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INFLUENCE OF ARBUSCULAR MYCORRHIZA ON SALT TOLERANCE OF *KOSTELETZKYA VIRGINICA* (L.) C. PRESL EX A. GRAY

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Abstract

The aim of this study was to investigate the effect of *Glomus mosseae* (*G. mosseae*) on Na^+ intercept ability in root tissues of *Kosteletzkya virginica* (*K. avirginica*) grown under salt stress. Pot experiments in greenhouse were carried out in *K. avirginica* inoculated with *G. mosseae* under 1% NaCl stress. The Na^+, K^+ concentrations, distribution and growth parameters of *K. avirginica* were analyzed. Salinization reduced P and chlorophyll contents, root and shoot dry weight. Salinity dramatically increased Na^+ concentrations, but decreased K^+ contents and K^+ / Na^+ ratio in shoot and root significantly ($p \leq 0.05$). Inoculated plants showed higher P concentrations, dry weight in both roots and shoots than non-inoculated ones. Compared with non-inoculated plants, *G. mosseae* inoculation accumulated Na^+ mainly in the roots, and maintained higher K^+ / Na^+ ratio in the shoots. The X-ray microanalysis of root transverse section showed that roots endoderm of inoculated plants could strongly retain the transport of Na^+ to stellar parenchyma vessels maintaining more Na^+ in the roots whereas keep higher K^+ / Na^+ ratio in the shoots than that of non-inoculated seedlings. The elevated Na^+ intercept ability in root tissues of mycorrhizal plants may help in improving the tolerance of *K. avirginica* to salt stress.

Salinization of soils is a serious land degradation problem in arid and semi-arid areas and is increasing steadily in many parts of the world including China. Among the most common effects of soil salinity is growth inhibition by Na^+ and Cl^- (Ahmad *et al.* 2023). The use of plant growth-promoting microorganisms has been shown to be an economical and environmentally-friendly approach to counteract the adverse effects of salt stress (Estrada *et al.* 2013, Liu *et al.* 2023). The introduction of arbuscular mycorrhizal fungi (AMF) to sites with saline soils may improve the salt-tolerance and growth of plants (Giri *et al.* 2003, Estrada *et al.* 2013, Liu *et al.* 2023,). The role of AMF in salt stress conditions is still inconclusive. The improvement in the plant P status has been recommended as the most important strategy of salinity stress tolerance in AMF colonized plants (Estrada *et al.* 2013).

Kosteletzkya virginica is a perennial herbaceous halophyte of the Malvaceae family that is native to the brackish marshes of the mid-Atlantic and southeastern United States. It was introduced into Northern Jiangsu, China, by the Halophyte Research Laboratory of Nanjing University in 1993 as a species with the potential to improve saline soils in order to develop saline agriculture (Qin *et al.* 2015). The roots of *K. avirginica* could form symbiotic associations with AMF and *Glomus mosseae* inoculation could improve seedlings growth under salt stress (Zhang *et al.* 2014, Zhang *et al.* 2014, Ruiz-Lozano and Azcón 2000). The improvement of growth under salt stress after *G. mosseae* inoculation could be related to ion homeostasis regulation in plant cells such as selective absorption of K^+ and Na^+, but the detailed mechanism remains elusive. In this study, we aimed to elucidate the mechanism of improved salt-tolerance in *K. avirginica* inoculated with *G. mosseae*. We used *K. avirginica* seedlings inoculated with *G. mosseae* as the model to investigate how *G. mosseae* inoculation regulates Na^+, K^+ concentrations and growth of *K. avirginica* under NaCl stress.

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Seeds of *K. virginica*, collected in 2015 from Jinhai Agricultural Experimental Farm (Dafeng, Jiangsu, China), were surface-sterilized by soaking in a 5% NaCl solution for 10 min and rinsed with sterile distilled water. They were then transferred aseptically to Petri dishes filled with water and incubated for 4 days at 25 °C. One week after germination, three seedlings of uniform size were transferred to each pot that was placed on a 2-cm-deep plate, and plants were grown until April 10, 2016 in a greenhouse under controlled conditions (16 hrs of 220 μmol m^{-2} s^{-1} daylight intensity at 28°C, 8 hrs of night at 18°C, relative humidity of 65–85%).

The substrate used in this study was purchased from Red Sun Group (Nanjing, China). The substrate used was a 1/1 (v/v) mixture of washed sand and nutritious soil, which had been sterilized by autoclaving twice for 1 hr at 121℃. The substrate had the following characteristics: pH 7.2; organic matter content 1.35% (w/w); available-N, 0.0048% (w/w); available-P, 0.0025% (w/w); and extractable K, 0.0148% (w/w).

