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A study of salt secretion by mangroves of Rekawa Lagoon, Sri Lanka

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A method to measure the salt secretion by mangroves which are open to the sea spray was developed and used to measure the salt secretion by mangrove species of Rekawa lagoon, an ecosystem with the highest diversity of true mangroves in southern Sri Lanka. Out of the twelve species of mangroves, only four species i.e. *Acanthus ilicifolius*, *Aegiceras corniculatum*, *Avicennia marina*, and *Avicennia officinalis* proved to be able to secrete salts. Under the salinity regime (26.2 ± 4.41 ppt) existed during the experimental period, the salt secretion by leaves of these four species were 47.2 ± 18.3, 35.1 ± 16.0, 149.3 ± 45.9, and 81.6 ± 30.5 mg salt cm^{-2} day^{-1} respectively. This result corroborates the published records and, hence validates the technique used in this study to measure the salt secretion. These four species exhibited increases in salt secretion with increases in soil salinity, consistent with previous reports. Results of this study also shows that the capacity to secrete salts at any given salinity was different between four species, following an order of *Av. marina* > *Av. officinalis* > *Ac. ilicifolius*, and *Ae. corniculatum*. The salt secretion by these species immediately after reducing the soil salinity was increased significantly implying an opportunistic removal of salt, which was accumulated in the plant body under high saline condition. Capacity for salt secretion by the four species as well as the magnitude of the increase of salt secretion as a response to increasing soil salinity, vary in parallel to the variations in salt tolerance given in published reports for the same species.

Key words: Mangroves, Salt secretion, Salt tolerance, *Acanthus*, *Aegeceras*, *Avecennia*.

1. Introduction

The importance of the salt tolerant plants are increasing over the sea level rise due to global warming as lands unsuitable for normal terrestrial plants are increasing day by day and only salt tolerant plants can make them productive (Dahdouh-Guabas et al, 2005). Mangroves which are woody plants that grow in intertidal areas of lagoons, estuaries and sheltered bays in tropical and sub-tropical latitudes, are one of the major group of salt tolerant plants. Although the salinity is often considered as a “stress”, NaCl may also be a resource for halophytic species (Ball

2002). The classic growth response of halophytes including mangroves to increasing salt concentration is similar to that of nutrients, with variation in the shape of the response curve reflecting concentrations which are deficient, saturating and toxic to growth (Ball, 2002). However the level that becomes toxic is depends on the species. Although the toxic level or tolerance limit is comparatively higher for all the mangroves, the degree of tolerance varies among different mangrove species (Allen et al., 2003; Tomlinson, 1986) The order of salinity tolerance of mangrove species are thought as one of the reason for zonation pattern of mangrove communities in the intertidal zone (Kathiresan and Bingham,2001). The physiological tolerance of mangroves for high salt levels depends on the mechanisms they have to extract fresh water from salty water in the soil (Ball, 1996). Mangroves avoid heavy salt loads by one or more of the following mechanisms;

(a) Salt exclusion - Most of the mangroves avoid salts using ultrafilters in root systems, which exclude salts while extracting water from the soil. They keep salt ions as filtered out during the water absorption through this ultrafiltration mechanism, eg. *Rhizophora*, *Bruguiera*, and *Ceriops.*

(b) Salt secretion - Some mangroves take salty water up, and then secrete only the salts through specialized glands in the leaves called ‘salt glands’. eg. *Avicennia*, *Aegiceras.* (Dschida et al., 1992; Fitzgerald et al., 1992).

(c) Salt accumulation - It is reported that the salt concentrations in the sap of mangrove plants can also be reduced by transferring the salts into senescent leaves and/or to the bark of stem and aerial roots or their wood (Tomlinson, 1986). The transferred salts, particularly sodium and chloride ions, deposit and store in such parts. Naskar and Mandal (1999) reports that *Excoecarea* and *Lumnitzera* accumulate sodium and chloride ions in senescent leaves, but withdrawn potassium and phosphate ions prior to leaf senescence.

