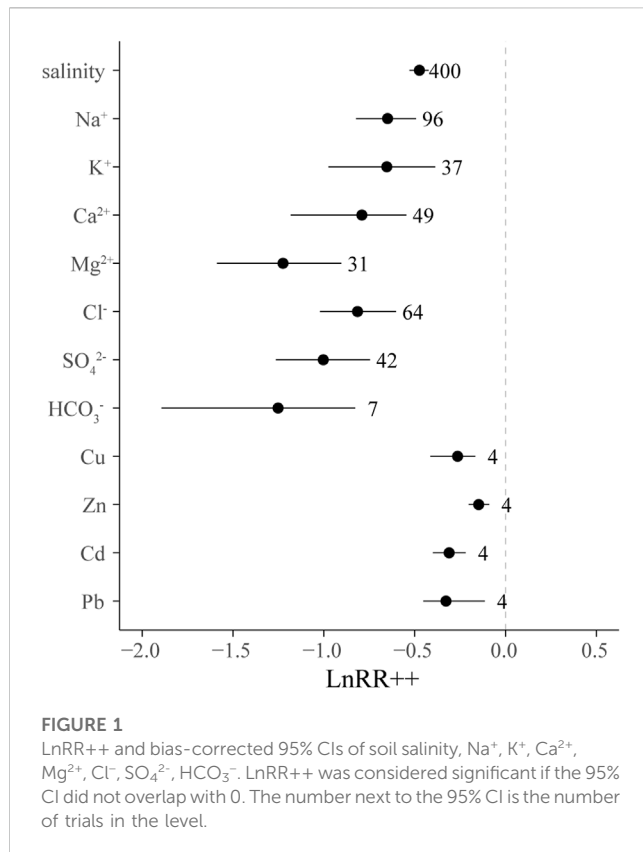
$$W_i^* = \frac{1}{v_i + \tau^2} \quad (4)$$

and the overall weighted natural logarithm response ratio (LnRR₊₊) of desalination to halophytes plantation was computed by:

$$\text{LnRR}_{++} = \frac{\sum_i \text{LnRR}_i \times W_i^*}{\sum_i W_i^*} \quad (5)$$

Their corresponding confidence intervals (CIs) were produced by bootstrapping function (3,999 iterations) (Leifheit et al., 2014; Alvarez et al., 2017; Hu et al., 2023). Positive values indicated an increase in soil salinity after halophytes plantation and negative values indicated a decrease in salinity. If 95% CIs were separated from zero-line, significant desalination effects were considered by halophytes, otherwise, there is no difference between the halophytes-planted groups and control.

LnRR₊₊ was transformed to effect size (%) according to the following equation:



$$Effect\ size\ (\%) = (e^{LnRR_{++}} - 1) \times 100\% \quad (6)$$

The Q test was performed to evaluate between-group heterogeneity and the subcategories. Categorical factors were considered statistically different if the significance level of Q statistics between groups was <0.05. Linear meta-regression was performed to examine the relationships between LnRR and continuous predictor variables using restricted maximum likelihood estimator (RMLE) method (Song et al., 2019; Sang et al., 2022). Publication bias was determined by using Egger's regression and fail-safe numbers (Supplementary Table S1) using "metafor" package in R software and MetaWin v. 2.1, respectively (Chen et al., 2013; Sang et al., 2022).

3 Results

3.1 Desalination performance of halophytes on a global scale

Positive values indicated an increase in soil salinity after halophytes cultivation and negative values indicated a decrease in salinity. If 95% CIs were separated from zero-line, significant desalination effects were considered by halophytes, otherwise, there is no difference between the halophytes-planted groups and control (Leifheit et al., 2014; Alvarez et al., 2017). Soil salinity was significantly decreased in halophytes field on average by 37.7% compared to control on a global scale ($p < 0.05$). Soluble ions (Na⁺, K⁺, Ca²⁺, Mg²⁺, Cl⁻, SO₄²⁻, HCO₃⁻) and heavy metal

concentrations (Cu, Zn, Cd, and Pb) significantly decreased as well ($p < 0.05$) (Figure 1).

3.2 The relationships between desalination and environmental factors

Meta-regression takes the result of each independent experiment as an index of effect, and analyzes the correlations with environmental factors, which can reveal the desalination performance of halophytes in different environments (Beyene et al., 2022). A convex linear correlation was found between LnRR_salinity and MAT in the range of -1.3°C–29.1°C, and LnRR_salinity was relatively high at around 13 °C ($R^2 = 0.08$, $p < 0.01$) (Figure 2). LnRR_salinity was negatively linear correlated with AI ($R^2 = 0.04$, $p < 0.01$), accompanied by a positive linear correlation with MAP ($R^2 = 0.04$, $p < 0.01$), but a negative linear correlation with PET ($R^2 = 0.03$, $p < 0.01$).

There is a concave linear relationship between sand content and LnRR, and LnRR_salinity increases significantly when it is greater than 75% ($R^2 = 0.12$, $p < 0.01$) (Figure 2). LnRR_salinity showed a negative linear correlation with pH value ($R^2 = 0.05$, $p < 0.01$), but no relationships between LnRR_salinity and bulk density or CaCO₃ content were found in the analysis ($p > 0.05$).