G. mosseae (Nicol. and Gerd.) was obtained from the Bank of Glomales in China. The inocula, which consisted of spores (2,830 spores per 100 g^{-1} soil), hyphae, and colonized root fragments, were collected from a 6-month-old pot culture of *G. mosseae* grown on sorghum in sterile sandy soil.

To study the effects of *G. mosseae* (Gm) on *K. avirginica* under NaCl stress, four treatments were designed: inoculated with Gm)10 g; inoculated with *G. mosseae* 10 g and 1% NaCl (Gm + NaCl); non-inoculated with *G. mosseae* control (-Gm); non-inoculated with *G. mosseae* and 1% NaCl (-Gm + NaCl). Each treatment was replicated six times in a randomized block design and each treatment was comprised of 30 pots (3 plants per pot). On June 18, 2016, healthy *K. avirginicas* with similar shape transplanted in the pots filled with 900 g cultivation substrate were selected as the experimental treatment. According to the design, per relevant pot received 10 g Gm inoculums by placing inoculum in soil below the *K. avirginica* seedlings prior to planting. The non-mycorrhizal control pots received an equivalent amount of inoculum sterilised twice at 121℃ for 30 min, together with a 0.25 μm-filtrate of unsterilised medium to provide similar microflora, but without viable AM fungi. Each pot stood on a 2 cm deep plate and kept in greenhouse on June 20, 2013. Plants were irrigated with a modified solution of Hoagland and Arnon (Hoagland and Arnon 1950) with all nutrients except P for 4 weeks. Then beginning to implement the salt stress test. The salinity of the substrate was based on the dry mass of the medium, and was tested as follows: 3 g of NaCl was dissolved in 300 ml of water, and poured the NaCl into per pot solution evenly three-times between day-7 and day-21 to avoid serious osmotic shock and to give a final NaCl concentration of 1% (w/v). Equal amount of distilled water was poured into the tray without NaCl treatment by the same method. Any occasional leakage was poured back into the tray after 1 h, and distilled water was added as necessary to maintain soil moisture. The pH of the substrate in all treatments was 7.2. After establishing salt stress, each pot was watered with 200 ml of Hoagland and Arnon nutrient solution (as above) every 3 d until day-60. Then, the roots, shoots and leaves of *K. avirginica* were harvested for further analysis.

Root and shoot tissues were analyzed for K^+ and Na^+ contents. Dried shoot tissues were digested in a Kjeldahl flask with 1 mL (9.2 M) $HClO_4$, 5 mL (14.3 M) HNO_3 and 0.5 ml (17.8 M) H_2SO_4. P concentrations of the root and shoot tissues were determined following the method of Allen (Allen 1989), and those of K^+ and Na^+ by flame photometry (Sengupta and Chaudhuri 2002). The 3th to 5th leaves from the end of *K. avirginica* were selected to test the chlorophyll concentrations (Zhang *et al.* 2014). All three plants in each pot were removed along with their roots at random and the number of the root length, the dry weights of roots and shoots and plant height of each *K. avirginica* were recorded. All shoots and roots tissues were dried in a forced-air oven at 80℃ for 72 hrs for dry weight determination. Shoot dry weight was the sum of leaves and stems.

To assess the extent of AMF colonization, the roots of three plants from each treatment were cleaned with 10% (w/v) KOH and stained with 0.05% (w/v) trypan blue (Phillips and Hayman 1970). The percentage of root length slained and colonized by AMF was estimated according to McGonigle *et al.* (McGonigle *et al.* 1990). The roots of each plant were cut into 1 cm long pieces, and 30 pieces from each plant were examined for their AMF content using a compound microscope (NLCD-307, Ningbo Yongxin Phenix Optical Ltd., Ningbo, P. R. China) at 100X magnification. A positive result for AMF colonization included the presence of vesicles or arbuscules, or the typical mycelium within the roots. The percentage of AMF colonization was calculated as follows:

AMF colonization (%) = Root length colonized / Root length observed × 100%.

The roots, shoots and leaves of the plants were rinsed with deionized water three times, and then dried at 80°C to a constant weight after filtration with Whatman paper. 0.1 g dry powder samples were then extracted with 5 ml 4 M HCl at 37°C overnight to release the free cations and centrifuged at 10,000 g for 10 min. The resulting supernatants of the extracts were diluted and Na^+ and K^+ determined with a Shimadzu AA-680 atomic absorption/flame spectrophotometer.

