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Research article

Low Na/K ratio in the leaves of mangroves mitigates salinity stress in estuarine ecosystem

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Abstract: Plants have their own genotype which allows them to absorb, accumulate or exclude nutrients particularly sodium (Na) and potassium (K) through their root system that are essential for physiological activities and growth in coastal wetlands. Dominant mangrove species such as *Avicennia alba, A. officinalis, A.maritima, Suaeda monoica, S. nudiflora, S. maritima* and *Acanthus ilicifolius* were selected from Andhra Pradesh coast to observe the sodium (Na) and potassium (K) accumulation in the leaves and the salinity in the aqueous soil solution in their respective rhizosphere. Results reveal that only *Acanthus ilicifolius* grew in low soil salinity of ~0.5 to 1.2 ppt. and are moderate accumulators of Na and K in the leaves. *Avicennia alba* is highly sensitive to salinity due to its high Na/K ratio in leaves. *A. officinalis* and *A. marina, S. nudiflora* and *S. maritima* show low Na/K ratio and are tolerant to salinity stress. *Acanthus ilicifolius* and *Suaeda monoica* show moderate ratio of Na/K in their leaves. The leaf epidermal modifications through salt glands (*Avicennia* and *Acanthus* spp.) and prevention of water loss by non-gladular trichomes as in case of *Avicennia* species helps in mitigation of salinity stress but their affinity towards K uptake and translocation to leaves primarily regulates the physiology and growth of plants to tolerate or succumb to salinity stresses. Except for *Suaeda monoica* both *S. nudiflora* and *S. maritima* are non-accumulators of Na and K showing their low ratio in leaves. K is an essential component in the leaves to mitigate increased salinity in the ecosystem despite the leaf epidermal morphological adaptations to exude excess salt. Plants which are efficient in K absorption are more tolerant to salinity stress while others are comparatively sensitive.
Keywords: Mangroves - Sodium - Potassium - Leaf epidermis - Salinity.

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INTRODUCTION

Coastal wetlands are vulnerable to direct impacts of changing climate that induces sea level fluctuations and salinity related ecological disturbances. Worldwide coastal biodiversity is sensitive to these dynamic frequent changes and several species are at the verge of extinction. Anthropogenic activities enhance the deterioration of coastal ecology not conducive for different mangrove species. Mangroves and associates confined to intertidal areas are subjected to high salinity in two ways. Firstly, through sea water inundation (Morrow & Nickerson 1973, Tomlinson 1986) and secondly, at the leaf level through the deposition of airborne salt spray (Boyce 1954). Adaptability, tolerance and susceptibility are the three major physiological processes (Farooqui *et al.* 1995) that the biotic forms have in their genes to abate stress conditions. The total concentration of salts translocated through root system needs to be regulated within the growing plant tissues (Paliyavuth *et al.* 2004). The roots of *Avicennia* species have the ability to filter over 90% of salt from the water they uptake (Scholander *et al.* 1962, Drennan & Pammenter 1982). In addition to this, the ions are stored in the leaf hypodermis, followed by active excretion through glands on the leaf surface (Waisel *et al.* 1986, Smith *et al.* 1989, Dschida *et al.* 1992, Balsamo & Thomson 1995). Salt glands are the special adaptive structures (multicellular trichomes) which are predominantly found on the leaves and stems of halophytic species in particular. These are efficient desalination devices capable of salt excretion from plant tissues (Fahn 2000). The function of stomatal

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conductance in any plant species is regulated through the osmotic processes during which potassium plays a major role in maintaining the turgor pressure of guard cells (Dietrich *et al.* 2001).