3.3 Cultivated practices regulating the desalination performance

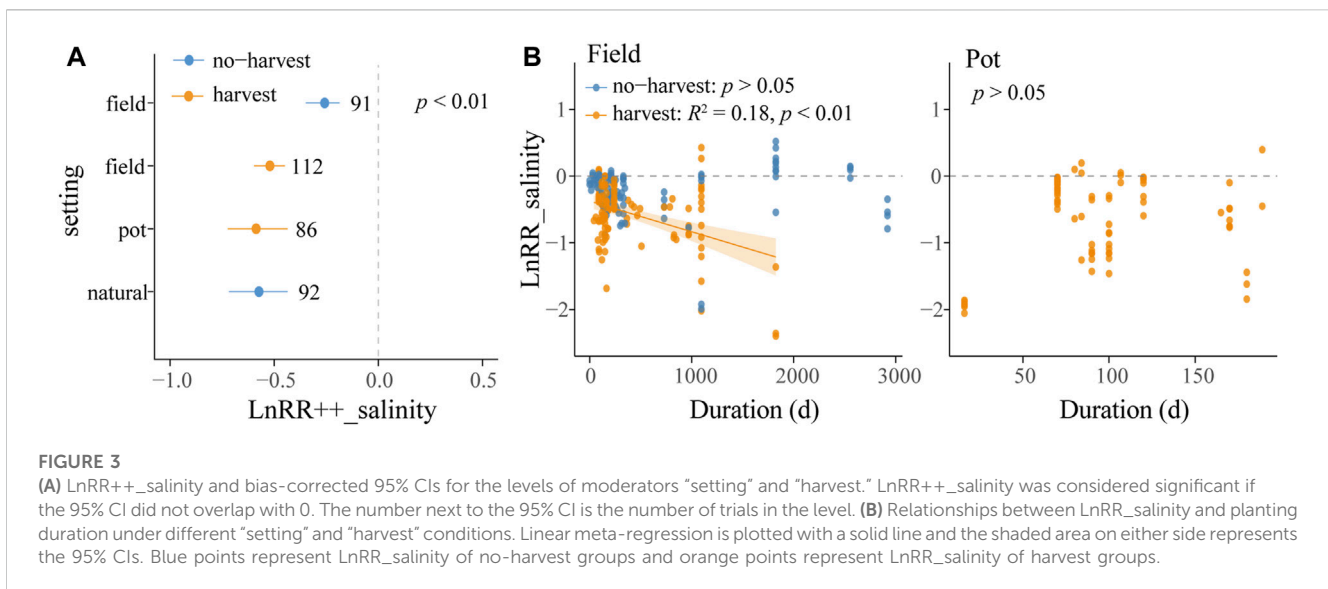
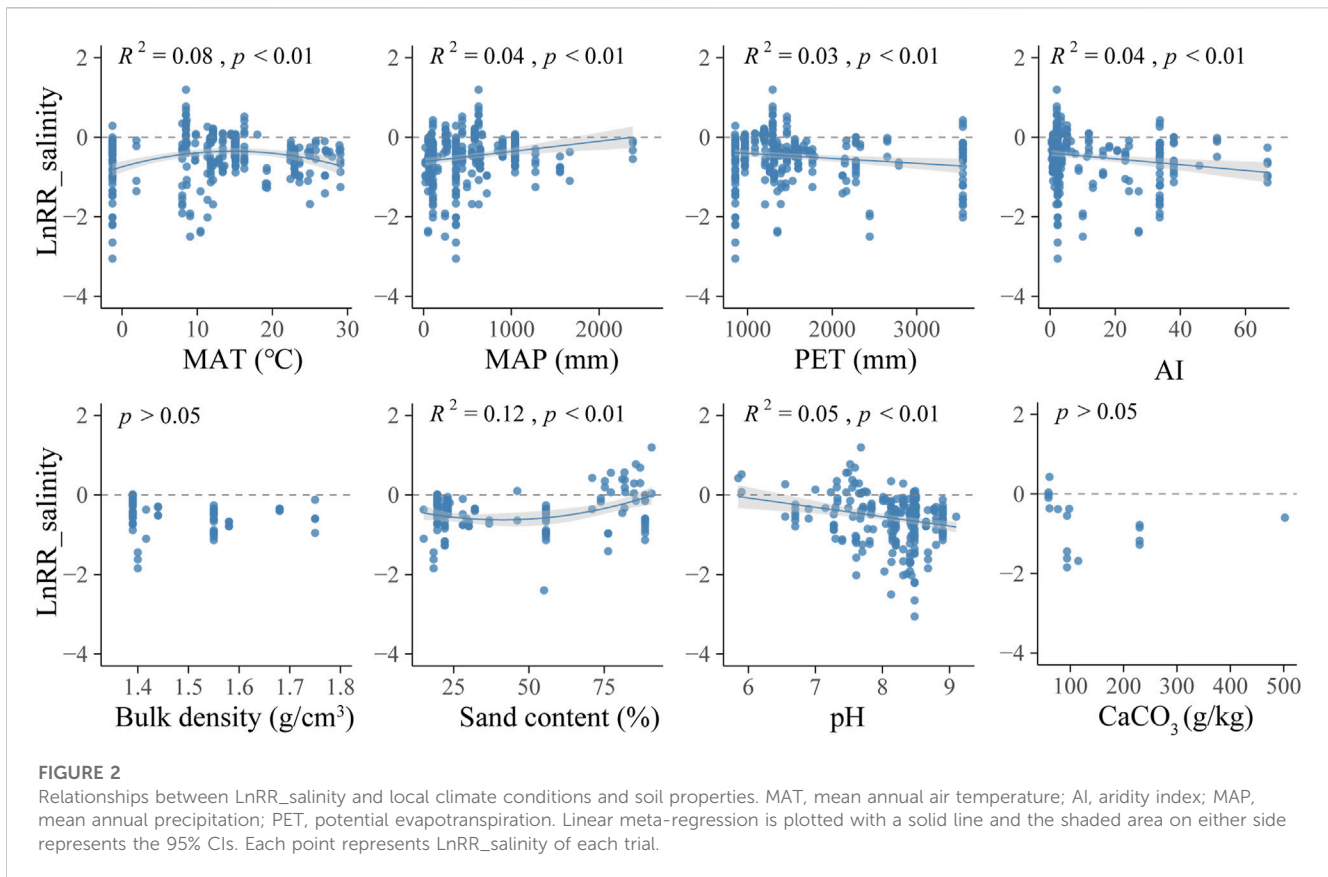
Experiment settings significantly influenced LnRR++_salinity, and LnRR++_salinity exhibited a significant difference between harvest practices in field experiments ($p < 0.05$). Effect sizes were -22.3% ($p < 0.05$) in field experiments under no-harvest conditions, -39.4% ($p < 0.05$) in field experiments under harvest conditions, -42.3% ($p < 0.05$) in pot experiments, and -43.3% ($p < 0.05$) in natural experiments ($p < 0.05$) (Figure 3).

