Ability of multicellular salt glands in *Tamarix* species to secrete Na^+ and K^+ selectively

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The present study aimed to determine the mechanism of cation-selective secretion by multicellular salt glands. Using a hydroponic culture system, the secretion and accumulation of Na^+ and K^+ in *Tamarix ramosissima* and *T. laxa* under different salt stresses (NaCl, KCl and NaCl+KCl) were studied. Additionally, the effects of salt gland inhibitors (orthovanadate, Ba^{2+} , ouabain, tetraethylammonium (TEA) and verapamil) on Na^+ and K^+ secretion and accumulation were examined. Treatment with NaCl (at 0–200 mmol L⁻¹ levels) significantly increased Na^+ secretion, whereas KCl treatment (at 0–200 mmol L⁻¹ levels) significantly increased K^+ secretion. The ratio of secretion to accumulation of Na^+ was higher than that of K^+ . The changes in Na^+ and K^+ secretion differed after adding different ions into the single-salt solutions. Addition of NaCl to the KCl solution (at 100 mmol L⁻¹ level, respectively) led to a significant decrease in K^+ secretion rate, whereas addition of KCl to the NaCl solution (at 100 mmol L⁻¹ level, respectively) had little impact on the Na^+ secretion rate. These results indicated that Na^+ secretion in *Tamarix* was highly selective. In addition, Na^+ secretion was significantly inhibited by orthovanadate, ouabain, TEA and verapamil, and K^+ secretion was significantly inhibited by ouabain, TEA and verapamil. The different impacts of orthovanadate on Na^+ and K^+ secretion might be the primary cause for the different Na^+ and K^+ secretion abilities of multicellular salt glands in *Tamarix*.

***Tamarix*, salt gland, inhibitor, ion secretion, salt stress**

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Soil salinity is an important limiting factor for plant growth. Throughout plant evolution, plants growing in saline environments have developed specific organs, such as salt glands in recretohalophytes. Salt glands vary greatly among plants and can be divided into multicellular salt glands, bicellular salt glands and salt bladders according to their structure [1]. These glands also differ in their functions. One of the functions of salt glands is to secrete cations preferentially. The cation secretory abilities of the multicellular salt glands of dicotyledons are as follows: divalent cation>monovalent

cation in *Tamarix aphylla*; $\text{Na}^+ > \text{K}^+ > \text{Ca}^{2+}$ in *Glaux maritima*; $\text{Na}^+ = \text{K}^+ > \text{Ca}^{2+}$ in *Limonium vulgare* [2–4]. Most salt glands of dicotyledons secrete Na^+ preferentially. Selective secretion of salts is considered to be the result of long-term adaptation to the saline environment. However, the mechanism for the preferential secretion of certain ions has not been elucidated [5–7].

Salt gland inhibitors have been used to investigate the salt-secreting functions of salt glands by many researchers. In a study of the subcellular ultrastructure of the salt glands in *Tamarix aphylla*, Thomson *et al.* [8] observed a large number of mitochondria in the secretory cells of this species;

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this finding indicated that the intercellular transportation of ions in the salt glands was an energy-consuming process. Balsamo *et al.* [9] successfully isolated mesophyll cells and secreting cells from the salt glands of *Ceratostigma plum-baginoides*. After detection, it was found that the total AT-Pase level in the plasma of the secreting cells was four-fold that of the mesophyll cells, and the activity of the former was more sensitive to the mitochondrial inhibitor Na-azide and plasma membrane inhibitor Vanadate; therefore, it was further deduced that H⁺-ATPase played an important role in the ion secretion. Kobayashi [10] found that the bicellular salt glands of Rhodes grass showed higher ability to secrete Na⁺ than K⁺, and that the plasma membrane H⁺-ATPase inhibitors, ion channel inhibitors, Na⁺-K⁺-ATPase inhibitors, and Ca²⁺ and K⁺ channel inhibitors had different effects on Na⁺ and K⁺ secretion; these findings indicated that the preferential Na⁺ secretion in salt glands might be due to the different secretory channels for different ions. The results of recent research showed that ion secretion of multicellular salt glands was regulated by several salt gland inhibitors, such as proton pump inhibitors, Ca²⁺ pump inhibitors and K⁺ channel inhibitors [9–13]. However, yet to be elucidated is whether multicellular salt glands, of which the subcellular structure is more complicated than that of bicellular salt glands, demonstrate a secretion preference for certain ions; if this is the case, the mechanism behind this process is also unknown.