Plants exhibit various adaptive strategies in response to different abiotic stresses such as salinity, which limits the plant growth and productivity (Munns 2002). *Avicennia* grows in the slightly elevated and mostly in adverse and frequently changing part of the intertidal habitat. The surface could be often dry for extended periods and salts increase in the substratum due to its upward movement in the soil column through capillary action. Three species of *Avicennia* such as *A. alba, A. marina* and *A. officinalis* are in general encountered along the Indian coastal zone along with *Suaeda* species (*S. maritima, S. monoica* and *S. nudiflora*) and *Acanthus ilicifolius*. However, *A. marina, A. oficinalis, S. nudiflora* and *Acanthus ilicifolius* are common in the coastal belt of India and form pure stands. The east coast of India is characterized by shallow coastal wetlands which are more affected by even the slightest change in climate induced sea level changes enhanced by anthropogenic activities. It estimated that about 1.76 lakhs hectares of land in Andhra Pradesh are affected by salinity, in the districts of Prakasam, Guntur, Krishna and East Godavari. The soil along the coast (about 10–15 km from the sea) is mostly sandy in nature and of marine origin. The sub-soil water is also found to be generally rich in salt content in certain areas. The salt tolerance potential varies from genotype to genotype and species to species within the plant kingdom (Moisender *et al.* 2002). The present study highlights the leaf epidermal morphology to mitigate salinity stress and Na/K ratio in the leaves responsible for species zonation of three dominant plant genera such as *Avicennia, Acanthus* and *Suaeda* in coastal wetlands.

MATERIAL AND METHODS

Sediment soil of 50 cm depth from ground surface was collected from around the rhizosphere of *Avicennia alba, A. officinalis, A. marina, Suaeda monoica, S. nudiflora, S. maritima* and *Acanthus ilicifolius*. These were sub-sampled at an interval of 10 cm to measure the total dissolved salts (salinity). The salinity was measured in the aqueous soil solution in order to know the concentration of salts available for the absorption by plants. For this ten sites were selected to collect the soil from rhizosphere of the respective plant species. Since the salinity variation was not much in a 50 cm sediment profile, the salinity given in table 1 is the average of 5 sub-samples in 50 cm deep sediment. The sample numbers 1–10 (Table 1) are 10 different soil cores. The salinity was measured in aqueous soil solution. For this 10g air dried soil sample was dissolved in 100ml of deionized water and kept overnight after rigorous shaking for 1hr. Samples were homogenized for 30 minutes prior to salinity measurement in ppt (parts per thousand) by using 'Orion-5 Star' (Thermo-Orion, Scientific Equipment, USA) at standardized 20°C temp.

Table 1. Average salinity (5 sub-samples of 50 cm core) in the soil rhizosphere of studied plants (*Salinity in ppt- parts per thousand).

Core Numbers	*Avicennia alba*	*Avicennia officinalis*	*Avicennia marina*	*Suaeda monoica*	*Suaeda nudiflora*	*Suaeda maritima*	*Acanthus ilicifolius*
1	2.2	1.5	3.0	2.1	3.0	2.4	1.0
2	2.8	1.8	3.2	1.2	3.2	2.6	0.7
3	1.2	1.0	3.5	1.5	4.0	2.0	0.8
4	1.5	0.9	2.9	1.2	4.1	2.8	0.9
5	1.9	1.2	2.5	1.4	3.2	3.7	1.1
6	3.0	1.3	1.9	1.5	3.8	2.8	1.0
7	2.3	1.6	3.8	1.0	4.5	3.6	0.9
8	2.1	1.9	2.9	2.0	4.3	4.0	1.2
9	1.2	2.0	1.9	2.8	4.2	3.1	0.5
10	1.6	1.3	2.0	1.7	3.1	2.5	0.7
Average (*ppt)	1.98	1.45	2.76	1.64	3.74	2.85	0.88

Ten mature leaf samples each of *Avicennia alba, A. officinalis, A. marina, Suaeda monoica, S. nudiflora* and *S. maritima* along with *Acanthus ilicifolius* were collected randomly from the coastal areas of Krishna- Godavari delta (Fig. 1 & 2). The Sodium (Na) and Potassium (K) was measured by Flame photometer (ELICO-CL-360) in 10 g air dried leaf samples which was acid digested (nitric acid and perchloric acid). The residue was made up to 100 ml using deionized water before the analysis. For morphological study the leaves were boiled in water and glycerine (60:40) with few drops of conc. nitric acid until the peel appeared separated. The peel was brushed off in clear water to remove the tissues and later mounted on slides in glycerinated medium. The upper and lower epidermal surface was observed under Olympus BX-51 and the photographs taken with DP-26 camera. The contributions of AF include microscopic observations, chemical analysis of leaves/soil and compilation of the manuscript. Ranjana contributed by processing of the samples and microscopic observations. YJ contributed in giving suggestions and providing partial input in the analysis of results and discussion.

