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REVIEW: PART OF A SPECIAL ISSUE ON HALOPHYTES AND SALINE ADAPTATIONS

Using euhalophytes to understand salt tolerance and to develop saline agriculture: *Suaeda salsa* as a promising model

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• **Background** As important components in saline agriculture, halophytes can help to provide food for a growing world population. In addition to being potential crops in their own right, halophytes are also potential sources of salt-resistance genes that might help plant breeders and molecular biologists increase the salt tolerance of conventional crop plants. One especially promising halophyte is *Suaeda salsa*, a euhalophytic herb that occurs both on inland saline soils and in the intertidal zone. The species produces dimorphic seeds: black seeds are sensitive to salinity and remain dormant in light under high salt concentrations, while brown seeds can germinate under high salinity (e.g. 600 mM NaCl) regardless of light. Consequently, the species is useful for studying the mechanisms by which dimorphic seeds are adapted to saline environments. *S. salsa* has succulent leaves and is highly salt tolerant (e.g. its optimal NaCl concentration for growth is 200 mM). A series of *S. salsa* genes related to salt tolerance have been cloned and their functions tested: these include *SsNHX1*, *SsHKT1*, *SsAPX*, *SsCAT1*, *SsP5CS* and *SsBADH*. The species is economically important because its fresh branches have high value as a vegetable, and its seed oil is edible and rich in unsaturated fatty acids. Because it can remove salts and heavy metals from saline soils, *S. salsa* can also be used in the restoration of salinized or contaminated saline land.

• **Scope** Because of its economic and ecological value in saline agriculture, *S. salsa* is one of the most important halophytes in China. In this review, the value of *S. salsa* as a source of food, medicine and forage is discussed. Its uses in the restoration of salinized or contaminated land and as a source of salt-resistance genes are also considered.

Key words: Amaranthaceae, dimorphic seeds, food, forage, germination, halophyte, heavy metal, medicine, saline agriculture, salt-resistance genes, salt tolerance, *Suaeda salsa*, succulence.

INTRODUCTION

More than 800 million ha of land worldwide, or about 6 % of the world's total land area, are salt-affected (Munns, 2005). Global annual losses in agricultural production from salt-affected land are in excess of US$12 billion and rising. At the same time, the increasing amount of arable land being lost to urban sprawl is forcing agricultural production into marginal areas (Shabala, 2013). One tool that can be useful for dealing with salt-affected land is halophytic plants.

Le Houérou (1993) estimated that there are 5000–6000 halophytic species, which represent about 2 % of all angiosperms. Flowers and Colmer (2008) defined halophytes as those plants that are able to survive and reproduce in environments where the salt concentration is $\geq$200 mM NaCl, which reduced the number of halophytes to about 1 % of the world flora. Such differences highlight the arbitrary nature of the definitions. Among halophytic species, only a small number (fewer than 500 species) are tolerant of seawater salinity (Flowers *et al.*, 2010); most halophytes can resist only lower salt concentrations. In a saline agricultural system, the salinity of the soil is perhaps half that of seawater (Rozema and Flowers, 2008), and so it seems possible that some halophytes could be developed as salt-tolerant crops. A better understanding of how halophytes tolerate saline soils could also help plant breeders and molecular biologists increase the salt tolerance of conventional crop plants (Glenn and Brown, 1999).

According to a survey of plants that are able to grow and reproduce when salt concentrations range from 0·8 to 4·2 % based on dry soil, China contains about 587 halophytic species (Zhao *et al.*, 2011). Halophytic species are currently widely studied in China because of their value for the development of saline agriculture. An example is the euhalophytic herb *Suaeda salsa*. Euhalophytes, which can dilute salt within their succulent leaves or stems and thus have high salt tolerance, are valuable for understanding how dicotyledonous plants can tolerate salt (Flowers and Colmer, 2008; Huchzermeyer and Flowers, 2013; Rozema and Schat, 2013). The potential of several highly salt-tolerant, succulent halophytes in the Amaranthaceae (especially species of *Suaeda* and *Salicornia*) for use in saline agriculture has been reported in a series of papers (Rozema and Flowers, 2008; Glenn *et al.*, 2013; Rozema and Schat, 2013; Ventura and Sagi, 2013). *S. salsa* is highly salt tolerant; the optimal NaCl concentration for its growth is 200 mM, and it grows as well with 400 mM NaCl as with 10 mM NaCl (Song *et al.*, 2009). A series of genes related to *S. salsa* salt tolerance have been cloned and their functions tested, i.e. the species is a promising model for understanding salt tolerance. At the same time, fresh branches of the species have substantial value as a vegetable, and its seed oil is edible and is rich in unsaturated fatty acids, and thus the species can be used for developing saline agriculture. Plant breeders in China have been attempting to increase *S. salsa* seed yield in saline soils (Shao *et al.*, 2004). Here, we review the value of *S. salsa* from economic and ecological perspectives. We also consider its value as a model halophyte in the Amaranthaceae.

BIOLOGICAL AND ECOLOGICAL CHARACTERISTICS OF *S. SALSA*

Suaeda salsa Pall. (Caryophyllales, Amaranthaceae, Chenopodioideae) is a leaf-succulent halophytic herb with high salt tolerance during germination and seedling stages (W. Li *et al.*, 2005; Song *et al.*, 2008). The species is distributed in Europe and Asia. Although *S. salsa* in China grows in areas that differ greatly in geography and ecology, it grows better in littoral saline soils, for example the Yellow River Delta, than in saline inland soils of arid zones, such as the Zhunger Basin in China (X. Li *et al.*, 2012). *S. salsa* cannot be found in soils that contain <5 g of salt kg^{-1} dry soil, and the optimal salt concentration for its growth is between 15 and 20 g kg^{-1} dry soil (Gu, 1999). When the salt concentration in soil exceeds 20 g kg^{-1} dry soil in inland saline soil or in the intertidal zone, *S. salsa* forms a monospecific community (Table 1) (Gu, 1999). The species occurs both in coastal salt marshes and in saline inland sites in China (Song *et al.*, 2008). *S. salsa* leaves and stems are green in inland saline soils but red–violet in the intertidal zone during the entire growth period; the red–violet colour is due to the accumulation of betacyanin (Fig. 1). *S. salsa* seeds germinate in late April. The plants flower from July onwards, and seeds begin to mature in late September (Gu, 1999). An adult plant that is representative of the inland *S. salsa* population is shown in Fig. 2.

DIMORPHIC SEEDS

Germination and dormancy

The term seed heteromorphism refers to the production by individual plants of seeds with different form or behaviour (Gul *et al.*, 2013). Seed heteromorphism has been reported in 26 families, 129 genera and 292 species of angiosperms; these plants are mainly members of the Asteraceae and Chenopodiaceae (now the Amaranthaceae) that grow in highly variable environments such as arid regions, semi-arid regions, deserts and saline soils. Seed heteromorphism is generally considered to be an adaptive strategy that enables plants to escape from sib competition and to tolerate a changeable environment (L. Wang *et al.*, 2010).

TABLE 1. *The abundance of* Suaeda salsa *and accompanying plant species as related to soil salt content (reproduced from Gu, 1999)*

Salt content (g kg^{-1} dry soil)	*Suaeda salsa*	*Aeluropus littoralis*	*Imperata cylindrica*	*Artemisia* spp.	*Phragmites australis*
<5		+	+ +	+ + +	+ + +
5–10	+	+ +	+ + +	+ + +	+ + +
10–15	+ +	+ + +	+ +	+ +	+
15–20	+ + +	+			
20–30	+ +				
>30	+				

Plus signs indicate the abundance of the plant species.

