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BRIEF COMMUNICATION

Differences in responses of moderately salt-tolerant and salt-sensitive tree species to heterogeneous salinity

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Abstract

Growth responses of the moderately salt-tolerant velvet ash (*Fraxinus velutina*) and salt-sensitive poplar (*Populus* × *euramericana*) were investigated under heterogeneous root zone salinity. The salinity treatments imposed on the two root zones (lower-higher) were 137-137 (uniform), 103-171, 68-205, 34-239, and 0-273 mM NaCl for velvet ash, and 51-51 (uniform), 34-68, 17-85, and 0-103 mM NaCl for poplar. The leaf gas exchange of the plants was measured one month after these treatments were implemented, and the plants were sampled 75 d after treatment to measure other physiological parameters. Net photosynthetic rate, transpiration rate, total biomass, and fine root compensatory growth increased as the difference in salinity between the two root zones (*i.e.*, salinity heterogeneity) increased in velvet ash. These parameters showed no significant difference among the treatments in poplar. The leaf Na^+ content was lower under heterogeneous salinity than under uniform salinity in both tested species. The leaf proline content in velvet ash decreased under heterogeneous salinity compared to that under uniform salinity, whereas that of poplar increased. The soluble sugar content of velvet ash leaves increased under heterogeneous salinity, whereas no changes were observed in poplar. The increased fine root biomass in the lower salinity zone promoted velvet ash growth by decreasing the leaf Na^+ and Cl^- content under heterogeneous salinity. The poplar's undifferentiated root distribution and gas exchange in response to the heterogeneous salinity were attributed to its salt sensitivity.

Additional key words: *Fraxinus velutina*, photosynthesis, poplar, *Populus* × *euramericana*, transpiration, velvet ash.

Studies on plant salt tolerance have been widely conducted. Most of these studies were performed under uniform salinity. However, the spatial distribution of salts in the soil is highly variable (Bazihizina *et al.* 2012a,b). There may be a high variation in salinity even in the rhizosphere of a single plant (Li *et al.* 2011). Therefore, studies on growth responses to heterogeneous salinity are essential for understanding plant growth under natural saline conditions. Studies on moderately salt-tolerant crops, such as tomato (Mulholland *et al.* 2002), cotton (Dong *et al.* 2010, Kong *et al.* 2012) and alfalfa (Sun *et al.* 2016), have shown that plant growth under heterogeneous salinity is more dependent on the lowest rather than on the highest salinity level in the root zone, even when the mean salinity is the same. However, in extremely salt-tolerant or salt-sensitive plants, the responses are different from those of moderately salt-tolerant plants. The halophyte *Atriplex nummularia* shows similar growth under uniform and heterogeneous salinity (Bazihizina *et al.* 2012b). The growth of a salt-

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Abbreviations: CC - fine root compensation coefficient; E - transpiration rate; P_N - net photosynthetic rate; PVC - polyvinyl chloride; SS - soluble sugar.

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sensitive species *Capsicum annuum* with one half of the roots subjected to non-saline conditions depended on the highest salinity around the second root half (Lycoskoufis *et al.* 2005). Cucumber, which is also a salt-sensitive species, had the same yield under heterogeneous and uniform salinity treatments (Mulholland *et al.* 2002). These results indicate that the growth responses of different plants to heterogeneous salinity are species specific.

Improvement in the growth of plants under heterogeneous salinity was found to be related to the distribution of roots. More roots in lower-salinity zones improves water absorption by plants (Shani *et al.* 1993, Bazihizina *et al.* 2009, Sun *et al.* 2016). Bazihizina (2009) reported that leaf water potential is negatively correlated with lower salinity in a heterogeneous root zone. The increase in biomass and yield in the heterogeneous salinity treatment compared to that under uniform salinity can be due to increased gas exchange (Dong *et al.* 2010, Kong *et al.* 2012) and decreased leaf Na^+ content (Sun *et al.* 2016). Heterogeneous salinity leads to lower Na^+ accumulation in cotton leaves compared to that under uniform salinity (Kong *et al.* 2012). The backward transportation of Na^+ from the leaves to the roots occurs when half of the roots experienced non-saline conditions (Kong *et al.* 2012, Sun *et al.* 2016). However, little is known about Cl^-, proline, and soluble sugar accumulation in plants under heterogeneous salinity, which are important responses of plants to salinity.