The harvested root segments, including the tip and 1 cm or more of the root, were dipped in 5% agar, inserted to a depth of 1.0 cm in a copper holder, and immediately sliced free-hand with a razor blade to get transverse sections, and then frozen in liquid nitrogen. The samples were freeze–dried, carbon coated in a high vacuum sputter coater, and stored in a desiccator. Samples were analyzed in S-3000N scanning electron microscope equipped with an energy-dispersive X-ray detector (HORIBA).

Counts per second of [K^+] and [Na^+] were measured in roots from different treatments mentioned above. Five tissues, i.e., epidermis cells, epicortex cells, cortex cells, endoderm cells, and stele cells in each root transverse section were analyzed. More than three transverse sections of each treatment were observed and three location spots of the same tissue of each section were analyzed.

Salinization induced significant reduction of the shoot and root dry weight without mycorrhizal inoculation, while Gm + NaCl counteracted such reductions significantly ($p < 0.05$, Table 1). Gm + NaCl showed significantly higher effects on these growth parameters than those of -Gm + NaCl ($p < 0.05$, Table 1). Under NaCl stress, the AMF colonization was decreased significantly ($p < 0.05$, Table 1). More P was distributed to roots compared to shoots in the same non - NaCl treatment, while reverse results were observed under NaCl stress (Table 2). Although P concentrations in the roots of *K. avirginica* were severely reduced by NaCl stress, higher P concentrations were observed in the shoots. However, inoculation with *G. mosseae* strongly enhanced P concentrations in both roots and shoots ($p < 0.05$). Gm + NaCl also showed higher chlorophyll concentrations than -Gm + NaCl ($p < 0.05$, Table 2).

Na^+ content of Gm in roots was markedly higher than that in -Gm ($p < 0.05$, Fig. 1A). Compared with -Gm and Gm, the Na^+ content in roots and shoots of both -Gm + NaCl and Gm + NaCl increased significantly, and Na^+ content of Gm + NaCl in roots was significantly higher than that of -Gm + NaCl, while Na^+ content of Gm + NaCl in shoots was very significantly lower than that of –Gm + NaCl ($p < 0.05$) (Fig. 1A). The K^+ content in shoots of Gm was significantly higher than that of Gm ($p \leq 0.05$) (Fig. 1B). Compared with -Gm and Gm, the K^+ content in roots of -Gm + NaCl and Gm + NaCl decreased by 35.12 and 40.10%, respectively, while K^+ content in shoots decreased by 26.21% and 18.44%, respectively (Fig. 1B). However, the K^+ content of the shoots was obviously higher than the roots no matter before or after salt treatment (Fig. 1B). Compared with -Gm and Gm, K^+ / Na^+ ratio in roots and shoots of both -Gm + NaCl and Gm + NaCl had a

substantial drop. K^+ / Na^+ ratio of Gm in roots was significantly lower than that of Gm, and K^+ / Na^+ ratio of Gm + NaCl in shoots was significantly higher than that of -Gm + NaCl ($p < 0.05$, Fig. 1C).

Table 1. Effects of *Glomus mosseae* on AMF colonization, root and shoot dry weight of *K. avirginica* grown under NaCl stress.

Treatments	Shoot dry weight (g / plant)	Root dry weight (g /plant)	AMF colonization (%)
-Gm	3.63 ± 0.6	0.46 ± 0.02	0
-Gm + NaCl	2.67 ± 0.2	0.45 ± 0.03	0
Gm	4.31 ± 0.7	0.57 ± 0.01	49.5 ± 3.2
Gm + NaCl	3.07 ± 0.3	0.58 ± 0.02	25.7 ± 2.1

Table 2. Effects of *Glomus mosseae on* P and chlorophyll concentrations of *K. avirginica* grown under NaCl stress.

Treatments	P concentrations			Chlorophyll conc. (mg/g)
	Shoot (mg/kg DW)	Root (mg/kg DW)	Total (μg/plant)	
-Gm	18.3 ± 5.2	19.9 ± 2.7	4.8 ± 0.1	3.58 ± 0.4
-Gm + NaCl	20.5 ± 4.3	9.3 ± 2.1	2.9 ± 0.2	1.43 ± 0.2
Gm	23.6 ± 4.1	27.2 ± 6.8	9.7 ± 0.4	4.22 ± 0.7
Gm + NaCl	28.3 ± 4.6	20.5 ± 6.1	7.4 ± 0.3	2.64 ± 0.2

