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Saline soil desalination by honeysuckle (*Lonicera japonica* Thunb.) depends on salt resistance mechanism

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ABSTRACT

Honeysuckle (*Lonicera japonica* Thunb.) is a traditional medicinal plant in China. This study aimed to investigate the relation between salt tolerance mechanism in honeysuckle and phytodesalination of saline soil through field trial. In April, 2014, honeysuckle plants were transplanted to non-saline and moderate saline plots. Six months later, Na^+ concentration, Na^+ adsorption ratio and electrical conductance in tilth soil were significantly lowered by honeysuckle in moderate saline plots, suggesting that saline soil was desalinized. Due to the inhibition on plant growth, the estimated phytodesalination capacity by shoot Na^+ accumulation was only 8.71 kg Na^+ ha^{-1}, which seemed very limited compared with succulent halophytes. Therefore, soil desalination by honeysuckle should depend on Na^+ leaching rather than shoot Na^+ accumulation. Respiration rate and Na^+ extrusion in roots were elevated by salinity, and they were significantly and positively correlated, indicating the importance of root respiration for resisting Na^+ uptake. The elevated root respiration might aid in dissolving calcite by releasing more CO_2 into soil, and consistently, Ca^{2+} concentration in tilth soil was remarkably increased by honeysuckle in moderate saline plots in contrast to no significant change in non-saline plots. As a result, Na^+ leaching could be facilitated, as Na^+ at the exchange site would be efficiently replaced by Ca^{2+}. In conclusion, salt-induced elevation of root respiration enhanced salt resistance of honeysuckle by increasing Na^+ extrusion and could assist in desalinizing saline soil by improving Na^+ leaching.

1. Introduction

There is large area of abandoned saline land in coastal zone in the world, and a promising choice is to develop saline agriculture by using salt tolerant economic crops in these regions (Rozema and Flowers, 2008; Panta et al., 2014; Qin et al., 2015). Salinity inhibits plant growth and reduces crop yield. However, saline soil can be rehabilitated by plants with the decrease of soil salinity and Na^+ concentration, and this plant-based method is called phytoremediation (Qadir et al., 2007). In contrast to applying chemical reagents, phytoremediation is low-cost and environmentally friendly for desalinizing saline soil (Qadir and Oster, 2004).

Na^+ can interfere with metabolism in plant cell and is the primary toxic component for plant growth (Zhu, 2003; Munns and Tester, 2008). High soil Na^+ concentration is considered as the principle limiting factor for plant growth in coastal land, and accordingly, phytoremediation mainly aims to reduce Na^+ concentration in saline soil (Qadir et al., 2007). There are two major phytoremediation mechanisms including shoot Na^+ accumulation and improving Na^+ leaching to deeper soil. In regions with poor drainage and low precipitation, shoot Na^+ accumulation seems more important. Compared with glycophytes, succulent halophytes can efficiently sequester Na^+ into vacuole for protecting cytoplasm against ionic toxicity (Flowers and Colmer, 2008; Lv et al., 2012), and the accumulated Na^+ serves as a cheaper osmolyte than organic compounds to resist salt-induced osmotic stress (Munns and Tester, 2008). Consequently, succulent halophytes can accumulate a large amount of Na^+ in the shoot and are optimal materials for soil remediation in these regions (Zhao, 1991; Ravindran et al., 2007; Rabhi et al., 2009). Noticeably, Jlassi et al. (2013) estimated that *Sulla carnosa*, an indifferent halophyte, could desalinize moderate saline soil by accumulating considerable Na^+ in the shoot, because Na^+ concentration was diluted to prevent toxicity on shoot tissues by virtue of high leaf expansion rate. Thereby,

Abbreviations: EC, electrical conductivity; NMT, non-invasive micro-test technique; SAR, sodium adsorption ratio; TF, translocation factor.

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the phytoremediation approach through shoot Na^+ accumulation depends on special salt tolerant mechanisms in plants.

