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ORIGINAL RESEARCH

Ultrastructural Characteristics of Three Chenopod Halophytes Lacking Salt Excretion Structures

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Abstract Plants maintained in high soil salinity generally develop particular structures to either tolerate or survive such adverse environments. Excretion of excess ions by special salt glands or other similar structures is a well-known phenomenon for regulating the mineral content of many halophytes. However, the three chenopod halophytes of *Suaeda* inhabit high saline soils, yet they exhibit no signs of salt excretion structures. The current study has been undertaken to assess the structural attributes of these halophytes to reveal their cellular characteristics during growth in salt tolerance. Transmission and scanning electron microscopy, as well as ion chromatography, have been employed for the study. One of the most noticeable features uncovered was the epidermal cutinization shown to be heavy on the outer epidermis and characterized externally by thick wax plates. Numerous vesicles and membranous invagination in the vacuoles were common features within the mesophyll cytoplasm. Invaginations of the vacuolar and/or plasma membrane frequently formed secondary vacuoles which later became distinct, membrane-bound compartments. Significant accumulation of solid sodium chloride salts was well demonstrated in the vacuoles of air-dried epidermis. Finally, salt tolerance mechanisms in these *Suaeda* have been discussed with respect to other halophyte modifications that improve salt tolerance in various ways.

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Introduction

Most plants do not require sodium or chloride ions from the soil and are unable to survive high saline environments. In high salinity, plant cells have a lower water potential than the solution surrounding the roots, causing water to move out of the roots by osmosis. For these plants, absorption of water from the soil only exacerbates the problem of high salinity. Some halophytes, however, are able to grow in salinic environments such as deserts, salt marshes, and coastal areas (Raven et al. 1992).

Salinity affects metabolic processes of plants and induces changes in their morphology and anatomy (Sen and Rajpurohit 1982). These plants have evolved mechanisms for dealing with high sodium concentrations, and for some, sodium appears to be a required element (Zhu 2001; Wang et al. 2007). The adaptation of halophytes has been known to vary among species (Waisel 1972; Fahn 2000; Kim et al. 2002); plants adapted successfully to and maintained in high soil salinity generally develop certain structures to either tolerate or survive such environments.

Excretion of ions by special salt glands or other excretion structures is a well-known mechanism for regulating the mineral content of many halophytes (Waisel 1972; Fahn 2000). Compartmentation of sodium ions in vacuoles is another adaptation that plays a significant role at the cellular level (Zhu 2001; Mansour and Salama 2004; Guo et al. 2006; Wang et al. 2007). Development of such structures is essential for some halophytes to avoid internal ion imbalance and hyperosmotic stress for survival (Zhu 2001). However, the three chenopod

halophytes of *Suaeda asparagoides*, *Suaeda japonica*, and *Suaeda maritima*, exist in high saline soils without wilting or enduring cellular damage, yet they exhibit no signs of internal or external salt excretion structures. The current literature examining the structural attributes of these *Suaeda* species allowing for their survival in high salinity is sparse. Thus, the present study has been undertaken to assess the structural features of these halophytes to reveal their cellular characteristics during growth in salt tolerance.

Materials and Methods

Plant Materials

About 10–15 mature plants each of *S. asparagoides* MAKINO, *S. japonica* MAKINO, and *S. maritima* (L.) Dumort were collected, according to Lee (1996), from the coastal area of Byeonsanbando, Buan-gun, Jeonbuk, Korea, from September through October of 2007. With *S. maritima,* both green- and red-leaved plants were used for electron microscopy to determine the effect of pigment change on subcellular differentiation. For the plants grown in their natural high saline habitat, leaf tissues were sampled immediately on site. Plants of *S. maritima* transferred and reared under a 16-h photoperiod at 24°C to 28°C for several months were used as non-salt conditioned tissues for comparison.

