Front. Biol. 2010, 5(2): 164–170
DOI 10.1007/s11515-010-0032-7

REVIEW

Progress in mechanism of salt excretion in recretohalopytes

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Abstract The recretohalophyte with specialized salt-secreting structures including salt glands and salt bladders can secrete salt from their bodies and easily adapt themselves to many kinds of salt habitats. Salt glands and salt bladders, arose from dermatogen cells, are excretory organs specially adapted for dealing with ionic homeostasis in the cells of recretohalophytes. The main function of salt glands or salt bladders is to secrete excess ions that invade the plant. The structures of salt glands or salt bladders differ among plant species. In addition to structural differences, salt glands also differ in their secretion abilities. In this review, we mainly focus on recent progress in the mechanism of salt excretion of salt glands and salt bladders, and in particular, emphasize the vesicle-mediated secretion systems from the vacuole to the plasmalemma and the possibly involved membrane-bound translocating proteins for salt secretion of plant gland secretory cell.

Keywords mechanism, salt excretion, recretohalopytes, salt bladders, salt glands

1 Introduction

Halophytes, plants that survive to reproduce in environments where the salt is around 200 mmol/L NaCl or more, constitute about 1% of the world's flora (Flowers and Colmer, 2008). Halophytes are divided into euhalophytes, recretohalophytes and pseuhalophytes according to their physiological mechanism of salinity tolerance, morphologic structures and ecological characteristics (Breckle, 1995). Recretohalophytes include exo-recretohalpphytes with salt glands and endo-recretohalophytes with salt bladders. The most remarkable morphological characteristics of recretohalophytes are the salt-secreting structures (salt glands and salt bladders) that can excrete or sequestrate excessive salts from metabolically active tissues (Zhou et al., 2001). Salt glands and salt bladders are prevalent on stem and leaf surface of recretohalophytes. They play an important role in regulating ion balance, maintaining the stability of osmotic pressure and enhancing the salinity tolerance (Zhang et al., 2003).

Structures of salt glands vary greatly in different plants, but they are very similar in the same plant families. They can be multicellular, as observed in dicotyledonous species such as Plumbaginaceae and Tamaricaceae (Waisel, 1972), or bicellular, as reported for the Poaceae (Liphschitz and Waisel, 1974; Fahn, 1979; Somaru et al., 2002). Salt bladder is usually composed of a stalk (1 to 4 stalk cells) and an enlarged bubble-shaped cell with a diameter of 80–200 μm (Zhao and Li, 1999). The aerial surfaces of the common ice plant, *Mesembryanthemum crystallinum* (Aizoaceae) are covered with giant (typically 500 μm in diameter) salt bladder cells. *Mesembryanthemum crystallinum*, however, appears to incorporate NaCl into salt bladders without the associated activity of such gland stalk cells (Agarie et al., 2007).

2 Salt secretion mechanism of salt bladders

How do the endo-recretohalophytes with salt bladders uptake, transport and sequester salt into salt bladders is not clear. However, from microprobe data the cytoplasmic concentration of $[K^+ + Na^+]$ in the leaves is about 200 mmol/L and shows high selectivity of K^+ in relation to Na^+. Na^+ and Cl^- are accumulated largely in the vacuoles of the bladder, epidermal, hypodermal and, to a lesser extent, in the mesophyll cells (Storey, 1983). The general ionic distribution between cells and cell compartments of the mature leaf of *Atriplex spongiosa* are diagrammatically summarized in Fig. 1. After the ions enter the bladders, they are temporarily stored in bladders, and will be released after rupture of bladders caused by salt pressure (Ish-Shalom-Gordon and Dubinsky, 1990) or damage factors such as high winds, heavy rain, or touch (Zhao and Li, 1999). It is clear that the enhanced sodium

Received January 19, 2010; accepted February 26, 2010

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accumulation in the epidermal bladder cells of the halophyte *Mesembryanthemum crystallinum* correlates with tonoplast Na^+/H^+ antiport and H^+-translocating ATPase (V-ATPase) activities, which are higher in salt bladders than surrounding cell types (Barkla et al., 1995, 2002). However, how the ions in the apoplast of mesophyll cell are polar transported to bladder cell needs further study.