Tamarix is an important bush plant that grows widely in sandy wastelands and in saline-alkali areas of arid and semiarid regions. It has attracted attention for its specific biological and ecological characteristics as well as its important roles in ecology and the social economy [13,14]. As an important morphological trait for adaptation to saline environments, the salt glands of *Tamarix* have been studied since the 1950s. The flow of ions between the eight subcells of the salt gland was considered to be driven by hydrostatic pressure [15]. However, with the discovery of ion channels and the use of a variety of inhibitors in recent years, whether the ion secretion is due to active transport has once again become a focus for research on salt secretion mechanisms [9,10]. In early research into the salt secretion characteristics of the salt glands of *Tamarix* growing in fields and cultured artificially in phytotrons, it was discovered that Na⁺ was the chief ion secreted [7,16–18]. However, the concentration of each ion in the plant root environment varied significantly in these experiments. Therefore, whether *Tamarix* preferentially secretes Na⁺ when the concentration of each ion is identical requires clarification. In addition, considering that the salt glands in *Tamarix* are multicellular, no reports have answered questions such as whether the ion secretion involves energy-consuming active transport and why the salt glands preferentially secrete Na⁺. Therefore, in the present study, the influences of different salt environments and salt gland inhibitors on ion secretion and accu-

mulation in *T. ramosissima* and *T. laxa* were investigated. The aim of the current study is to provide a theoretical basis for investigating the function of salt glands and revealing the ecophysiological characteristics of dicotyledons adapted to saline environments.

1 Materials and methods

1.1 Plant materials and culture conditions

One-year-old branches of *T. ramosissima* and *T. laxa* were collected from the Turpan Desert Botanical Garden at the Chinese Academy of Sciences (40°51'N, 89°11'E). Branches with a diameter of about 0.5 cm were selected and cut into 10-cm-long pieces. All branches were soaked in water for 24 h and then disinfected in 0.5% potassium permanganate solution for 30 min followed by washing with tap water. The bases of the branches were soaked in 0.1% ABT rooting powder solution for 10 h and planted in quartz sand medium for rooting and sprouting. After sprouting, the cuttings were sprayed with half-strength Hoagland nutrient solution every 3 days. The experiments were conducted in phytotrons at the Xinjiang Institute of Ecology and Geography with temperatures of (34±3)°C (day)/(28±3)°C (night), 40%–65% relative humidity, and light intensity of 12000 lx with a 14/10 h (light/dark) photoperiod. The cuttings were cultured for 15 d.

1.2 Experimental design

After the shoots had grown 4–6 cm, plants of identical height were selected, rinsed with deionized water to remove sand from the roots, and placed in deionized water in containers of height 30 cm and diameter 20 cm (with two plants per container). The water was continuously aerated for 24 h each day.

The plants were divided into three groups: (i) a dose-response group, to which 0, 50, 100, 150 or 200 mmol L⁻¹ NaCl or KCl was applied in the culture solution; (ii) a Na-K competition group, which were treated with 100 mmol L⁻¹ NaCl plus 100 mmol L⁻¹ KCl; and (iii) an inhibitor-treated group, to which one of the following salt gland inhibitors were added to either 100 mmol L⁻¹ NaCl or KCl nutrient solutions, with inhibitor-free solutions as the control. The inhibitors and their concentrations were orthovanadate (1.5 mmol L⁻¹), Ba²⁺ (3 mmol L⁻¹), ouabain (3 mmol L⁻¹), tetraethylammonium (TEA-Cl) (12 mmol L⁻¹), and verapamil (3 mmol L⁻¹).