Electron Microscopy

For transmission electron microscopy (TEM), the mid-portion of freshly collected leaf samples were sliced under the dissecting microscope and immediately subjected to the following procedures: approximately 4–6 mm^2 sections of tissue from each species were fixed in 3% glutaraldehyde in 0.01 M phosphate buffer (pH 7.2) at room temperature for 3 h (Kim et al. 2000). The fixed tissues were rinsed three times in the same buffer and post-fixed in 2% osmium tetroxide overnight at 4°C. After three rinses in the buffer, they were dehydrated through a graded acetone series, substituted, and embedded in low-viscosity Spurr resin. Ca. 60–90 nm ultrathin sections were cut with the Ultracut-S ultramicrotome using a diamond knife. Grids coated with 0.3% chloroform-diethanol formvar were used for the sections. They were double stained with 2% uranyl acetate and 0.5% lead citrate for 45 min each and examined with the Hitachi-H 7100 TEM at the Korea Basic Science Institute (KBSI) Daegu Center. For scanning electron microscopy (SEM), ca. 10–20 mm^2 of healthy leaf pieces were processed by the same method of TEM fixation and dehydration as described above, with the exception of the substitution step, in which isoamyl acetate was used after dehydration, and further dehydration to critical point and ca. 10 nm sputter coating with platinum were performed before examination with the Hitachi-S 4200 SEM at the KBSI Daegu Center.

Element Analysis and Ion Chromatography

The scanning electron microscopy-energy dispersive spectroscopy (SEM-EDS) X-ray spectroscope attached to the Hitachi-S 4200 SEM was utilized for analysis of the elements distributed in *S. maritima* epidermal cells. Five elements, including Na and Cl, discerned by weight percentage, were analyzed from the epidermal peel that had been air-dried naturally. The dried epidermal peels were placed on aluminum stubs with double-sided tape and coated with platinum gold before examination. NaCl concentrations from the *S. maritima* leaves were estimated by following the modified method of Kim et al. (2002). Dried leaves (1 g) milled with UDY cyclone sample mill was boiled at 95°C for 1 h in a 25-ml measuring flask. Distilled water was added to make a final volume of 25 ml and filtered with a GF/C filter of pore size 0.45 μm. Filtrates were diluted 1/100 times with double-distilled water. Cation (K^+, Na^+, Mg^{2+}, Ca^{2+}) analysis was done with inductively coupled plasma (Jobinyvon 38 Plus), and anion (Cl^-) analysis was performed with titrators (Mettler Toledo Titrarors DL50).

Results

The three *Suaeda* species examined in this study exhibited no apparent signs of salt excretion structures, yet were well maintained without wilting or enduring cellular damage. All three species exhibited centric and bifacial leaf arrangements consisting of epidermis, mesophyll, water storage tissue, and veins. The mesophyll tissue differentiation into the palisade and spongy parenchyma was not clearly evident; however, it was apparent that it surrounded the central water storage tissue. One of the most remarkable features uncovered during the study was heavy epidermal cutinization. Unlike the thin cuticles noted on the epidermis of non-saline conditioned tissues (Fig. 1a), the cuticles from plants grown in high salinity were found to be conspicuously dense on thick, outer epidermal walls (Fig. 1b). The epidermal cells were sizeable and each occupied by a prominent central vacuole. Along the vacuolar membrane, numerous irregular, membrane-bound structures were continuously formed. The radial and inner tangential walls of the epidermal cells were also unusually thick compared to the relatively thin walls of the sub-epidermal and mesophyll cells (Fig. 1c).