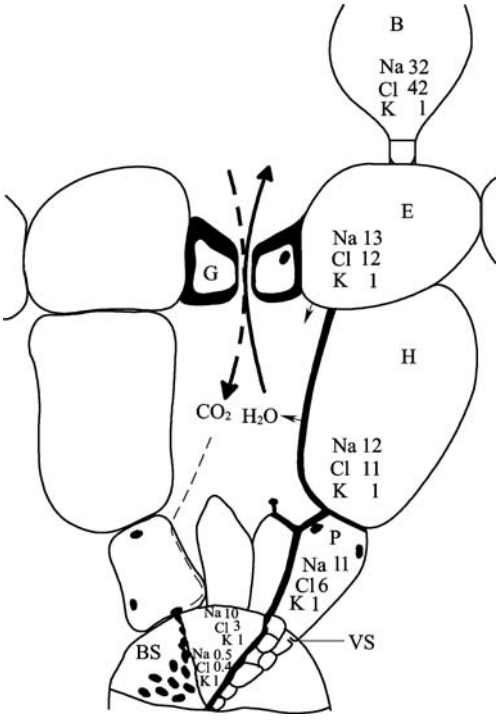


Fig. 1 Schematic diagram of ionic distribution in the mature leaf of *Atriplex spongiosa* grown under condition of 600 mmol/L NaCl. BS: bundle sheath cell cytoplasm and vacuole; VS: vascular system; P: palisade cell (vacuole); H: hypodermal cell (vacuole); E: epidermal cell (vacuole); B: bladder cell (vacuole); G: guard cell. Arrows show CO_2 and H_2O movements across stoma. Reproduced from Storey et al. (1983).

3 Salt secretion mechanism of salt glands

3.1 Secreted substances and the preference of cations for secretion of salt glands

The secreted fluid of salt glands contains various substances. Nevertheless, salt glands mainly secrete inorganic ions such as Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, NO_3^-, SO_4^{2-}, PO_4^{3-} (Thomson, 1975). In addition, salt glands can also secrete some unfamiliar ions, such as Cs^+, Rb^+, Br^-, I^- (Hill, 1967). Various organic substances such as soluble sugars, amino acids, small-molecule proteins were also found in the secreted fluid (Pollack and Waisel, 1970).

It is clear that the secretion ability increases with external concentration of, and time of exposure to salt (Pollak and Waisel, 1970; Liphschitz and Waisel, 1974; Marcum and Murdoch, 1992). However, the preference of cations for secretion is different in different plants. In the multicellular glands of dicotyledonous plants, there are diverse differences among species: divalent cations > monovalent cations in *Tamarix aphylla*, $Na^+ > K^+ > Ca^{2+}$ in *Glaux maritima*, $K^+ > Ca^{2+} > Na^+$ in *Armeria maritime*, $Na^+ = K^+ > Ca^{2+}$ in *Limonium vulgare* and $Na^+ > K^+$ in *Limonium sinense* (Fig. 2) (Berry, 1970; Rozema et al., 1981; Ding et al., 2009a). In contrast, a strong preference for the secretion of Na^+ is common in the bicellular glands of the Gramineae (Pollak and Waisel, 1970; Rozema et al., 1981; Wieneke et al., 1987). The increase of Ca^{2+} concentration markedly enhances salt-secretion rates of salt glands in the leaves of *Limonium bicolor* (Ding et al., 2010). These results suggest that secreted substances and its concentrations are dependent on plant species, salt and its concentration in the medium, and Ca^{2+} possibly involves in the regulation of salt secretion of salt glands.

