ISSN 1021-4437, Russian Journal of Plant Physiology, 2022, Vol. 69:75. © Pleiades Publishing, Ltd., 2022.

RESEARCH PAPERS

Heterogeneous Salt Concentrations in Soil Affects *Pyrus calleryana* Decne. Growth

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Received December 20, 2021; revised December 20, 2021; accepted December 21, 2021

Abstract– The uneven salt distribution in soil plays an important role in regulating plant growth. To explore the effect of heterogeneous soil salt stress on the growth of *Pyrus calleryana* Decne., container seedlings were placed in a split-root container for salt stress treatment. Five salt stress root treatments were performed, including a control non-salt stress treatment, two localized salt stress treatments, and two whole-root uniform salt-stress treatments. Our results indicate that salt stress was directly related to the reduced growth and photosynthesis. Seedlings under localized salt stress treatments (0/100 and 0/200) showed significantly larger increases in biomass than those under uniform salt stress treatments (100/100 and 200/200).Under localized salt stress treatment (0/100), the compensatory growth of fine roots (d < 2 mm) occurred in the salt-free side of the plant container, and the fine root biomass, root length, surface area, root volume, root tip number, branch number, and crossing number on the non-salt-stressed side were significantly higher compared to those on the salt-stressed side. Under the localized salt-stress treatment of 0/200, the salt concentration exceeded the lethal concentration for roots, which led to the growth of fine roots on the salt-free side. Our results indicate that the compensatory growth of L-side fine roots increased the photosynthetic rate and dry matter accumulation, and reduced the inhibition on the growth of *Pyrus calleryana* under local salt stress compared with uniform salt stress.

Keywords: *Pyrus calleryana*, localized salt stress, biomass, photosynthesis, root distribution

DOI: 10.1134/S1021443722040094

INTRODUCTION

In the Yellow River Delta, soil salinity is the primary environmental factor that supports plant diversity and diverse ecosystem functions; however, there are large areas of low productivity saline-alkaline land that have been abandoned for a relatively long time [1]. Therefore, the utilization and improvement of saline-alkaline land have become crucial in this region. Several studies have shown that the spatial heterogeneity of soil is a general characteristic of natural ecosystems [2, 3]. Within this context, the heterogeneity of the spatial distribution of saline soil is an important characteristic. Furthermore, the uneven distribution of salt in soil plays an important role in maintaining plant growth [4]. Therefore, understanding the mutual feedback relationship between soil salinity and root growth is important for revealing the mechanism of plants adapting to saline environment and formulating appropriate irrigation and improvement measures to improve the utilization rate of saline soil.

Among all the plant organs, root systems are the most vulnerable to saline-alkaline stress. As roots tend to avoid growing in saline areas, the distribution, characteristics, and growth of roots under saline-alkaline stress are the most direct adaptive plant characteristics to absorb and utilize soil nutrients effectively [5]. Under natural conditions, the distribution of salt in the soil is uneven due to the influence of natural and anthropogenic factors, such as precipitation, transpiration, irrigation, and cultivation. Furthermore, the salt stress environments of various root zones within the same plant can also differ.

As vital organs that enable plants to obtain underground resources directly, root systems can resist and avoid saline-alkaline environments by improving their root morphology [6]. For example, studies have shown that uneven salt stress can reduce plant damage, as roots within low salt areas develop characteristics related to the compensatory absorption of water or nutrients [7–9]. In a previous study [10], fine roots of *Fraxinus velutina* located in localized salt stress regions provided water to the leaves of the plants via increased growth in non-stressed areas. This reduced the Na^+ accumulation in leaves and an increase in the K^+ con-

Abbreviations: L—left side; R—right side; H2—plant height after treatment; H1—plant height before treatment; P_n—net photosynthetic rate; G_s—stomatal conductance; C_i—intercellular CO_2 concentration; TR– transpiration rate.