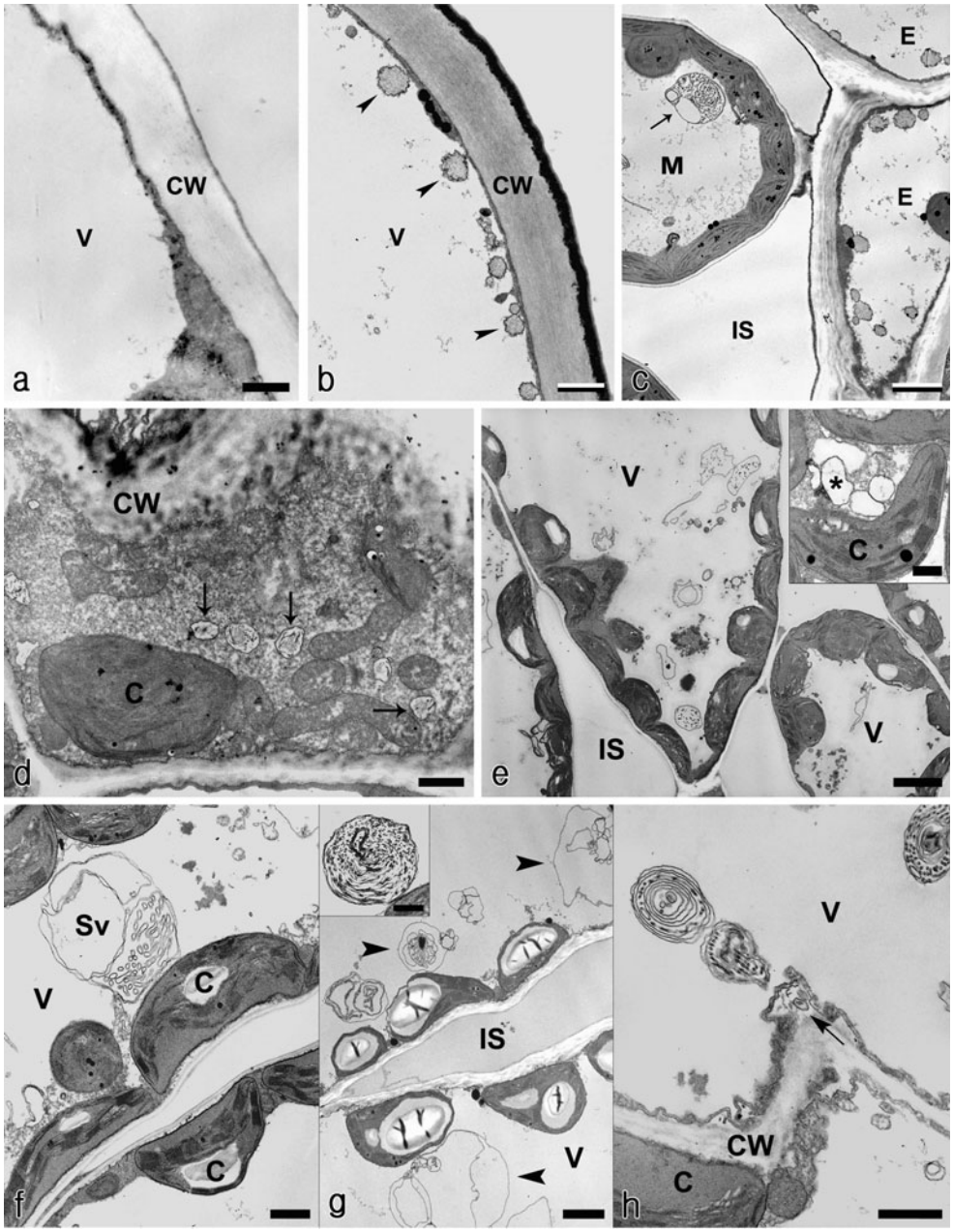

Fig. 1 Transmission electron micrographs of cellular features examined from plants grown in non-saline (**a**) and saline conditions (**b**–**h**). **a** A partial view of the epidermal cell with a thin cuticle, taken from a plant grown under non-saline conditions. *Bar*=1.1 μm. **b** A prominent central vacuole with numerous irregular, membrane-bound structures (*arrowheads*) lining the vacuolar membrane. *Bar*=1.0 μm. **c** Unusually thick radial and tangential epidermal walls alongside relatively thin-walled sub-epidermal cells. *Bar*=2.0 μm. **d** Numerous small vacuoles containing fibrillar materials found within the dense cytoplasm of a young mesophyll cell. *Bar*=1.0 μm. **e** A prominent central vacuole with membranous invaginations in the mature mesophyll cell. *Bar*=3.0 μm. *Inset*: several vacuoles (*asterisk*) confined to restricted cytoplasm. *Bar*=0.5 μm. **f** A distinct, membrane-bound secondary vacuole formed within the primary vacuole. *Bar*=1.0 μm. **g** Membrane invaginations (*arrowheads*) of variable size occurring in the vacuole. *Bar*=1.5 μm. *Inset*: peculiar membrane configurations are formed due to intergradations of vesicular or tubular membranes. *Bar*=2.0 μm. **h** Complex membrane invaginations (*an arrow*) resulting in the formation of plasmalemasome-like structures. *Bar*=1.0 μm. *C* chloroplast, *CW* cell wall, *E* epidermis, *IS* intercellular space, *M* mesophyll cell, *S* salt crystal, *Sv* secondary vacuole, *V* vacuole, *W* wax plate. All figures represent *S. maritima*, except **e** (*inset*) (*S. asparagoides*) and **g** (*S. japonica*)

In young mesophyll cells, small vacuoles filled with fibrillar materials were scattered throughout dense cytoplasm (Fig. 1d); while a central vacuole was prominent in mature mesophyll cells (Fig. 1e), in which numerous small vesicles and membranous invaginations of variable size were the most common features. The frequency at which

these invaginations occurred along the plasma or vacuolar membrane was variable; however, in many cases, they formed secondary vacuoles within the primary vacuole (Fig. 1f–g). Some secondary vacuoles occurred near the plasma membrane, while others developed from a distance. The secondary vacuoles often became distinct, membrane-bound compartments in which the vacuolar membranes occasionally fused with the plasma membrane. Such vacuoles often contained vesicular, spherical, tubular, fibrillar, or membranous contents (Fig. 1g, inset) that may have partially originated from the secondary vacuolar membrane. Because of their considerable size, they often protruded