

Review

Physiological Significance of Morpho-Anatomical Features of Halophytes with Particular Reference to Cholistan Flora

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ABSTRACT

Desert flora shows a range of morphological and anatomical features under natural and simulated saline conditions. The morphological characteristics include smaller leaves, fewer stomata, increased succulence, thick cuticle and deposition of wax. The anatomical ones include salt secretory trichomes and glands at leaf level, thick and many layered epidermis and well developed water storing tissues in the cortex of stem, and reduced cortical area, widening of casparian band and enhanced development of root endodermis. Of these, the most important ones are salt-secretory trichomes and salt glands. With few structural differences, they are similar functionally and are associated with the secretion of ions. In this review an attempt has been made to present a detailed account of salt glands and trichomes in relations to their functions, together with the pathways and mechanisms of ion-secretion, in the halophytes endemic to desert environments.

Key Words: Apoplast; Cholistan; Cuticle; Ion-secretion; Salt glands; Symplast; Trichomes

INTRODUCTION

Vegetation in desert suffers vagaries of nature like water, heat and salt stresses. Such constraints are extremely detrimental to plant growth and development. The plants inhabiting desert environments have developed, over the ages, certain features which help them to thrive under adverse conditions. Such features are often displayed in the morphology and anatomy of plants.

In Pakistan, Cholistan represents a vast desert spread over about 26,000 km² area in the south (Rao *et al.*, 1989). It mainly comprises of sand dunes and saline tracts, where salinity levels rise up to 40 dS m⁻¹. The desert temperature shoots to more than 50°C during summer, hence aggravating the problems of aridity. Despite of this, Cholistan enjoys quite a diversified vegetation cover including grasses, herbs, shrubs and trees (Rao & Babar, 1990). Desert plants have acquired certain features which enable them to tide over the harsh conditions of salinity. Unfortunately, few studies have been conducted about the development and role of salinity-related features of plants from Cholistan. This review encompasses an account of physiological significance of morpho-anatomical features of desert halophytes raised in natural and simulated saline habitats.

ADAPTATIONS IN NATURAL SALINE HABITATS

Morphological. Most obvious morphological adaptations of plants from desert-saline habitats are smaller leaves, fewer stomata per unit leaf area, increased succulence, thickness of leaf cuticle and deposition of wax (Gale, 1975; Mass & Nieman, 1978). These adaptations play a crucial role in

conserving water for sustained plant growth under saline conditions. More recently, a substantial ecotypic variability has been reported in *Cenchrus ciliaris*, which enables this grass to withstand in harsh condition particularly during periods of severe drought (Hameed *et al.*, 2002).

Anatomical. These are the most conspicuous adaptations found throughout the plant body (Dickison, 2000). At leaf level, there are certain appendages which help the plant to secrete excess of salts from the main body. Most important among them are salt secretory trichome (e.g. *Atriplex* spp.). Second type is that of multicellular salt glands which occur in many flowering plants of desert and coastal habitats, and are confined to the members of families including Poaceae, Aviceeniaceae, Acanthaceae, Frankiaceae, Plumbaginaceae and Tamaricaceae (Mauseth, 1988; Thomson *et al.*, 1988; Marcum & Murdoch, 1994).

The desert plants usually have succulent stems which are characterized by a well developed water storing tissue in the cortex and pith (Lyshede, 1977; Dickison, 2000). Many layered epidermis may be thick walled, covered with thick cuticle and coated with wax. For example in *Anbassis* sp., the epidermis is eight to eleven layered and stomata occur at the base of an obliquely oriented stomatal crypt (Bokhari & Wendelbo, 1978). In contrast, the stem of halophyte *Salicornia fruticosa* has a simple cortex and single layered epidermis which is thin walled. The photosynthetic tissue has palisade and parenchymatous cells for storage of water (Fahn, 1990).