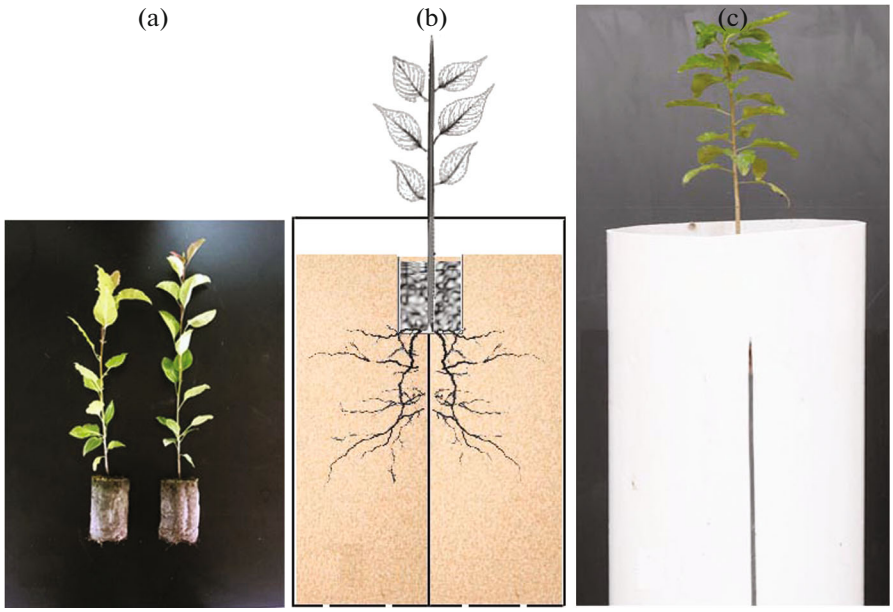

Fig. 1. Representation of (a) *Pyrus calleryana s*eedlings; (b) sand culture root-dividing container; and (c) the experimental setup with the seedling in the root-dividing container.

tent, thereby alleviating the adverse effects of salt stress on the plants. Furthermore, under root splitting conditions related to different salt treatments, the uneven distribution of salt has been shown to promote overall plant growth and significantly improve the yield and starch content of maize [11]. Additionally, the inhibitory effect of localized root salt stress on the growth of cotton (*Gossypium hirsutum*) [12] and *Atriplex nummularia* [13] was significantly lower than the effect of complete root salt stress. Photosynthesis is an important physiological process that is directly related to plant growth. Notably, the ion toxicity and water stress of wheat under localized salt stress were lower than those under uniform salt stress, thereby influencing plant photosynthesis [14].

Pyrus calleryana is a deciduous tree in the Rosaceae family. It is native to China and has a strong salt tolerance. In addition, it is one of the primary ornamental trees in the Yellow River Delta. At present, soil salinization poses a threat to the biosphere and the environment. Climate warming intensifies soil water evaporation, which increases soil salt accumulation [15–17]. As plant salt tolerance to varying levels of salt stress is representative of the actual environment, we analyzed plant growth, photosynthesis, and the root structure and distribution characteristics of *P. calleryana* seedlings using root treatments that corresponded to localized salt stress. The purpose is to analyze the effect of root local salt stress on plant growth of *P. calleryana*, reveal the distribution characteristics of root system of *P. calleryana*, explore the feasibility of local salt desalination technology in saline alkali land, and provide theoretical basis for original soil greening in saline alkali land.

MATERIALS AND METHODS

Plant materials. The experiment was conducted at the Dongying branch of the Shandong Academy of Forestry Sciences. The year-old seedlings of *P. calleryana* were planted in a light substrate non-woven container that allowed for root air pruning. This meant that when the roots grew beyond the non-woven container, the air naturally pruned the roots, thereby ensuring that the root lengths outside the container were approximately identical (Fig. 1a). Containers with a diameter of 5.5 cm and a height of 7.5 cm were used, with a substrate of peat, perlite, and vermiculite in a 7 : 2 : 1 ratio, respectively. In mid-April 2019, the seeds were sown in non-woven containers and placed in a greenhouse. The containers and seedlings were moved to the seedling yard for standby at the end of May.

Preparation of root dividing container. We used PVC plastic pipes (20 × 35 cm) and aluminum-plastic plates (3-mm thick) to construct the root-dividing containers (Fig. 1). The description and production process was based on previously developed methods [5]. For practicality, the completed root-dividing containers were placed into plastic flowerpots with an upper diameter of 23 cm. Treated sand was sieved to 2 mm and added to both sides of the root-dividing container. A small amount of coarse gravel was placed in the bottom of the container for drainage.

Transplanting. In early July 2019, seedlings with a height of approximately 20 cm were selected for saline stress experiments. After removing the outer non-woven fabric, the seedlings were transplanted into flowerpots with a middle partition to ensure that the

root system could grow evenly on both sides of the partition (Figs. 1b, 1c).

Experimental design and treatments. Five salt stress root treatments were used in the experiment, including a control non-salt stress treatment (0 mmol/L on both sides of the partition), two localized salt stress treatments (L: 0 mmol/L, R: 100 mmol/L; L: 0 mmol/L, R: 200 mmol/L), and two uniform salt stress treatments (100 mmol/L or 200 mmol/L on both sides of the partition). Hereafter these treatments are abbreviated as 0/0, 0/100, 0/200, 100/100, and 200/200, respectively. L and R represent the NaCl stress concentration on the left and right sides of the rooting container, respectively. Each treatment was replicated five times.