into the primary vacuole and occupied a sizeable volume of the cell. Within secondary vacuoles, the tubular structures retained relatively uniform width and appeared smooth in outline, in contrast to more complex structures. The secondary vacuoles appeared individually in some sections, but at times appeared in a complex series of membrane configurations due to intergradations of vesicular, spherical, or tubular membranes. The vacuolar membranes of *S. maritima* continued to form complex invaginations that may have originated from a set of concentrically arranged membranes resembling plasmalemasomes or myelin sheath (Fig. 1h) protruding into the primary vacuole. While it is possible that these membrane configurations are cytoplasmic in origin, evidence of their association with Golgi or endoplasmic reticulum could not be verified. Little to no traces of salts was detected in the mesophyll tissues near the vein. Further, no significant subcellular differentiation was detected between green and red leaves during examination.

The leaves of *Suaeda* demonstrated a typically xerophytic nature in morphology, while the epidermal and mesophyll cells dynamically formed peculiar membrane invaginations at the cellular level. Along with a very thin cuticle (Fig. 1a), a thin epidermal wax layer (Fig. 2a) was observed in plants grown under non-saline conditions. Furthermore, salts were virtually not found internally in the epidermis (Fig. 2b), whereas the epidermis of cells grown in high saline conditions had a visibly high salt content. The examined leaf epidermis of *Suaeda* was not only covered with thick wax plates on the surface, but the stomatal guard cells were also thickly coated and laid in a slight depression within the waxy layer (Fig. 2c). A considerable accumulation of crystallized sodium chloride salts was well demonstrated within the vacuoles of epidermal cells that had been peeled and dried at room temperature (Fig. 2d). The crystallized salts were also found, to a lesser degree, in the guard cells. Several intact secondary vacuoles within the primary vacuole were clearly visible in these cells (Fig. 2e), and clusters of solidified salt crystals were scattered throughout the inner vacuolar surface (Fig. 2e–f). Findings of the element analysis done by SEM-EDS of the solid crystals indicated that the crystals were undoubtedly sodium chloride salts (Fig. 3). According to this analysis, the five elements of Na, Cl, K, Si, and Ca were the primary constituents of these salts. Among these elements, Na and Cl comprised the majority, occupying 52.9% and 29.9%, respectively, of the total weight (Table 1).