After 15 d in deionized water, the culture solution was replaced with the appropriate salt solution. The salt treatments were applied for 48 h. Each treatment contained six replicates. The salt gland inhibitors and references for the methods used are listed in Table 1.

Table 1 Ion transport inhibitors and references for the methods used

Inhibitor	Action site	Reference for method	Manufacturer
Orthovanadate (Na_3VO_4)	H^+ -ATPase (P-type)	Balsamo & Thomson [9]; Briskin <i>et al.</i> [11]	Guangzhou Weibo Chemical Co., Ltd.
Ba^{2+} (BaCl_2)	Cation channels/transport agents	Maathuis & Amtmann [19]; Véry & Sentenac [20]	Tianjin Kaitong Chemical Reagent Co., Ltd.
Ouabain	Na^+ - K^+ -ATPase	Brown <i>et al.</i> [21]; Davis & Jaworski. [22]	Wako Co.
Tetraethylammonium (TEA-Cl)	K^+ channel	Maathuis & Amtmann. [19]; Véry & Sentenac. [20]	Alexis Co.
Verapamil ($\text{C}_{27}\text{H}_{38}\text{N}_2\text{O}_4 \cdot \text{HCl}$)	Ca^{2+} channel and K^+ channel	Véry & Sentenac. [20]; Kobayashi <i>et al.</i> [10]	Sigma Co.

1.3 Determination standard and method

1.3.1 Collection of salt gland secretions

After 24 h treatment, the marked sections of foliages were excised and immediately placed in test tubes with 20 mL deionized water and shaken for 20 s. For convenience of determination and calculation of the ion secretion rate, the deionized water containing salt gland secretions were marked in accordance with the excised foliage. At the end of the experiment, each marked excised foliage was dried, weighed and its ion content determined. Rates of ion secretion rate were expressed in $\mu\text{mol g}^{-1} \text{h}^{-1}$.

1.3.2 Na^+ , K^+ detection and proportions of ion accumulated in plant tissues

After the wash in deionized water, the marked foliages were incubated at 105°C for 30 min to deactivate enzymes, and then oven-dried to a constant weight at 80°C and the dry weight was recorded. The dried plant samples were crushed and ashed at 550°C in a muffle furnace and then dissolved in 20 mL dilute nitric acid. The Na^+ and K^+ ion contents of the plant samples and their secretions were detected using atomic absorption spectrometry (SOLAARS-2, Thermo Electron, USA).

The proportion of ion accumulated in the tissues to the total amount secretion represented the affinity of Na^+ and K^+ to the plants.

1.4 Statistical analyses

The data were analyzed by means of a one-way ANOVA using SPSS 11.0 (SPSS, Inc., Chicago, USA). Homogeneity tests and data standardization (if necessary) were performed before analysis. Multiple comparisons were performed for data of the dose-response group and Na-K competition group using Tukey's test. Data from the inhibitor-treated group and control were compared using Dunnett's method.

2 Results and analyses

2.1 Effect of different salt concentrations on ion secretion

Under NaCl stress, the two *Tamarix* species secreted much

more Na^+ than K^+ ($P < 0.05$). The salt concentration in the root environment significantly affected Na^+ secretion ($P < 0.05$) but not K^+ secretion ($P > 0.05$). With increasing ion concentration in the root environment, the Na^+ secretion rate in *T. ramosissima* gradually decreased and peaked at 50 mmol L^{-1} NaCl. In contrast, the Na^+ secretion rate in *T. laxa* gradually increased and peaked at 200 mmol L^{-1} NaCl. The K^+ secretion rates in the two *Tamarix* species remained at a relatively low level and were not affected by the salt concentration in the root environment (Figure 1).