Seed dimorphism and polymorphism are known for many halophytic species, for example *Atriplex patens* (He and Li, 1995), *Suaeda moquinii* (Khan *et al.*, 2001), *Suaeda aralocaspica* (L. Wang *et al.*, 2008) and *Suaeda acuminata* (H. L. Wang *et al.*, 2012). *S. salsa* also produces dimorphic seeds (W. Li *et al.*, 2005; Song *et al.*, 2008), i.e. soft brown seeds and hard black seeds. Brown seeds absorbed water more quickly than black seeds; brown seeds have a higher germination rate than black seeds under salinity, while black seeds are more sensitive than brown seeds to salinity in the absence of light; the optimal NaCl concentration for germination is about 400 mM for brown seeds and about 100 mM for black seeds (W. Li *et al.*, 2005). In *S. acuminata*, the two seed types (brown vs. black seed) absorbed water at different rates with brown seeds imbibing water faster; germination percentages of brown seeds were significantly higher than those of black seeds in all temperature and light regimes tested (H. L. Wang *et al.*, 2012). This indicates that heteromorphic seeds present different germination characteristic to help their mother plants adapt to a changeable environment.

After *S. salsa* seeds were stored for 1 year at approximately 20 °C and 30–40 % relative humidity, germination decreased for brown seeds but increased for black seeds regardless of salinity. Stratification and gibberellic acid (GA_4) treatments improved germination of black seeds but had little effect on brown seeds (W. Li *et al.*, 2008). The latter authors hypothesized that GA_4 may be the active form of endogenous gibberellin that releases dormancy and promotes germination of black seeds of *S. salsa*, and that certain environmental factors (e.g. stratification, soil salinity and storage) may affect *S. salsa* seed germination by affecting the biosynthesis of gibberellins, especially GA_4 (W. Li *et al.*, 2008). In another desert annual halophyte, *S. acuminata*, germination of black seeds was promoted by exogenous gibberellic acid (GA_3) but not by 8 weeks of cold stratification (H. L. Wang *et al.*, 2012). In non-dormant *S. acuminata* brown seeds, contents of zeatin riboside (ZR), GA_3 and abscisic acid (ABA) were significantly higher than in dormant black seeds, while contents of indole-3-acetic acid (IAA) were significantly higher in black than in brown seeds (H. L. Wang *et al.*, 2012). These results indicated that interactions among ZR, ABA and GA_3 may affect the dormancy of both seed types. The role of endogenous hormones in the dormancy and germination of dimorphic *S. salsa* seeds warrants further investigation.

Seed development under salinity

In a greenhouse sand-culture experiment, X. Li *et al.* (2011) found that salinity during the seed maturation stage benefited *S. salsa* in that it maintained brown seed (black seed of *S. salsa* was not used in the literature of this section) viability and ensured seedling emergence and population establishment. A preliminary study showed that, at 500 mM NaCl, the PG (phosphatidylglycerol) and SQDG (sulfoquinovosyldiacylglycerol) levels and the DGDG/MGDG (digalactosyldiacylglycerol/monogalactosyldiacylglycerol) ratio were higher in germinated brown seeds whose source plants had been cultured with 500 mM rather than with 1 mM NaCl. When brown seeds were incubated with 600 mM NaCl, the conductivity and malondialdehyde (MDA) concentration in the embryos were greater if the source plants had been cultured in 1 mM rather than in 500 mM NaCl. These results indicate that salinity during seed maturation

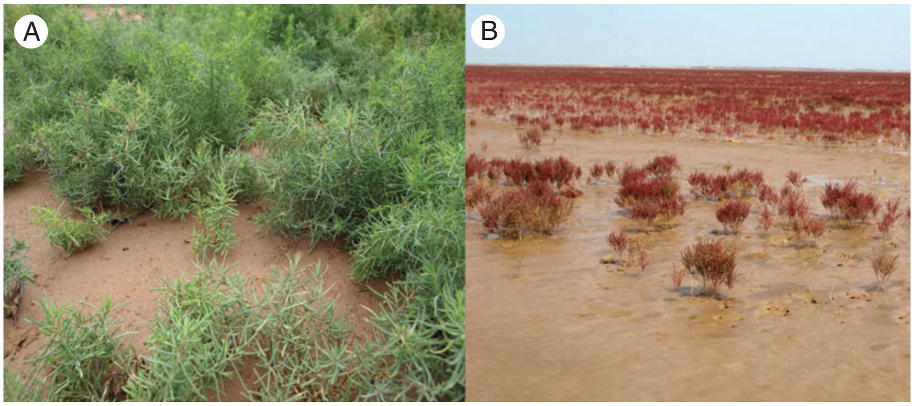

Fig. 1. *Suaeda salsa* growing at an inland site with saline soil (A) and at an intertidal zone (B).

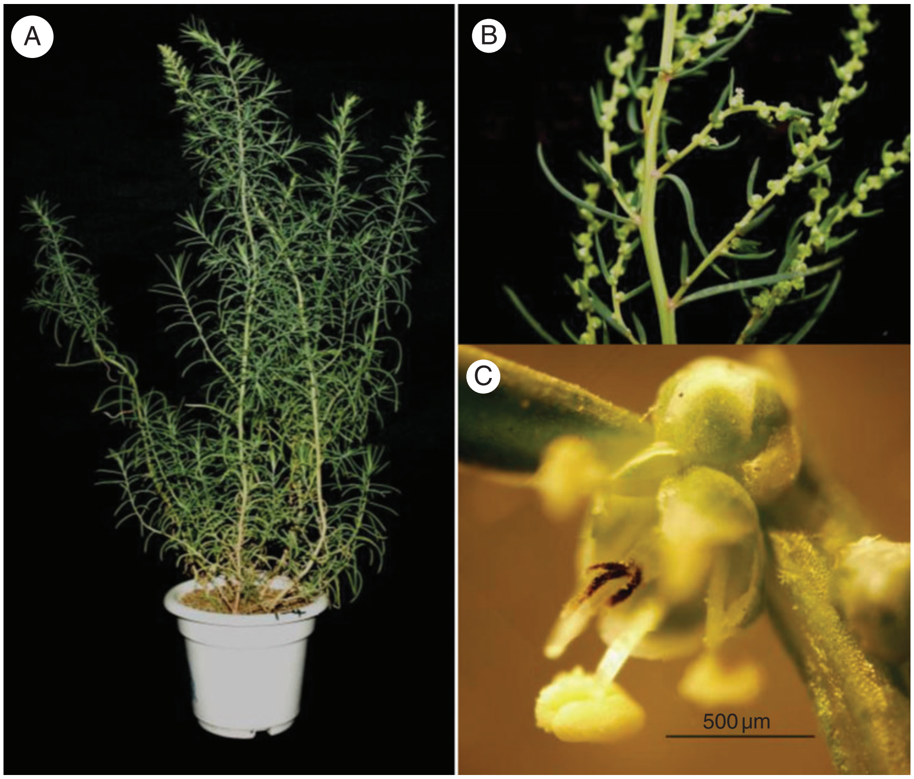

Fig. 2. A *Suaeda salsa* plant growing from seed of a plant occurring in inland saline soil. The above-ground plant (A), the flowering branches (B) and flower (C). The bar in C indicates 0·5 mm.

may increase the salt tolerance of seeds by changing the lipid composition of membranes (Zhou *et al*., 2014). The mechanism that explains why the viability of *S. salsa* seeds relies on salt during plant culture remains to be determined.