To ensure that the seedlings grew evenly on both sides of the rooting container, 1/3 of a modified Hoagland's nutrient solution was added (once every five-days), followed by 1/3 of a modified Hoagland's nutrient solution containing different concentrations of NaCl ten days later. Thus, the salt-stress-free side of the container was directly irrigated with nutrient solution, while the salt stress side was irrigated with a nutrient solution of a corresponding NaCl concentration. After the experiment, the seedlings were irrigated with a nutrient solution once every ten days, with the solution leaching from the hole at the bottom of the container.

Growth measurement. The heights (cm) of *P. calleryana* seedlings were measured using the conventional method at different growth stages, and the relative growth rate of the plant height was calculated. The formula used was as follows:

$$V = \frac{\mathrm{H2} - \mathrm{H1}}{\mathrm{H1}} \times 100\%,$$

V is the relative growth rate of plant height; H2 is the plant height after treatment; and H1 is the plant height before treatment.

Determination of photosynthetic index. After 15 days of treatment, the net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration of the leaves were measured using a Li-6400 portable photosynthesis instrument (LI-COR, United States). A red/blue LED light source was used with a light intensity of 1000 μmol/m^2 s. Measurements were taken from 10:00 to 11:00 a.m. Five replicates were performed per treatment.

After 15 days of treatment, chlorophyll fluorescence parameters of the leaves were measured using an OS-30p+ plant stress measuring instrument (OPTI-sciences). Three leaves were selected from each seedling, and the central part of the leaves was clamped with dark clips for dark adaptation. After 40 min of dark adaptation, the F_v/F_m (maximal photochemical efficiency of PSII in the dark) values of the leaves were measured, with five replicates for each treatment.

Determination of root biomass. After 60 days of salt stress treatment, entire seedlings were harvested, including the above and belowground parts. The roots were sampled and slowly cleaned with tap water to wash away the sand on both sides of the root-dividing container. Root biomass was recorded by cutting the roots outside and along the bottom of the substrate (Fig. 1). The root system was divided into two parts, namely, those inside and those outside the substrate. The growth characteristics of the fine roots were recorded only for those growing outside the substrate.

The roots were measured individually with a Vernier caliper and graded according to coarseness (<2, 2–5, and >5 mm). The length, surface area, volume, and average diameter of fine roots (≤2 mm) were measured using the WinRhizo root analysis system (Regent Instruments Inc.), while the aboveground and root biomass of the plant was determined after drying at 105°C for 0.5 min, and then at 70°C for 48 h to achieve a constant weight.

Statistical analysis. We used Excel 2010 and Data Processing System (DPS) 15.10 for data processing and one-way ANOVA and Least Significant Difference (LSD) tests to compare differences between various data groups ($P < 0.05$). Results are expressed as the mean ± standard deviation.

RESULTS

Effects of Salt Stress on Growth

Our results indicated that, in general, the growth of *P. calleryana* seedlings was significantly inhibited under salt stress (Fig. 2, Table 1). Both uniform and localized salt stress treatments reduced plant height, biomass, and the root/shoot ratio. After the 100/100 and 200/200 complete salt stress treatments, the seedling growth was inhibited, and the leaves became smaller, necrotic or wilted. Seedling senescence occurred after 38 and 21 days of salt stress treatment, respectively, and the relative growth rates of plant heights were 6.80 and 0.33% for the 100/100 and 200/200 treatments, respectively. Under the localized salt stress treatments of 0/100 and 0/200, relative growth rates were 22.93 and 16.53%, respectively, significantly higher than those under uniform salt stress ($P < 0.05$).

Regarding biomass, root salt stress significantly affected the above and belowground biomass of *P. calleryana* seedlings. Compared to uniform salt stress, seedling biomass under localized salt stress treatments of 0/100 and 0/200 increased by 39.63 and 113.74%, respectively. Specifically, the aboveground biomass increased by 27.82 and 106.39%, respectively, while the belowground biomass increased by 53.56 and 122.99%, respectively. Thus, the aboveground biomass was significantly higher than the belowground biomass ($P < 0.05$).