As shown in Figure 2, under KCl stress, the K^+ secretion rate in *T. laxa* and *T. ramosissima* increased with the increase of salt concentration in the root environment and was significantly higher than the Na^+ secretion rate ($P < 0.05$). As for Na^+ , the K^+ secretion rate showed similar trends between the two *Tamarix* species. The Na^+ secretion rate remained at a relatively low level in all KCl treatments, and no significant difference was shown ($P > 0.05$) (Figure 2).

For both *Tamarix* species, the addition of KCl to NaCl solutions had no significant effect on the Na^+ secretion rate compared with that of the NaCl solution alone ($P > 0.05$), whereas the addition of NaCl to KCl solutions led to a significantly lower K^+ secretion rate than that of KCl solution alone ($P < 0.05$). In addition, both *Tamarix* species showed a significantly higher Na^+ secretion rate compared with K^+ in the NaCl+KCl mixed solution (Figure 3).

2.2 Effect of different salt treatments on the accumulated ion content

The accumulated Na^+ content in *T. ramosissima* and *T. laxa* increased rapidly with the increase in NaCl concentration in the root environment, and the rate of Na^+ accumulation was significantly higher ($P < 0.05$) than that of K^+ (Figure 4).

Under KCl stress, the accumulated K^+ contents of both *Tamarix* species showed a positively linear trend, whereas the Na^+ contents remained at a relatively low level and were unaffected by the salt concentration in the root environment ($P > 0.05$) (Figure 5).

As shown in Figure 6, the Na^+ content in *T. laxa* and *T. ramosissima* showed no significant difference between the NaCl treatment and NaCl+KCl treatment ($P > 0.05$). The same findings were observed for K^+ content ($P > 0.05$).

With 50 mmol NaCl treatment, the secretion and accu-

Figure 1 The effect of NaCl concentration on the secretion of Na^+ and K^+ in *T. ramosissima* (A) and *T. laxa* (B).

Figure 2 The effects of different KCl concentrations on the secretion of Na^+ and K^+ in *T. ramosissima* (A) and *T. laxa* (B).

Figure 3 The effects of 100 mmol of NaCl, KCl and Na+K solutions on secretion of Na^+ and K^+ in *T. ramosissima* (A) and *T. laxa* (B).

Figure 4 The effects of different NaCl concentrations on the accumulated Na^+ and K^+ content of *T. ramosissima* (A) and *T. laxa* (B).

Figure 5 The effects of the KCl concentration on the accumulated Na^+ and K^+ content of *T. ramosissima* (A) and *T. laxa* (B).

mulation of Na⁺ in both *Tamarix* species were significantly higher ($P<0.05$) than the control, whereas K⁺ secretion showed no significant difference ($P>0.05$). With 50 mmol KCl treatment, K⁺ secretion and accumulation in the both *Tamarix* species were significantly higher ($P<0.05$) than the control ($P<0.05$), whereas the Na⁺ secretion showed no significant difference ($P>0.05$). In all treatments, the Na⁺ secretion was equal to or higher than accumulation, whereas K⁺ secretion was significantly lower than accumulation. These results indicated that Na⁺ secretion took precedence over K⁺ secretion in the *Tamarix* species (Table 2).

2.3 Effects of salt gland inhibitors on ion secretion

Without inhibitors, ion secretion in the two *Tamarix* species significantly increased with the increase of salt concentration in the root environment ($P<0.01$, t -test). However, with addition of salt gland inhibitors, except for Ba²⁺, the Na⁺ secretion rate in NaCl-treated samples significantly decreased ($P<0.05$) (Figure 7A, Table 3). In contrast, in the KCl-treated samples, the addition of three inhibitors significantly decreased the K⁺ secretion rate, but orthovanadate

and Ba²⁺ had no significant effect ($P>0.05$) (Figure 7B, Table 3).