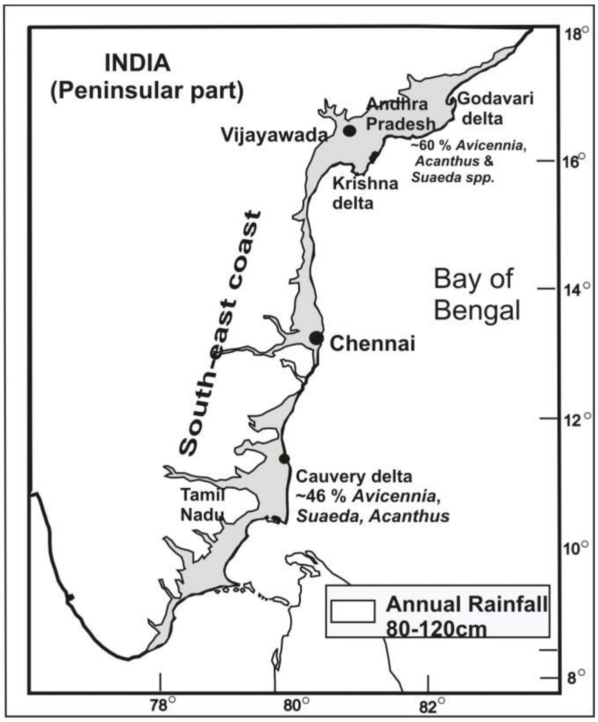

Figure 1. Map showing south-east coast and the percentage of salt tolerant mangroves.