Discussion

Salinity represents one of the most important environmental stresses in plants. In fact, for most plants, highly saline soils usually cause an ion imbalance, creating a hyperosmotic stress. Plants that inhabit such environments are able to overcome this stress by way of developing a salt tolerance mechanism. Plants with salt tolerance have the ability to maintain growth in saline conditions relative to non-saline conditions (Moller and Tester 2007) through a complex mechanism that has been shown to work as an interplay of physiological processes during salt tolerance controlled by a group of proteins (Askari et al. 2006) or genes (Mansour and Salama 2004; Yun 2005). Despite the fact that research in the area of salinity stress has been carried out for years, the mechanism of salt tolerance in plants has yet to be elucidated. Salinity usually affects metabolite processes of plants and induces morphological and anatomical changes (Sen and Rajpurohit 1982; Tester and Davenport 2003; Mansour and Salama 2004). Structural changes caused by salinity include an increase in succulence, cuticle thickening, development of stomata, inhibition of differentiation, and earlier occurrence of lignification (Waisel 1972; Sen and Rajpurohit 1982; Robinson et al. 1997). The *Suaeda* examined in this study exhibited a moderate degree of succulence, cuticle thickening, and sunken stomata. In other *Suaeda* growing along the coast, a strong correlation has been reported between morphological and physiological variation and plasticity of environmental changes (Ihm et al. 2004).

Mechanisms of salt tolerance can vary by halophyte species. It can be achieved by a combination of osmotic adjustment of the cytoplasm, salt extrusion across the plasma membrane, or salt accumulation in vacuoles (Zhu 2001; Mimura et al. 2003). In particular, the latter of the three is an appropriate way of adaptation in cases in which the cells have a considerably large vacuole as in the studied *Suaeda* species. The *Suaeda* have shown numerous primary and secondary vacuoles, as seen in Fig. 1e–h throughout the epidermis and mesophyll cells. Many studies have been carried out concerning the plasma membrane and tonoplast—particularly the tonoplast of the halophyte. They play an important role in regulating tolerance to external salt, as the vacuolar ions contribute to osmotic