Seed photosynthesis allows biosynthetic fluxes by providing ATP and oxygen, which are readily used for respiration and biosynthesis (Weber *et al*., 2005). Rolletschek *et al*. (2003) showed that oxygen production in maturing cotyledons of *Vicia faba* was able to reach 50 % of atmospheric oxygen concentration within approx. 5 min. In a field investigation, X. Li *et al*. (2012) reported that oxygen production was greater in maturing embryos of *S. salsa* brown seeds in the intertidal population than in the inland population (the oxygen production in fresh embryos was 4 times greater per embryo, and 3 times greater per gram fresh weight of embryo for the intertidal population than for the inland population), which may be related to the greater proportion of brown seeds in the intertidal than in the inland population (Song *et al*., 2008).

Cotyledons in embryos of maturing brown seeds of the inland and intertidal populations of *S. salsa* are green and contain chlorophyll, although the chlorophyll content in the embryos is much lower in mature seeds than in maturing seeds of both populations (X. Li *et al*., 2012). However, the embryos of mature *S. salsa* seeds did not photosynthesize during germination

(X. Li *et al*., 2012). In contrast, cotyledons of mature seeds of the desert halophyte *Suaeda physophora* are dark green and photosynthetically active during germination (Y. Li *et al*., 2008; S. R. Zhang *et al*., 2010). *S. physophora* is a common plant species in the Zhunger Basin, Xinjiang, north-western China, which is one of the driest regions in the world (Song *et al*., 2005). Chlorophyll in mature seeds of *S. physophora* may help the species to establish in saline and arid regions. In a field investigation, Zhang (2009) identified about 20 halophytic species that contain chlorophyll in the cotyledons of mature seeds. All of these species, which include *Salsola foliosa*, *S. acuminata*, *Halogeton glomeratus* and *S. physophora*, are succulent halophytes in the Amaranthaceae and are distributed in the inland saline arid zone in China. However, none of the halophytes in littoral saline soils in China, such as *S. salsa*, *Suaeda glauca* and *Kochia scoparia*, contains chlorophyll in the cotyledons of mature seeds. The question arises: Why do mature seeds of halophytes such as *S. salsa* in littoral saline soils contain very little chlorophyll while mature seeds of halophytes such as *S. physophora* in the inland saline arid zone of the Zhunger Basin contain substantial chlorophyll (Fig. 3)? The probable answer relates to differences in moisture availability. Suitable conditions for germination in the Zhunger Basin are limited to short periods in early spring when there is snowmelt or intermittent rainfall. Because moisture availability is limited, seeds must germinate as soon as possible. Thus, green cotyledons may benefit these species in that they enhance seedling growth and establishment under arid conditions (S. R. Zhang *et al*., 2010). In the littoral saline soils, by contrast, there is more rainfall and water is not so limiting as in arid regions. Thus, the rapid growth and establishment of *S. salsa* seedlings does not seem to depend on photosynthesis during germination.

SOURCES OF SALT-TOLERANCE GENES

Na^+ accumulation in vacuoles

As noted earlier, *S. salsa* is highly salt tolerant and is a good source for genes that confer salt tolerance. A series of *S. salsa* genes related to salt tolerance have been cloned and their functions tested (Table 2). By affecting the accumulation of inorganic cations and anions, some of these genes help regulate the osmotic balance in the vacuole, a very important feature of halophytes (Short and Colmer, 1999). The roots of *Suaeda maritima* have two low-affinity Na^+-uptake pathways: pathway 1 regulates Na^+ uptake under low salinity (e.g. 25 mM NaCl), and pathway 2 regulates Na^+ uptake under high salinity (e.g. 150 mM NaCl). Pathway 1 might be mediated by a high-affinity K transporter-type transporter, and pathway 2 by an AKT1-type channel (S. M. Wang *et al*., 2007). The Na^+/H^+ antiporter in the tonoplast plays a central

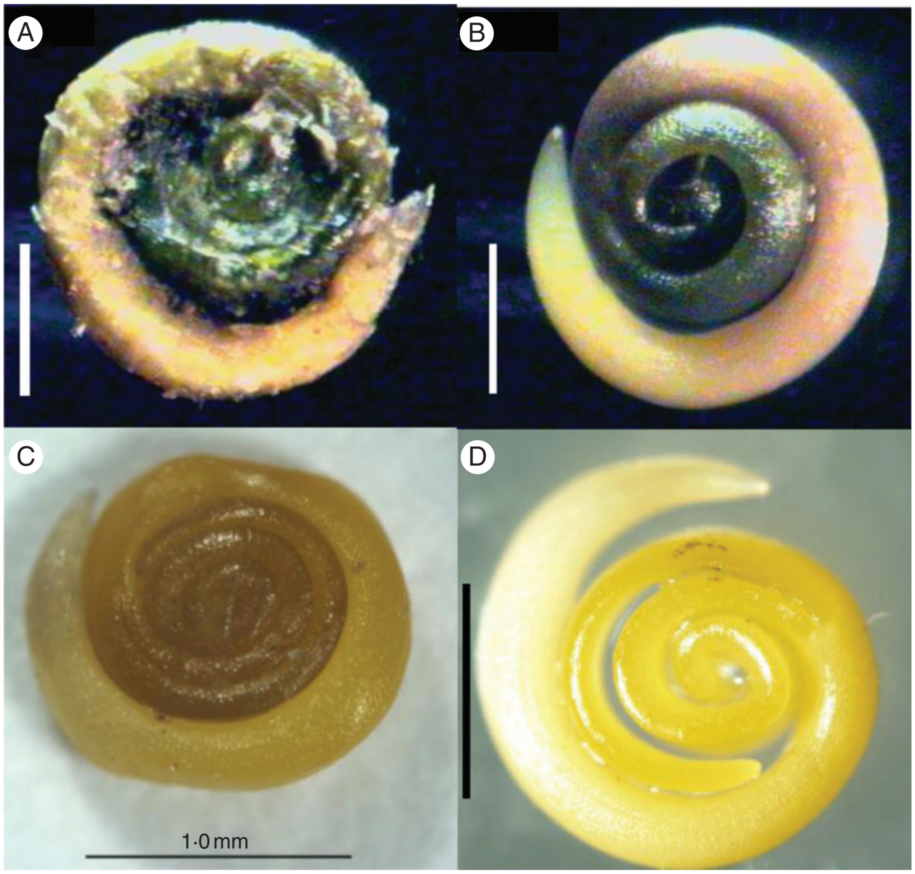

FIG. 3. Morphology of the embryos in *Suaeda physophora* and *Suaeda salsa* seeds. The embryo in a mature *S. physophora* seed without moistening (A) and after moistening with distilled water for 12 h (B). The embryo in a mature brown *S. salsa* seed from saline inland soil without moistening (C) and after moistening with distilled water for 10 h (D). Scale bars = 1 mm. The photographs in A and B are reproduced from S. R. Zhang *et al*. (2010), the photograph in C is reproduced from Song *et al*. (2008) and the photograph in D is reproduced from X. Li *et al*. (2012).