2.4 Effect of salt gland inhibitors on foliar ion contents

Of the salt gland inhibitors used, all except Ba²⁺ showed no significant effect on Na⁺ content, whereas all of the inhibitors showed little effect on the K⁺ content of *T. ramosissima* and *T. laxa* ($P>0.05$) (Figure 8, Table 4).

3 Discussion and conclusion

Tamarix displayed different ion secretion patterns in response to different salt treatments. Compared with the control (salt-free), the Na⁺ and K⁺ secretion rate of the salt glands significantly increased with the increase of salt concentration in the root environment (Figures 1 and 2). However, the ratio of Na⁺ secretion to the foliar Na⁺ content was higher than the ratio for K⁺ (Table 2). In addition, the Na-K competition experiment demonstrated that the addition of NaCl to the KCl treatment significantly inhibited K⁺ secre-

Figure 6 The effects of 100 mmol of NaCl, KCl and Na+K solutions on the accumulated Na⁺ and K⁺ content of *T. ramosissima* (A) and *T. laxa* (B).

Table 2 The effects of salt treatments on foliar Na⁺ and K⁺ secretion and accumulation in *T. ramosissima* and *T. laxa*^{a)}

Ions		<i>T. ramosissima</i>			<i>T. laxa</i>		
		NaCl (μmol g ⁻¹)	CK (μmol g ⁻¹)	KCl (μmol g ⁻¹)	NaCl (μmol g ⁻¹)	CK (μmol g ⁻¹)	KCl (μmol g ⁻¹)
Na ⁺	Secreted	345.6±10.0a	158.4±10.4b	105.5.0±5.7c	249.4±17.8a	100.4±18.9b	113.4±9.3b
	Accumulated	325.0±32.6a	57.6±4.4b	60.5±4.8b	333.4±14.6a	51.5±5.1b	68.4±5.4b
K ⁺	Secreted	3.7±0.8b	1.6±0.2b	88.0 ±7.6a	15.1±1.1b	8.5±1.6b	88.8±5.5a
	Accumulated	228.2±36.2a	42.4±2.4b	354.3±32.4a	189.5±27.5a	30.3±3.8b	323.1±45.2a

a) All data are means of six replications±SE (n=6); different letters indicate a significant difference at $P<0.05$.

Figure 7 The effect of five salt gland inhibitors on the Na⁺ (A) and K⁺ (B) secretion rate in *T. ramosissima* and *T. laxa*.

Table 3 Results of a paired samples *t*-test comparing the different salt gland inhibitor treatments and the control on the Na⁺ and K⁺ secretion in *T. ramosissima* and *T. laxa*^{a)}

Treatments	<i>T. ramosissima</i>		<i>T. laxa</i>	
	Na ⁺	K ⁺	Na ⁺	K ⁺
+Van	11.43*	1.74	8.53*	2.02
+Ba	1.58	0.46	2.54	3.44
+Oua	7.84*	3.69*	11.60*	10.94*
+TEA	8.79*	9.73*	14.44*	7.46*
+Ver	3.98*	10.02*	6.89*	6.89*

a) *, *P*<0.05. **Figure 8** The effect of different inhibitors on accumulation of Na⁺ (A) and K⁺ (B) in the foliage of *T. ramosissima* and *T. laxa*.**Table 4** Results of a paired samples *t*-test comparing the different inhibitor treatments and controls on accumulation of Na⁺ and K⁺ in *T. ramosissima* and *T. laxa*^{a)}

Treatments	<i>T. ramosissima</i>		<i>T. laxa</i>	
	Na ⁺	K ⁺	Na ⁺	K ⁺
+Van	1.27	0.37	1.85	0.81
+Ba	5.59*	1.49	5.16*	1.14
+Oua	1.86	1.52	1.85	1.03
+TEA	1.59	1.19	0.45	0.92
+Ver	1.83	0.57	0.37	1.30

a) *, *P*<0.05.