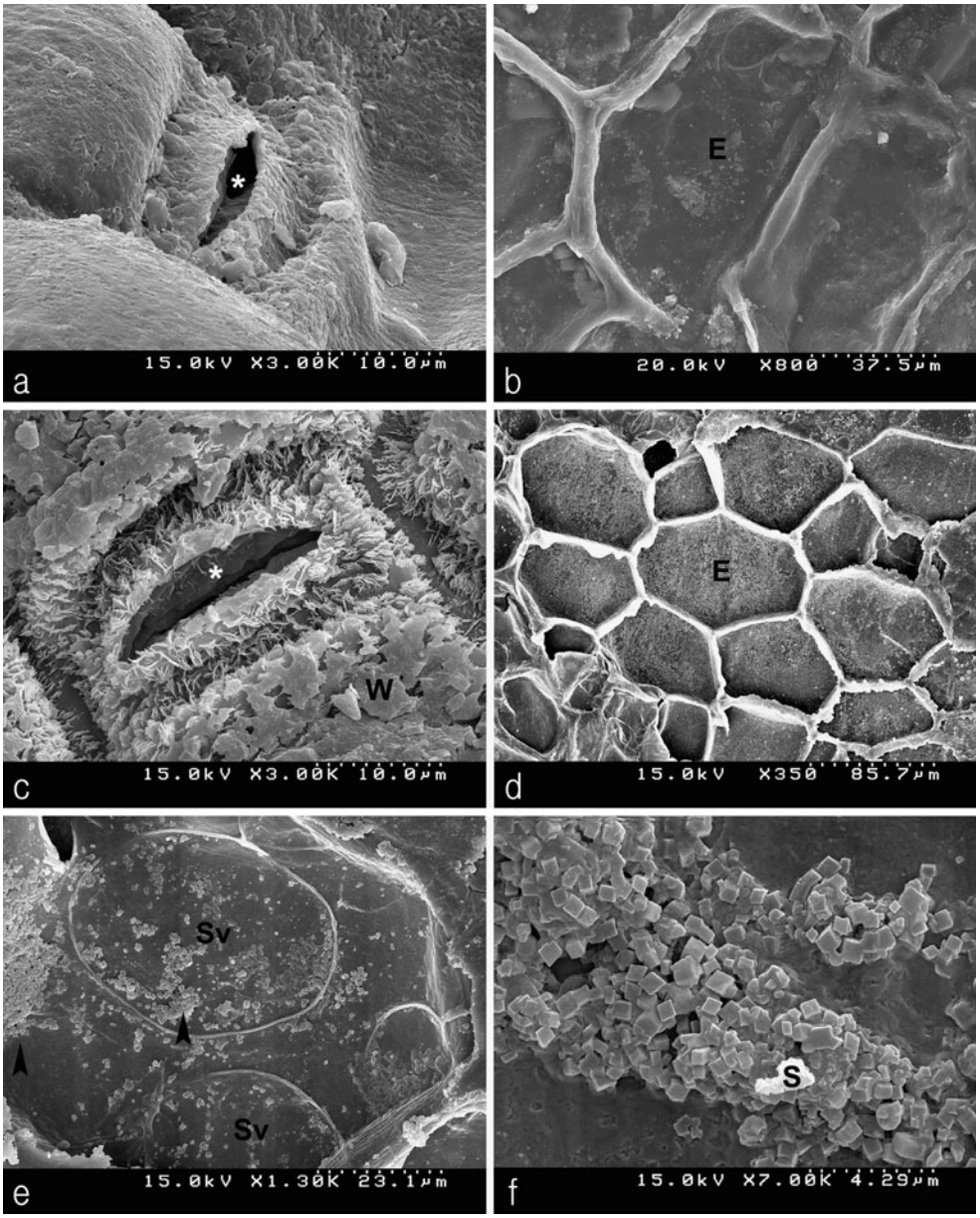

Fig. 2 Scanning electron micrographs of the epidermis obtained from plants grown in non-saline (**a**–**b**) and saline conditions (**c**–**f**). **a** Thin epidermal wax layer from a plant grown in non-saline conditions. *Asterisk* indicates stomata. **b** Peeled epidermal cells as seen from the cytoplasmic side, taken from a plant grown under non-saline conditions. **c** Thick wax plates on the epidermal surface. *Asterisk* indicates stomata. **d** A low magnification view of the peeled epidermis showing crystallized salts distributed throughout the cells. **e** Secondary vacuoles and clusters of crystallized salts (*arrowheads*) encountered in the air-dried epidermal cell. **f** Close-up of the solidified salt crystals. For the abbreviations found in the corresponding artwork of this figure, please refer to Fig. 1

adjustment of the cell (Guo et al. 2006; Wang et al. 2007). Accumulation of ions in the vacuole serves to avoid an increase in the ionic strength of the cytoplasm and increase cellular osmolality to counter osmotic stress (Mimura et al. 2003).