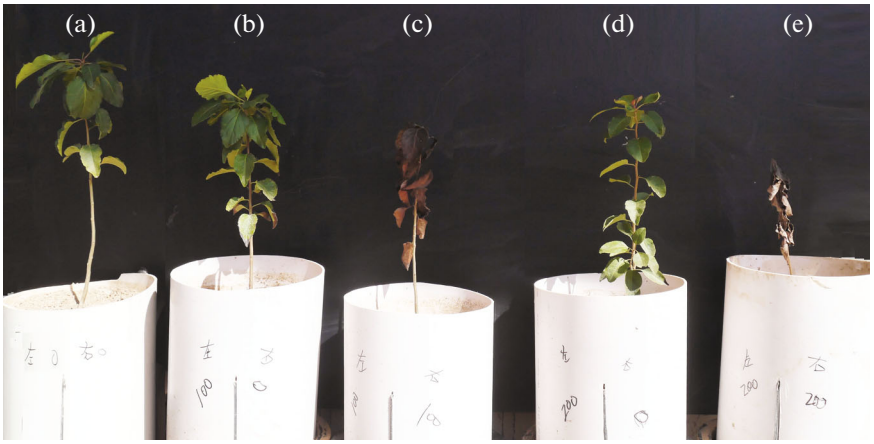

Fig. 2. Growth of *Pyrus calleryana* seedlings after 60 days of salt stress treatments at (a) 0/0 (0 mmol/L on both sides of the partition); (b) 0/100 (L: 0 mmol/L, R: 100 mmol/L); (c) 100/100 (100 mmol/L on both sides of the partition; (d) 0/200 (L: 0 mmol/L, R: 200 mmol/L); and (e) 200/200 (200 mmol/L on both sides of the partition).

Effect of Salt Stress on Photosynthesis

Our results indicate that salt stress led to a decrease in the net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (TR) (Table 2). The photosynthesis of local salt stress (0/100) was not significantly lower than that of the control (0/0). Photosynthesis remained at a controlled level. Compared to the 100/100 full salt stress treatment, the P_n, G_s, C_i, and TR of the localized 0/100 salt stress treatment increased by 26.64, 158.33, 31.24, and 97.54%, and compared with the 200/200 treatment, increases were 138.33, 210.00, 9.45, and 124.02%, respectively. Furthermore, the 0/200 treatmentproduced increases of 9.87, 100.00, 3.25, and 56.16%, respectively, compared to the 100/100 treatment, and caused increases of 89.34, 120.00, 23.81, and 77.09%, respectively, compared to the 200/200 treatment. In short, localized salt stress alleviated the effect of uniform salt stress on the photosynthetic characteristics of *P. calleryana* seedlings.

Chlorophyll fluorescence parameters indicated that the F_v/F_m of leaves decreased under salt stress conditions (Table 2). Under uniform salt stress, F_v/F_m decreased significantly with increased salt concentration and decreased more than under localized salt stress. Compared with the 100/100 and 200/200 complete salt stress treatments, the F_v/F_m of the 0/100 and 0/200 partial treatments increased by 25.04 and 93.78%, and 18.14 and 83.08%, respectively. These results indicate that, compared with uniform salt stress, localized salt stress alleviated the inhibition of light response centers and reduced the degree of stress in *P. calleryana* seedlings.

Effect of Salt Stress on Root Distribution

Our results indicate that salt stress reduced the root biomass of *P. calleryana* seedlings (Fig. 3, Table 3). Under uniform salt stress, an increase in salt concentration resulted in a decrease in coarse, fine, and total root biomass. These results differed significantly from that of the 0/0 treatment ($P < 0.05$). Compared to the 100/100 treatment, there was no significant difference in coarse root biomass in the L (salt-free)and R (salt stress)regions of the containers, but significant differences in fine root and total root biomass were observed, with the total root biomass decreasing by 80.21%.

Table 1. Effects of different salt stress treatments on the growth of *Pyrus calleryana* seedlings.

Treatments, mmol/L	Plant height	Dry weight of shoot, g		Dry weight of root, g		Root/shoot ratio	Total, g
		leaf	branch	coarse root (>2 mm)	fine root (<2 mm)		
0/0	31.74 ± 0.81a	2.51 ± 0.12a	2.84 ± 0.10a	4.66 ± 0.17a	2.46 ± 0.10a	1.33 ± 0.03a	12.47 ± 0.37a
0/100	30.41 ± 1.07a	2.21 ± 0.17b	2.66 ± 0.07a	2.51 ± 0.11b	2.45 ± 0.10a	1.02 ± 0.03b	9.83 ± 0.34b
100/100	25.45 ± 0.25c	1.67 ± 0.07c	2.14 ± 0.16c	2.03 ± 0.08d	1.20 ± 0.08c	0.85 ± 0.01c	7.04 ± 0.25c
0/200	27.66 ± 0.71b	2.08 ± 0.09b	2.44 ± 0.11b	2.26 ± 0.11c	1.62 ± 0.18b	0.86 ± 0.04c	8.40 ± 0.39d
200/200	23.40 ± 1.19d	1.13 ± 0.050d	1.06 ± 0.07d	1.43 ± 0.06e	0.31 ± 0.09d	0.79 ± 0.09c	3.93 ± 0.04e

The biomass of the belowground parts includes the root system in the substrate; different lowercase letters indicate