In the range of 0 to about 3,000 days experiment duration, a negative linear correlation was found between LnRR_salinity and experiment duration in harvested field conditions ($R^2 = 0.18$, $p < 0.05$) (Figure 3), and no correlation was detected in no-harvested conditions and pot experiments. No correlation was found between LnRR_salinity and experiment duration in the range of 0–180 days ($p > 0.05$).

Desalination effects showed significant differences among different soil layers ($p < 0.05$) (Figure 4). Effect sizes of annual halophytes were -39.4% ($p < 0.05$), -19.9% ($p < 0.05$) and -2.66% ($p > 0.05$) in 0–30 cm, 30–60 cm, and >60 cm soil layers, respectively. Those of perennial halophytes were -39.1% ($p < 0.05$), -47.0% ($p < 0.05$) and -27.1% ($p > 0.05$) in 0–30 cm, 30–60 cm and >60 cm soil layers, respectively.

3.4 Shoot salt accumulation in halophytes

LnRR_salinity was negatively correlated with shoot biomass ($R^2 = 0.08$, $p < 0.01$) and Cl⁻ removal by shoot biomass ($R^2 = 0.16$, $p = 0.03$), and positively correlated with shoot Na⁺ content ($R^2 = 0.07$, $p = 0.04$). In pot experiments, a negative linear correlation



was found between LnRR_salinity and shoot biomass ($R^2 = 0.11, p < 0.01$), shoot Cl^- content ($R^2 = 0.42, p < 0.01$) and Cl^- removal by shoot biomass ($R^2 = 0.44, p = 0.03$), and no relationship was found between LnRR_salinity and shoot Na^+ content and Na^+ removal by shoot ($p > 0.05$). In field experiments, no linear correlation was

found between LnRR_salinity and shoot biomass, shoot Na^+ content, shoot Cl^- content, Na^+ removal by shoot biomass or Cl^- removal by shoot biomass ($p > 0.05$) (Figure 5).

In both pot and field experiments, no relationship was found between LnRR_salinity and shoot K^+ content or shoot Na^+/K^+ ($p > 0.05$).

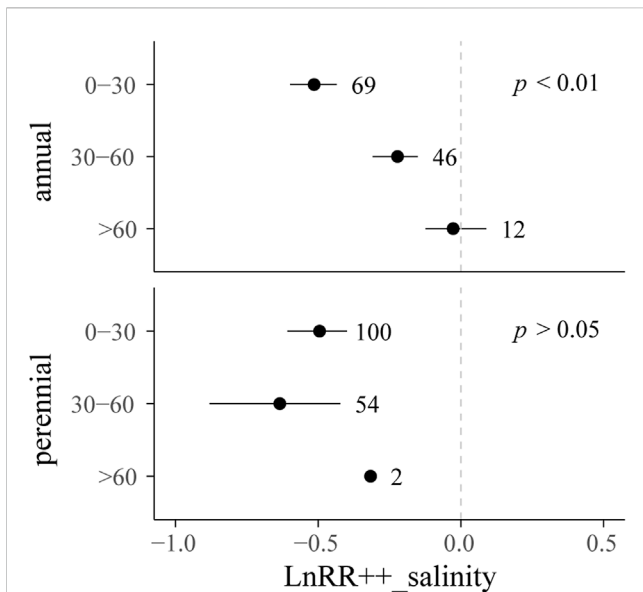


FIGURE 4
LnRR++_salinity and bias-corrected 95% CIs for the levels of moderators "lifeform" and "soil layer." LnRR++_salinity was considered significant if the 95% CI did not overlap with 0. The number next to the 95% CI is the number of trials in the level.