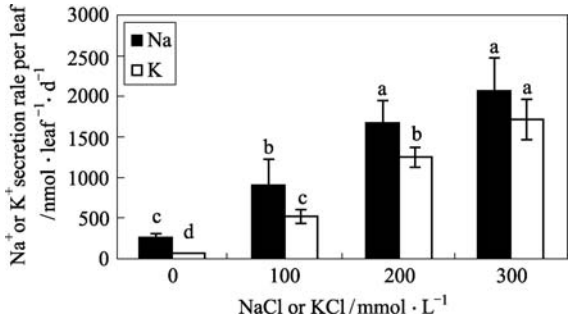


Fig. 2 Effects of NaCl and KCl on the rate of salt-secretion by the adaxial surface of the fourth leaf of *Limonium sinense* plants treated with NaCl and KCl for 25 days. Means within NaCl or KCl treatment that have the same letters are not significantly different at $P < 0.05$. Vertical bars represent standard deviations (n = 5). Reproduced from Ding et al. (2009a).

Up to now, the salt secreting mechanism of salt glands in plants is still not clear. However, the following hypotheses of salt secretion are proposed based on the studies on physiological analysis of salt secretion of salt glands.

3.2 Physiological mechanism of salt secretion

It is well known that ions enter salt glands against an electrochemical concentration gradient. Secretion is an active physiological process and is temperature dependent (Dschida et al., 1992). Under controlled conditions, salt secretion tends to be heavily dependent on the salinity of any treatment solution (Rozema and Riphagen, 1977; Batanouny et al., 1992) and the humidity of the air (Pollak and Waisel, 1979). The sodium concentration in the secreted fluid was found to be always higher than its

concentration in the leaves, xylem and medium (Arisz et al., 1955). Experiments on effects of temperature and metabolic inhibitors on the rates of secretion indicate that secretion is energy dependent (Arisz et al., 1955). Presumably, the energy source is adenosine-triphosphate (ATP) (Hill and Hill, 1973). Orthovanadate is known to be an inhibitor of the plasma membrane H^+-ATPase. In both bicellular and multicellular glands, it has been reported that the inhibitors of plasma membrane H^+-ATPases inhibit Na^+ secretion (Dschida et al., 1992; Bhatti and Sarwar, 1993), and that these salt gland cells have a high plasma membrane ATPase activity (Balsamo and Thomson, 1996; Naidoo and Naidoo, 1999). Therefore, H^+-ATPase is believed to play an important role in salt secretion of the salt glands by establishing an electrochemical proton gradient across the plasma membranes. It is reasonable to assume that the ATP is supplied by the mitochondria of the gland cells since these cells lack chloroplasts, and ultrastructural studies indicate that the mitochondrial fractional volume of the secretory cells is considerably higher than that of most other plant cells (Faraday and Thomson, 1986; Vassilyev and Stepanova, 1990). However, Hill and Hill (1973) suggested that the ATP essential for secretion in the light is produced in the mesophyll and diffuses symplastically to the glands. Therefore, further studies are required to determine whether ATP consumed by salt gland cells is generated by mesophyll cells surrounding salt gland or by the mitochondria of the gland cells. In brief, salt secretion is an active physiological process, and ATP is supplied either by chloroplast or motochondrion.

3.2.1 Salt secretion is caused by osmotic potential of gland cells

Arisz (1955) proposed that ions are accumulated in salt glands actively and subsequently the osmotic potentials in gland cells increase significantly, which results in a remarkable increase of hydrostatic pressure. After the salt glands' pressure reaches the highest level, the ions are excreted out of salt gland cells by periodic micro-droplets, thus to rescind the hydrostatic pressure. Obviously, salt glands' secretion should be a physical process.