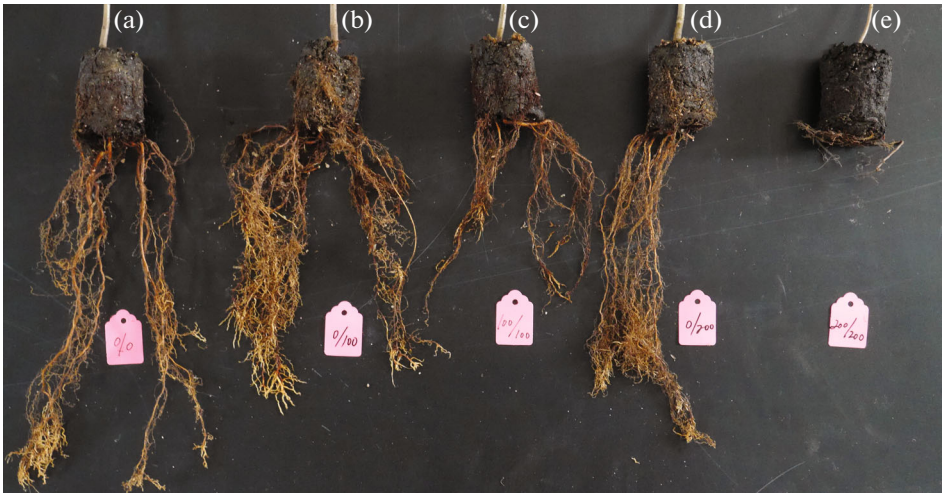

Fig. 3. Root distribution of *Pyrus calleryana* seedlings after 60 days under various salt stress treatments including (a) 0/0 (0 mmol/L on both sides of the partition); (b) 0/100 (L: 0 mmol/L, R: 100 mmol/L); (c) 100/100 (100 mmol/L on both sides of the partition; (d) 0/200 (L: 0 mmol/L, R: 200 mmol/L); and (e) 200/200 (200 mmol/L on both sides of the partition).

Compared with the 0/0 control treatment, the coarse and total root biomass of the 0/100 and 0/200 treatments showed a significant decrease ($P < 0.05$). However, the fine root biomass on the L side increased by 38.24% and 23.53%, respectively. Compared with the 0/100 treatment, there was no significant difference in the coarse and fine root biomass on the L side, but there was a significant difference on the R side after the salt stress treatment ($P < 0.05$). Under localized salt stress, the biomass of the coarse and fine roots on the L side (no salt stress) was significantly higher than that on the R side. Under the 0/100 treatment, the biomass of the coarse and fine roots in the L side increased by 90.91% and 161.11%, respectively, com-

Table 2. Effects of different salt stress treatments on photosynthetic and chlorophyll fluorescence parameters of *Pyrus calleryana* seedlings, including net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (TR)

Treatment, mmol/L	P_n, μmol/m^2 s	G_s, mol [H_2O]/m^2 s	C_i, μmol CO_2 mol	TR, mmol/m^2 s	F_v/F_m
0/0	15.42 ± 1.56a	0.35 ± 0.05a	313.79 ± 18.86a	4.36 ± 0.46a	0.827 ± 0.10a
0/100	14.12 ± 1.20a	0.31 ± 0.01a	316.59 ± 8.91a	4.01 ± 0.16a	0.779 ± 0.13b
100/100	11.15 ± 1.45c	0.12 ± 0.03c	289.28 ± 22.14b	2.03 ± 0.47c	0.623 ± 0.17d
0/200	12.25 ± 2.52b	0.22 ± 0.02b	298.67 ± 16.57ab	3.17 ± 0.17b	0.736 ± 0.15c
200/200	6.47 ± 0.40d	0.10 ± 0.03c	241.23 ± 22.32c	1.79 ± 0.39d	0.402 ± 0.12e

Lowercase letters indicate significant differences among different stress treatments ($P < 0.05$).

Table 3. Root biomass distribution of *Pyrus calleryana* seedlings under various salt stress treatments

Treatment, mmol/L	NaCl, mmol/L		Coarse roots (>2 mm), g		Fine roots (<2 mm), g		Total, g
	L	R	L	R	L	R	
0/0	0	0	0.94 ± 0.13Aa	1.09 ± 0.09Aa	1.02 ± 0.11Ab	0.83 ± 0.06Aa	3.88 ± 0.16a
0/100	0	100	0.21 ± 0.05Abc	0.11 ± 0.03Bb	1.41 ± 0.10Aa	0.54 ± 0.05Bb	2.27 ± 0.17b
100/100	100	100	0.14 ± 0.04Abc	0.17 ± 0.04Ab	0.39 ± 0.06Ac	0.26 ± 0.03Ac	0.96 ± 0.13d
0/200	0	200	0.29 ± 0.09Ab	0.00 ± 0.00Bc	1.26 ± 0.07Aa	0.00 ± 0.00Bd	1.55 ± 0.16c
200/200	200	200	0.09 ± 0.02Ac	0.10 ± 0.03Ab	0.00 ± 0.00Ad	0.00 ± 0.00Ad	0.19 ± 0.05e

The biomass of coarse and fine roots does not include the root systems in the matrix. Different capital letters indicate significant differences in different regions (L/R) under the same stress treatments ($P < 0.05$), and different lowercase letters indicate significant differences in the same region (L/R) under different stress treatments ($P < 0.05$).