3.5 The relationships between desalination and response of soil properties

Correlations between desalination performance and LnRR_salinity of soil properties can help to reveal the underground mechanisms during desalination (Wang et al., 2021; Beyene et al., 2022). LnRR_salinity exhibited significantly positive linear correlated with LnRR_BD ($R^2 = 0.30, p < 0.01$), LnRR_pH ($R^2 = 0.02, p = 0.04$), and LnRR_AK ($R^2 = 0.19, p < 0.01$), negative correlated with LnRR_SOC ($R^2 = 0.11, p = 0.04$), LnRR_TN ($R^2 = 0.08, p = 0.01$), and LnRR_MB ($R^2 = 0.82, p < 0.01$), and not correlated with LnRR_AP ($p > 0.05$) (Figure 6).

4 Discussion

4.1 Climate and soil properties affecting desalination by halophytes

It has been studied that MAT is one of the most important drivers affecting the salinization process, and plants could mitigate the sensitivity of soil surface temperature change with air temperature (Han et al., 2010; Ma et al., 2018; Eswar et al., 2021). The convex linear regression between LnRR_salinity

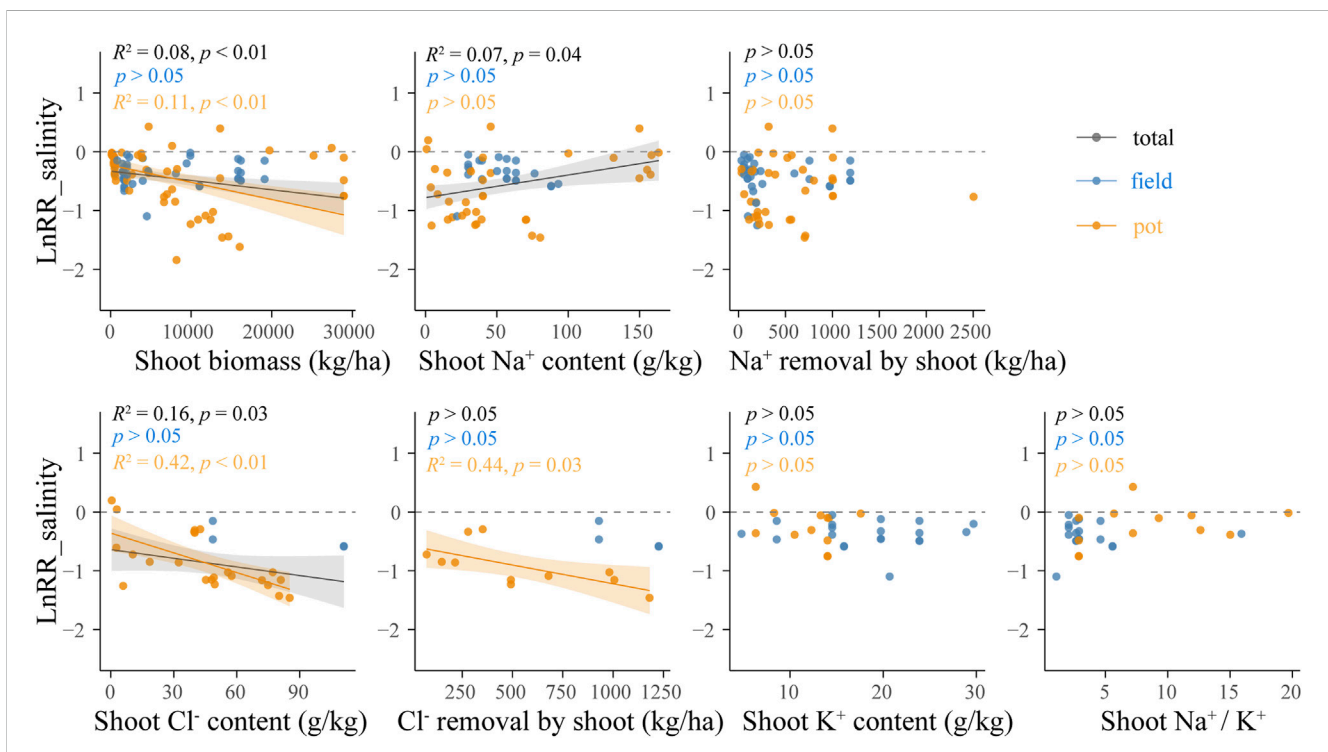


FIGURE 5
Relationships between LnRR_salinity and shoot biomass, shoot Na⁺, K⁺ and Cl⁻ content, Na⁺ and Cl⁻ removal by shoot, and shoot Na⁺/K⁺ under field and pot conditions. Linear meta-regression is plotted with a solid line and the shaded area on either side represents the 95% CIs. Black: all data; blue: field; orange: pot.