3.2.2 Salt secretion is similar to animal flow transport system

This hypothesis is proposed by Levering and Thomson (1971, 1972). The salt gland in *Spartina foliosa* is composed of two cells, a large basal cell and a smaller, dome-shaped cap cell which is located on a neck-like protrusion of the basal cell. There is no cuticular layer separating the salt gland from the mesophyll tissue. The most unique feature of the glands in *Spartina* is the occurrence of an extensive system of partitioning membranes in the basal cells. These partitioning membranes are infoldings of the plasmalemma which extend from the wall protuberances as a double-membrane system throughout the basal cell (Fig. 3). The ultrastructure of the basal cell in *Spartina* is thus remarkably similar to the absorptive and secretory epithelial cells in animal tissue. Based on the ultrastructure and the organization of the salt gland of *Spartina*, the following hypothesis is proposed for the mechanism of salt secretion. There is an active secretion of ions into the channels of the partitioning membranes of the basal cells. This is possibly accomplished with the utilization of energy supplied by the associated mitochondria (Copeland, 1967). If a coupled solute-water-transport system might be assumed (Diamond and Bossert, 1967), water moving passively into the extracellular channels in the basal cell would exert sufficient pressure to cause movement of ions into the cap-cell wall and out through the pores of the cuticle.

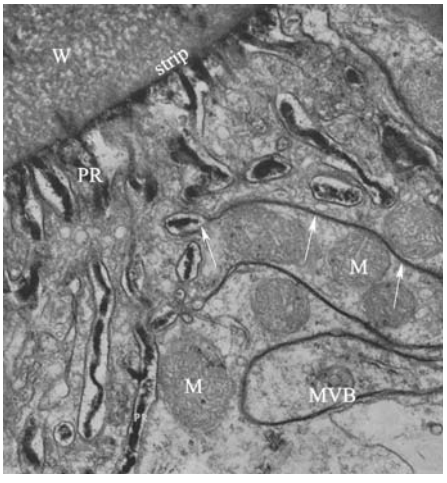


Fig. 3 Ultrastructure of the *Spartina foliosa* salt gland. Note that wall protuberances (PR) originate from the wall (W) located between the basal and the cap cell of *Spartina foliosa* salt gland. This is the only wall in the entire gland complex which bears protuberances. The protuberances extend only into the basal cell. Note the "flaky" substructure of the wall except for the small basal strip (strip) where the protuberances originate. Several mitochondria (M) and a multivesicular body (MVB) are present. The membranes (MEM, arrows) which surround the protuberances extend into the cytoplasm and partition it. (× 25600). Reproduced from Levering and Thomson (1971).

3.2.3 Salt secretion is the opposite process of exocytosis

The existence of a vesicle-mediated system for metabolite transport from the vacuole to the cell membrane was initially advanced by Ziegler and Lüttge (1967) in their studies of the secretory salt glands of *Limonium vulgare*. They observed that salt-secreting cells lacked a conspicuous large central vacuole. Instead, the cells contained a

series of smaller "vacuole-like" membrane vesicles, many of which were seen in close proximity to the cell membrane (Fig. 4). More importantly, the tonoplast of the "vacuole-like" vesicles often appeared to fuse with the plasmalemma (Fig. 4) in agreement with a vesicle-mediated secretion process. The experiments of Thomson et al. (1969) offered the most convincing evidence for the vacuole as the site for ion accumulation in secreting cells. When *Tamarix aphylla* plants were grown in a solution containing rubidium, electron dense accumulations appeared in their "microvacuoles" (Fig. 5). The darkly stained vesicles were visible in micrographs, and in many instances their membranes appeared fusing with the plasmalemma (Fig. 5). However, it was shown that in most glands of *Limonium platyphyllum*, chloride transport was accompanied by the displacement of vacuoles toward the cell periphery and by the establishment of plasmalemma contact sites with the tonoplast which appeared similar to gap junctions in animal epithelial cells. No evidence for the exocytosis of vacuoles was found (Vassilyev and Stepanova, 1990). They proposed that the active step in NaCl secretion was the influx of ions into the vacuole; the efflux was believed to be passive, and occurs from the vacuole into the periplasmic space through channels in the contacting area of tonoplast and plasmalemma.