In contrast to non-leaching condition, Qadir et al. (2003) reported that Na^+ removal by shoot harvest of alfalfa contributed to only 1–2% of the total removed Na^+ in saline soil under irrigated condition, and root activity favored Na^+ leaching to deeper soil. Root respiration increases partial pressure of CO_2, assists in dissolving calcite, provides a source of Ca^{2+} to replace Na^+ at the exchange site of soil, and then facilitates Na^+ leaching (Qadir et al., 2005). Similarly, Na^+ removal through leaching was mainly responsible for total soil sodium removal in spite of the great shoot Na^+ accumulation in a halophyte, *Atriplex halimus* (Gharaibeh et al., 2011). Even for the succulent halophyte, *Suaeda fruticosa*, Na^+ leaching enhancement resulting from root effect was inferred to help remediate saline natural biotope (Rabhi et al., 2010). Thus, root respiration may play an important role in phytoremediation of saline soil under leaching condition. However, the role of root respiration in relation between salt tolerance and Na^+ removal from the soil is still unclear.

Honeysuckle (*Lonicera japonica* Thunb.) is a traditional medicinal plant and native to East Asia. Its flower is rich in two bioactive phenolic constituents, chlorogenic acid and galuteolin, and has been used as Chinese medicine for a long time (Chen et al., 2005). Honeysuckle is an ideal material to exploit coastal saline land due to its strong environmental adaptability and high economic value. Salinity can stimulate the synthesis of phenolic biosynthesis (Ksouri et al., 2007; Lim et al., 2012; Petridis et al., 2012; Colla et al., 2013; Borgognone et al., 2014), and the bioactive constituents of honeysuckle belong to phenolic compounds. Thus, there is a potential advantage that salinity may enhance medicinal quality of honeysuckle. In a recent study, we identified a salt tolerant honeysuckle cultivar by using hydroponic experiment and revealed that its tolerance originated from the control of Na^+ uptake and internal Na^+ transport (Yan et al., 2015a). In this study, we aimed to investigate phytoremediation effect of honeysuckle on moderate saline soil and explore the role of root respiration in the relation between salt tolerance and phytoremediation through field trial. Accordingly, honeysuckle plants were grown in non-saline and moderate saline plots for investigating the effects of salinity on root respiration, root Na^+ efflux, plant growth and shoot Na^+ accumulation. In addition, salinity and Na^+ concentration were contrasted between soil samples from plant inside (distributed with roots) and outside (distributed without roots) in non-saline and moderate saline plots. Our study can deepen the knowledge about phytoremediation of saline soil and may provide a reference for developing saline agriculture in coastal zone.

2. Materials and methods

2.1. Experimental site

The experiment site was established in Dongying Halophyte Arboretum, Dongying Academy of Agricultural Sciences, Shandong province, China (37°24′N, 118°39′E and 8.8 m above sea level). This area belongs to warm temperate continental monsoon climate. The annual average temperature and precipitation are 12.8 °C and 555.9 mm in this site.

2.2. Field trial design

Bare-rooted honeysuckle plants (two years old, Jiufengyihao cultivar) were bought from Jiujianpeng Agricultural Technology Limited Company (Pingyi, Shangdong, China) and planted in non-saline area in the arboretum in November, 2013. Four replicate plots were, respectively, constructed in non-saline and moderate saline areas, and the plot size was 3 m × 4 m. The initial soil nutrients, salinity and pH are listed in Table 1. To avoid border effects, plots were separated with ridges of 0.6 m wide and 0.3 m high, and 0.5 m around the plots was left as isolation belt. The plots were ploughed up and applied with compound fertilization at 750 kg ha^{-1}. In April, 2014, forty five plants were transplanted to each plot, and plant and row spacing were 0.5 m and 0.75 m. Plant inside and outside, respectively, indicate the sites which are less than 0.15 m and at least 0.35 m distance from the plants. Roots were mainly distributed in plant inside and hardly reached the outside. Thus, root metabolism could affect soil properties in plant inside rather than the outside, and soil from plant outside was sampled as control to reflect the effects of planting honeysuckle on soil salinity.

Table 1
Soil nutrients, salinity and pH in non-saline and moderate saline areas. Data in the table indicate the mean of five replicate samples (±SD). Within each row, different letters indicate significant difference at $P < 0.05$.