Table 4. Growth characteristics of fine roots of *Pyrus calleryana* seedlings under different salt stress treatments

Treatment (mmol/L)	NaCl, mmol/L		Length, m		Surface area, cm^2		Volume, cm^3		Average diameter, mm	
	L	R	L	R	L	R	L	R	L	R
0/0	0	0	5.79 ± 0.14Ac	5.66 ± 0.28Aa	30.99 ± 2.81Ab	28.83 ± 2.48Aa	0.13 ± 0.02Ac	0.12 ± 0.02Aa	0.17± 0.02Ab	0.16 ± 0.01Ab
0/100	0	100	11.22 ± 1.60Ab	4.62 ± 0.33Bb	71.23 ± 5.48Aa	26.42 ± 3.75Ba	0.37 ± 0.01Aa	0.12 ± 0.03Ba	0.20 ± 0.02Aa	0.18 ± 0.02Aa
100/100	100	100	4.59 ± 0.26Ac	3.79 ± 0.19Ac	26.43 ± 3.08Ab	20.03 ± 1.55Bb	0.12 ± 0.02Ac	0.09 ± 0.01Ab	0.18 ± 0.01Ab	0.16 ± 0.01Ab
0/200	0	200	13.77 ± 0.71Aa	0.00 ± 0.00Bd	71.17 ± 5.10Aa	0.00 ± 00Bc	0.30 ± 0.02Ab	0.00 ± 0.00Bc	0.17 ± 0.01Ab	0.00 ± 0.00Bc
200/200	200	200	0.00 ± 0.00Ad	0.00 ± 0.00Ad	0.00 ± 0.00Ac	0.00 ± 0.00Ac	0.00 ± 0.00Ad	0.00 ± 0.00Ac	0.00 ± 0.00Ac	0.00 ± 0.00Ac

The growth characteristics of fine roots do not include the root system in the matrix. Different capital letters indicate significant differences in different regions (L/R) under the same stress treatments ($P < 0.05$), and different lowercase letters indicate significant differences in the same area (L/R) under different stress treatments ($P < 0.05$).

pared to that on the R side. However, under the 0/200 treatment, the growth of coarse and fine roots on the R side was significantly inhibited, while the compensatory growth of coarse and fine roots on the L side increased significantly.

Under the uniform salt stress treatments, an increase in salt stress corresponded to a decrease in fine root length, surface area, and root volume (Table 4). However, there was no clear change in the average diameter of the fine roots. The calculation results showed that there was no significant difference between the 100/100 treatment and 0/0 control in fine root length, surface area and root volume in L side, while that of the R side decreased significantly by 33.04, 30.52, and 25.00%, respectively. Under the 200/200 treatment, root growth and development were inhibited by high salt stress, and no root growth occurred on either side.

Under the 0/100 treatment, the growth of fine roots increased significantly on the L side ($P < 0.05$), while the root length, surface area, and root volume also increased by 142.86, 169.61, and 208.33%, respectively, compared with that on the R side. Compared to the 0/0 treatment, the root length, surface area, and root volume on the L side increased by 93.78, 129.85, and 184.62%, respectively, while that on the R side decreased 18.37, 8.36, and 0.05%, respectively. Under the 0/200 treatment, the new fine roots on the R side were significantly inhibited by high salt stress, leading to the growth of fine, lateral roots on the L side (no salt stress) ($P < 0.05$). However, the heterogeneity of the fine roots was significantly affected by salt stress in the 0/200 treatment and increased on the L side by 137.82, 129.65, and 130.77%, respectively, compared with the control treatment.

Our results indicate that uniform salt stress reduced the number of root tips, branches, and intersections of fine roots, while localized salt stress significantly increased the number of root tips, branches, and intersections on the side of the container non-stressed side (L side) ($P < 0.05$) (Fig. 4). Compared with the 0/0 control treatment, the number of root tips, branches, and intersections in the L and R areas of the 100/100 treatment decreased by 36.88, 35.89, and 30.84%, respectively, and 36.36, 22.78, and 39.04%, respectively. Under the 200/200 treatment, root growth and development were inhibited, and senescence occurred when the stress limit of seedlings was exceeded. Under the 0/100 treatment, the number of root tips, branches, and intersections of the fine roots on the non-stressed side (L side) increased significantly by 138.14, 109.89, and 135.63%, respectively ($P < 0.05$). Compared with the 0/0 treatment, the 0/100 treatment significantly increased the number of root tips, branches, and intersections on the L side by 34.93, 99.11, and 122.34%, respectively, and decreased the number of root tips and intersections on the R side by 27.72 and 4.61%, respectively, while the number of branches increased by 6.31%. The number of root tips, branches, and intersections on the L side in the 0/200 treatment increased significantly by 69.70, 130.69, and 197.61%, respectively, compared with the 0/0 control treatment.