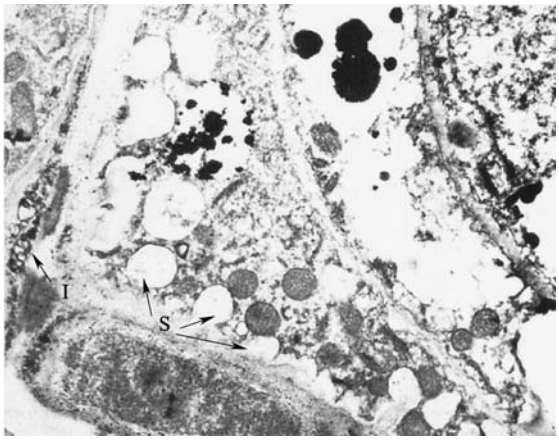
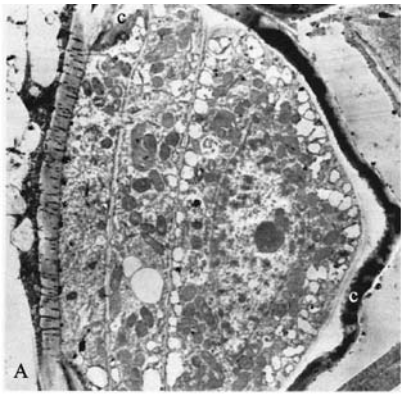
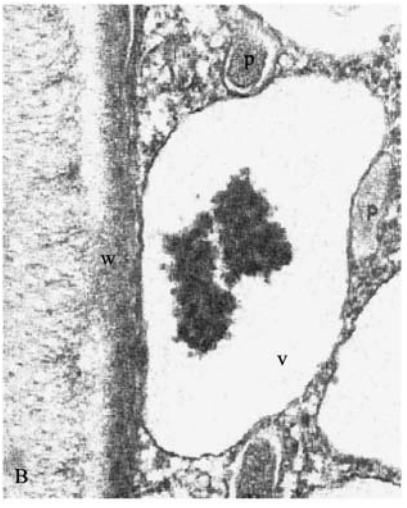


Fig. 4 Electromicrograph view of a secretory cell of the *Limonium vulgare* salt gland during secretion. Note the apparent fusion of small vesicles with the plasma membrane (arrows). Reproduced from Dr. A E Hill (Hill and Hill, 1967).





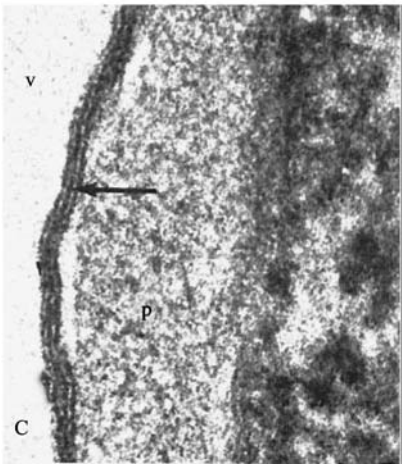


Fig. 5 Ultrastructure of a salt gland of *Tamarix aphylla*. A: longitudinal section through a salt gland of *Tamarix aphylla*, the transfusion area can be seen at the left base wall. Note the proliferation of small vacuoles around the periphery of the secretory cell and their apparent association with the plasmalemma at the wall extension areas. B: close association between a small vacuole and the plasmalemma in a secreting cell. Rubidium dense areas are clearly visible. C: high magnification of the contact point between the tonoplast and the plasmalemma. c: Cuticle; v: vacuole; w: cell wall; p: cell wall protrusions. A is reproduced from Dr. W W Thomson (Thomson and Liu, 1967). B and C are reproduced from Dr. W W Thomson (Thomson et al., 1969).