Table 2. *Cloned genes in* Suaeda salsa *and their probable functions*

Gene	Probable function	Reference(s)
SsHKT1	K^+ uptake under K^+ starvation or salt stress	Shao *et al.* (2006)
SsNHX1	Na^+/H^+ antiporter across the tonoplast membrane	Ma *et al.* (2004)
SsVHA-H	Encoding H subunit of V-H^+-ATPase	Y. Li *et al.* (2006)
SsVHA-B	Encoding B subunit of V-H^+-ATPase	P. H. Li *et al.* (2004)
SsSOS1	Na^+/H^+ antiporter across the plasma membrane	S. Y. Wang *et al.* (2013), Duan *et al.* (2013)
SsPIP	Encoding an aquaporin located in plasma membrane	Liu (2003)
SsCAX1	Ca^{2+}/H^+ antiporter at tonoplast	Han *et al.* (2011)
SsP5CS	Encoding Δ1-pyrroline-5-carboxylate synthase involved in proline synthesis	P. P. Wang *et al.* (2002*a*)
SsBADH	Encoding betaine aldehyde dehydrogenase involved in betaine synthesis	S. H. Wang *et al.* (2007)
SsCMO	Encoding choline monooxygenase involved in betaine synthesis	S. H. Wang *et al.* (2007)
SsINPS	Encoding *myo*-inositol-1-phosphate (I-1-P) synthase involved in *myo*-inositol synthesis	P. P. Wang *et al.* (2002*b*)
SsGST	Encoding glutathione *S*-transferase	L. P. Wang *et al.* (2002), Qi *et al.* (2004)
SsCAT1	Encoding catalase	Ma *et al.* (2003)
SsCAT2	Encoding catalase	Ma *et al.* (2003)
SsAPX	Encoding ascorbate peroxidase	Ma *et al.* (2002)
Ss.sAPX	Encoding stroma ascorbate peroxidase	K. Li *et al.* (2012)
SsTypA1	Encoding a member of the TypA/BipA GTPase gene family involved in oxidative stress	F. Wang *et al.* (2008)
SsPrxQ	Encoding peroxiredoxin Q involved in oxidative stress under salinity and low temperature	Guo *et al.* (2004)
SsMAPKK	Encoding mitogen-activated protein kinase kinase involved in resistance to high salinity, low temperature and drought	Yin (2003)
SsNCEDI	Encoding 9-*cis*-epoxyearotenoid dioxygenase involved in ABA synthesis	Cao (2004)
SsDREB	Transcription factor involved in drought and salt resistance	Liu *et al.* (2011)
SsEF-1α	Encoding an alpha subunit of translation elongation factor-1 alpha, which is involved in resistance to high salinity, low temperature, osmotic stress and oxidative stress	Sun *et al.* (2004)

role in salinity tolerance, and its activity is tightly controlled by the electrochemical H^+-gradient across the tonoplast, a gradient that is generated by V-H^+-ATPase and V-H^+-PPase (Lv *et al.*, 2012). Efficient vacuolar sequestration of cytotoxic Na^+ is considered an important feature of halophytes. This sequestration requires that Na^+ be pumped into the vacuole against the electrochemical gradient and that Na^+ in the vacuole be prevented from leaking back into the cytosol (Bonales-Alatorre *et al.*, 2013). The NHX Na^+/H^+ antiporters are thought to contribute to the vacuolar compartmentalization of Na^+ (Hasegawa, 2013). As indicated by SEMeX-ray and TEMeX-ray microanalyses, Na^+ in *Salicornia europaea* is predominantly compartmentalized in the vacuoles of shoot endodermal cells. Accordingly, the transcript amounts of *SeNHX1*, *SeVHA-A* and *SeVP1* (responsible for Na^+/H^+ antiporter, V-H^+-ATPase and V-H^+-PPase, respectively, in *S. europaea*) in shoots increase significantly with an increase in NaCl concentration, suggesting that these genes and their encoded proteins are important for Na^+ sequestration in vacuoles (Lv *et al.*, 2012). In *S. salasa*, northern blot analysis indicated that *SsNHX1* expression in leaves was up-regulated by 500 mM NaCl stress. The *SsNHX1* product is probably an Na^+/H^+ antiporter that may play important roles in the salt tolerance of *S. salsa* (Ma *et al.*, 2004). Further study showed that, when exposed to 300 mM NaCl, tomato (*Solanum esculentum*) transformed with *SsNHX1* accumulated less leaf cytosolic Na^+ and maintained a higher K^+/Na^+ ratio than the wild-type; the dry weight, the net photosynthetic rate (Pn) and chlorophyll concentration in leaves were also much higher in transgenic plants than the wild-type (Zhao, 2006). A similar result was shown in rice (*Oryza sativa* L. 'Zhonghua No.11') transformed with *SsNHX1* under saline conditions (Zhao *et al.*, 2006). For example, the K^+/Na^+ ratio in leaves of transgenic rice plants was much higher than the wild-type at 300 mM NaCl; Pn and F_v/F_m ratio declined in both experimental lines under salinity, but a remarkable decrease occurred in the wild-type compared with the transformed plants after exposure to 300 mM NaCl; for example, there was a 91·7 and 18·4 % reduction of the Pn and F_v/F_m ratio, respectively in wild-type, whereas only 54·4 and 7·5 %, respectively in transgenic rice plants (Zhao *et al.*, 2006). These results indicate that *SsNHX1* contributes to salt tolerance. Meanwhile, under salt stress the up-regulation of the vacuolar H^+-ATPase (V-H^+-ATPase) genes, *SsVHA-H* and *SsVHA-B*, and the increase in the activity of V-H^+-ATPase provide the proton driving force for sequestering Na^+ in leaf vacuoles of *S. salsa* (P. H. Li *et al.*, 2004; Y. Li *et al.*, 2006).

Na^+ and Cl^- exclusion by roots

The ability to regulate Na^+ or Cl^- uptake and transport to the shoot is crucial for salt tolerance in plants (Greenway and Munns, 1980; Tester and Davenport, 2003; Munns, 2005). In *S. maritima*, comparison of the external Na^+ with that in the xylem indicated that Na^+ was more strongly excluded from the transpiration stream as salinity increased (Clipson and Flowers, 1987). In a hydroponic experiment, the ability of roots to exclude Na^+ and Cl^- was greater under saline conditions in an intertidal population than in an inland population of *S. salsa*. Moreover, X-ray microanalysis showed that *S. salsa* roots of the intertidal population accumulated more $[Na^+]$ and $[Cl^-]$ in both the cortex and the stele than the roots of the inland population (Song *et al.*, 2011). The results may explain why leaves of the intertidal population accumulated less Na^+ and Cl^- than the leaves of the inland population (Song *et al.*, 2011).

Na^+ efflux across the plasma membrane is attributed to the Salt-Overly-Sensitive1 (SOS1) Na^+/H^+ antiporter. SOS1 functions in root and shoot cells, and mediates Na^+ efflux to the apoplast against the electrochemical potential via secondary active transport driven by the H^+ gradient across the plasma membrane established by H^+-ATPase. The expression of *SsSOS1* in roots, stems and leaves is induced by salt stress (Duan *et al.*, 2013; S. Y. Wang *et al.*, 2013). Researchers have suggested that *SsSOS1* may mediate Na^+ efflux in leaves and roots but reduce

Na^+ long-distance transfer in stems, which may minimize Na^+ toxicity (Duan *et al.*, 2013).