DISCUSSION

Generally, the growth of plants under salt stress is a direct indicator of salt tolerance, with plant growth and biomass being inhibited to varying degrees related to changes in the degree of saline stress [18, 19]. In this study, we investigated the effects of different salt stress treatments on above and belowground biomass and plant heights of *P. calleryana* seedlings. Notably, plant biomass under localized salt stress was significantly higher than that under uniform salt stress, which corresponds to the results of similar salt stress studies on *Citrus reticulata* [20], *Medicago sativa* [9], and *Fraxinus velutina* [10]. Results from our study showed that

seedlings grew normally under localized salt stress treatments of 0/100 and 0/200 mmol/L, while under uniform salt stress treatments with concentrations of 100/100 and 200/200 mmol/L, plant senescence occurred after 38 and 21 days, respectively. These concentrations were much higher than the lethal salt stress concentration, indicating that localized salt stress can effectively alleviate the effects of high salt stress on the growth of *P. calleryana*.

Notably, studies have shown that the self-regulation of plant biomass allocation patterns is a plasticity mechanism that allows plants to adapt to salt stress, often consistent with the prediction of optimal allocation theory [21, 22]. In this study, the root/shoot ratio of *P. calleryana* seedlings decreased significantly with increased salt concentration, but this decrease was alleviated under localized salt stress. This differed from the increase in the root/shoot ratio of wheat [14] and *Atriplex nummularia* [13] and is primarily related to the fact that the salt concentration used in this experiment was higher than the lethal salt stress concentration of *P. calleryana*. Root biomass showed a significant downward trend under salt stress, with the decrease in the aboveground biomass being lower than that in the root biomass. This is the primary reason for the decrease in the root/shoot ratio and the delayed senescence of the plant under uniform stress conditions.

The inhibition of plant growth by salt stress is related to a decrease in the photosynthetic efficiency of plants through the disruption of metabolic processes [3]. Studies have shown that under salt stress, plant photosynthesis is inhibited, together with physiological drought, leaf stomatal closure, and a decrease in transpiration and photosynthetic rates [23–25]. A previous study [26] noted that high concentrations of Na^+ under salt stress conditions can inhibit the selective absorption of K^+ by roots, thereby destroying the ion balance in cells and reducing the photosynthetic efficiency of *P. calleryana*. Furthermore, Xie et al. [27] suggested that stomatal closure is a major factor leading to reduced photosynthesis in *P. calleryana*. The inhibition of photosynthesis under salt stress is primarily caused by stomatal closure, which blocks the supply of CO_2 and results in the destruction of the photosynthetic unit [28]. In our study, all salt stress treatments reduced the P_n, G_s, TR, and F_v/F_m of *P. calleryana*. However, under the localized salt stress treatment of 0/100, C_i was approximately identical to that of the control treatment, and there was little difference in the other photosynthetic parameters. We suggest that the root zone located on the salt-free side of the container provided sufficient water for the seedlings to ensure that photosynthesis was not significantly inhibited. In addition, compared with uniform salt stress, localized salt stress significantly reduced the inhibition of photosynthesis and was correlated to an increase in F_v/F_m, stomatal conductance, and net photosynthetic rate, thereby promoting the accumulation of photosynthetic products in the roots and shoots.