tion, while the addition of KCl to the NaCl treatment had no significant effect on Na⁺ secretion (Figure 3). These results indicated that the salt glands of *Tamarix* secreted Na⁺ preferentially to K⁺. Preferential secretion of Na⁺ by salt glands is reported for other plant species, such as Plumbaginaceae, Avicenniaceae, Tamaricaceae, Frankeniaceae, *Reaumuria soongorica* and *Sporobolus spicatus* [4,6,17,18]. Previous research on the functions of *Tamarix* salt glands found that *T. aphylla* had a higher secretion rate of bivalent cations—such as Ca²⁺ and Mg²⁺—than monovalent cations such as Na⁺; this species also secreted Si, which led to a general conclusion that ion secretion was not selective in *Tamarix* salt glands [23]. After studying the ion secretion mechanisms of two *Tamarix* species from Xinjiang Province subjected to different salt treatments, it was found that, although the secreted ion species from multicellular salt glands were influenced by the ion composition in the root environment, salt glands preferentially secreted Na⁺ when the concentrations of Na⁺ and K⁺ were the same. Furthermore, ion-selective secretion might be an important survival

strategy for *Tamarix* by which plants rapidly regulate the internal ionic equilibrium to adjust to the saline environment, as in other dicotyledons.

Salt glands are important for ion homeostasis regulation in dicotyledons. Internal ionic equilibrium under salt stress is a comprehensive reflection of a variety of salt resistance mechanisms. Internal Na⁺ and K⁺ contents in *Tamarix* are mainly affected by the types and concentrations of salts in the root environment [7]. In the two *Tamarix* species treated with NaCl, when the salt concentration exceeded 50 mmol in the root environment, Na⁺ accumulation was significantly higher than that of K⁺ (*P*<0.05), while the K⁺ accumulation was significantly higher than that of Na⁺ with KCl treatment (*P*<0.05) (Figures 4 and 5). In addition, the internal ion levels and salt gland secretory abilities mutually regulated each other; however, the response mechanism differed for Na⁺ and K⁺. In the separate NaCl and KCl treatments, with the increase of salt level in the root environment, internal Na⁺ accumulation increased as the ion-secreting ability decreased (Figures 1A and 4A). In contrast, K⁺ secretion was positively regulated by internal K⁺ accumulation; that is, the secretory ability of the salt glands significantly increased with internal K⁺ accumulation (*P*<0.05) (Figures 2A and 5A). However, no wilting of the leaves occurred during the entire experiment. These results indicated that the excessive accumulation of Na⁺, which was induced by the decreased Na⁺ secretion, might function as an osmotic potential regulator to enhance water absorption by plants in a saline environment. On the other hand, high concentrations of K⁺ are toxic to cell metabolism, whereas low concentrations of K⁺ have little contribution to osmotic potential regulation. Therefore, the K⁺ secretion rate was increased during the

KCl treatment to maintain the internal equilibrium of K^+ (Figures 2 and 5). Zhao *et al.* [24] found that KCl treatment decreased internal Na^+ but increased internal K^+ accumulation in *Suaeda salsa*, *Atriplex centralasiatica* and *Limonium bicolor* seedlings; however, high internal K^+ concentrations inhibit plant growth, and similar phenomena have been reported in other plant species, indicating that high concentrations of K^+ (not Na^+) were more toxic to the physiological metabolism of seedlings [25–27]. Although no inhibitory effects of high K^+ concentrations on *Tamarix* plant growth have been noted during the short-term studies, the effects of long-term KCl stress on *Tamarix* growth require further study. Furthermore, the affinity between ions and plants might also be an important factor for the selective secretion of ions. As shown in Figures 3 and 6, the proportions of Na^+ and K^+ accumulated in plant tissues of *T. ramosissima* were 3.67 and 11.04, respectively, and those of *T. laxa* were 3.06 and 8.43, respectively (Figures 3 and 6); this indicates that the *Tamarix* species had a higher affinity to K^+ , which led to decreased K^+ secretion. Similar results have been reported in previous studies on *Sporobolus spicatus* and Rhodes grass [6,10].