In comparison with Na^+, less attention has been paid to Cl^- homeostasis under salinity. The uptake of Cl^- from low external concentrations is thought to be via $Cl^-:2H^+$ symport, but at the higher concentrations at which halophytes normally grow influx is likely to be via an anion channel; in this case, the Cl^- concentration remains low in the cytoplasm if the membrane is depolarized (Flowers and Colmer, 2008). The cytoplasmic concentration of Cl^- in *S. maritima* has been estimated to be 86 mM, about half that for Na^+ (Flowers and Yeo, 1988). If this difference in concentration existed across the root plasma membrane, the Nernst potential would be about −33 mV. Uptake into the vacuole could be mediated by H^+ exchange. Recently, a bumetanide-sensitive cation–Cl^- co-transporter has been discovered in *Arabidopsis* and warrants further investigation in halophytes. However, there are no data obtained by direct measurement using ion-specific microelectrodes in the cells of *S. maritima* (Flowers and Colmer, 2008). In both inland and intertidal populations of *S. salsa*, the concentration of Cl^- in leaves was about 30–40 % lower than that of Na^+ based on tissue water (Song *et al.*, 2011). However, the physiological and molecular mechanisms of Cl^- uptake and transfer in *S. salsa* under salinity remain unclear.

K^+ homeostasis

HKT class 1 (HKT1) proteins typically exhibit high Na^+ selectivity, while class 2 (HKT2) proteins are more selective for K^+ than Na^+ or are non-selective (Hasegawa, 2013). Recently, molecular experiments reveal that the sustained activation of K (+) outward current may be the result of an unexpected $O_2\cdot^{-1}$ post-transcriptional regulation of the guard cell outward-rectifying K (+) (GORK) channels. This consists of a probable new mode of regulating the processing of the GORK mRNA, in a reactive oxygen species (ROS)-dependent manner, which allows sustained K (+) effluxes during programmed cell death (PCD). These results provide new mechanistic insights into K (+) channel regulation during an oxidative stress response (Tran *et al.*, 2013).

In *S. salsa*, *SsHKT1* proteins increase under conditions of K^+ starvation or salt stress, which suggests that *SsHKT1* is important for K^+ uptake, especially under low K^+ and high salinity (Shao *et al.*, 2006). Further study demonstrated that transgenic *Arabidopsis* plants overexpressing *SsHKT1;1* showed enhanced salt tolerance and increased shoot K^+ concentrations, whereas no significant changes in shoot Na^+ concentrations were observed. The K^+ transporters in the roots selectively mediated K^+ uptake irrespective of external Na^+, and their inhibitor N-ethylmaleimide (NEM) did not affect Na^+ uptake at low K^+ in *S. salsa*. The results provide strong *in vivo* evidence that *SsHKT1;1* mainly acts as a potassium transporter in heterologous expression systems and in *S. salsa*. The results also indicate that *SsHKT1;1* contributes to salt tolerance by helping maintain cytosolic cation homeostasis in general and by helping maintain K^+ nutrition under salinity in particular (Shao *et al.*, 2014).

The role of Ca^{2+} in maintaining K^+ and Na^+ homeostasis

Ca^{2+} is an important cation in plant responses to stress. Many stresses induce the increase of cytosolic Ca^{2+} concentrations (Kaplan *et al.*, 2006). Ca^{2+} can activate high-affinity K^+ uptake, substantially increasing K^+-selective uptake over Na^+-selective uptake (Hasegawa, 2013). Ca^{2+} can ameliorate Na^+ toxicity in plants by decreasing Na^+ influx via non-selective cation channels; elevated external Ca^{2+} concentrations also inhibit Na^+-induced K^+ efflux via outwardly directed, K^+-permeable channels (Shabala *et al.*, 2006). Therefore, Ca^{2+} is very important in maintaining K^+ and Na^+ homeostasis under salinity. In contrast to AtCAX1, which is inactive under salinity, SsCAX1 might play an important role in lowering the cytosolic Ca^{2+} burst induced by salt stress. First, SsCAX1 expression and protein levels were both increased markedly to sequester exogenous Ca^{2+} in vacuoles in the presence of 100 mM $CaCl_2$ and 100 mM NaCl. In addition, salt stress significantly induced the transcription of V-H^+-ATPase subunit c and increased the activities of V-H^+-ATPase, which provided more energy to the Ca^{2+}/H^+ antiporter as well as to the Na^+/H^+ antiporter. As a result, cytosolic Ca^{2+} and Na^+ homeostasis were maintained (Han *et al.*, 2011).

Succulence

An important characteristic of halophytes is succulence, which is associated with an increase in cell size, a decrease in surface area per tissue volume and a high water content per unit surface area (Waisel, 1972). Succulence in leaves or stems is an adaptive feature that enables dicotyledonous halophytes to regulate their internal ion concentrations (Short and Colmer, 1999). Some findings suggest that, like increased light and aridity, Na^+ can induce an increase in succulence (Jennings, 1968); the author suggested that these three factors exert the same effect on plant cells, i.e. they all bring about an increase in ATP synthesis (Jennings, 1968). V-H^+-ATPase can provide energy to the tonoplast Na^+/H^+ antiporter, which can be induced to increase Na^+ in vacuoles (Han *et al.*, 2011). Uptake of Na^+ and Cl^- into halophyte cells may occur via gated cation and anion channels or even vesicles (Glenn and Brown, 1999). Electron micrographs of the succulent euhalophytes *S. europaea* and *Suaeda arcuata* growing with 400 mM NaCl showed pinocytic invaginations on the cell membrane and vesicular bodies in the vacuoles, which indicated that ion transport from the apoplast to the vacuole in above-ground organs of salt-accumulating halophytes is carried out by means of pinocytosis (Kurkova and Balnokin, 1994). Accumulation of Na^+ and Cl^- in the vacuole by the tonoplast Na^+/H^+ antiporter or vesicular transport can decrease cell water potential, which benefits water uptake of plants under salinity and which therefore increases stem or leaf succulence. However, the actual mechanism remains unclear. Many extremely salt-tolerant plant species are stem- or leaf-succulent euhalophytes. For example, the halophyte *S. maritima* grows optimally at moderate salinities (about 200 mM NaCl), and the optimal growth is accompanied by an increase in succulence and other morphological changes (Yeo and Flowers, 1980; Hajibagheri *et al.*, 1984). When *S. salsa* plants from inland saline soil and from an intertidal zone were exposed to 600 mM NaCl, leaf water content was >8 and 10 mL g^{-1} dry weight, respectively (Song *et al.*, 2009). When *S. aralocaspica*, *Suaeda eltonica* and *Suaeda heterophylla* were treated with salinity, the cross-sectional area of leaves increased, and there was a noticeable increase in the size of chlorenchyma and other cells. However, how cells regulate their size is largely unknown (Park *et al.*, 2009).

Aquaporins (AQPs) facilitate water movement across biomembranes. Currently, two types of plant AQPs have received the most attention, and these are referred to as plasma membrane AQPs (PIPs) and tonoplast AQPs (TIPs) based on their subcellular localization. The transcriptional level of *SsPIP* (Southern blot analysis showed that there was only one copy of *SsPIP* in the *S. salsa* genome) in *S. salsa* leaves was increased after treatment with 400 mM NaCl (Liu, 2003). Immunoblot analyses of PIP located in plasma membrane-enriched fractions of *S. salsa* seedlings also showed a significant increase under salinity (Qi *et al.*, 2009). The results suggest that AQPs may correlate with the increase in leaf succulence of *S. salsa* under salinity (Qi *et al.*, 2009). However, further research is needed to clarify AQP activity under salinity.

Salinity tolerance is a physiologically and genetically complex trait (Flowers, 2004). Because succulence is an important morphological adaptation that increases salinity tolerance, a better understanding of the physiological and molecular processes underlying the succulence induced by salinity may help plant breeders and molecular biologists increase the salt tolerance of conventional crop plants.