Parameters	Non-saline area	Moderate saline area
Organic matter content (mg g^{-1})	27.72 ± 0.51a	27.40 ± 1.46a
Total nitrogen content (mg g^{-1})	1.12 ± 0.11a	1.14 ± 0.11a
Available phosphorus content (mg g^{-1})	9.41 ± 1.21a	11.56 ± 2.45a
Available potassium content (mg g^{-1})	0.35 ± 0.11a	0.31 ± 0.09a
Na^+ content (mg g^{-1})	0.31 ± 0.05a	0.61 ± 0.20b
Electrical conductance (μs cm^{-1})	486 ± 29a	910 ± 119b
Sodium adsorption ratio	9.51 ± 0.92a	16.43 ± 2.12b
Soil pH	7.65 ± 0.31a	7.81 ± 0.27a

2.3. Soil sampling and analysis

In October, 2014, composite soil samples from 0–20 and 20–40 cm depth were collected from three randomly selected sites from plant inside and outside in each plot. Honeysuckle roots were mainly distributed in tilth soil with depth of 0–20 cm. Soil samples were ground to pass through 1 mm sieve, extracted with deionized water at the ratio of 1:5 (w/v) and then filtrated. The filtrate was collected for measuring Na^+, K^+, Ca^{2+} and Mg^{2+} content by using an atomic absorption spectrophotometer (TAS-990, China). Electrical conductivity (EC) was detected by using a conductivity meter (DDSJ-308A, China). Sodium adsorption ratio (SAR) is a classic parameter to indicate soil sodicity and calculated as: $SAR = Na^+/[(Ca^{2+} + Mg^{2+})/2]^{1/2}$, and the unit of ions concentration in this equation is mM (Murtaza et al., 2009). Before honeysuckle plants were transplanted to the plots, soil was sampled for analyzing the initial nutrients. Soil organic matter, total nitrogen, available phosphorous and available potassium contents were measured, respectively, by using $K_2Cr_2O_7$ external heating, Kjeldahl digestion, Mo-Sb colorimetric, and flame photometric methods (Jiao et al., 2013).

2.4. Plant sampling and analysis

In June and October, 2014, plants were harvested, rinsed with deionized water and wiped with tissues. Roots, leaves and veins were separated, dried at 105 °C for 10 min, and then dried at 70 °C to constant weight. The extraction of Na^+ was performed according to Song et al. (2011). Deionized H_2O (25 ml) was added to 0.1 g dried plant powder and boiled for 2 h. The supernatant was diluted 50 times with deionized H_2O for measuring Na^+ content by using an atomic absorption spectrophotometer (TAS-990, China). Na^+ translocation factors (TF) indicate Na^+ transport from root to the aerial part. TF1 and TF2 were calculated as: TF1 = Vine Na^+ concentration/Root Na^+ concentration and TF2 = Leaf Na^+ concentration/Root Na^+ concentration. Shoot Na^+ concentration was calculated as vine dry weight × Na^+ concentration of vine + leaf dry weight × Na^+ concentration of leaf. On the basis of plot area, shoot