Transverse sections of the roots of *K. avirginica* seedlings were scanned by X-ray microanalysis, beginning with the outermost tissues and proceeding to the middle in the following orders: epidermis cells, epicortex cells, cortex cells, endoderm cells, and stele cells. The scan results were transformed to data by the professional software (Table 3). In the roots of –Gm and Gm groups without NaCl treatment, K^+ content gradually increased from the outer root tissues to the middle ones (Table 3). On the other hand, Na^+ content was generally lower, and the internal Na^+ content was obviously lower than that in the external tissues ($p < 0.05$, Table 3). However, either inoculated seedlings or non-inoculated seedlings, Na^+ changes in the epidermis, epicortex and cortex are small ($p < 0.05$, Table 3). When exposed to NaCl stress, Na^+ content had a significant increase in all tissues of -Gm and Gm groups ($p < 0.05$, Table 3). Na^+ content in stele of Gm + NaCl decreased significantly than that of -Gm + NaCl ($p < 0.05$, Table 3), however, Na^+ contents in other tissues of Gm + NaCl increased obviously than that of Gm + NaCl ($p < 0.05$, Table 3). In addition, K^+ was mainly concentrated in the endoderm cells in Gm group under saline conditions (Table 3).

Salt stress is one of the main factors limiting the growth and yield of economic plants, while sodium is the main salts of salt damage. Under salt stress, the regionalization of Na^+ may be one of the possible survival strategies of plants, such as Na^+ intercepts in the root to inhibit the transport to the shoots (Zhu *et al*. 2006, Kronzucker and Britto 2011). Endodermis exists between the cortex and stele of plant roots, and the cells of endodermis is composed of some hydrophobic substances which have a blocking effect on ion diffusion (Zhu *et al.* 2006). Its role is to control ions into the xylem conduit (Gaymard *et al.*1998, Plett and Møller 2010, Hasegawa 2013). Because of the barrier function of casparian bands in endodermis, the Na^+ from the soil needs a symplast pathway to enter the column tube, and then transport to the shoots with the transpiration flow. This process

needs to be done twice through the process of the plasma membrane, one is through the root epidermal or cortical cell plasmalemma into the symplast pathway; another one is through the parenchymal cell plasmalemma of xylem to enter in the apoplastic space of the column tube (Gaymard *et al.*1998, Tester and Davenport 2003, Ma *et al.* 2013).

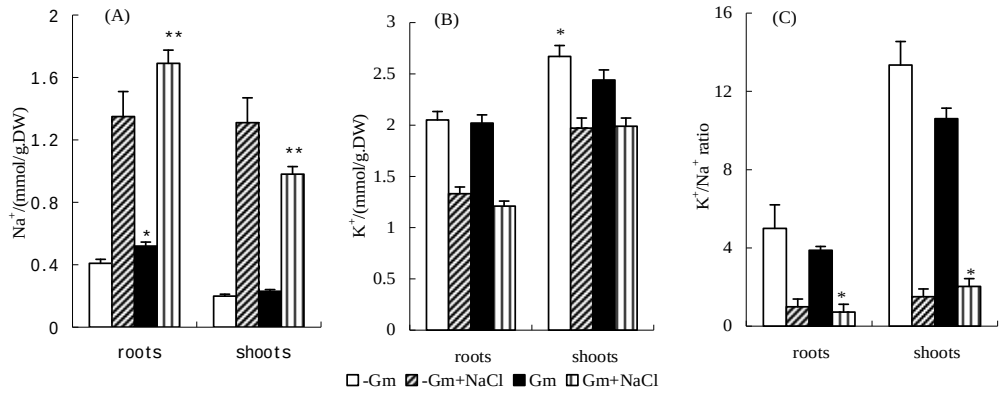

Fig. 1. Effects of *Glomus mosseae* on contents of Na^+ and K^+, and K^+ / Na^+ ratio in roots and shoots of *Kosteletzkya avirginica* under NaCl stress: (A) Na^+ content; (B) K^+ content; (C) K^+ / Na^+ ratio. * $p < 0.05$; * * $p < 0.01$.

Table 3. Effects of *Glomus mosseae* on mean relative contents of Na^+ and K^+, and K^+ / Na^+ ratio in different tissues of *K. avirginica* root transverse section under NaCl stress.