Mangroves avoid heavy salt loads through a combination of above processes (Kathiresan and Bingham, 2001). However, all the mangrove species do not possess these mechanisms in the same order. Particularly the salt secretion takes place only in four, out of 20 true mangrove genera in the world, i.e. *Acanthus*, *Aegialitis*, *Aegicerous* and *Avicennia.* The salt ‘glands’ that secrete sodium chloride to control the salt balance in the plant body of these genera could be the most distinctive structure developed in mangrove leaves. Salt glands occur on the surface of both side of leaves in these genera, but are not necessarily equally frequent on upper and lower surfaces (Tomlinson, 1986). In most of the cases, it is more abundant in adaxial surface (Hong and Eong, 1984). The precise mechanism of salt secretion is not understood, but it is an active process, as evidenced by ATPase activity in the plasmalemma of the secretary cells and the possibility of stopping the salt secretion by metabolic inhibitors (Drennan et al., 1992, Tomlinson, 1986). The salt secreting mangrove species allow more salt into the xylem than do the non-secreting species. Therefore, the NaCl concentration of salt secreting mangroves is about 10 times higher than that of non-secreting mangroves (Tomlinson, 1986). However, they still exclude about 90% of the salts (Scholander et al., 1962). Although the salinity tolerances of some mangrove species have been studied, much information on salt tolerance remains to be discovered. Particularly, the studies on the salt secretion by mangroves are scarce. Still the precise mechanism of salt secretion is not known. Even the little knowledge on the salt balance of salt secreting mangroves may not be universal as the salt balance or water use characteristics of the same species are reported to vary depending on climatic and edaphic factors (Youssef and Saenger, 1988). Therefore it is important to conduct studies to enrich the knowledge on salt secretion by mangroves. It is vital as the importance of salt tolerant plants is increasing day by day due to continuing climatic changes.

1.1. Objectives

This is a preliminary study on the salt secretion by mangroves in Sri Lanka. The study aims firstly to measure the salt secretion by mangroves *in situ*, and compare the rate of salt secretion by different species, which are in the same community under the same environmental condition. Secondly, this project aims also to study the variation of salt secretion by mangroves with the variation of soil salinity under green house condition. Effects of the previous exposure to higher or lower salinity on the salt secretion by mangroves under subsequent salinity regime were also studied as it gives an implication on effects of fluctuating salinity levels in the natural environment on the salt secretion by mangroves.

2. Materials and methods

2.1. In situ measurement of salt secretion by mangroves

The salt secreting mangrove species are listed in the literature. But, as a preliminary step, it was decided to test all the true mangrove species, which are co-existing in a same community, for salt secretion. If the expected results are obtained, then the methodology used to measure the salt secretion in this study gets validated. Moreover, the capacity of salt secretion by different species can be copared as they were measured under the same environmental conditions. All the true mangroves in Rekawa lagoon, in southern Sri Lanka, were selected for this study as it is located nearby and having highest species diversity of true mangroves in the southern Sri Lanka. Moreover almost all the species which are reported as common mangroves in Sri Lanka, occur in Rekawa lagoon also.

Followings are the mangrove species from Rekawa lagoon, selected for this study

(1) *Acanthus ilicifolius**
(2) *Aegiceras corniculatum*
(3) *Avicennia marina*
(4) *Avicennia officinalis*
(5) *Bruguiera gymnorriza*
(6) *Bruguiera sexangula*
(7) *Ceriops tagal*
(8) *Excoecaria agallocha*
(9) *Heritiera littoralis*
(10) *Lumnitzera racemosa*
(11) *Rhizophora mucronata*
(12) *Sonneratia caseolaris*

(* According to Tomlinson, 1986, this species is considered as a mangrove associate).

In order to distinguish salt secreting mangroves and compare the level of secretion between species, the salt secretion by these mangroves were quantified *in situ*.

Quantification of the salt secretion in the field was rather difficult without a proper control, because salt brought by the sea spray could also be deposited on mangrove leaves. It is unavoidable, as all the mangroves are located near to the sea. Covering the plants or plant parts from the sea spray during the experiment, cannot be recommended as it may affect the normal physiological processes of plants and hence the salt secretion too. Therefore, a proper control for the in situ measurement of the salt secretion was planned and included as follows to the methodology to measure the salt secretion *in situ.*

Three individuals from each species were selected for the test and two closely located twigs, each having at least 10 leaves, were selected from each of the three individuals. One twig from each individual was cut in water and left the cut end in double distilled water for about half an hour to continue transpiration replacing the salty xylem sap by distilled water. Then the leaves of the cut twig were washed thoroughly by distilled water and the twig was tethered to the same place of the mother plant with the same orientation. Leaves of the other twig were also washed thoroughly by double distilled water and blotted dry. Both twigs from each individual were left for 24hours and then, 10 leaves from each twig was carefully removed and washed in 50ml of double distilled water to get all the salts on the surface of leaves into the water. Then, area of all the leaves used to collect secreted salts was quantified manually using millimeter papers on which the exact size and shape of leaves are marked. The salinities of two 50ml solutions, one containing salts from leaves of the detached twig and the other from the intact twig, were quantified separately using a salinometer (Hanna, Conductivity/ Salinity meter, Modle HI 9835). The amount of salt collected from leaves of each twig was standardized as **'mg salt cm^{-2} day^{-1}'**. The 'detached twig' in this experiment was considered as the 'control'. If there is a value for the amount of salts corresponds to detached twig, it should be purely due to salts deposited on leaves by the sea spray and it should be common for the intact twig also. Therefore the salt secretion by leaves of each individual was corrected as follows;