Tree species, which have large roots, are expected to be greatly affected by heterogeneous salinity. In addition, previous studies, which have been based on single species, provide no information on growth differences among trees with different salt tolerance. In the present study, we selected two tree species, moderately salt tolerant velvet ash (*Fraxinus velutina* Torr.; Du *et al.*, 2013), and salt sensitive hybrid poplar (*Populus* × *euramericana* Guinier; Sixto *et al.* 2005, Chen and Polle 2010) to compare their growth and physiological responses to heterogeneous salinity.

The velvet ash seedlings were grown in tissue culture, and cuttings from young branches of poplar were grown in small pots in a greenhouse. When the height of the plants reached 10 - 12 cm, they were transplanted into the split-root pots. Polyvinyl chloride (PVC) tubes with an inner diameter of 25 cm and height of 40 cm were used. A round PVC board attached to the end of the tube served as the bottom of each pot. A rectangular PVC board 40 cm long and 25 cm wide was inserted centrally into each pot to separate the root zone into two equal parts. On top of the board, a 7.5 × 7.5 cm hole was cut to place the plant. The crevices of the pot were sealed. Four holes, 1 cm in diameter, were drilled into the bottom of the pots for drainage. The root zones of the pots were filled with 11 kg of clean sand with particles 0.05 - 0.1 mm in diameter. Each plant was placed centrally into a split-root pot. After trans-plantation, 400 cm^3 of a half-strength Hoagland solution (Arnon and Hoagland 1940) was added into each root zone of the pots and then every 4 d. Thirty days later, when the plants were approximately 30 cm in height and roots had developed in both root zones of the pots, the heterogeneous salinity treatments were implemented. Equal mean salinity treatments were applied based on the salinity at which a 50 % reduction in growth in comparison to 0 mM NaCl was observed for both tested species. For velvet ash, the mean NaCl concentration of the two root zones of each pot was set at 137 mM NaCl (Xu *et al.* 1994), and this was used in both root zones for the uniform salinity treatment. Four heterogeneous salinity treatments, 103-171, 68-205, 34-239, and 0-273 mM NaCl (lower-higher root zone salinity) were applied. Poplar is much more sensitive to salinity, as low Na^+ accumulation in leaves can reduce the water content and growth rate (Chen *et al.* 2002, Janz *et al.* 2012); therefore, the mean NaCl concentration of the two root zones was set at 51 mM NaCl and this concentration was used in both root zones for the uniform salinity treatment. Three heterogeneous salinity treatments, 34-68, 17-85, and 0-103 mM NaCl, were applied. NaCl was added to a full-strength Hoagland solution to obtain the desired concentrations. To avoid the accumulation of salt in the pots, an additional 500 cm^3 of the treatment solution was irrigated into each root zone of the split-root pots. As a result, the electrical conductivity of the drainage water at the end of each irrigation event was almost the same as that of the irrigation solution. Plastic film was used to prevent evaporation from the pots. There were 6 replicates for each treatment. The salinity treatments lasted 75 d. During the treatments, the day/night temperature range was 14 - 16/22 - 28 °C, a relative humidity 50 - 60 %, a 12-h photoperiod, and an irradiance of 600 - 1 000 $\mu mol\ m^{-2}\ s^{-1}$.

Leaf gas exchange parameters were measured from 09:00 to 11:00 h on two consecutive sunny days after the salinity treatments had been implemented for 30 d in the uppermost fully expanded leaves using a *Li-6400* photosynthesis system (*Li-COR*, Lincoln, NE, USA). The ambient relative humidity was 50 - 60 %, and the leaf and air temperatures were both 20 - 25 °C. The rate of air flow and the photosynthetically active radiation were set at 500 $\mu mol\ s^{-1}$ and 800 $\mu mol\ m^{-2}\ s^{-1}$, respectively. At the end of experiment, shoot height was measured. The leaves and shoots were sampled separately. The roots in each zone of the pots were carefully washed with water and divided into fine roots (diameter < 1 mm) and coarse roots (diameter > 1 mm). The root stump in the small pot, which did not belong to either of the root zones, was also sampled. The leaf, stem, stump, coarse root, and fine root samples were dried at 85 °C for 3 d.