The roots of saline desert plants have reduced cortex to shorten the distance between epidermis and stele. The casparian strip is much wider in the highly dry and salt marsh habitat plants, as compared to mesophytes. In saline

habitat plants, the endodermis and exodermis (hypodermis with casparian band) represent barriers of variable resistance to the radial flow of water and ions from cortex to the stele under prevailing conditions (Hose *et al.*, 2001; Taiz & Zeiger, 2002). Such adaptation is advantageous for efficient functioning of endodermis, when the protoplasts are attached to the large portions of the radial and transverse walls of endodermal cells (Fahn, 1990).

ADAPTATIONS IN SIMULATED SALINE HABITATS

The plants of desert-saline area when grown in artificial saline media show differential morpho-anatomical responses as a consequence of presumably altered physiological mechanisms. Given below is a brief account of morpho-anatomical changes in arid zone plants grown under simulated highly saline conditions.

Morphological. Most prominent features are the reductions in growth and related parameters (Nabi & Courdet, 1995; Akram, 1997). Desert plants exposed to saline media show distinct halo-tolerance potential (Hamid, 1995). Applied salinity brings about a significant reduction in the leaf area but increases leaf succulence (Longstreth & Nobel, 1979). Exposure of the ecotypes of halophytic grass *Sporobolus locladus* to relatively low levels of salinity promotes growth and improves leaf angle and position for optimum interception of sunlight (Hamid, 1995). This supports the view that low concentration of salts is required for promoting growth of halophytes (Jennings, 1976; Ohta *et al.*, 1988). Stem of desert plants, under salinity, are often thin and roots also show much thinning and constriction (Gale, 1975; Hamid, 1995).

Anatomical. Both halophytes and non-halophytes exhibit remarkable anatomical changes when exposed to elevated levels of salinity (Mass & Nieman, 1978). However, most conspicuous changes are notable in leaf. Longstreth and Nobel (1979) reported a smaller increase in mesophyll area/leaf area in *Atriplex patula* (halophyte) than *Phaseolus vulgaris* and *Gossypium hirsutum* (glycophytes). This revealed a greater tendency of atriplex to maintain constant mesophyll area. This is an adaptive feature which reflects greater degree of shielding to photosynthetic mechanisms from harmful effects of salts.

Zoysiagrass (*Zoysia* spp.) does not show any change in the density of salt glands when grown under salinity (Marcum & Murdoch, 1990). Enhanced salt tolerance of *Zoysia* spp. is proportional to a greater density of salt glands in different species followed by exclusion of shoot ions from leaf gland secretion (Marcum *et al.*, 1998).

In the root epidermis and root hairs of *Atriplex hastata*, the wall turberances develop on the inner side in response to higher salt treatment (Longstreth & Nobel, 1979). The epidermal cells thus become transfer cells (Kramer *et al.*, 1978). However, at lower levels of salinity, endodermis, pericycle, and thick cuticle develop, and the induction of aerenchyma and hollowness of pith occurs in *Sporobolus locladus* (Hamid, 1995).

STRUCTURE OF SALT SECRETORY FEATURES

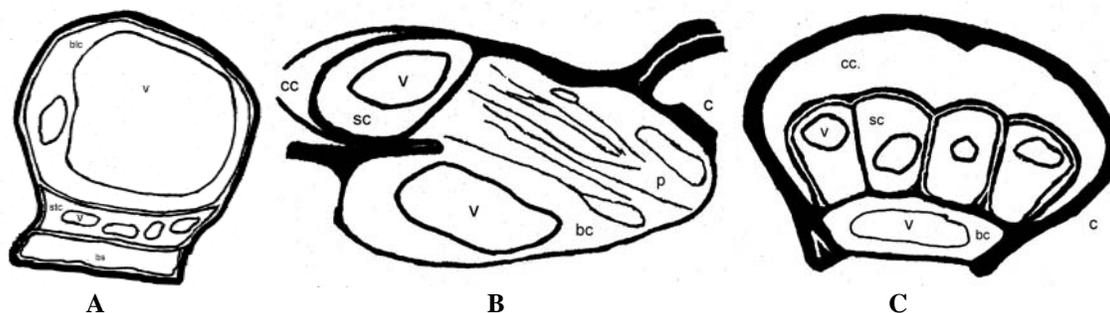
As mentioned above, the arid zone plants have adopted special features to off-load the excess of ions. They include salt secretory trichomes and salt glands; general structure and function of which are briefly given below:

Trichomes. Salt secretory trichomes, characteristics of *Atriplex* spp., are bladder-like hairs projecting out of leaf surface. They consist of a large secretory or bladder cell on the top (Fig. 1a) and a stalk consisting of one or sometimes a few cells (Samaoui, 1971; Dickison, 2000). All these cells contain mitochondria, dictyosomes, ribosomes, endoplasmic reticulum and a large flattened nucleus. The chloroplasts are rudimentary or partially developed. The only difference lies in that a single large vacuole is present in bladder cell and many small vacuoles in the stalk cell (Osmond *et al.*, 1969). A symplastic continuum exists from the mesophyll cells to the bladder cell for the movement of ions. The external walls of bladder and stalk cells are cutinized, while inner primary walls are not (Thomson & Platt-Aloia, 1979). The salts are released to outside environment by leaf shedding.

Salt Glands. These are multicellular, more prominent and elaborate in structure. In grasses, the glands are generally bicelled, i.e., an outer cap cell and a subtending basal cell (Fig. 1b). They may be sunken, subsunken, extending out of epidermis (Liphshitz & Waisel, 1974; Marcum & Murdoch, 1994) or lie recumbent to the leaf surface in parallel rows atop intercostals ridges (Marcum *et al.*, 1998).

In dicotyledonous species, the salt glands are multicellular, consisting of basal and secretory cells. The number of cells may vary from six up to forty in different genera (Fahn, 1990). For example, in *Tamarix* spp. the salt glands consist of two basal collecting cell and outer six highly cytoplasmic secretory cells (Mauseth, 1988). However, the glands of *Avicennia* (Fig. 1c) and *Glaux* comprise of several secretory cells positioned above a single disc-shaped basal cell (Rozema *et al.*, 1977). The position of the gland may be a lateral register with epidermis (*Tamarix*), present in epidermal depression (*Glaux*) or projecting out of abaxial surface of leaf-like trichomes (*Avicennia*) (Thomson *et al.*, 1988).

Fig. 1. Typical structure of salt secretory trichomes of atriplex (A) and salt glands of grasses (B) and dicots (C). Letters represent vacuole (v), bladder cell (blc), stalk cell (stc), secretory cell (sc), collecting chamber (cc), partitioning membranes (p) and cuticle (c)



At ultrastructural level, the basal and stalk cells of grasses and dicot glands contain some microbodies, a large flattened nucleus, endoplasmic reticulum, ribosomes, many mitochondria, rudimentary plastids and small vacuoles (Thomson, 1975). Most striking features are many and extensive invaginations of plasmalemma i.e., partitioning membranes extending into the basal cell from the wall between basal cell and cap cell (Oross & Thomson, 1982). Moreover, numerous small vesicles occur near plasmalemma to carry the ions (Shimony, 1973). The glands are covered by an expanded cuticle, over the secretory cell and form a collecting chamber with the outer cap cell wall. A symplastic continuity, due to the presence of plasmodesmata, exists between the basal and cap cells and basal and mesophyll cells (Zeigler & Lutge, 1967).

PATHWAYS OF SECRETION

Thomson *et al.* (1988) have suggested three possibilities: (a) direct apoplastic flow of solutes to the glands, (b) symplastic movement via plasmodesmata and (c) some combination of the two (Fig. 2).

Apoplastic pathway. Both in the glands of grasses and dicot plants, the inner primary walls of stalk cell or basal cells are not cutinized (Oross & Thomson, 1982). So an apoplastic continuum from mesophyll to the gland cells exists. Atkinson *et al.* (1967) by feeding radioactive Cl^- to high salinity grown leaves showed that specific activity of secreted Cl^- was greater than that present in the leaf. This indicated that Cl^- passed directly to the glands without coming in equilibrium with the major Cl^- pool within the leaf cells. Ionic lanthanum fed to the cut branches, leaf discs, leaf petioles or leaf bases revealed that deposits were detected throughout the apoplast of leaves as well as transfusion zone at the base of the gland of *Tamarix*, walls of the stalk and bladder cells of the *Atriplex* (Campbell *et al.*,