Ion secretion in *T. ramosissima* and *T. laxa* was affected to a certain degree by salt gland inhibitors, indicating that ion secretion in salt glands was an active transport process with the participation of a variety of proton pumps, carrier proteins and ion channels (Figures 7 and 8, Tables 3 and 4). In addition, the different impacts of the inhibitors on Na^+ and K^+ secretion also indicated different secretory pathways for Na^+ and K^+ . For example, orthovanadate significantly inhibited Na^+ secretion but showed little effect on K^+ secretion in the two *Tamarix* species. This indicates that the carrier proteins inhibited by orthovanadate participated in Na^+ secretion but not K^+ secretion, which might also play a vital role in the preference for Na^+ secretion in salt glands (Figure 7, Table 3).

Ba^{2+} is an inhibitor of a number of transport proteins and cation channels [13,20]. Kobayashi *et al.* originally verified the inhibitory ability of Ba^{2+} on the ion secretion of bicellular salt glands and noted that Ba^{2+} inhibited Na^+ secretion but not K^+ secretion in the salt glands of Rhodes grass [10]. In the present study, Ba^{2+} demonstrated no significant inhibition on Na^+ and K^+ secretion in multicellular salt glands (Figure 7, Table 3); however, the Na^+ content in the foliages of the *Tamarix* species decreased significantly whereas the K^+ contents showed no significant difference in response to Ba^{2+} (Figure 8, Table 4). Previous studies on rice roots found that Ba^{2+} inhibited Na^+ absorption in roots and thus decreased Na^+ accumulation in aboveground parts [13]. However, in the same study, Ba^{2+} had no significant effect on K^+ absorption [13]. Therefore, whether or not the significant decrease in Na^+ contents in foliages of *Tamarix* is related to the inhibition by Ba^{2+} of Na^+ absorption by the roots remains to be seen.

Ouabain, TEA and verapamil showed significant inhibi-

tory effects on Na^+ and K^+ secretion in *Tamarix* (Figure 7, Table 3). The effect of verapamil on K^+ secretion in *T. ramosissima* was highly significant; the K^+ secretion in the verapamil treated samples was close to that in the salt-free control (Figure 7B). In contrast, the effect of verapamil on Na^+ secretion was not as significant. Therefore, ion channels responding to verapamil might be more important for K^+ secretion.

Orthovanadate is a specific inhibitor of plasma membrane H^+ -ATPase; inhibition of plasma membrane H^+ -ATPase might lead to a decrease in the Na^+ secretion rate in both multicellular salt glands and salt bladders [11,12]. Plasma membrane H^+ -ATPase plays an important role in the salt secretion of salt glands by producing a transmembrane electrochemical potential. In the present study, orthovanadate was the only inhibitor showing different effects on Na^+ and K^+ secretion (Table 3). Therefore, it was deduced that an electrochemical proton gradient generated by plasma membrane H^+ -ATPase showed higher activity during Na^+ secretion but not K^+ secretion.

In conclusion, the secretion of Na^+ takes precedence over K^+ in the multicellular salt glands of *T. ramosissima* and *T. laxa*. The five salt gland inhibitors showed different effects on Na^+ and K^+ secretion in the two *Tamarix* species. Orthovanadate, which is a specific inhibitor of plasma membrane H^+ -ATPase, significantly inhibited Na^+ secretion whereas its effects on K^+ secretion were not significant. The difference in Na^+ and K^+ secretion ability might be an important reason for the preferential secretion of Na^+ . However, the transmembrane transport of ions might occur at any site during their migration from mesophyll cells into the collecting cells of salt glands [6,28]. The specific sites that lead to different Na^+ and K^+ secretory abilities require further study.

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