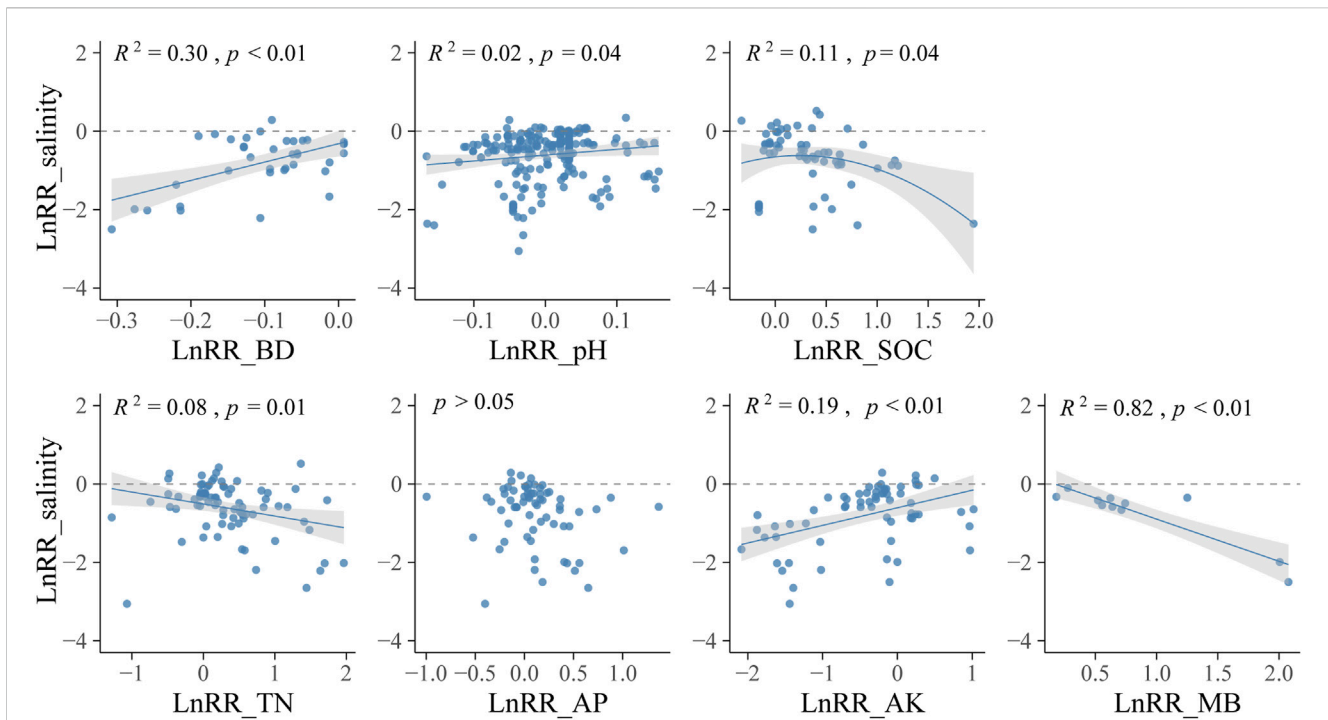


FIGURE 6 Relationships between LnRR_salinity and LnRR_salinity of soil properties. BD, bulk density; SOC, soil organic carbon; TN, total nitrogen; AP, available phosphorus; AK, available potassium; MB, microbial biomass. Linear meta-regression is plotted with a solid line and the shaded area on either side represents the 95% CIs. Each point represents LnRR_salinity of each trial.