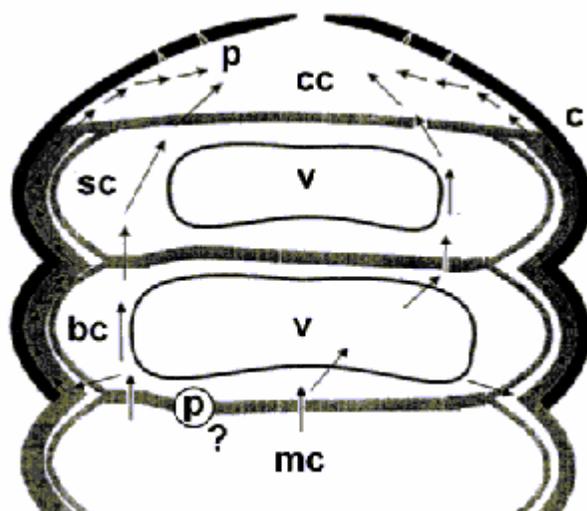
1974) and the walls of the basal cells of *Cynodon* (Oross & Thomson, 1982). Moreover, heavy enrichment of Cl^- in the mesophyll cell walls and the walls of transfusion zone of the gland of high salinity grown leaves, also gave credence to the apoplastic flow of ions (Campbell & Thomson, 1975). These evidences indicate that apoplast is open to the base of the gland and forms primary pathway of ion movement.

Symplastic pathway. Although the presence of plasmodesmata between the mesophyll, basal and cap cells of glands forms this pathway of ion movement, the supporting evidence is scarce. This is particularly true in case of plants grown under highly saline conditions. Zeiger and Lutge (1967) in *Limonium* reported that Cl^- deposits were associated with plasmodesmata of the transfusion zone and concluded that Cl^- was symplastically transported to the glands. Pollak and Waisel (1970) reported that salinity grown *Aeluropus* secreted Na^+ at a lower rate. The amount of Na^+ secreted and that present in the leaf was almost the same, which indicated that Na^+ was transported symplastically.

Symplastic movement of ions has also been suggested from the electrophysiological studies, Osmond *et al.* (1969) have shown the electrical coupling between leaf mesophyll cell and vacuoles of basal cells of *Atriplex*. Moreover, the light induced changes in the membrane potential of the mesophyll cells were detectable in basal cells of the gland (Thomson *et al.*, 1988), which confirmed that the signal moved symplastically.

Apoplastic-symplastic combined pathway. Campbell and Thomson (1975) using silver chloride deposits in salinity grown leaves of *Tamarix* showed that most of the deposits were associated with plasmodesmata of the transfusion zone as well as walls of salt-loaded leaves; however in control plants, the deposits were only detected in association with the plasmodesmata. This supports to the view that ions move preferentially through apoplast in high salt grown plants.

Fig. 2. Schematic representation of apoplastic and symplastic movement of ions from mesophyll to the collecting chamber of a salt gland. Letters represent mesophyll cell (mc), basala cell (bc), secretory cell (sc), collecting chamber (cc) and pores (p) in the cuticle ©. Possibility of ion pump in the transfusion zone of mesophyll and basal cells. Long arrows indicate symplastic movement across plasmodesmata, plasma membrane and tonoplast, while short arrows indicate apoplastic movement via cell wall spaces



NATURE OF SECRETED MATERIALS

The excess of salts in growth media is, presumably, secreted in a major bulk. A complete analysis of the secreted materials indicated a variety of anions and cations. For instance, in *Tamarix*, Ca^{2+} , Mg^{2+} , Na^+ , K^+ , Cl^- , SO_4^{2-} , NO_3^- , PO_4^{3-} , HCO_3^- and even Br^- was found to be secreted (Pollak and Waisel, 1970; Thomson *et al.*, 1988). Kleinkopf and Wallace (1974) found that 25% of the leaf K, Ca, Cu, Mn, B, Al, Si, Ti, Mo, Sr and Ba were secreted by the salt glands. Similarly, Ca^{2+} , Mg^{2+} , Na^+ , K^+ , Cl^- , in *Limonium* (Faraday & Thomson, 1986), and Ca^{2+} , Mg^{2+} , Na^+ , K^+ , Cl^- and HCO_3^- in *Armeria* (Baumister & Ziffus, 1981) have been reported to be secreted via salt glands of leaf.