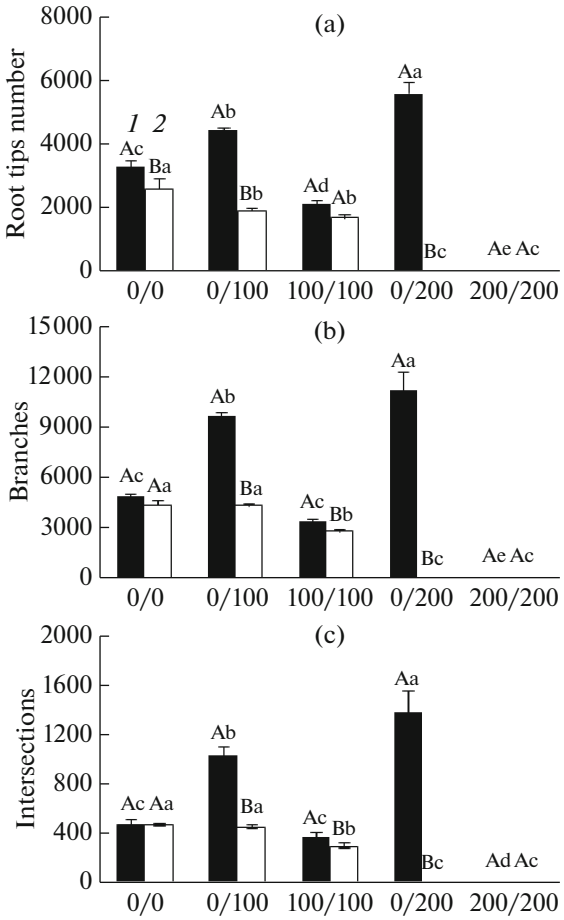

Fig. 4. Number of root tips (a), branches (b), and intersections (c) of the root system of *Pyrus calleryana* seedlings under different salt stress conditions. (1) Number of root tips on left root system of seedling (L) under 0/0 salt free stress; (2) number of root tips on right root system of seedling (R) under 0/0 salt free stress. The fine root branching structure does not include the root system in the matrix. Different capital letters indicate significant differences in different regions (L/R) under the same stress ($P < 0.05$), and different lowercase letters indicate significant differences in the same regions (L/R) under different stress conditions ($P < 0.05$).

Root biomass distribution is an important index for measuring the ability of plants to obtain resources. Under salt stress conditions, root systems can adapt to the environment through the growth and redistribution of roots with different diameters [29, 30]. Although localized salt stress inhibited the root growth of *P. calleryana* seedlings in our study, total root growth under localized salt stress increased significantly compared to the growth of roots exposed to uniform salt stress. The large amount of root growth that occurred on the salt-free side of the divided container, especially the increase of fine roots, effectively promoted the root absorption of water and nutrients, thereby alleviating the inhibition of salt stress. Fur-

thermore, under localized salt stress, the increase in root biomass in the salt-free area has been linked to an increase of indoleacetic acid (IAA) in the root system [31, 32], which compensates for the inhibition of the root system on the salt-stressed side of the container. Under localized salt stress, the increase in fine roots on the non-salt side increased the total contact area between roots and soil, allowing the roots to absorb extra water and nutrients. This effect indicated that localized salt stress resulted in the compensatory growth of roots on the salt-free side, and the root compensation was related to stress intensity.

These results correspond with previous studies showing that fine roots can affect the migration of salt and water in the soil around roots, which is conducive to maintaining the balance of soil salt surrounding the root growth zone to create the most suitable environment for root growth [33]. A previous study has reported that spatiotemporal heterogeneity regulates the root dynamics in mangrove forests [34]. Another study highlighted that in *Quercus virginiana* and *Quercus acutissima* [35], a low-salt environment promoted the growth of fine roots, whereas a high-salt environment inhibited the growth of fine roots. In our study, the length, surface area, and volume, as well as the number of root tips, branches, and intersections, increased to varying degrees, with the growth of the fine roots not being significantly inhibited under localized stress. This indicates that *P. calleryana* can maintain root activity under salt-stress conditions by reducing the root diameter and increasing the number of root tips.

At present, *P. calleryana* is the main greening tree species in the mild saline-alkaline area of the Yellow River Delta. This study systematically investigated the mechanism underlying the response of *P. calleryana* seedlings to heterogeneous salt stress at the whole-plant level. Our findings provide theoretical support for planting *P. calleryana* for the local desalination of heavily saline-alkaline land. However, we carried out a pot experiment with *P. calleryana* at the seedling stage, which has certain limitations in time and field application. Under the proposed new branch of soil science, microzone soil science [36], the changes and effects of heterogeneous salt stress on the whole growth cycle of seedlings under field environmental conditions requires further study. Under saline conditions, heterogeneous salt stress can promote the growth of *P. calleryana* plants, and fine roots have an evident compensatory effect in the non-salt-stress regions. Thus, local desalination under heterogeneous salt stress can significantly alleviate the inhibition of *P. calleryana* growth by high salt stress. The results can provide theoretical guidance for native *P. calleryana* soil greening in saline-alkaline areas.

ACKNOWLEDGMENTS

The authors wish to thank the anonymous reviewers for their constructive comments.

FUNDING

This research was funded by the Key R & D programs in Shandong (project no. 2019GNC106130).

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

Statement on the welfare of humans or animals. This article does not contain any studies involving humans or animals performed by any of the authors.

AUTHOR CONTRIBUTIONS

Y.L. and H.W. conceived and designed the experiments; Y.L. H.W, and Z.W. performed the experiments, analyzed the data, and drafted the manuscript; Q.Y., J.ZH, and L.W aided in analyzing the data and performing the experiments. All authors have read and agreed to the published version of the manuscript.

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