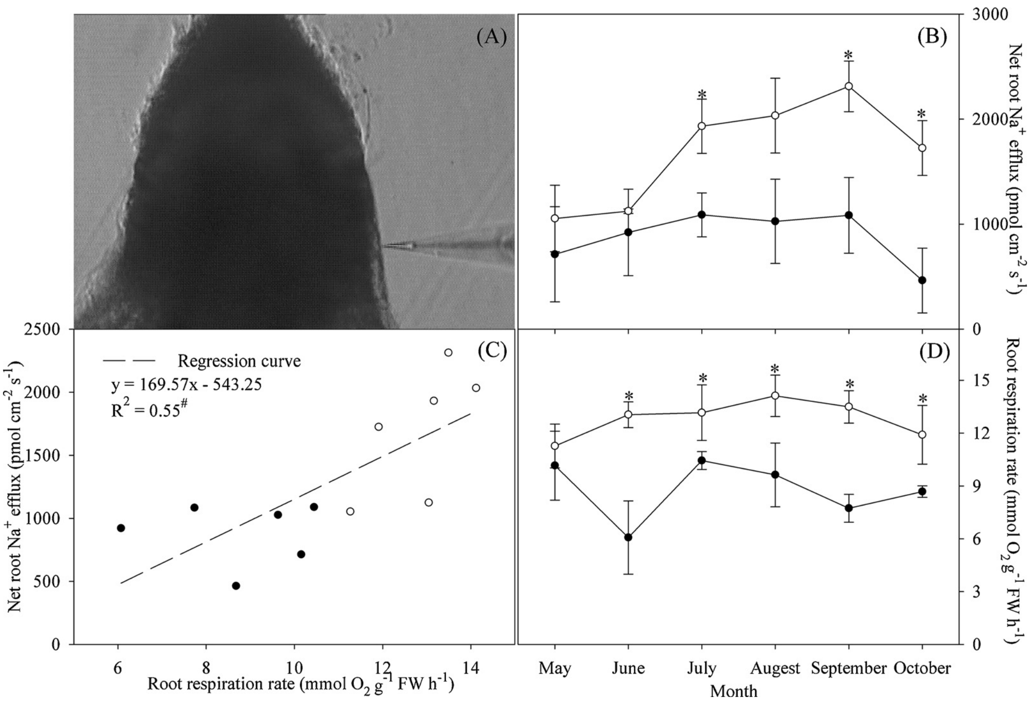

Fig. 1. The non-invasive ion-selective electrode closed to the root (A), Net root Na^+ efflux (B), root respiration rate (D) and the regression between root respiration and Na^+ efflux (C) in honeysuckle grown in non-saline (closed symbol) and moderate saline (open symbol) plots. Data in the figure indicate the mean of four replicate plots (±SD). Significant difference induced by salinity is indicated by asterisks: * $P < 0.05$. # Indicates that the correlation was significant at $P < 0.05$.

dry weight per hectare was estimated to indicate plant productivity, and phytodesalinaton capacity by shoot Na^+ accumulation was determined by multiplying plant productivity and shoot Na^+ concentration.

Newly developed roots were sampled for measuring root Na^+ flux by using non-invasive micro-test technique (NMT) according to our recent study (Yan et al., 2015a). The measured positions could be visualized and defined under NMT microscope (Fig. 1A). Ion flux measurements were started from the apex and went along the root axis until 3000 μm at interval of 500 μm. The average value of Na^+ efflux was calculated and shown in Fig. 1B. Newly developed roots (0.1 g fresh weight) were sampled and transferred to an air-tight cuvette, and respiration rate was detected as a decrease of the oxygen concentration at 25 °C by using a Clark-type oxygen electrode (Hansatech, England) (Millenaar et al., 2002).

2.5. Statistical analysis

One-way ANOVA was carried out by using SPSS 16.0 (SPSS Inc., Chicago, IL, USA) for comparing plant growth, root respiration, root Na^+ efflux, TF and Na^+ concentration between the plants from non-saline and moderate saline plots. EC, SAR, Na^+ and Ca^{2+} concentration between soil samples from plant inside and outside were also contrasted through one-way ANOVA. The values presented are the mean of samples collected from four replicate plots. The comparisons of means were determined through bonferroni test, and the difference was considered significant at $P < 0.05$. Regression analysis between root respiration and root Na^+ efflux was carried out by using SPSS 16.0 to demonstrate potential positive relationship between them, because root respiration could provide necessary power for excluding Na^+.

3. Results

3.1. Biomass, Na^+ concentration and Na^+ translocation factor

Root, vine and leaf dry weight significantly decreased in the plants in moderate saline plots compared with non-saline plots, and the decrease was up to 23.71%, 41.78% and 28.93% in October, 2014 (Table 2). However, Na^+ concentration in root, vine and leaf was greatly elevated in plants in moderate saline plots in contrast to non-saline plots, and the elevation reached 69.06%, 21.67% and 44.96% in October, 2014 (Table 2). TF1 and TF2 were decreased by moderate salinity, and both of them become significantly lower in plants in moderate saline plots than those in non-saline plots in October, 2014 (Table 2).

Table 2
Biomass, Na^+ concentration, Na^+ translocation factor in honeysuckle grown in non-saline and moderate saline plots. DW indicates dry weight. TF1 and TF2, respectively, indicate Na^+ translocation factor from root to vine and leaf. Data in the table indicate the mean of four replicate plots (±SD). Within each row, different letters indicate significant difference at $P < 0.05$ at the same sampling time.