Osmotic stress tolerance

All halophytes must meet the challenge of osmotic adjustment in response to a low external water potential, and osmotic adjustment involves both inorganic and organic solutes (Munns, 2005; Flowers and Colmer, 2008; Munns and Tester, 2008). Glycinebetaine and proline are two important organic osmotica involved in osmotic adjustment in certain halophytes (Flowers and Colmer, 2008). The halophyte *S. maritima* accumulated glycinebetaine when grown in the presence of NaCl, and glycinebetaine is considered to act as a non-toxic cytoplasmic osmoticum that maintains the intracellular osmotic balance between the cytoplasm and the NaCl in the vacuole (Flowers and Hall, 1978; Hall *et al.*, 1978). When another leaf-succulent halophyte, *Suaeda fruticosa*, was treated with 600 mM NaCl, the glycinebetaine content in shoots was 220 mM based on tissue water, suggesting that glycinebetaine plays a role in the osmotic adjustment (Khan *et al.*, 2000). At 200 mM NaCl, the average level of glycinebetaine in salt-treated plants was 33 mM kg^{-1} fresh weight in leaves of *S. aralocaspica*, *S. eltonica* and *S. heterophylla*, and if all glycinebetaine accumulated in the cytoplasm, the concentration would be 10 times higher than that or about 330 mM. Thus, if glycinebetaine accumulates in the cytoplasm, it could significantly contribute to the cytoplasmic osmotic potential (Park *et al.*, 2009). Glycinebetaine, however, often accumulates specifically in the chloroplasts of chenopods such as *Spinacia okracea* (Hanson *et al.*, 1985) and not in the whole cytoplasm. In *S. salsa* treated with 400 mM NaCl, the glycinebetaine concentration exceeded 25 mM kg^{-1} fresh weight and was inferred to play an important role in *S. salsa* osmotic adjustment (Liu *et al.*, 1994).

Under salinity, the contribution of proline to osmotic potential (Ψs) was <0·2 % in *S. physophora* (Song *et al.*, 2006) and <0·5 % in *S. salsa* (Zhang and Zhao, 1998). *S. maritima* accumulates higher levels of proline in its leaves under salt conditions than *S. europaea*. However, the glycinebetaine content in leaves is greater in *S. europaea* than in *S. maritima* (Moghaieb *et al.*, 2004). Tipirdamaz *et al.* (2006) suggested that 'species that behaved as glycinebetaine accumulators contained little proline and *vice versa*'. Thus, the cytoplasmic osmoticum glycinebetaine may play a more important role than proline in osmotic adjustment in *S. salsa* under high-salinity conditions (Song *et al.*, 2006). It follows that the role of compatible solutes in osmotic adjustment seems to vary among halophytes.

Besides their role in osmotic adjustment, compatible solutes may also have many other roles including the protection of enzymes and membranes, and ROS scavenging (Bohnert and Shen, 1999). They are even potent blockers of ROS-activated K^+ channels (Cuin and Shabala, 2005, 2007). For example, low (0·5–5 mM) concentrations of exogenously supplied proline or glycinebetaine significantly reduced NaCl-induced K^+ efflux from barley roots in a dose–response manner (Cuin and Shabala, 2005). Low (5 mM) concentrations of glycinebetaine and proline significantly reduced $OH^\bullet$-induced K^+ efflux. A significant reduction in K^+ efflux was found using osmolytes for which free radical scavenging activity had and had not been demonstrated. These results indicate that, in addition to free radical scavenging, glycinebetaine and proline must have other roles in mitigating the damaging effects of oxidative stress (Cuin and Shabala, 2007).

Two genes involved in glycinebetaine synthesis have been molecularly characterized in several halophytes in the genus *Suaeda*. Western blots showed that the protein levels of choline monooxygenase (CMO) and glycinebetaine aldehyde dehydrogenase (BADH), enzymes that catalyse the synthesis of glycinebetaine from choline, increase under salt stress in *S. aralocaspica* (Park *et al.*, 2009). In *S. salsa*, *SsBADH* and *SsCMO* were cloned and their functions evaluated. Transgenic tobacco with *SsCMO* exhibited an increase in tolerance to salt stress (S. H. Wang *et al.*, 2007). Moreover, *SsP5CS* (involved in proline synthesis) and *SsINPS* (involved in *myo*-inositol synthesis) in *S. salsa* were cloned, and the expression levels of *SsP5CS* (P. P. Wang *et al.*, 2002*a*) and *SsINPS* were upregulated by salinity (P. P. Wang *et al.*, 2002*b*).

Oxidative stress

High salinity can lead to the formation of ROS, and timely scavenging of ROS is critical in plant salt tolerance. Halophytes are equipped with powerful antioxidant systems, including enzymatic and non-enzymatic components, which are thought to protect important biomolecules such as lipoproteins and DNA from the damage caused by ROS (Oueslati *et al.*, 2012*a*). The activity of both catalase (CAT) and superoxide dismutase (SOD) in *S. maritima* increased significantly 10 d after the initial application of 255 mM NaCl; treatment with 255 mM NaCl also resulted in the synthesis of new isoforms of both CAT and SOD (Mallik *et al.*, 2011). In *S. salsa*, activities of Mn-SOD and several isoforms of Fe-SOD and CuZn-SOD were detected in leaf extracts, and the results indicated that these SOD isoforms may increase the tolerance to oxidative stress under salinity (B. S. Wang *et al.*, 2004). Several genes involved in oxidative stress tolerance of *S. salsa*, such as *SsGST*, *SsPrxQ*, *SsCAT1*, *SsCAT2*, *SsAPX*, *Ss.sAPX* and *SsTypA1*, have been cloned and their functions tested (Ma *et al.*, 2002, 2003; L. P. Wang *et al.*, 2002; Guo *et al.*, 2004; Qi *et al.*, 2004; F. Wang *et al.*, 2008; K. Li *et al.*, 2012). For example, the overexpression of *Ss.sAPX* (a gene of the stromal APX in *S. salsa*) increased the germination, cotyledon growth, survival rate, and salt tolerance in transgenic *Arabidopsis* plants (K. Li *et al.*, 2012). Under salinity, the transgenic plants had longer roots, higher total chlorophyll content, higher total APX activity, less cell membrane damage (as indicated by MDA levels) and lower H_2O_2 content than the wild-type. The results suggest that *Ss.sAPX* may play an important role in the protection against salt-induced oxidative stress in higher plants (K. Li *et al.*, 2012).

UTILIZATION AS FOOD, MEDICINE, FORAGE AND BIOENERGY

As food

With the rapid growth of human populations and the irreversible spread of soil salinization in arid and semi-arid regions, the competition for fresh water and arable land among agricultural, domestic and industrial interests has increased tremendously (Rozema and Flowers, 2008). The problems resulting from reduced availability of fresh water and non-saline land might be partially reduced by the domestication of halophytes, because many of these salt-adapted plants can be used as vegetables and might also be developed as oilseed crops (Weber *et al.*, 2007; Rozema and Schat, 2013). Several halophytes in the genus *Suaeda* have the potential to become oilseed crops. For example, the seed oil content of *S. aralocaspica* was >29 % on a dry weight basis, and both black and brown seeds contain about 93 % unsaturated fatty acids, with linoleic (>68 %) and oleic acid (>20 %) being the most abundant (L. Wang *et al.*, 2012). Its high seed oil content and significant percentage of polyunsaturated fatty acids make the halophyte *S. aralocaspica* a promising source of high-quality edible oil (L. Wang *et al.*, 2012). Weber *et al.* (2007) evaluated the seeds of six halophytes (*Arthrocnemum indicum*, *Alhaji maurorum*, *Cressa cretica*, *Halopyrum mucronatum*, *Haloxylon stocksii* and *S. fruticosa*) as sources of edible oil. The results indicated that the seeds of these halophytes and of *S. fruticosa* in particular (the oils of this species contained 74 % unsaturated fatty acids) could be used as a source of oil for human consumption. This suggests that *Suaeda* spp. have great potential as oilseed crops.