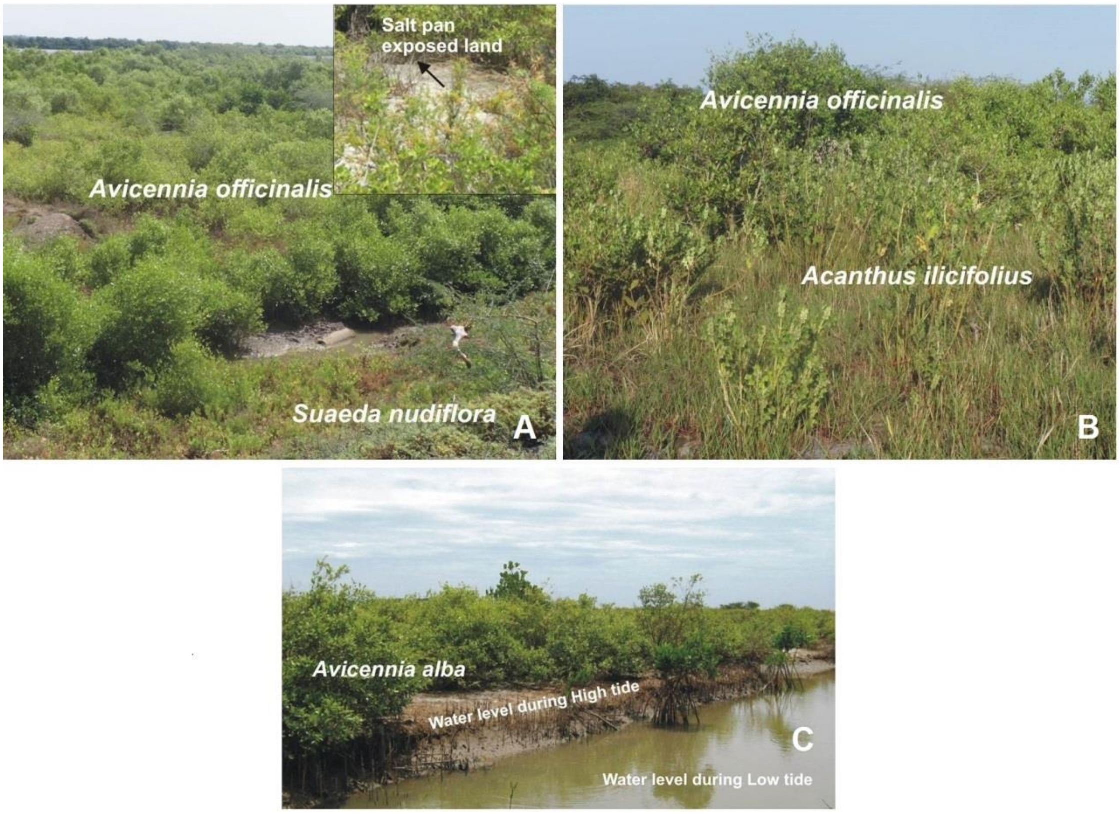

Figure 2. A, *Avicennia marina* and *A. officinalis* along with *Suaeda nudiflora* and *S. maritima* on highlands that are often inundated by tides but not regularly. Inset, showing interspersed salt accumulation on the surface; **B,** *Avicennia officinalis* along the back water channel towards land and *Acanthus ilicifolius* on highlands; **C,** *Avicennia alba*, regularly inundated by high tides twice a day (near shore).

RESULTS

Salinity in aqueous soil solution

The soil samples in the vicinity of roots of *Avicennia alba* shows minimum 1.2 and maximum 3.0 ppt (Table 1). The average soil salinity in 10 sites where *A. alba* was growing shows 1.98 ppt in the aqueous soil solution. The average soil salinity was 1.45 ppt in the region where *A. officinalis* was growing. The minimum salinity was 1 and the maximum was 2.0. Out of all the *Avicennia* species the highest soil salinity was in the soil where *A. marina* was growing. The average salinity in soil was 2.76. The minimum was 1.9 and the maximum was 3.8.

Among the three species of *Suaeda* the highest average salinity (3.74) in aqueous soil solution was recorded where *S. nudiflora* was growing followed by *S. maritima* (2.85) and *S. monoica* (1.64). The minimum salinity was recorded in the rhizosphere of *S. monoica* (1 ppt) followed by *S. maritima* (2) and *S. nudiflora* (3). The maximum salinity was recorded in *S. nudiflora (*4.5 ppt) followed by *S. maritima* (3.7) and *S. monoica* (2.8). The lowest average salinity was recorded in the vicinity of *Acanthus ilicifolius* (0.88 ppt). The minimum concentration in the soil was 0.7 ppt and the maximum salinity recorded was 1.2 ppt.

Table 2. Sodium, Potassium in the leaves (10 samples) of dominant plant taxa recorded along the Krishna Godavari delta, east coast of India.

		Avicennia alba	*Avicennia officinalis*	*Avicennia marina*	*Suaeda monoica*	*Suaeda nudiflora*	*Suaeda maritima*	*Acanthus ilicifolius*
Sodium (Na)	**1**	98.5	160.0	48.8	83.0	7.9	12.0	82.3
	2	112.8	165.8	51.8	92.0	12.0	8.0	98.0
	3	120.8	170.7	54.8	74.0	20.0	7.0	76.0
	4	99.0	165.0	55.0	83.0	19.0	13.0	78.0
	5	100.5	175.0	37.0	89.0	21.0	8.0	89.0
	6	125	165.0	49.0	96.0	8.0	9.0	100.0
	7	123	168.0	52.0	92.0	7.9	10.0	95.0
	8	97.0	155.0	55.0	72.0	9.0	12.0	99.0
	9	89.0	162.0	38.0	79.0	10.0	9.0	81.0
	10	90.8	155.0	56.0	89.0	14.0	13.0	72.0
Average		105.64	164.15	49.74	84.9	12.88	10.10	87.03
Potassium (K)	**1**	10.1	32.0	21.2	11.0	1.9	5.0	17.8
	2	11.9	35.8	25.2	20.0	3.0	2.0	28.0
	3	12.0	37.2	30.6	11.0	6.0	2.0	15.0
	4	9.5	32.0	30.0	14.0	5.0	5.0	15.0
	5	9.0	38.0	22.0	12.0	8.0	5.0	18.0
	6	12.0	35.0	23.0	14.0	2.0	3.0	19.0
	7	12.0	35.5	26.0	12.0	2.0	5.0	24.0
	8	9.0	30.0	26.0	11.0	4.0	4.0	23.0
	9	9.0	32.0	23.0	13.0	7.0	4.0	19.0
	10	10.0	32.0	26.0	15.0	7.0	6.0	15.0
Average		10.45	33.95	25.30	13.30	4.59	4.10	19.38
Na/K	**1**	9.8	5.0	2.3	7.5	4.0	2.4	4.6
	2	9.5	4.6	2.1	4.6	4.0	4.0	3.5
	3	10.1	4.6	1.8	6.7	3.3	3.5	5.1
	4	10.4	5.2	1.8	5.9	3.8	2.6	5.2
	5	11.2	4.6	1.7	7.4	2.6	1.6	4.9
	6	10.4	4.7	2.1	6.9	4.0	3.0	5.3
	7	10.3	4.7	2.0	7.7	4.0	2.0	4.0
	8	10.8	5.2	2.1	6.5	2.3	3.0	4.3
	9	9.9	5.1	1.7	6.1	1.4	2.3	4.3
	10	9.1	4.8	2.2	5.9	2.0	2.2	4.8
Average		10.15	4.85	1.98	6.52	3.14	2.66	4.60