Parameters	Non-saline (June, 2014)	Moderate saline (June, 2014)	Non-saline (October, 2014)	Moderate saline (October, 2014)
Root DW per plant (g)	2.30 ± 0.12a	1.42 ± 0.23b	6.41 ± 0.42a	4.89 ± 0.37b
Vine DW per plant (g)	2.56 ± 0.40a	1.24 ± 0.39b	42.56 ± 4.95a	24.78 ± 6.11b
Leaf DW per plant (g)	3.09 ± 0.51a	1.78 ± 0.39b	51.98 ± 4.12a	36.94 ± 2.99b
Root Na^+ content (mg g^{-1} DW)	4.99 ± 0.32b	9.06 ± 1.01a	6.40 ± 0.67b	10.82 ± 0.91a
Vine Na^+ content (mg g^{-1} DW)	2.58 ± 0.34b	3.87 ± 0.45a	2.40 ± 0.71a	2.92 ± 0.82a
Leaf Na^+ content (mg g^{-1} DW)	1.78 ± 0.42b	2.37 ± 0.61a	2.58 ± 0.42b	3.74 ± 0.65a
TF1 (Vine Na^+/root Na^+)	0.52 ± 0.11a	0.43 ± 0.09a	0.38 ± 0.12a	0.27 ± 0.05b
TF2 (Leaf Na^+/root Na^+)	0.36 ± 0.10a	0.26 ± 0.07b	0.41 ± 0.09a	0.32 ± 0.07b

Table 3
The estimated plant productivity and phytodesalinaton capacity by shoot Na^+ accumulation (PHD capacity) in honeysuckle and some succulent halophytes grown in saline soil. Plant productivity was the estimated shoot dry weight per hectare, and PHD capacity was calculated by multiplying plant productivity and shoot Na^+ concentration. DW indicates dry weight.

Species	Plant productivity ($t\,DW\,ha^{-1}$)	PHD capacity ($kg\,Na^+\,ha^{-1}$)	Experimental design	Reference
Lonicera japonica	2.57	8.71	Field experiment	This study
Sulla carnosa	5.24	320	Pot experiment	Jlassi et al. (2013)
Sesuvium portulacastrum	6.63	2504	Pot experiment	Rabhi et al. (2009)
Arthrocnemum indicum	2.32	711	Pot experiment	Rabhi et al. (2009)
Suaeda fruticosa	1.38	802	Pot experiment	Rabhi et al. (2009)
Suaeda salsa	12.69	3330	Pot experiment	Zhao (1991)
Tecticornia indica	–	752	Field experiment	Rabhi et al. (2010)
Suaeda fruticosa	–	215	Field experiment	Rabhi et al. (2010)
Suaeda maritima	–	504	Field experiment	Ravindran et al. (2007)
Sesuvium portulacastrum	–	474	Field experiment	Ravindran et al. (2007)

3.2. Root respiration and Na^+ efflux

Since June, 2014, root respiration was markedly elevated by moderate salinity, and similarly, greater root Na^+ efflux was observed in plants in moderate saline plots compared with non-saline plots (Fig. 1B and D). The regression analysis suggested that root respiration was significantly and positively correlated with root Na^+ efflux (Fig. 1C).

3.3. The estimated productivity and phytodesalinaton capacity

The estimated plant productivity was lower in *L. japonica* than the succulent halophytes such as *Suaeda salsa*, *Sesuvium portulacastrum* and *S. carnosa*, but it was even higher compared with other succulent halophytes such as *Arthrocnemum indicum* and *S. fruticosa* (Table 3). However, phytodesalinaton capacity of *L. japonica* was only 8.71 $kg\,Na^+\,ha^{-1}$, which was very limited compared with these succulent halophytes (Table 3).

3.4. Soil EC, SAR, Na^+ and Ca^{2+} concentration

In October, 2014, EC, SAR and Na^+ were significantly lowered, whereas Ca^{2+} was remarkably increased in tilth soil from plant inside compared with the outside in moderate plots (Fig. 2). No significant difference was observed in soil EC, SAR, Na^+ and Ca^{2+} concentration between soil samples from plant inside and outside in non-saline plots as well as in deeper soil below tilth layer in moderate saline plots (Fig. 2).