MECHANISM OF ION SECRETION

The trichomes and salt glands have minimally developed chloroplasts but numerous fully developed mitochondria. This indicates that secretion is an active process (Thomson *et al.*, 1988). Studies have revealed that ionic concentration of the secretion fluid is greater than the root medium. This suggests that somewhere in the stem-leaf-gland continuum, the secretion against the concentration gradient occurs (Osmond *et al.*, 1969; Hill, 1973), which requires energy. This implies that the active sites (energy consuming sites) are located at the points of coupling

between the basal cells of gland and mesophyll cells from where the salts are secreted from the gland i.e., the plasmalemma of secretory cells (Thomson *et al.*, 1988).

The energy requirement of secretion process was confirmed using inhibitors of photosynthesis in the presence of light and uncouplers of carbon fixation in dark (Hill & Hill, 1976). This revealed that as apposed to mesophyll photosynthesis (i.e. 90%), the secretory cell photosynthetic activity (i.e., 10%) was insufficient to trigger the uptake of ions. From this, Hill and Hill (1973) concluded that ATP, derived mainly from respiration and partially from cyclic photophosphorylation of mesophyll cells, is utilized for the movement of ions to the gland cells. It has been argued that since ion secretion consumes energy, some sort of pump is involved in this process (Hill & Hill, 1973). As the glands are exit points of secreted fluid, it is likely that they are the locations of active process. This notion is further strengthened by high mitochondrial density in the secretory cells of the glands of all plants (Thomson *et al.*, 1988).

The evidence that the pumps are located in the mesophyll came from the electrophysiological studies, wherein electrical coupling has been reported between mesophyll and secretory cells (Hill & Hill, 1976). Contrarily, the apoplastic transport of ions implies that solutes are transported into the apoplast of the glands by secretory cells and accumulated in the collecting chamber (Fig. 2). Solute linked movement of water into the chamber results in its expansion. With sufficient expansion, the saline

solution is released to the surface of the leaf with the opening of the pores in the cuticle. Platt-Aloia *et al.* (1983) using transmission and freeze fracture electron microscopic observations reported that the small vacuoles, containing secretory materials, in different gland cells may fuse with plasmalemma of the secretory cells, and release the material to the apoplast of the glands.

Since the salt secretion is an active process, involves transport across membrane and utilizes ATP, attention has been shifted to ATPase, mainly the glandular. Two types of ATPase have been reported. Kylin and Gee (1970) have reported the cation-stimulated ATPase in the homogenate of salt secretory leaves of *Avicennia*, whereas Hill and Hill (1973, 1976) have reported anion-stimulated ATPase in microsomal fractions isolated from salt grown secretory leaves of *Limonium*. The activity of ATPase is correlated with the activity of gland, which suggests an important role of this enzyme in secretion process (Thomson *et al.*, 1988).

The secreted ions may flow back into the plant. To prevent it, the secretory cells of salt glands have longitudinal side walls, heavily cutinized, with cutin permeating the cell wall layers, whereas, the stalk cell acts like an apoplastic barrier to the flow of ions (Mauseth, 1988).

FUTURE RESEARCH PROSPECTS

The halophytic vegetation of Cholistan is highly diversified and needs to be comprehensively explored for the occurrence of morpho-anatomical adaptations and their physiological significance. As a unique desert, it is likely that Cholistan flora possesses a wide range of useful features of salt tolerance. Rao *et al.* (1989) and Rao and Babar (1990) have given a nice account of the phytosociology of Cholistan vegetation, which can be used as a baseline information for further studies. Future work from microscopic to molecular levels is likely to yield novel information on the classification of plants according to nature and type of stress tolerance features, structure and function of salt secretory systems, nature of secreted material and mechanism(s) of ion secretion.

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