3.3 Perspectives of the mechanism of salt gland secretion

3.3.1 The possible membrane-bound translocating proteins involved in salt gland secretion

Studies on process and mechanism of salt secretion in recretohalophytes have revealed characteristics of the ultrastructure of salt glands and salt bladders, as well as

some basic mechanisms in salt secretion process. However, further research will be important for revealing the molecular mechanism underlying this process. It is well known that ions cannot cross the bilayer of cellular membranes. Therefore, membrane-bound translocating proteins are believed to participate in salt secretion process. In plants, salt overly sensitive 1 (SOS1) in the plasma membrane are critical for growth in high salinity, removing toxic Na^+ from the cytoplasm by transport out of the cell (Qiu et al., 2003). Na^+ extrusion through these Na^+/H^+ antiporters is driven by an inwardly directed proton gradient created by H^+-ATPases (Shi et al., 2002). However, it is still unknown whether this plasmalemma Na^+/H^+ exchanger is involved in glandular Na^+ secretion process. It is clear that the immediate energy supply for salt secretion process in shark rectal gland derives from the active transport of Na^+ back out across the basolateral membrane by the Na^+/K^+-ATPase (Riordan et al., 1994). The existence of this type of P-type ATPase such as Na^+/K^+-ATPase has not been reported in plants and no genes encoding the enzyme exist in the *Arabidopsis* or rice genomes. Therefore, there is currently no reason to predict their existence in plants, but neither can their presence be ruled out. When PpENA1 apparently gives *Physcomitrella* a clear selective advantage under moderate salt stress, it is intriguing that Na^+-ATPases are absent in vascular plants (Lunde et al., 2007). Both Na^+ and K^+ secretion in the salt glands of Rhodes grass can be inhibited by ouabain (an inhibitor of Na^+/K^+-ATPase in animal cells) (Kobayash et al., 2007). However, the conclusion that Na^+/K^+-ATPases play an important role in salt secretion of the salt glands cannot be fully supported by only using the pharmacological agent. It is very interesting to study whether a plant Na^+/K^+-ATPase exists and may function in plant salt glands. In animals, the cation-Cl^- co-transporter (CCC) family is essential for adequate homeostasis of the most abundant electrolytes, K^+ , Na^+ and Cl^-, and plays a key role in the regulation of intracellular Cl^- content in secretory and absorptive epithelia (Russel, 2000; Delpire and Mount, 2002; Hebert et al., 2004; Gamba, 2005). It is clear that a Na^+: K^+: Cl^- cotransporter plays an important role in shark rectal gland NaCl secretion (Riordan et al., 1994). Colmenero-Flores et al. (2007) have cloned an *Arabidopsis thaliana* cDNA encoding a *bona fide* Na^+: K^+: Cl^- co-transporter (AT1G30450) involved in plant development and ion homeostasis. Given the participation of CCC proteins in salt transport in secretory epithelia in animal systems, it is interesting to study whether a plant Na^+: K^+: Cl^- cotransporter functions in the salt secretion of plant salt glands.

3.3.2 Is the opposite process of exocytosis really involved in salt gland secretion?

This review describes existing evidence supporting the presence of a vesicle-mediated pathway for salt secretion in plant salt glands. It should be noted that the bulk of evidence in support of a vesicle-mediated vacuolar export system in salt gland cells is derived primarily from cytological and anatomical studies, many of which contain little or no physiological and biochemical data, so we cannot ignore the likelihood that some calculated rates of secretion are impossibly high to be accounted for by vesicle transport to the plasmalemma (Echeverría, 2000). In view of the vacuole as the location where salts accumulate, ionic specific fluorescent probe can be used to trace the "vacuole-like" small vacuoles during salt secretion, and X-ray microanalysis can also be used to analyze whether salts accumulate in these small vacuoles.

The exocyst, an evolutionarily conserved protein complex, is required for tethering and fusion of the vesicles and plasma membrane at the sites of polarized exocytosis (Munson and Novick, 2006). The exocyst is comprised of eight subunits: SEC3, SEC5, SEC6 SEC8, SEC10, SEC15, EXO70, and EXO84 (Boyd et al., 2004; Hsu et al., 2004; Tsuboi et al., 2005). Homologues of all exocyst subunits have been identified in the genome of *Arabidopsis* (Elias et al., 2003), rice, poplar and the moss *Physcomitrella patens* (Chong et al., 2009). In other multicellular organisms such as insects and mammals, in which also exocytosis for different types of secretion occurs, the exocyst is involved in some, but not all types of polarized exocytosis (He and Guo, 2009). In plants, to our knowledge, only the exocyst genes have been proposed as a tethering complex. If the plant exocyst is involved in exocytosis for various types of secretion, the plant specific expansion of the EXO70 family of genes may represent a means of regulation of the plant exocyst during exocytosis processes for different purposes (Zhang et al., 2010). It is very interesting to investigate whether the EXO70 family of genes is involved in salt gland secretion. In order to study the molecular mechanism of salt gland secretion, an efficient transformation model plant of recretohalophytes needs urgently to be established.