Tissues of *K. avirginica*	Ion (%)	-Gm	-Gm+ NaCl	Gm	Gm + NaCl
Epidermis	K^+	58.8 ± 4.2	60.6 ± 3.1	52.9 ± 4.7	56.4 ± 4.0
	Na^+	29.1 ± 3.9	53.2 ± 4.4	30.4 ± 5.4	54.8 ± 3.3
	K^+ / Na^+	2.02 ± 0.23	1.14 ± 0.15	1.74 ± 0.22	1.03 ± 0.19
Epicortex	K^+	71.8 ± 7.2	86.8 ± 5.7	74.4 ± 5.5	78.0 ± 4.9
	Na^+	27.7 ± 3.3	78.2 ± 4.3	30.6 ± 4.5	80.4 ± 3.6
	K^+ / Na^+	2.59 ± 0.15	1.11 ± 0.22	2.43 ± 0.26	0.97 ± 0.12
Cortex	K^+	73.9 ± 5.5	75.2 ± 4.9	84.5 ± 6.7	57.4 ± 6.3
	Na^+	24.3 ± 3.6	100.2 ± 5.7	31.3 ± 3.1	110.4 ± 3.0
	K^+ / Na^+	3.04 ± 0.18	0.75 ± 0.07	2.7 ± 0.13	0.52 ± 0.12
Endoderm	K^+	94.4 ± 6.2	90.0 ± 3.8	97.8 ± 9.4	87.3 ± 6.3
	Na^+	10.8 ± 4.1	55.2 ± 4.0	21.6 ± 4.2	61.5 ± 3.8
	K^+ / Na^+	8.74 ± 0.18	1.63 ± 0.12	4.53 ± 0.22	1.42 ± 0.13
Stele	K^+	103.7 ± 8.6	66.1 ± 5.7	105.6 ±7.0	64.3 ± 6.3
	Na^+	8.4 ± 2.8	40.8 ± 3.9	7.3 ± 3.0	23.2 ± 5.0
	K^+ / Na^+	12.35 ± 0.83	1.62 ± 0.14	14.46 ± 0.76	2.77 ± 0.27

In the endoderm of mycorrhizal seedlings, the Na^+ increased significantly, while it decreased in the column, which may be associated with casparian bond limited Na^+ from exodermis input to the column tube and then transport to the shoots. Under NaCl stress, this barrier function of

inoculated seedlings increased significantly, this may be the one mechanism by which mycorrhizal seedlings intercepted Na^+ in the root. Under NaCl treatment, the K^+ in the endoderm of mycorrhizal plants also increased, but reduced significantly in the column. This may be associated with salt treatment enhanced the thickness of casparian bond. Our results showed that the difference between inoculated seedlings and non-inoculated seedlings of *K. avirginica* isn't the capability of Na^+ entering the epidermis and cortex, but mainly affected by the capacity of Na^+ loading to the column tube. In the parenchymal cell of xylem in root of mycorrhizal seedlings which have more strong salt-tolerance ability, the ability of Na^+ transporting outward is significantly less than the non-inoculated seedlings. The tolerance of the *K. avirginica* seedlings depended mainly on the capacity of Na^+ loading to the column tube.

High K^+ / Na^+ ratios are maintained and could influence the ionic balance of the cytoplasm or Na^+ efflux from plants (Giri *et al.* 2007). In the absence of salt stress, inoculation with the fungi maintained relatively lower K^+ / Na^+ (higher Na^+ / K^+) ratios in *K. avirginica* roots, and plants showed highest root and shoot dry weights, compared with non-inoculated plants. These findings indicate that lower K^+ / Na^+ ratios (within limited levels) had positive effects on the growth of *K. avirginica* under non-salt-treated conditions. However, positive correlations were observed between shoot and root dry weights and K^+ / Na^+ ratios in the stele, between AM colonization and K^+ / Na^+ ratios in the epidermis and stele. These results suggest that the capacity of plants to maintain a higher cytosolic K^+ / Na^+ ratio is one of the key determinants of salt tolerance in plants inoculated with AM fungus (Zhang and Shi 2013, Liu *et al.* 2023).

In conclusion, under NaCl stress, the roots of mycorrhizal *K. avirginica* intercepted more Na^+ than the shoots done, while the K^+ content of the shoots was obviously higher than the roots. The NaCl-tolerant capacity of *K. avirginica* seedlings depended mainly on the ability of the root endoderm hindering Na^+ transporting to the column tube and limiting Na^+ loading, and the Na^+ interceptive ability of mycorrhizal seedlings in roots and K^+ / Na^+ ratio in shoots were stronger than that of non-inoculated seedlings. The elevated Na^+ intercepting ability in root tissues of mycorrhizal plants may help improve the tolerance of *K. avirginica* to NaCl Stress.

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