Sodium and potassium in leaves

The leaf samples of *A. alba* show the minimum 99 mg g^{-1} and maximum 125 mg $g^{-1}$of sodium concentration. The minimum concentration in *A. officinalis* was 155 mg g^{-1} and maximum 175 mg g^{-1}. The high sodium concentration in the leaves of *Avicennia officinalis* and *A. alba* was an average of 164 and 105 mg g^{-1}, respectively followed by *A. marina* which shows three times lower concentration (average 50 mg g^{-1}). The minimum concentration of sodium in *A. marina* was 38 mg g^{-1} and maximum 56. The potassium concentration was however, highest in *A. officinalis* followed by *A. marina* and *A. alba* (Table 2). The Na/K ratio varied between these three species. While it was highest in *A. alba* (~10.15), it was low in *A. officinalis* (~4.85) followed by *A. marina* (~1.98). The Highest Na accumulation was in *Suaeda monoica* followed by several times low Na in *S. nudiflora* and *S. maritima*. Similar trend was recorded in K concentration in the leaves of these three species. *Acanthus ilicifolius* has the affinity to absorb and accumulate Na and K (87 and 19 mg g^{-1}, respectively) in the leaves but the high concentration of K (low Na/K ratio) in the leaves along with the adaptability feature such as salt glands to exude excess salt enables it to tolerate salinity stresses.

Leaf epidermal morphological adaptability

The salt glands observed in *Avicennia* species and *Acanthus ilicifolius* are a distinctive multicellular trichome. In both the genera, glandular hairs are found on the upper leaf surface and much more densely in the abaxial indumentums (Metcalfe & Chalk 1957). On the upper leaf surface they are sunken in shallow pits (Fig. 3A, B). In *Avicennia* species the non-glandular trichomes are many in number so much so that the stomata become obscure and are hardly visible (Fig. 3C). In the lower surface they occur scattered among long non-glandular hairs composed of three or four cells (Fig. 3D). The non-glandular hairs /trichomes are not present in *Acanthus ilicifolius*. It is only the glandular trichomes that are present on the upper and lower leaf surface (Fig. 3E–H). The salt gland has two to four vacuolated cells at the level of the epidermis, the stalk cell with an almost completely cutinized wall, and four to eight terminal cells. The terminal cells have a thin, perforated cuticle which separates from the cell walls apically, leaving an enclosed cavity between them. The secreted salt evaporates or is washed during rainy season. The *Suaeda* species do not show any glandular or non-glandular trichomes (Farooqui *et al.* 2009) either to excrete salt or to resist excess transpiration through the non-glandular trichomes. However, the leaves of *Suaeda* are needle like and succulent in nature, particularly *S. nudiflora*. The succulent leaves and low salt accumulation in *Suaeda* species helps them to adapt in salt stressed conditions when the physiologically active water becomes low in the pore water of the substrate.