4. Discussion

4.1. Salt tolerance and phytoremediation mechanism in honeysuckle

Salinity suppressed honeysuckle growth due to the significant lowered root, vine and leaf dry weight in plants in moderate saline plots compared with non-saline plots (Table 2). The inhibition on plant growth is a common finding in glycophytes exposed to salinity, which mainly results from the depression on carbon assimilation induced by ionic toxicity and osmotic stress (Kalaji et al., 2011; Chao et al., 2013; Ashrafi et al., 2015; Snedden et al., 2015). In parallel with the reduction of plant growth, Na^+ concentration was significantly increased by moderate salinity in plant tissues including root, vine and leaf (Table 2). As similar with halophytes, Na^+ accumulation in glycophytes is usually increased by

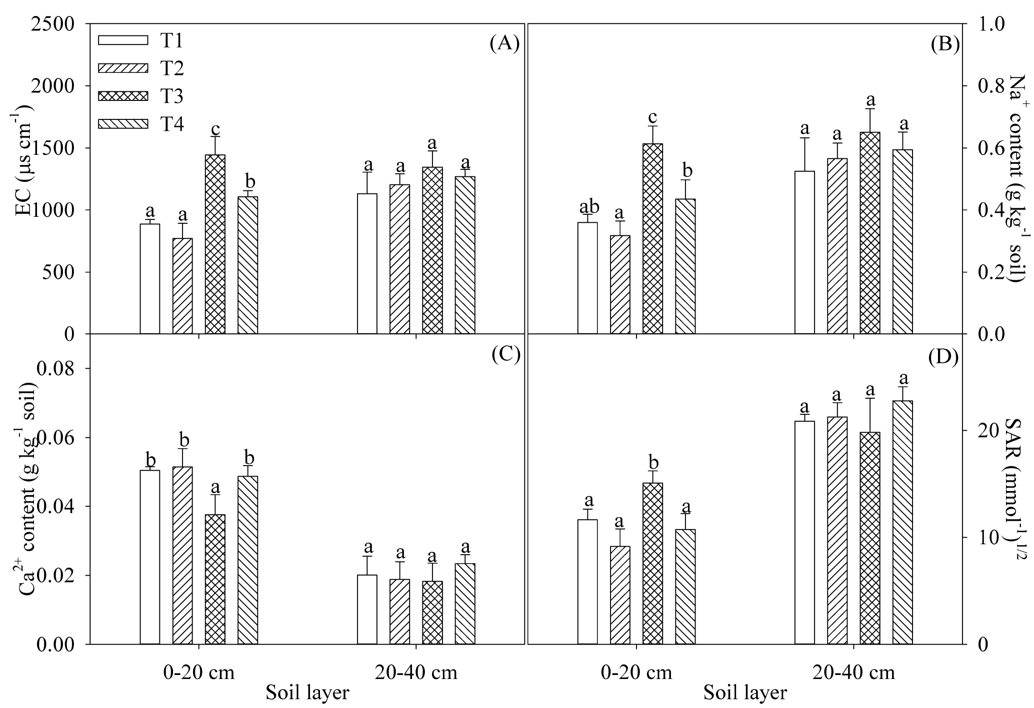

Fig. 2. Soil electrical conductance (EC) (A), Na^+ (B), Ca^{2+} (C) and sodium adsorption ratio (SAR) (D) from plant inside and outside in non-saline and moderate saline plots in October, 2014. Data in the figure indicate the mean of four replicate plots (±SD). Different letters on error bars indicate significant difference at $P < 0.05$ among soil samples at the same layer. T1, T2, T3 and T4, respectively, indicate soil samples from plant outside and inside in non-saline and moderate saline plots.