High salt stress disrupts homeostasis with regard to water potential and ion balance, and this has effects at both the cellular and whole plant levels (Zhu 2001). One major aspect of plant adaptation to saline environments is developing a capacity for lowering the osmotic potential of the plant body. In particular, ion retention and osmotic adjustment by the plant tissue are important considerations for plant growth in saline habitats (Tester and Davenport 2003). Salinity affects many aspects of plant metabolism and can also induce certain structural changes. In fact, succulence is one of the most common features of halophytes, often considered an adaptation to salinity that aids in the reduction of internal salt concentrations (Sen and Rajpurohit 1982; Mimura et al. 2003). Many halophytes, however, reduce their internal salt content by way of their roots or with the aid of salt glands by salt extrusion (Waisel 1972; Poljakoff-Mayber 1975; Flower et al. 1977; Ramadan 1998; Bamidele 2007).

Considering the fact that salt tolerance can be attained only in plants in which cells function normally and can endure a high salt condition without apparent damage, the examined *Suaeda* are salt-tolerant plants that have adapted to saline environments without developing any special morphological structures. Evidence of this is seen in their epidermal tissues. Except for thick wax plates over the

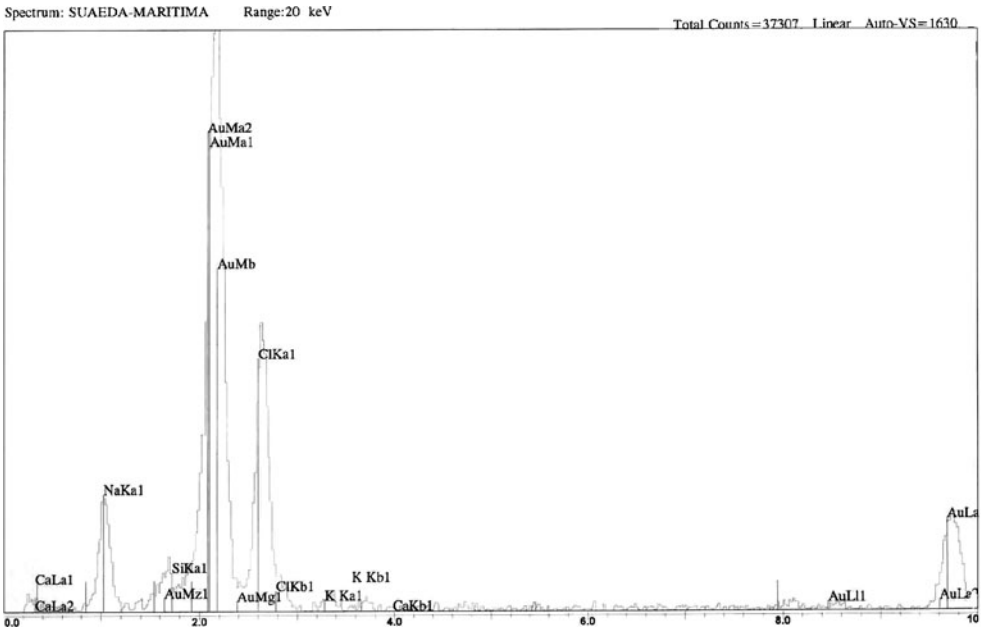

Fig. 3 SEM-EDS element analysis of the solid crystals in the epidermal cells of *S. maritima*. The detection of Au is due to the aluminum stub used for sample preparation

cuticle layer, as seen in *S. maritima* grown in the presence of sodium chloride (Hajibagheri et al. 1983), the *Sueada* exhibited no signs of salt excretion structures internally or externally, despite their continued inhabitance of high saline soils. Salt in these species may be concentrated in the vacuoles of epidermal cells without displaying any signs of wilting or cellular damage. They exhibited xerophytic or succulent cellular characteristics during growth in salt tolerance. As previously stated, one of the most noticeable features was found to be heavy cutinization occurring in the outer walls of the epidermal surfaces. In the study, controls were included from plants grown in non-saline conditions in order to appropriately assess the effect of salt stress on the development of certain plant features as part of an adaptive mechanism. Comparison data from the controls indicate that the cuticle thickening observed in the study is most likely a direct effect of adaptation to a high saline environment, and further can be considered an important feature contributing to the salt tolerance mechanism of halophytes.