DISCUSSION

All along the south- east coast of India, one can encounter pure forms of *Avicennia officinalis*, *A. marina*, *Suaeda maritima* and *S. Nudiflora* in most of the intertidal zones (Orissa, Tamil Nadu, Andhra Pradesh). These are in general scrubby bushes that are spread in large areas (Fig. 3) interspersed between salty substrates devoid of any vegetation. *Avicennia officinalis* and *A. alba* record high Na in their leaves that shows its affinity for Na absorption and translocation in the shoot system. Out of these *Avicennia marina*, is the lowest Na accumulator. However, the accumulation of K was least in *A. alba* and it was three times higher in *A. officinalis* followed by slight decrease in the values of K in *A. marina*. Thus, results show that both *A. officinalis* and *A. marina* have the affinity for potassium uptake and its translocation in the shoot system and in the leaves. The Na/K ratio was highest in *A. alba* and comparatively it is 52 % low in *A. officinalis* and 80 % low in *A. marina*. These two species with low Na/K ratio are recorded in abundance in the coastal wetlands of India, thereby, indicating that K is an essential component in the shoot system to mitigate increased salinity in the ecosystem despite the similar leaf epidermal morphological features adapted to exude excess salt accumulation in all the three species. The tolerance of all halophytes to salinity depends on controlled uptake and compartmentalization of Na and K and the synthesis of compatible solutes, even where salt glands are functional to exude excess salts (Flowers & Colmer 2008). Potassium plays an essential role in many physiological processes and the main function to regulate the turgor in stomatal cells helps mitigate the water stresses caused by high salinity when the physiologically active water becomes low for plants in wetlands.

Therefore, in India, *Avicennia alba* occurs only in mangrove forests from Sunderbans of West Bengal, Orissa, Andhra Pradesh (Coringa) but are either stray or absent from other mangrove areas in the south-east coast with increased salinity (Farooqui 2010, Srivastava *et al.* 2012). It is however not recorded from Saurashtra and Kutch areas where the high salinity exists in the coastal land due to dry and arid climatic conditions. *Avicennia marina* and *A. Officinalis* are distributed throughout in the mangrove areas due to its wide salinity tolerance perhaps due to its affinity for K absorption.

The association of *Acanthus ilicifolius* along with *Avicennia officinalis* and *A. marina* is restricted to landward zones. In general, *Acanthus* tends to grow in the areas of good fresh water input in the coastal wetlands with low salinity. Results show that its Na/K ratio is similar to *A. officinalis.* Its affinity for potassium uptake is similar to *A. marina*. Thus, low Na/K ratio coupled with salt glands for salt exudation enables the