The differential root growth between the two root zones was estimated using the compensation coefficient (Mou *et al.* 1997). The root compensation coefficient is the ratio of the difference between the fine root biomass in the lower and higher salinity zones to the total fine root biomass of the whole plant. The leaf soluble sugar and proline content were determined using the methods of Yemm and Willis (1954) and Bates (1973), respectively, with a spectrophotometer (*UV-1750*, *Shimadzu*, Kyoto, Japan). The Na^+ content in the leaves and fine roots was determined using an atomic absorption spectrophotometer (*WYC-402C*, *Shengfen*, Shenyang, China) according to Xu *et al.* (2011). The Cl^- content was determined using the silver nitrate titration method (Lao 1988).

The means and standard deviations (SDs) were calculated, and the measured parameters were compared using the least significant difference test (*LSD*) in *SPSS 16.0*. The figure was prepared using *SigmaPlot v. 11.0* (*Systat Software*, Chicago, IL, USA).

Our results show that the shoot height of velvet ash in the 0-273 mM NaCl treatment was significantly higher than that in all the other treatments except for the 34-239 mM NaCl treatment. In poplar, no significant change in plant height was observed among the treatments (Table 1). For the total biomass of velvet ash, the 0-273 mM NaCl treatment significantly increased the total biomass compared to the other treatments, and the root biomass increased with increasing salinity heterogeneity (Fig. 1*A*). Poplar showed a slight but non-significant increase in total plant and root biomass under some heterogeneous salinity treatments (Fig. 1*B*).

Table 1. Shoot height, leaf net photosynthetic rate (P_N), transpiration rate (E), fine root compensation coefficient (CC), leaf proline content, and soluble sugar (SS) content of velvet ash and poplar treated with 137-137, 103-171, 68-205, 34-239, and 0-273 mM NaCl and 51-51, 34-68, 17-85, and 0-103 mM NaCl (lower-higher) in root zones, respectively. Means ± SDs, *n* = 6. Different letters indicate significant differences among the treatments for the same species ($P < 0.05$). The fine root compensation coefficient is the ratio of the difference between the fine root biomass in the lower and higher salinity zones to the total fine root biomass.

Species	NaCl [mM]	Shoot height [cm]	P_N [μmol (CO_2) $m^{-2} s^{-1}$]	E [mmol (H_2O) $m^{-2} s^{-1}$]	CC	Leaf proline [mg g^{-1} (d.m.)]	Leaf SS [mg g^{-1} (d.m.)]
Velvet ash	137-137	68.57 ± 3.52^b	12.82 ± 1.60^c	5.43 ± 1.24^b	-0.03 ± 0.21^b	7.38 ± 3.26^a	7.78 ± 1.41^b
	103-171	68.63 ± 1.72^b	12.58 ± 1.69^c	5.43 ± 0.83^b	0.04 ± 0.25^b	5.85 ± 2.79^{ab}	9.70 ± 1.26^a
	68-205	68.43 ± 1.29^b	13.64 ± 1.38^{bc}	5.66 ± 0.48^b	0.16 ± 0.25^{ab}	5.45 ± 1.56^b	10.11 ± 1.73^a
	34-239	71.25 ± 2.42^{ab}	14.46 ± 1.30^{ab}	6.42 ± 0.20^a	0.44 ± 0.38^a	4.19 ± 2.22^b	10.24 ± 0.99^a
	0-273	73.88 ± 1.38^a	15.61 ± 1.25^a	6.71 ± 0.45^a	0.52 ± 0.21^a	3.12 ± 1.71^b	9.76 ± 1.24^a
Poplar	51-51	90.33 ± 10.17^a	10.98 ± 2.99^a	4.39 ± 1.62^a	0.01 ± 0.17^a	2.06 ± 1.17^b	7.65 ± 2.22^a
	17-85	93.00 ± 11.54^a	10.97 ± 1.70^a	5.74 ± 0.61^a	0.02 ± 0.10^a	6.82 ± 1.65^a	8.10 ± 0.71^a
	34-68	93.67 ± 6.95^a	12.07 ± 3.09a	6.44 ± 2.02^a	0.10 ± 0.08^a	7.71 ± 1.53^a	7.44 ± 1.16^a
	0-103	90.33 ± 6.53^a	11.71 ± 1.70^a	6.42 ± 1.66^a	-0.01 ± 0.26^a	5.54 ± 2.45^a	6.50 ± 1.82^a