3.3.3 Proposed model of salt gland secretion

Based on our present knowledge, it is difficult to draw a clear conclusion regarding the mechanism of salt gland secretion. However, from the available information described above, it is possible to visualize the likelihood of a vesicle-mediated system and possibly involved membrane-bound translocating proteins for salt gland secretion (Fig. 6). Na^+ enters salt gland cells by K^+ outwardly rectifying channels (KORC), non-selective cation channels (NSCC), high-affinity K^+ transporter 1 (HKT1) and *Arabidopsis* K^+ transporter 1 (AKT1). Na^+ in cytoplasm of secretory cells can be excreted by the collaboration of H^+-ATPase, SOS1, Na-K-Cl cotransporter (NKCC) and Na^+/K^+-ATPase at the plasmalemma directly

or sequestrated to the microvacuoles temporarily and then excreted by the following ways: (1) salts are excreted when the microvacuoles fuse with the plasmalemma; (2) microvacuoles dock onto the plasmalemma without fusion. The two membranes (tonoplast and plasmalemma) form "junctional complexes" where channels on both membranes connect allowing passage of solutes from the vesicle to the exterior.

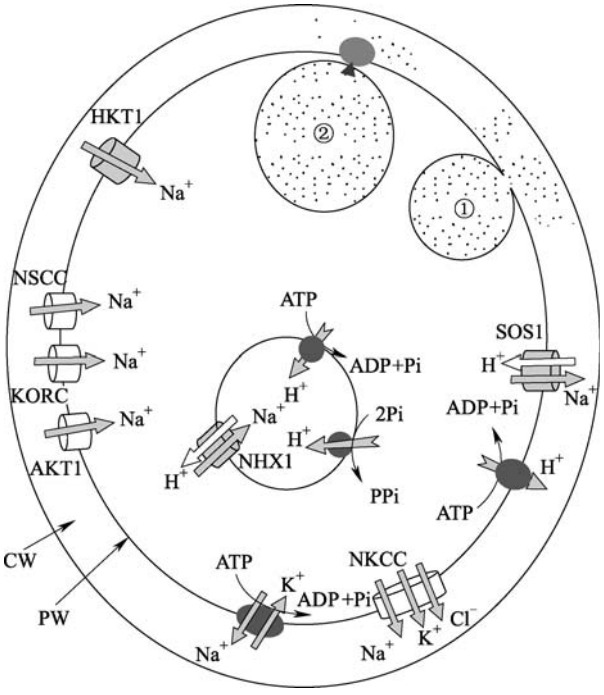


Fig. 6 Diagrammatic representation of vesicle-mediated secretion systems from the vacuole to the plasmalemma and possibly involved membrane-bound translocating proteins for salt secretion of plant gland secretory cell. Note vesicle-mediated secretion systems: ① microvacuoles fuse with the plasmalemma; ②"junctional complexes" allow the direct transfer of salts to the apoplast. Juxtaposition of membrane-bound carriers located at the tonoplast and the plasmalemma, Na^+ can be excreted by collaboration of H^+-ATPase, salt overly sensitive 1 (SOS1), Na-K-Cl cotransporter (NKCC) and Na^+/K^+-ATPase at the plasmalemma. Red arrowheads represent tonoplast-bound carriers, and the direction indicates the flow of salts.

Acknowledgements We are grateful for the financial support from the National Natural Science Foundation of China (Grant No. 30870138) and the High Technology Research and Development Program of China (No. 2007AA091701).

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