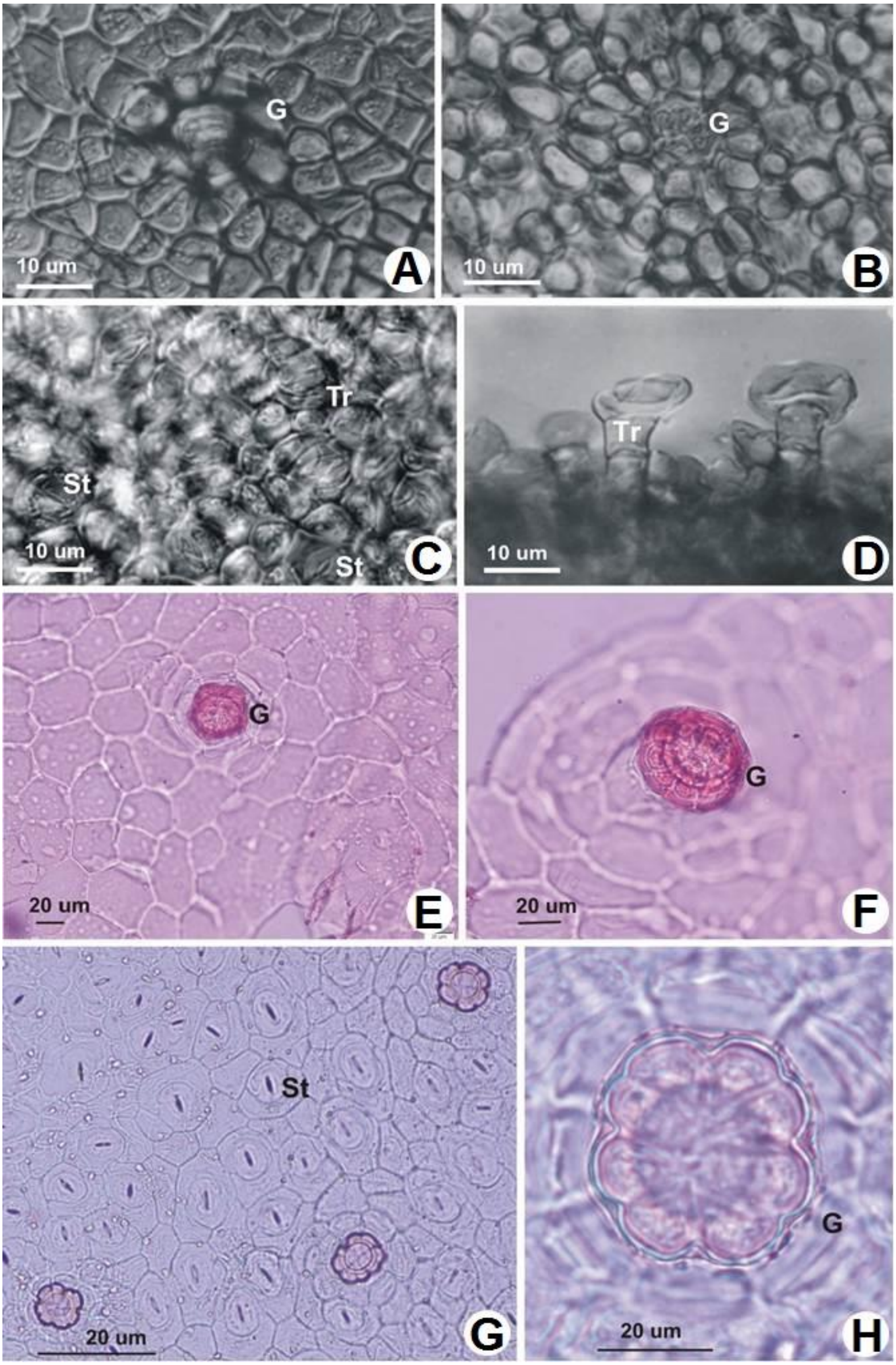

Figure 3. A, The Upper leaf epidermal illustration of salt glands (G) in *Avicennia alba*; **B,** The upper leaf epidermis of *A. officinalis* showing salt glands (G); **C,** Lower leaf epidermis showing non-glandular trichomes (tr) and obscured stomata (st); **D,** Enlarged view of Non-glandular trichomes in *A. officinalis* (stained with Safranin); **E,** Upper leaf epidermis of *Acanthus ilicifolius* showing multicellular peltate trichome known to secrete salts (salt glands).

species to survive the low to moderate salinity stress. But unlike *Avicennia*, lack of non-glandular trichomes in *Acanthus* does not help this species to restrict excess water loss during transpiration under salinity stress conditions. Therefore, it prefers to grow in low salinity zones and not in high salinity areas despite having salt glands for excess salt exudation and low Na/K ratio.

The affinity for Na and K uptake was highest in *S. monoica* with high Na/K ratio. Thus, this plant species is therefore, not found in abundance in the study area perhaps due its high salt accumulation without any functional adaptability features in the leaves to exude excess salt. The only adaptation is that it tends to increase the volume of the needle like succulent leaf. The experimental analysis showed that increased salinity in the substrate tends to increase the thickness of the cuticle in *Suaeda* which helps in the restriction of water evaporated during the transpiration (Hajibaghera *et al.* 1983) Uphof (1941) noted that the epidermis of xero-succulents and coastal halophytes is characterized by a thick cuticle and a cover of waxy layers. Thus cuticular resistance plays a major role in decreasing transpiration rates, a phenomenon frequently observed under saline conditions (Waisel 1972, Yeo 1981) and a decreased flux of water through the root system would mitigate against excessive ion transport to the shoot.