The fine root biomass of velvet ash increased with decreasing NaCl concentration in both salinity zones of the heterogeneous salinity treatment (Fig. 1*C*). The fine root biomass in the zone with 0 mM NaCl was significantly higher than that in the other treatments, being almost three-fold that in the 273 mM zone. The difference in fine root biomass between the lower and higher salinity zones correlated with the compensation coefficient of the fine roots, which increased with an increase in salinity heterogeneity. In velvet ash, the compensation coefficients of the fine roots increased with an increasing difference in salinity between the two zones (Table 1). For poplar, the fine root biomass in each root zone and the total fine root biomass showed no significant difference among the treatments (Fig. 1*D*). The fine root compensation coefficients of poplar were close to zero and showed no significant difference among the four treatments (Table 1).

The net photosynthetic rate (P_N) of velvet ash generally increased with an increasing difference in salinity between the two root zones (*i.e.*, increasing salinity heterogeneity). The photosynthetic and transpiration (E) rates in the 0-273 and 34-239 mM NaCl treatments were significantly higher than those in the 137-137 and 103-171 mM treatments. In poplar, there was no significant difference among the treatments in terms of P_N or E (Table 1).

In velvet ash, the leaf proline content decreased with increasing salinity heterogeneity (Table 1). In the heterogeneous salinity treatments, it was lower than that in the uniform salinity treatment. The leaf soluble sugar content was significantly higher in the heterogeneous salinity treatments than in the uniform salinity treatment. The leaf proline content in poplar, in contrast to that in velvet ash, increased significantly in the heterogeneous salinity treatments (Table 1). No significant difference in the soluble sugar content of poplar was found among the treatments.

The Na^+ content in velvet ash leaves and fine roots decreased with an increase in salinity heterogeneity (Fig. 1*E*). The Na^+ content in leaves was significantly lower than that in fine roots. The root Na^+ content in the lower salinity zones was lower than that in the higher salinity zones for each heterogeneous salinity treatment. The Cl^- content in leaves and fine roots also decreased with increasing salinity heterogeneity and was much higher in the leaves than in the fine roots (Fig. 1*G*). The Cl^- content of fine roots in the lower salinity zones was lower than that in the higher salinity zones in all the heterogeneous salinity treatments. In poplar, the leaf Na^+ content in the heterogeneous salinity treatments was significantly lower than that in the uniform salinity treatment (Fig. 1*F*). The Na^+ content in fine roots in the lower salinity zones was lower than that in the higher salinity zones in each of the heterogeneous salinity treatments. The Na^+ content in leaves was significantly lower than that in fine roots in all treatments. The Cl^- content in leaves was significantly higher than that in fine roots in all the treatments. The Cl^- content in leaves in the heterogeneous salinity treatments was slightly lower than that in the uniform salinity treatment (Fig. 1*H*). No difference in Cl^- content in the fine roots was observed