Numerous vesicles and membranous invaginations were common features observed in the *Suaeda* cytoplasm. Secondary vacuoles, frequently noted throughout the study, may function as a site of ion accumulation and osmotic uptake of water. The ions accumulated in the secondary vacuoles may then migrate to and fuse with the plasmalemma, releasing the ionic contents into the walls. Recently, the extent of vacuolation has been included as one of the intrinsic properties in plants having salinity tolerance (Moller and Tester 2007). Once released into the walls, the salt is effectively removed from the plant, as backflow along the walls into the leaf is blocked by the cuticularized zone around the outer epidermal cell. Cell membranes are important in the response of the cells to various types of solutes (Guo et al. 2006). Whether salts become sequestered in the secondary vacuoles is not yet known; however, this is a highly likely scenario since the element analysis of the epidermal peel, as seen in Fig. 3 and Table 1, clearly demonstrated high concentrations of sodium and chloride ions.

Table 1 clearly revealed Na and Cl as the major compositional elements of *S. maritima* leaves, together comprising 82.77% in the element analysis. The NaCl salt content of *S. maritima* leaves may constitute up to 14.5% of their dry weight. The optimal concentration of NaCl for growth varies from 0.05 to 0.1 M NaCl depending on plant age (Hajibagheri et al. 1983). A considerable accumulation of sodium and chloride in the vacuoles has previously been suggested (Flowers 1985; Tester and Davenport 2003). Plant vacuoles serve as important storage compartments for many ions and small molecules that are needed for cell homeostasis and protection against various stresses (Hirschi 2001; Bassham 2002). A rapid increase in vacuolar volume has been reported when plants were under salt stress (Mimura et al. 2003).

Table 1 Analysis of the mineral elements of *S. maritima* using SEM-EDS

Element	Counts/s	Atomic percent	Weight percent
Na	21.23	39.03	29.90
Si	11.19	10.77	10.07
Cl	61.65	44.76	52.87
K	3.69	3.41	4.44
Ca	2.27	2.04	2.72

As revealed in other halophytes (Waisel 1972), excess accumulation of chloride reduces uptake of phosphate and nitrate, and such reduction has been known to result in a reddish coloration. In *Suaeda*, however, no significant change in pigmentation was reported in salt-stressed plants examined previously (Lu et al. 2002). While salt stress has been shown to result in a significant accumulation of sodium and chloride in leaves (Lu et al. 2002), the contents of chlorophyll a and b and other pigments were not simultaneously analyzed. No significant subcellular differentiation was noticed in the examined green- and red-leaved *Suaeda* plants in the present study.

Vacuoles of various size and content have frequently been observed in the secretory cells of the salt gland, and the possibility that vacuoles might be directly involved in a general mechanism of secretion has previously been suggested (Thomson 1975; Fahn 2000). It appears as though salt accumulation in the microvacuoles of salt glands and membrane invaginations in the vacuoles of the *Suaeda* leaves may be related phenomena. According to Zhu (2001), any sodium ions that manage to get into cells can be stored in vacuoles and exported out of the cell. Vacuolar compartmentation is then a very economical means for preventing sodium toxicity in the cytoplasm, as the ion imbalance resulting from excess sodium can create a hyperosmotic stress and pose a challenge for survival. Thus, the aforementioned study findings and reasoning allow for the speculation that these *Suaeda* have evolved mechanisms to tolerate highly saline soils not only by forming numerous membranous invaginations within the cells, but also by accumulating thick wax plates externally in the epidermis, both of which function to preserve intracellular homeostasis and allow for survival in environments of high salinity.

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