The seed yield of *S. salsa* is about 2000kg ha^{-1} in saline soils where the soil salt content is about 5 g kg^{-1} dry soil. Plant breeders and other researchers in China have been attempting to increase the plant biomass and seed yield of *S. salsa* in saline soil. For example, the artificial cultivation of *S. salsa* can increase its seed yield one- to two-fold, while breeding for high yield can increase *S. salsa* seed yield two- to three-fold; and the excessive saline water irrigation can increase the shoot biomass of *S. Salsa* efficiently (Shao *et al.*, 2004). The oil content is >20 % in dry seeds of *S. salsa*. The oil contains seven kinds of fatty acids, and unsaturated fatty acids account for 90·7 %, with linoleic acid, oleic acid and linolenic acid accounting for 68·7, 13·9, and 4·2 %, respectively (Table 3). Therefore, *S. salsa* produces a high-quality oil that is fit for human consumption (Li and Fan, 2010). Besides *Suaeda* spp., *Salicornia bigelovii* is also thought to have potential as a high-quality oil-seed crop. The species can produce about 2000kg ha^{-1} of seeds over a 200-d growing cycle (Rozema and Flowers, 2008).

When grown in saline inland soils, *S. salsa* is green (Fig. 1A), and the fresh branches are highly valued as a vegetable. The contents of protein, crude fibre, carotenoids, amino acids and vitamin C in fresh branches of *S. salsa* are 2·3 mg g^{-1} f. wt, 63·7 mg g^{-1} f. wt, 106·5 μg g^{-1} f. wt, 30·4 μg g^{-1} f. wt and 1·3 mg 100 g^{-1} f. wt, respectively. The content of nitrate, by contrast, is only 1·13 μg g^{-1} f. wt, i.e. the fresh branches of *S. salsa* are safe for human consumption with respect to nitrates (Zhao *et al.*, 2010). Like *S. salsa*, species of the annual genus *Salicornia* and of the perennial genus *Sarcocornia* can also be used as leafy vegetable crops, not only because of their salty taste but also because of their high nutritional value in terms of minerals and antioxidant vitamins, such as vitamin C and β-carotene. In addition, total polyphenol, β-carotene and ureides, all of which have antioxidant activity, increased in *Salicornia* and *Sarcocornia* spp. as the percentage of seawater used for irrigation increased (Ventura *et al.*, 2011).

TABLE 3. *The composition and relative content of fatty acids in the seed oil of* Suaeda salsa *(reproduced from Gu, 1999)*

Fatty acid	Molecular formula	Relative content (%)
Terephthalic acid	$C_8H_8O_4$	0·82
11-Hexadecenoic acid	$C_{16}H_{30}O_2$	0·45
Palmitoleic acid	$C_{16}H_{30}O_2$	3·36
Palmitic acid	$C_{16}H_{32}O_2$	6·59
Linoleic acid	$C_{18}H_{32}O_2$	68·74
Oleic acid	$C_{18}H_{34}O_2$	13·93
Stearic acid	$C_{18}H_{36}O_2$	1·93
Linolenic acid	$C_{18}H_{30}O_2$	4·17

As medicine

Many halophytes have high contents of polyphenols and other bioactive compounds and are promising sources of pharmaceuticals. *Mesembryanthemum edule*, for example, is a traditional remedy for treatment of fungal and bacterial infections, sinusitis, diarrhoea, infantile eczema and tuberculosis. *Tamarix gallica* has been used as an astringent, detergent, diuretic, expectorant and laxative (Oueslatia *et al.*, 2012*a*). Oueslatia *et al.* (2012*b*) assessed the *in vitro* and *ex vivo* antioxidant activities of acetone extracts of *S. fruticosa*, *Suaeda pruinosa*, *Suaeda mollis* and *S. maritima* in Tunisia. The results showed that *S. mollis* has the highest DPPH• scavenging ability followed by *S. pruinosa*, *S. fruticosa* and *S. maritima*, while *S. fruticosa* had the highest antioxidant ability (as determined by the inhibition of β-carotene bleaching) and a high total antioxidant capacity (Oueslatia *et al.*, 2012*b*). These results show that antioxidant activity differs among *Suaeda* species. In another paper, Oueslatia *et al.* (2012*a*) reported that the edible halophyte *S. fruticosa* is a valuable source of antioxidants that have novel anti-inflammatory and anti-cancer capacities. Astragalin (kaempferol-3-O-glucoside), which was isolated from extracts of *Suaeda asparagoides*, can function as an antioxidant in biological systems, particularly on skin exposed to solar radiation, and can protect cellular membranes against ROS (Park *et al.*, 2012). An experiment with *S. maritima* showed that maritima-supplemented diets protect haematological and biochemical properties (total protein, glucose and calcium levels), improve innate immunity, and protect against *Miamiensis avidus* infection in the olive flounder (Harikrishnan *et al.*, 2012). *Salicornia* plants are also a promising source of pharmaceutical compounds. For example, isorhamnetin 3-O-β-D-glucopyranoside isolated from *Salicornia herbacea* protects against ROS-induced cellular damage (Kong *et al.*, 2009).

Leaves and stems of *S. salsa* in the intertidal zone are red–violet (Fig. 1B) and during the entire growth period they accumulate betacyanin. Betacyanins are probably involved in the regulation of ROS in stressed plants (C. Q. Wang *et al*., 2006). Betalains have been used as natural additives for food, drug and cosmetic products. The content of flavanols in *S. salsa* is much higher in July (98·8 mg g^{-1} d. wt) than in other months, and July extracts have the highest antioxidant activity *in vitro* (Z. S. Zhang *et al*., 2010). In inland saline sites, the average Se content is 10 times greater in fresh branches of *S. salsa* (0·02 mg kg^{-1} f. wt) than in non-halophytic crops (Gu, 1999). Therefore, the species is regarded as a potential resource for cancer prevention (Ding *et al*., 2008). Because of its high content of unsaturated fatty acids, the seed oil of *S. salsa* is used to decrease blood sugar and blood pressure, to dilate blood vessels, to prevent heart disease and to develop disease immunity (Ding *et al*., 2008).

Fourteen fatty acid methyl esters have been identified in the product formulated from the extracts of *S. salsa* seedlings, and hexadecanoic acid methyl ester (25·9 %), 9,12-octadecandienoic acid methyl ester (28·3 %) and 9,12,15-octadecatrienoic acid methyl ester (9·0 %) are major extract components. Ten fatty acid methyl esters dominated by 9,12-octadecadienoic acid methyl ester (83·4 %) are present in the extracts of seeds. These extracts evidently inhibit ear swelling of normal and adrenalectomized mice, decrease vascular permeability and suppress the formation of granuloma. The anti-inflammatory activity of the extracts from seeds and seedlings results from the suppression of inflammatory mediators, the decrease in the content of MDA from inflammatory exudates and accordingly the increase in catalase activity (Zheng *et al*., 2003). Therefore, *S. salsa* is valued as a source of medicine.