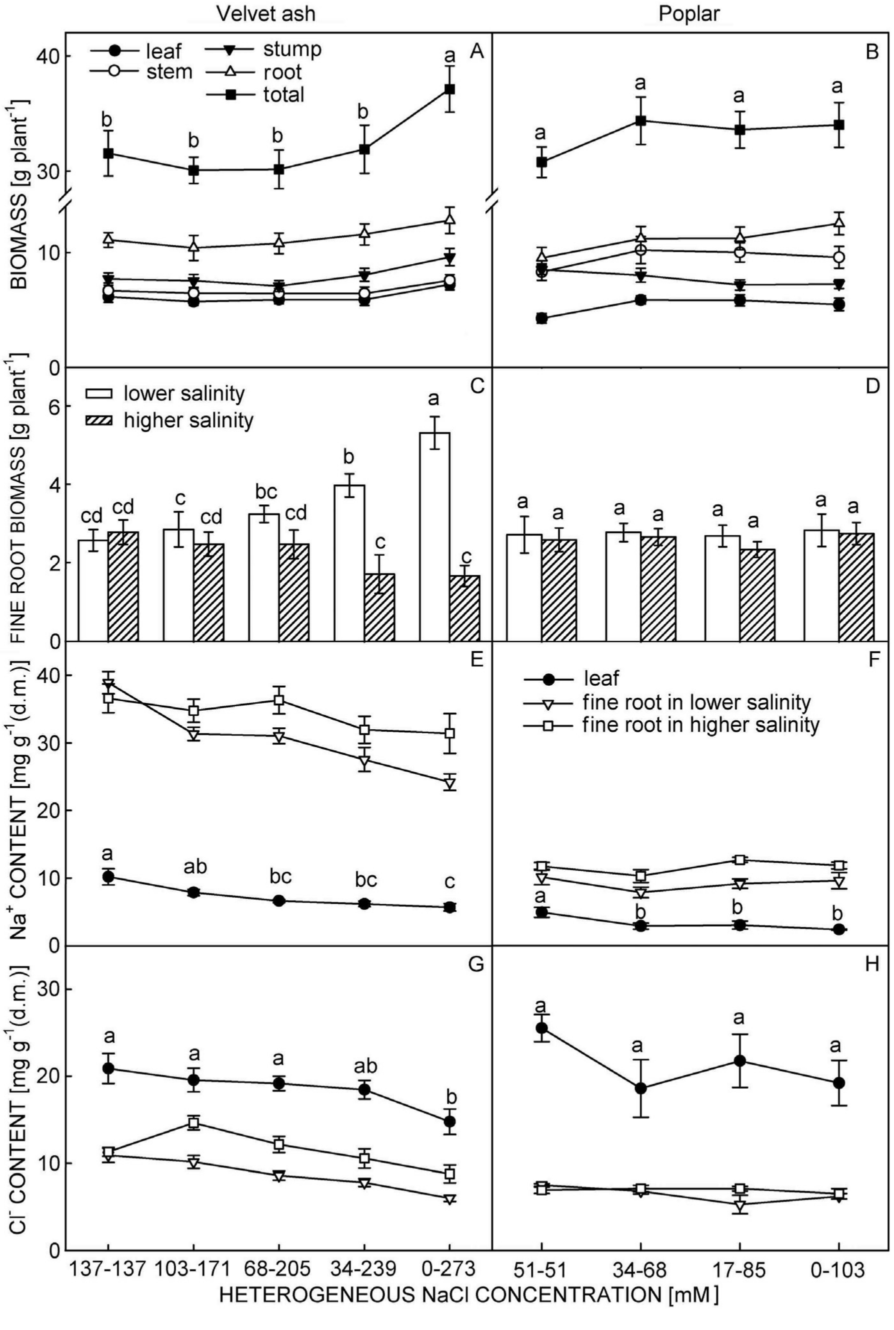

Fig. 1. Leaf, stem, stump, root, and total biomass (*A* and *B*), fine root biomass in lower and higher salinity zones (*C* and *D*), content of Na^+ (*E* and *F*) and Cl^- (*G* and *H*) in the leaves and fine roots of velvet ash and poplar treated with 137-137, 103-171, 68-205, 34-239, and 0-273 mM NaCl and 51-51, 34-68, 17-85, and 0-103 mM NaCl, respectively. Means ± SEs, $n = 6$. Different letters indicate significant differences among the treatments for the same species ($P < 0.05$).

among the treatments. In velvet ash, the significant increase in growth under the 0-273 mM NaCl treatment may have resulted from decreased leaf Na^+ and Cl^- content and increased photosynthesis.