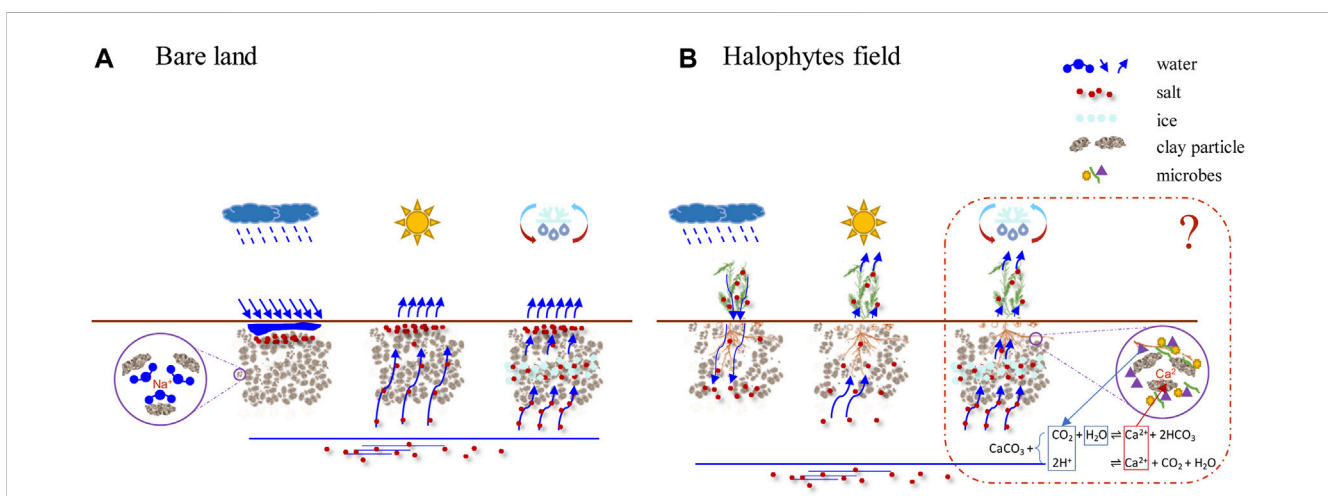


FIGURE 7 Role of halophytes in soil desalination. (A) Bare land, (B) Halophytes field. Basically, we proposed that halophytes cultivation would decrease soil salt content, improve soil structure, and increase soil organic carbon, nutrients, and microbial biomass in the rooting zone. The relevant mechanisms were compiled from the results of previous publications (Panta et al., 2014; Nouri et al., 2017) and this study, including aboveground salt accumulation, an increase of salt leaching, land cover decreasing evaporation, and water table reduction. The red dotted line box shows the differences with previous studies and possible mechanisms that need further clarification, including the contribution of CaCO₃ dissolution to desalination and the required environmental conditions, the multiple roles of microbes in halophytes desalination, and the possible influence of salt accumulation caused by freeze-thaw cycles.

and MAT in the range of -1.3°C – 30°C showed larger effects of halophytes desalination in cold and hot regions. This was consistent with the results of previous studies indicating that in hot areas, soil desalination by halophytes could be attributed to canopy shading resulting in the alleviation of the high-

temperature driving salinization process, such as soil evaporation (Panta et al., 2014; Jian et al., 2015; Nouri et al., 2017; Eswar et al., 2021). The amplification of soil desalination effects in cold areas might be related to the influence on soil freeze-thaw process. Salt in the soil profile would accumulate at

the surface layer in the freezing period and initial evaporation period due to large evaporation, which are also the main causes of soil salinization in cold and arid areas (Han et al., 2010; Zong et al., 2022). The increase of vegetation or stubble or soil moisture may migrate the temperature change and reduce the evaporation, which might influence the accumulation of salt on the soil surface (Flerchinger et al., 2003; Wu et al., 2019; Qin et al., 2021).

There was a negative correlation between LnRR_salinity and AI, indicating that in arid and semiarid areas, most of which secondary salinized, soil desalinization by halophytes could be better than in wet areas with high rainfall and low evaporation. As Esvar et al. (2021) pointed out, the underlying mechanisms of salinization are different between arid areas and humid coastal areas. In arid areas, scarce precipitation and a large amount of evaporation occur, and vegetation could reduce soil evaporation by increasing coverage and improving soil texture (Puigdefábregas, 2005; Jian et al., 2015; Cao et al., 2020). While in coastal areas with high precipitation providing downward forces, salinization is often caused by seawater movements, i.e., intrusion and floods (Katabchi et al., 2016; Khanom, 2016; Pauw et al., 2017). Therefore, halophytes applied in such areas should be better considered to gradually improve soil properties in the meantime provide economic benefits. Relationships between desalinization and environmental conditions indirectly corroborated the importance of land cover by halophytes in inhibiting salinity by reducing surface temperature and evaporation (Panta et al., 2014; Nouri et al., 2017).

Desalinization performance was better under low sand content conditions than that under high sand content conditions where salinity even increased. This was consistent with the results of previous studies in which soil with a high content of clay and silt particles has a strong ability to hold water and salt, and the reduction of soil salt content by halophytes in such conditions might be partially due to the penetration of soil by roots to increase soil pores and thus increase water infiltration and salt leaching (Jesus et al., 2015; Nunes et al., 2015). However, soil with high sand content has poor water and salt holding capacity and weakened upward-driven force, which might not only lead to relatively lower soil salt content before plantation but also increase soil water and salt holding capacity by the input of organic matter and their positive effects on soil aggregations (Zhang et al., 2016a; Cao et al., 2020; Li et al., 2020). This indicated that soil desalinization by halophytes may be more beneficial to reduce salt surface accumulation and increase salt leaching and infiltration in the areas with heavy topsoil and loose deep soil.

During the alkalization process, Na⁺ in the soil solution enters the soil colloid, so that the soil colloid contains more replaceable sodium (Litalien and Zeeb, 2020). When +1 charged cations dominate soils, clay particles are especially dispersed, resulting in a poor soil structure with few macropores and thus increasing water evaporation and reducing water infiltration (Litalien and Zeeb, 2020). In this study, it was found that desalinization was greater in the area of high pH, which may be owing to the efficient rhizosphere processes in such area. Soil pH value could be reduced by rhizosphere processes, such as root respiration or root exudates which further improve soil structure (Qadir et al., 1996; Qadir et al., 2005; Akhter et al., 2003).