The study reveals that all the three genera (*Avicennia*, *Acanthus* and *Suaeda*) adapted to saline coastal areas behave differently with respect to Na and K affinity and accumulation in their leaves. While *Avicennia* has two features (glandular trichomes and non-gladular trichomes), the *Acanthus* has only glandular trichomes for salt exudation and no other adaptability to mitigate excess water evaporation through stomata. *Suaeda* species show increased leaf volume with the increasing salinity in the substrate. Among all the physiological processes in plants, the salinity shows an inhibiting influence on the photosynthesis. This is not only attributed to stomatal closure leading to a reduction of intercellular CO_2 concentration, but also to non-stomatal factors like reduction in green pigments and leaf area. It is also depicted from literature that salt affects photosynthetic enzymes, chlorophylls and ionic contents (Misra *et al.* 1997). Salinity limits the growth and production by affecting ion balance, water status, mineral nutrition, etc. (Munns 1993). Salt glands are specialized adaptive structures found predominantly on the leaves and stems of halophytic species. They are considered to be efficient desalination devices capable of removing salts from the plant tissues via an energy-dependent secretion process. High concentrations of salts in the root zone decrease soil water potential and the availability of water (Lloyd *et al.* 1989). This deficiency in available water under saline conditions causes dehydration at cellular level and ultimately osmotic stress occurs. The excessive amounts of toxic ions like Na^+ and Cl^- create an ionic imbalance by reducing the uptake of beneficial ions such as K^+, Ca^{2+}, and Mn^{2+} (Hasegawa *et al.* 2000). Therefore, the present study reveals that plants which are efficient in K absorbtion are more tolerant to salinity stress while others are sensitive despite the leaf epidermal modifications to mitigate such stresses.

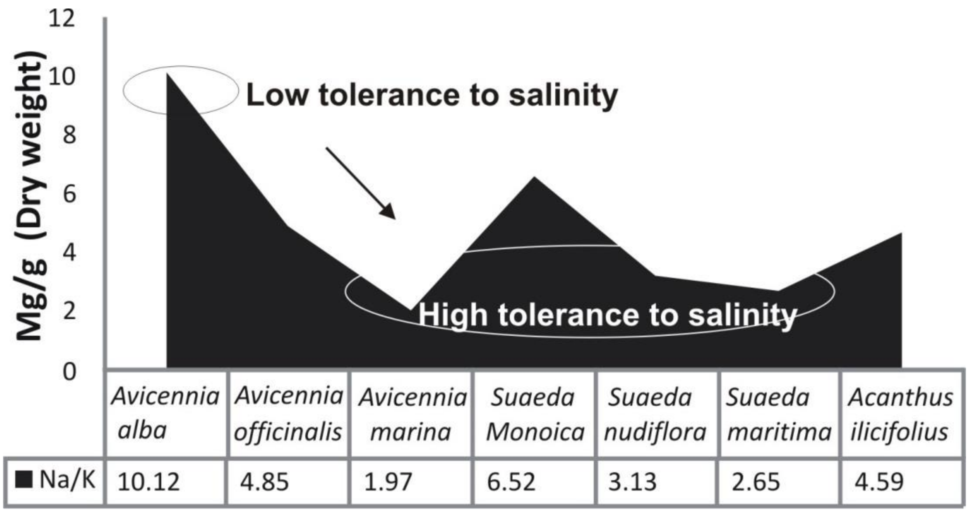

Figure 4. Relative affinities of dominant mangrove species to Na and K accumulation in the leaves.

Figure 4 shows that *Avicennia alba*, *S. monoica* and *Acanthus ilicifolius* are salt-sensitive mangroves/associates as the Na/K ratio is quite high but *A. officinalis*, *A. marina*, *S. nudiflora* and *S. maritima* are salt tolerant mangroves having affinity for K uptake as their Na/K ratio in the leaves is low. The K concentrations in the physiological processes of these species perhaps help in the mitigation of the salt stress in saline substrate and therefore, have become more abundant along the south-east coast competing with other species leading to local extinction of several other mangroves.

CONCLUSION

Salt stress has a significant effect on growth and distribution/zonation of mangroves relative to salinity in the substrate. Out of all the studied species, *Avicennia officinalis*, *A. marina, S. nudiflora* and *S. maritime* maintained the beneficial K ions in their leaf tissues, therefore, exhibit its dominance in saline substrate. *A. alba* and *S. monoica* are sensitive to salinity stresses as these have low affinity for K absorption. *Acanthus ilicifolius* too moderately sustains the salinity stress as the Na/K ratio is low but lacks leaf epidermal modifications to prevent water loss during transpiration except the glandular trichomes for salt excretion. Thus, potassium and sodium ions have a strong correlation with the salt tolerance potential in different plant species of studied mangroves. The current study also proves that Na/K ratios are the useful screening tools for salt tolerance at specific level in mangroves. The study can be used during the coastal zone management and strategies adopted for reforestation of mangroves in varied coastal ecosystems world over.

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