The lower proline content and higher soluble sugar content of leaves under heterogeneous salinity than under uniform salinity implies the existence of effective mechanisms for osmotic adjustment under saline conditions because the synthesis of soluble sugar is more energy-efficient than the synthesis of proline, and lower energy consumption is likely to promote plant growth under saline stress (An *et al.* 2005). The absorption of nutrients, water, and salts as well as the exclusion of salts are processes that occur mainly in the fine roots (Rewald *et al.* 2011). In velvet ash, the growth response to the series of heterogeneous salinity treatments might be largely attributed to the increase in total fine root biomass, which in turn depended mainly on the growth of fine roots in the lower salinity zone. The increase in the root compensation coefficient implies that velvet ash has the ability to adjust the distribution of its roots under heterogeneous salinity. The altered root distribution in response to the root environment might be related to hormonal adjustment of the roots in different salinity zones (Kong *et al.* 2016). Meanwhile, the average fine root diameter should decrease with increased salinity, and the change in root structure may affect ion absorption and so salt resistance. The growth, ion accumulation, and root distribution of velvet ash under heterogeneous salinity were consistent with previous reports on moderately salt-tolerant species (Mulholland *et al.* 2002, Dong *et al.* 2010, Kong *et al.* 2012, Sun *et al.* 2016).

In poplar, the slight increase in growth under heterogeneous salinity might be related to decreased Na^+ and Cl^- content (Chen *et al.* 2009), which might have alleviated salinity stress. However, growth was not significantly promoted under heterogeneous salinity, indicating the presence of other metabolic processes that had offset these advantages. The significant increase in proline content under heterogeneous salinity might be one of the factors that caused the greater consumption of photosynthates and energy. The relatively efficient process of osmotic adjustment, *i.e.*, the synthesis of soluble sugar rather than proline, did not appear to be active in poplar under heterogeneous salinity. The similar fine root growth in the two root zones differing in salinity indicated that this plant had no ability to adjust the distribution of roots in environments with heterogeneous salinity. The gas exchange, ion accumulation, and root distribution of poplar under heterogeneous salinity were consistent with previous reports on salt-sensitive species (Mulholland *et al.* 2002, Lycoskoufis *et al.* 2005).

Velvet ash actively responded to heterogeneous salinity, which was evident from the change in gas exchange, fine root growth, and soluble sugar synthesis. In contrast, the responses of poplar were not as evident, except for the increase in transpiration rate and proline content. The differences between the two species in response to heterogeneous salinity might be attributed to the differences in the patterns of fine root growth under heterogeneous salinity and the leaf Na^+ and Cl^- accumulation. Velvet ash is moderately salt tolerant (Xu *et al.* 1994, Du *et al.* 2013), and it is likely that indole acetic acid signalling in the roots triggers the differential growth of fine roots under heterogeneous salinity (Kong *et al.* 2016). Further, this species limited the transport of Na^+ and Cl^- from the roots to the leaves (Wang *et al.* 2009) and underwent osmotic adjustments (Zeng *et al.* 2015). Poplar is much more sensitive to salinity than velvet ash (Chen and Polle 2010) but did not produce more roots in the lower salinity zone under heterogeneous salinity. Uder salinity, it transported Na^+ and Cl^- to the leaves, which was the main cause of the reduction in plant growth. The difference in Na^+ and Cl^- accumulation in leaves may depend on the absorption of these ions by the fine roots. For poplar, the uniform ion content in the fine roots and root distribution under heterogeneous salinity led to undifferentiated leaf Na^+ and Cl^- accumulation. However, the decreased Na^+ and Cl^- content in the fine roots and the production of fewer fine roots in the higher salinity zone in velvet ash prevented the Na^+ and Cl^- accumulation in the leaves above a toxic level.

In future studies, the interactions among soluble sugar and proline synthesis, salt accumulation, root distribution, root structure, and other related mechanisms of the response to uniform and heterogeneous root zone salinity need to be further investigated.

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