4.2 Cultivated practices affecting desalinization by halophytes

The effect of experiment duration on LnRR_salinity was correlated only with field experiments under harvest conditions, showing that continuous planting of multiple growing seasons would decrease salinity to a greater degree. This was consistent with the results of previous studies indicating under non-harvest conditions, salt taken up by halophytes could be returned to the soil by leaf shedding on the surface, and this might even include salt taken up from groundwater (Feng et al., 2018; Cao et al., 2020). Whether in pot or field experiments planting for one growing season, no increase in desalinization was found with the extension of planting duration, indicating seasonal variations acting on phytodesalination capacity, because of different water movements and root respiration within seasons (Qadir et al., 2007; Rabhi et al., 2010b; Feng et al., 2018; Liang and Shi, 2021). The study of seasonal variations of halophytes desalinization could be helpful in the application of soil improvement performance and to arrange the later crops (Rabhi et al., 2010a; Rabhi et al., 2010b).

The desalinization of halophytes performed mainly within 0–60 cm soil layers, and the soil layer deeper than 60 cm was not the case. This was consistent with the results of previous reviews in which the desalinization effect was mainly limited to the rooting zone (Qadir et al., 2000). The roots of annual plants are mainly distributed in the range of 0–30 cm layer, while perennials have deeper root distribution and root biomass reserves underground (Barrett-Lennard, 2002; Monti and Zatta, 2009). Due to the differences in root growth between annual plants and perennial plants, the soil desalinization capacity of annual plants is greater in 0–30 cm layer than that of 30–60 cm layer, and perennial plants performed similarly in both layers. In addition, annual plants are fast-growing, and have a large amount of seed, while perennials are slow to establish but can be harvested continually after successful establishment. The species of different lifeforms can be selected according to different purposes (Nikalje et al., 2018).

4.3 Aboveground accumulation and root-soil interaction of desalinization by halophytes

Aboveground accumulation and root-soil interaction are two main parts of soil desalinization. Studies proved the potential of halophytes for salt uptake (Ravindran et al., 2007; Rabhi et al., 2009; Rabhi et al., 2010a), while Gharaibeh et al. (2011) suggested that salt uptake in aboveground biomass is a small percentage comparing with original salt content or salt input by irrigation in saline soils and, in consequence, root rhizosphere processes would be the main mechanism of desalinization. This analysis showed that harvest significantly increased desalinization, and desalinization was detected to be greater with larger shoot biomass, indicating the important contribution of aboveground salt accumulation to desalinization and that shoot biomass could be used as an indicator of the desalinization performance of halophytes. However, no correlation was detected between LnRR_salinity and Na⁺ or Cl⁻ removal of shoot in field

conditions, indicating root-soil interaction also played an important role in phytodesalination (Qadir et al., 1996; Qadir et al., 2005; Akhter et al., 2003; Liang and Shi, 2021). There have been some possible mechanisms of soil desalination in plant root-microbe-soil processes (Jesus et al., 2015; Rabhi et al., 2015; Liang and Shi, 2021). Respiration of roots and microorganisms, root exudates, and decomposition of organic matter generating acid matter reduce the soil pH of alkaline soil and dissolve CaCO_3 , and then Ca^{2+} exchange Na^+ from soil colloids (Qadir et al., 1996; Qadir et al., 2005); roots exudates and turnover and the propagation of microorganisms increase soil organic matter; roots gather and penetrate the soil to improve soil pore size and increase precipitation interception and runoff infiltration (Li et al., 2020; Rathore et al., 2022). In this study, desalination performance is accompanied by the decrease of BD and pH and the increase of SOC, TN, and MB, which further corroborates the important roles of root-soil interactions and the improvement of soil structure and soil fertility (Figure 6). However, no relationship between LnRR , salinity of soil salinity and CaCO_3 content. It should be noted that the precipitation and dissolution of CaCO_3 co-exist in soil, affected by climatic conditions, land use types, and soil properties. CaCO_3 content may show different trends during vegetation restoration (Liu et al., 2017; Gao et al., 2018; Xu et al., 2021). The change of CaCO_3 content and the contribution of CaCO_3 dissolution to phytodesalination needs further clarification.

Plant inputs stimulate the activity and size of the soil microbial community, which could enhance the nutrient cycle and reduce soil pH of saline-alkali soil (Li et al., 2022; Liu et al., 2022; Rathore et al., 2022). Microbial biomass and the resulting microbial necromass, part of which can be relatively recalcitrant, provides binders for aggregates that physically protect soil organic matters and improve soil structure (Bronick and Lal, 2005; Zhu et al., 2018; Zhu et al., 2020; Shao et al., 2022). In this study, MB increased in halophytes field, and the response showed a strong correlation with desalination effect, which highlights the importance of microbes in the process of soil improvement during desalination (Figure 6). In addition, microbes play a critical role in developing plant salt tolerance strategies by regulatory mechanisms including ions transportation and homeostasis, osmotic regulation, hormone balance, antioxidant mechanisms, and other stress signaling (Acuña et al., 2019; Salwan et al., 2019; Diao et al., 2022; Wang et al., 2022). The interaction between plants and microbes suggests that halophytes promote microbial colonization compared with bare land, and microbes could directly or indirectly affect soil desalination by improving soil properties and promoting plant growth (Figures 5, 6). However, many pieces of research focus on halophytes root-associated microbes improving salt tolerance of crops (Acuña et al., 2019; Salwan et al., 2019; Wang et al., 2022), and halophytes effects on soil pH, nutrients, structures, and microbes (Li et al., 2022; Liu et al., 2022; Rathore et al., 2022). There is a clear need for more studies on halophyte-microbe-soil interactions, especially the multiple roles of microbes in halophytes desalination.

