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## Na<sup>+</sup> uptake pathways in the halophyte *Suaeda maritima*

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**Key words:** Halophyte, Na<sup>+</sup> net uptake, <sup>22</sup>Na<sup>+</sup> influx, Na<sup>+</sup> uptake pathways

**Introduction** Reducing Na<sup>+</sup> influx must be the key step for controlling Na<sup>+</sup> accumulation compared with vacuolar Na<sup>+</sup> compartmentalization and Na<sup>+</sup> extrusion (Apse et al., 1999; Ma et al., 2004; Martínez-Atienza et al., 2007), neither of which would be sufficient alone. However, the pathways by which plants take up Na<sup>+</sup> are uncertain since Na<sup>+</sup> uptake by plant roots has largely been explored using species that accumulate little Na<sup>+</sup> into their leaves. By way of contrast, the halophyte *Suaeda maritima* accumulates, without injury, concentrations of the order of 400 mM NaCl in its leaves. Here we use *S. maritima* to examine Na<sup>+</sup> uptake pathways.

**Materials and methods** Twenty one to 23 day old seedlings were used to evaluate the effects of inhibitors of ion transport on growth and ion accumulation. Na<sup>+</sup> analysis was performed using an atomic absorption spectrophotometer. <sup>22</sup>Na<sup>+</sup> influx was evaluated according to the method described by Essah et al. (2003).

**Results** TEA<sup>+</sup>, Cs<sup>+</sup> and Ba<sup>2+</sup> significantly reduced the net uptake of Na<sup>+</sup> from 150 mM NaCl over 48 h, by 54%, 24% and 29%, respectively (Tables 1 and 2). TEA<sup>+</sup>, Cs<sup>+</sup> and Ba<sup>2+</sup> also significantly reduced <sup>22</sup>Na<sup>+</sup> influx by 47%, 30% and 31%, respectively (Figure 1). In contrast to the situation in 150 mM NaCl, neither TEA<sup>+</sup> nor Cs<sup>+</sup> significantly reduced net Na<sup>+</sup> uptake or <sup>22</sup>Na<sup>+</sup> influx in 25 mM NaCl (Table 1, Figure 1). Ba<sup>2+</sup> did significantly decrease net Na<sup>+</sup> uptake (by 47%) and <sup>22</sup>Na<sup>+</sup> influx (by 36% with 1 mM Ba<sup>2+</sup>) in 25 mM NaCl (Table 2, Figure 1).

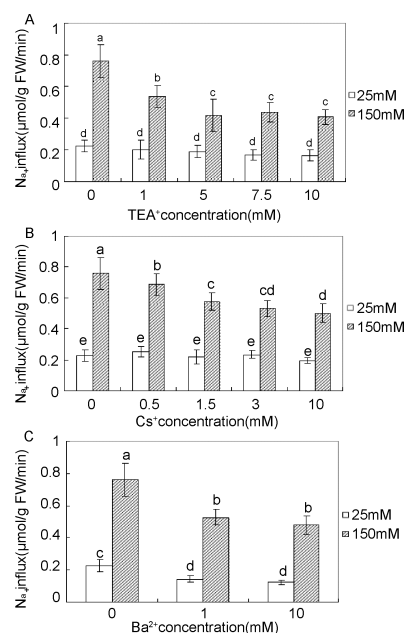
**Conclusions** We propose that two distinct low-affinity Na<sup>+</sup> uptake pathways exist in *S. maritima*: Pathway 1 is insensitive to TEA<sup>+</sup> or Cs<sup>+</sup>, but sensitive to Ba<sup>2+</sup> and mediates Na<sup>+</sup> uptake in low salinities (25 mM NaCl); Pathway 2 is sensitive to TEA<sup>+</sup>, Cs<sup>+</sup> and Ba<sup>2+</sup> and mediates Na<sup>+</sup> uptake in higher external salt concentrations (150 mM NaCl).

**Table 1** Effect of TEA<sup>+</sup> and Cs<sup>+</sup> on net Na<sup>+</sup> flux (μmol g<sup>-1</sup> fresh weight root min<sup>-1</sup>) of *S. maritima*.

NaCl concentration (mM)	Inhibition		
	None (control)	TEA <sup>+</sup> (10mM)	Cs <sup>+</sup> (3mM)
150	0.56 ± 0.04a	0.26 ± 0.03c	0.43 ± 0.03b
25	0.20 ± 0.02a	0.15 ± 0.01a	0.18 ± 0.03a

**Table 2** Effect of Ba<sup>2+</sup> on whole plant Na<sup>+</sup> content (μmol/plant) and root net Na<sup>+</sup> flux (μmol g<sup>-1</sup> fresh weight root min<sup>-1</sup>) of *S. maritima*.

	BT	25Na	25NaBa	150Na	150NaBa
Na <sup>+</sup> content	7.0 ± 0.56d	50 ± 5.61b	22 ± 1.4c	100 ± 7.7a	51 ± 4.4b
Na <sup>+</sup> netflux		0.19 ± 0.02c	0.10 ± 0.01d	0.43 ± 0.02a	0.31 ± 0.03b



**Figure 1** Root <sup>22</sup>Na<sup>+</sup> influx of *S. maritima* seedlings treated with different inhibitors.

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