salinity, because root Na^+ uptake is a passive process (Munns and Tester, 2008). However, plants have evolved protective mechanisms to actively exclude root Na^+ and restrict Na^+ transport to the shoot (Bojorquez-Quintal et al., 2014; Maathuis et al., 2014). As a result, leaf Na^+ accumulation can be alleviated in salt-resistant glycophytes under saline stress to prevent severe toxic damage (Sun et al., 2009; Hussain et al., 2012; Chen et al., 2013; Aparicio et al., 2014). In agreement with our hydroponic experiment (Yan et al., 2015a), the capacity of root Na^+ extrusion was significantly enhanced by salinity in this study (Fig. 1B), and Na^+ transport to shoot was restricted as well, indicated by the significant decrease in TF1 and TF2 (Table 2). These results further confirmed that honeysuckle was a Na^+-resistant plant, and shoot Na^+ accumulation was just a balance between active extrusion and passive uptake in honeysuckle under salinity. Thus, the significance of shoot Na^+ accumulation in honeysuckle did not conform to that in succulent halophytes, because Na^+ could be efficiently confined in vacuole and used as a cheaper osmolyte than organic compounds in succulent halophytes. Accordingly, succulent halophytes seem more appropriate for rehabilitating saline land by extracting soil Na^+ particularly in arid regions (Ravindran et al., 2007; Rabhi et al., 2009).

Although shoot Na^+ concentration in honeysuckle was significantly increased by salinity, the amount of accumulated Na^+ was still limited compared with succulent halophytes, and moreover, its biomass was greatly reduced (Table 2). Therefore, the estimated phytodesalination capacity was much lower in honeysuckle than succulent halophytes (Table 3), and then honeysuckle could hardly serve as a Na^+ accumulator for desalinizing saline soil. Nonetheless, soil in moderate saline plots was exactly desalinized due to the significant decrease in EC, Na^+ concentration and SAR in tilth soil from plant inside compared with the outside (Fig. 2A, B and D), and it could be inferred that root activity might enhance Na^+ leaching to deeper soil.

4.2. Status of root respiration at the relation between salt resistance and phytoremediation

Root respiration was remarkably elevated by salinity (Fig. 1D), and then more CO_2 would be released into soil, which could help dissolve calcite and increase soil Ca^{2+} concentration. Because Ca^{2+} could replace Na^+ at the exchange site of soil, Na^+ leaching through precipitation or irrigation was facilitated. In moderate saline plots, honeysuckle significantly increased Ca^{2+} concentration and decreased Na^+ concentration in tilth soil, indicated by higher Ca^{2+} concentration and lower Na^+ concentration in tilth soil from plant inside than the outside (Fig. 2B and C). In contrast, Ca^{2+} and Na^+ concentration in tilth soil of non-saline plots was not significantly affected by honeysuckle, as they did not show obvious difference between soil samples from plant inside and outside (Fig. 2B and C). Therefore, the elevated root respiration might aid in improving Na^+ leaching by increasing Ca^{2+} concentration in saline soil.

Root Na^+ extrusion depends on the performance of plasma membrane Na^+/H^+ antiporter and is an active defence behavior requiring driving force from ATP hydrolyzation (Bose et al., 2014; Yan et al., 2015b). A high respiration rate can provide necessary energy for defence processes such as Na^+ extrusion and Na^+ compartmentation by producing more ATP (Jacoby et al., 2011). Thus, rice salt tolerance was enhanced by facilitating Na^+ exclusion in line with the increase of root respiration (Malagoli et al., 2008). Consistently, a significant positive correlation between root respiration and Na^+ extrusion was observed in this study (Fig. 1C), suggesting that the elevated root respiration in honeysuckle contributed to resisting salinity. Thus, root respiration bridged salt resistance in honeysuckle and phytodesalination function. As far as we known, root respiration was rarely elevated in succulent halophytes to enhance root Na^+ exclusion under salinity, which was probably on account of the special salt tolerant mechanism, as the major carbon reserves might be deployed in shoots rather than roots to mediate tissue tolerance.

5. Conclusion

Moderate saline soil was rehabilitated by honeysuckle, as Na^+ concentration, SAR and EC in tilth soil were significantly reduced. Honeysuckle was confirmed as a Na^+-resistant plant by field trial in this study, and it could hardly desalinize saline soil by shoot Na^+ accumulation. Root respiration was elevated by salinity, which enhanced salt tolerance by increasing Na^+ extrusion and aided in desalinizing saline soil by improving Na^+ leaching. Thus, root respiration acted as a bridge linking salt tolerance and phytoremediation of saline soil.

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