In some areas, high soil salinity is accompanied with high concentrations of bioavailable heavy metals. This particularly occurs in coastal areas where received industrial and urban wastes, and in arid and semi-arid regions where mining and

agricultural practices contribute to the increase of both heavy metals and salinity (Duarte et al., 2010; Wang et al., 2014; Lutts and Lefèvre, 2015; Guan et al., 2018). In the face of the combination of salt and heavy metals pollution, it is impossible for glycophytes accumulators to remediate these soils, because glycophytes cannot survive in saline soils, contrary to halophytes. Halophytes are now receiving increasing attention as potential candidates for remediation of these heavy metal-polluted saline soils (Manousaki and Kalogerakis, 2011; Wang et al., 2014; Lutts and Lefèvre, 2015). Studies about phytoremediation by halophytes mainly focused on the effect of salinity on heavy metals accumulation and distribution characteristics (Manousaki and Kalogerakis, 2009; Zhang et al., 2016b; Kahli et al., 2021), and the mechanisms of salinity alleviating heavy metals toxicity and promoting growth (Ghnaya et al., 2007; Bankaji et al., 2016; Zhou et al., 2018; Patel and Parida, 2021), indicating the importance of salinity on heavy metals phytoremediation. These results could also suggest that the interactions of salt and heavy metals have effects on plant growth and, in turn, on desalination (Bankaji et al., 2016; Zhang et al., 2016b; Zhang et al., 2020). However, few studies investigated the salinity and heavy metals interaction effects on soil desalination. As the salinization process intensifies, soil desalination could be taken into consideration in the assessment of halophytes for the phytoremediation of heavy metals contaminated saline soils.

Na^+ and K^+ compete for binding sites of roots in saline soil due to the similarity of physical and chemical properties. Jesus et al. (2015) implied that plants that absorb a lot of potassium might increase the potential requirements for nutrients or indicate that the plants are highly selective to K^+ over Na^+ . As a consequence, sodium uptake would be less in this kind of plants. However, K^+ plays a vital role in plants, and halophytes need to maintain a certain ratio of sodium to potassium (Matinzadeh et al., 2013; Percey et al., 2016). This analysis showed that desalination capacity did not correlate with shoot K^+ content, indicating that halophytes with high selectivity for K^+ in their roots may not reduce their desalination capacity, which further suggests that appropriate K application could be permitted during phytodesalination.

In this study, desalination by halophytes was similar in the pot experiments and field experiments (Figure 3), and shoot Cl^- accumulation contributed more to desalination in pot experiments than in field experiments (Figure 5; Supplementary Figure S2). Pot experiments could control leaching (Qadir et al., 1996; Qadir et al., 2005; Rabhi et al., 2009; Gharaibeh et al., 2011), thereby soluble ions that should have been leached out of the rhizosphere would be absorbed by the plants. So, it should be noted that pot experiments would magnify the contribution of aboveground salt accumulation to desalination.

5 Conclusion and further perspectives

Our results provide insights into how the desalination performance depends on abiotic and biotic experimental conditions and its desalinated mechanisms. Results showed that desalination performance was better in cold and hot regions than in temperate regions, in dry regions than in wet regions, in alkaline saline soils than in neutral saline soils, and in conditions with low

sand content than high sand content. Under aboveground harvest treatment, desalinization increased with the years of cultivation, while no trends were detected under no harvest treatment, indicating the importance of aboveground accumulation. Desalinization was not related to soil CaCO₃ content but was accompanied by soil properties improvement, implying other root-soil interactions rather than CaCO₃ dissolution play important roles. Shoot biomass could be used as an indicator of the desalinization performance, and the performance would not be decreased due to the high uptake selectivity for K⁺ over Na⁺. Desalinization of annuals mainly happened in 0–30 cm soil layers, and that of perennials happened in 0–60 cm layers. Desalinization was similar in the pot experiments and field experiments, but it should be noted that pot experiments would magnify the contribution of aboveground salt accumulation to desalinization.

Our results corroborate some mechanisms of phytodesalination, including the decrease of evaporation and soil surface temperature, salt accumulation in shoot biomass, and the improvement of soil properties. Meanwhile, we found some mechanisms that need to be verified and explored (Figure 7). Future research should be focused on: to verify the change of soil CaCO₃, the contribution of CaCO₃ dissolution to desalinization, and its required environmental conditions; to uncover halophyte-microbe-soil interactions affecting desalinization, especially the multiple roles of microbes in halophytes desalinization; to explore how halophytes influence the process of salt accumulation caused by freeze-thaw cycles. Furthermore, the exploitation of the economic value of halophytes is still critical to popularize the technology of phytodesalination.

Data availability statement

The raw data supporting the conclusion of this article will be made available from the corresponding authors upon reasonable request, without undue reservation.

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Author contributions

SW and JL: conceptualization, writing and analysis. YL: analysis and methodology. YW: visualization. CT: supervision and funding acquisition. All authors contributed to the article and approved the submitted version.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2023.1198540/full#supplementary-material>

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