As forage and bioenergy

Halophytes can be used as forage. Sheep and goats fed diets containing *Salicornia*, *Suaeda* and *Atriplex* gained as much weight as those whose diets included hay without halophytes (Glenn *et al*., 1998). Moreover, the quality of the meat of the experimental animals was unaffected by a diet rich in halophytes (Glenn *et al*., 1998). Chenopods generally contain high contents of crude protein, sulphur and minerals, which are critical to ruminant health. Halophytes, however, also contain oxalate and can generate mineral toxicities and deficiencies, which are obviously harmful to animals (Norman *et al*., 2013). The high salt content of halophytes limits the amount an animal can eat. Increasing sodium in the diet significantly decreases feed intake, digestibility, live weight gain and wool growth either as a main effect or through an interaction with potassium (Masters *et al*., 2005). The strategy is to incorporate halophytes as part of a mixed diet for livestock, replacing conventional hay forage with halophytes to make up between 30 and 50 % of the total food intake of sheep and goats (Glenn and Brown, 1999). Like *S. salsa* branches, *S. salsa* seed meal has a high protein content (about 27 %). This means that both branches and seed meal of *S. salsa* can be used as forage; a mixed diet for livestock can contain about 10 % of *S. salsa* hay (Ding *et al*., 2008).

Regarding bioenergy, *S. salsa* oil can be used as a raw material to produce fatty acid methyl esters, which in turn can be used to produce biodiesel; about 97 % of *S. salsa* oil can be converted to fatty acid methyl esters (Yang *et al*., 2008). In addition, the air-dried *S. salsa* plant is a potential feedstock for bio-ethanol production and high value-added products. Xylose yield and glucose yield from air-dried *S. salsa* plants reach a maximum of 18·48 and 25·49 g per 100 g of raw material, respectively (S. X. Li *et al*., 2013).

UTILIZATION IN THE RESTORATION OF SALINIZED OR CONTAMINATED LAND

In the restoration of contaminated land

The large volumes of wastewater discharged from coastal aquaculture projects can be a serious source of pollution. Untreated effluent may damage coastal ecosystems (Brown *et al*., 1999). Under high-salinity irrigation, halophytes can be used as biofilters to remove nutrients from saline aquaculture wastewater. In a greenhouse experiment, for example, the succulent salt marsh species *Suaeda esteroa* and *S. bigelovii* performed better than the desert saltbush *Atriplex barclayana* in removing total nitrogen, inorganic nitrogen, and total and soluble reactive phosphorus (Brown *et al*., 1999). In *Salicornia brachiata*, quantitative reverse-transcriptase PCR showed that the *SbMT-2* gene is up-regulated by stresses induced by zinc, copper, salt, heat and drought. *Escherichia coli* cells expressing recombinant SbMT-2 were more tolerant than non-transformed cells to Zn^{2+}, Cu^{2+} and Cd^{2+}; the fusion protein SbMT-2 showed the highest affinity to zinc ions followed by copper and cadmium ions. These results indicated that the SbMT-2 protein has metal-binding characteristics and could therefore by useful in detoxification of heavy metals (Chaturvedi *et al*., 2012). *S. brachiata* has inherent resilience of varying abiotic tolerance, and therefore the *SbMT-2* gene could be a potential candidate to be used for enhanced metal tolerance and heavy metal phytoremediation under saline conditions (Chaturvedi *et al*., 2012). This indicates that certain succulent salt marsh species can be used as promising biofilters to remove nutrients from saline aquaculture wastewater.

In a field investigation, accumulation of copper (Cu), chromium (Cr), lead (Pb) and arsenic (As) was greater for *S. salsa* than for *Phragmites australis*, *Spartina alterniflora* or *Typha orientali*; the content of the four metals in *S. salsa* shoots was about 100, 40, 5 and 2 μg g^{-1} d. wt, respectively (Gao *et al*., 2010). Relative to salt-sensitive plants, halophytes such as *S. salsa* offer a greater potential for phytoremediation with respect to reducing the levels of toxic metals from saline soils. Using the scanning ion-selective electrode technique, L. Z. Li *et al*. (2012) analysed the pattern and rate of Cd^{2+} fluxes at different regions of the *S. salsa* root apex. The results indicated that Cd^{2+} influx into roots can be significantly suppressed by pretreatment with the Ca^{2+}-channel blockers $LaCl_3$ and verapamil. This means that Cd^{2+} may enter roots through non-selective Ca^{2+} channels, which suggests a theoretical basis for the phytoremediation of Cd^{2+} contamination by *S salsa* in saline coastal soils. Wu *et al*. (2012) found that the expression of INPS, CMO, BADH, CAT and Gpx (glutathione peroxidase) was elevated in the above-ground parts of *S. salsa* after combined Hg and salinity exposure. For Hg-treated *S. salsa* plants, the metabolic profiles of extracts from the above-ground parts of seedlings showed clear increases in the amino acids valine, leucine, isoleucine, threonine, alanine, glutamine and phenylalanine. These results indicate that Hg may induce oxidative stress and disturb protein bio-degradation and energy metabolism in *S. salsa*.

In the restoration of salinized land

Halophytes are ideally suited for the revegetation and remediation of salt-affected land (Shabala, 2013). *Atriplex nummularia*, for example, can achieve a biomass of 20–30 t ha^{-1} year^{-1} and accumulate between 20 and 40 % NaCl in its dry matter when irrigated with saline water. *S. fruticosa* can remove >2·5 t of salts ha^{-1} in a single harvest of the aerial parts of the plant each year (Shabala, 2013). *S. salsa* can also efficiently absorb and accumulate salts from saline soils. If planted at a density of 15 plants m^{-2} and if harvested at the end of the growing season, *S. salsa* could potentially remove 3–4 t of Na$^+$ ha^{-1} from saline soil, suggesting that it might be used to improve the quality of saline soils (Zhao, 1991).

In a field study at an inland site, the planting of *S. salsa* increased soil organic matter by 43 % and increased total soil nitrogen by 18 % relative to soil that was not planted (Lin *et al.*, 2005). In the same study, the planting of *S. salsa* increased numbers of actinomyces and fungi five- and 16-fold, respectively. This indicates that the planting of *S. salsa* has potential for improving coastal saline soils.

CONCLUSIONS

Although genetic engineering may generate crops for saline land, the selection of useful transgenes is hampered by a fundamental lack of knowledge about the mechanisms of salt resistance in halophytes (Rozema and Schat, 2013). The genetic background is better described in non-halophytes such as *Arabidopsis* (Bevan *et al.*, 2001) and rice (Huang *et al.*, 2013) than in euhalophytes, but *Arabidopsis*, rice and other non-halophytes cannot survive on saline land. The genomes of the halophytes *Eutrema halophilum* (Deng *et al.*, 2009) and *E. parvulum* (Dassanayake *et al.*, 2011) have been reported, and although these two species have been promulgated as valuable model halophytes (Deng *et al.*, 2009; Dassanayake *et al.*, 2011), their salt tolerance is lower than that of the euhalophytes *S. salsa* (Song *et al.*, 2009) and *S. europaea* (Lv *et al.*, 2012). Euhalophytes within the Amaranthaceae offer the best opportunity to understand how dicotyledonous plants can tolerate salt (Flowers and Colmer, 2008; Huchzermeyer and Flowers, 2013; Rozema and Schat, 2013). Therefore, elucidating the genetic background of certain model euhalophytes (e.g. *S. salsa* and *S. europaea*) is important. Regarding the utilization of *S. salsa*, further work is needed to increase *S. salsa* seed yield and to evaluate the value of *S. salsa* in the restoration of contaminated saline soils. The latter research should include the combined study of the physiological and molecular mechanisms of heavy metal uptake and transfer within *S. salsa* plants and the efficiency at which *S. salsa* removes heavy metals from saline soils in the field.

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