Salt secretion = (**'mg salt cm^{-2} day^{-1}'** corresponds to the intact twig) - (**'mg salt cm $^{-2}$ day^{-1}'** corresponds to the detached twig)

The above whole procedure was repeated three times during a six month period, to measure the salt secretion by same mangrove species (but using different individuals), when the salinity level of the lagoon water is different. Although the salinity level of lagoon water is not always same to that of soils in the intertidal zone, it is true that the soil salinity of the intertidal zone vary depending on the salinity of lagoon water. Therefore, on each occasion of measurement of salt secretion by mangrove plants in Rekawa lagoon, the salinity of lagoon water was also measured by a hand refratometer (ATAGO S/Mill-E, Japan)

2.2. Measurement of salt secretion under different soil salinities

Salt secreting mangrove species which were identified based on the results of *in situ* studies described in 2.1, were used for the *ex situ* measurement of salt secretion under different levels of the soil salinity.

Young individuals of each of salt secreting mangrove species with at least few twigs in each, were brought into the university green house and planted individually in plastic pots (with 20cm diameter and 30cm height) having few holes at the bottom, and filled with the soil brought from the same mangrove. Pots with young plants were placed individually on 7cm deep plastic trays to get extra water collected after watering. Water with salinities of 5, 15, 25, and 35 ppt were prepared separately by mixing seawater and tap water, and left in separate tanks to be used in the experiment. Initially all the pots in each species were irrigated once a day by the water with the salinity of 10 ppt. Excess water accumulated in trays were returned to the relevant tank every other day and salinity of the water in tanks were measured by a hand refractometer (ATAGO S/Mill-E, Japan) and adjusted by adding fresh water or sea water more, as necessary.

Ten pots with individual plants which were established and rooted up to the bottom of the pot, from each species were used in the experiment to measure the salt secretion under different salinity levels. Pots were assigned to five salinity levels, 0, 5, 15, 25, and 35 ppt, as two pots per one salinity level. Each plant was irrigated with excess water with the salinity assigned to it, twice a day and left for three days to get acclimatized to the particular salinity. Meanwhile, at least 10 mature leaves from each individual plant were selected and their area was quantified manually without detaching leaves, by marking the exact shape and size of each leaf on millimeter papers.

On the fourth day, the salt secretion during a 24 hour period, by leaves of which the area is known, were measured following the same method used for *in situ* measurements. (But a detached twig from each individual was not used in this *ex situ* experiment as it was verified that there was no sea-spray into the green house). During that period plants were irrigated three times with excess water having the same salinity assigned to each plant while keeping them in trays with excess water with the same salinity. The procedure was repeated four times, but each time, the assigning of plants of the same species into five salinity levels was done by re-randomization. Before each measurement, plants were left three days in trays with water having the same salinity assigned to the plant and irrigated twice a day with the same water. The salt secretion was standardized as **'mg salt cm^{-2} day^{-1}'**. The experiment was ended within 16 consecutive days in June 2006.

2.3. Measurement of salt secretion under fluctuating soil salinities

Same mangrove species, which were identified as salt secreting mangroves, were used to measure the salt secretion under fluctuating salinity levels. Same individual plants, which were used to measure the salt secretion under different salinities, were also used to measure the salt secretion under fluctuating salinities as follows.

Eight individual plants from each species were selected for this experiment and all of them were acclimatized to a moderate salinity by keeping them in trays with excess water of the salinity of 20 ppt for three days while irrigating plants twice a day with the same water. Then salt secretion of all these plants, during a 24 hour period under the same salinity, was measured following the same procedure that is described in above 2.1 and used to measure salt secretion under different salinities.

At the end of the 24 hour period, one half of the individuals of each species (i.e. four individuals) were transferred to trays with low saline water (i.e. 05 ppt) and the other half to trays with high saline water (i.e. 35ppt). Then the salt secretions of these plants during the two subsequent days (i.e. day two and day three) under the new salinity regime were measured separately. The salt secretion during the first day under moderate salinity, and during the second day and third day under low or high salinity was standardized as **‘mg salt cm^{-2} day^{-1}’**.

2.4. Data analysis

Mean and standard deviation values of in situ salt secretion by mangrove plants in Rekawa lagoon were calculated to distinguish salt secreting species. One-way ANOVA with Tukey-Kramer HSD test (Zar, 1984) was used to test significant differences of the rates of salt secretion among four of the salt secreting species as well as salt secretion of the same species under different salinity levels.

Correlation analysis was performed to find out the relationship between soil salinity and salt secretion in different species. Regression equations were established to explain significant correlations.

3. Results

3.1. Interspecific variations of the salt secretion

Out of the twelve mangrove species tested, only four species, *Acanthus ilicifolius*, *Aegiceras corniculatum*, *Avicennia marina* and *Avicennia officinalis* showed salt secretion. Mean values received for the amounts of salts collected from leaves of other eight species were zero or negative when corrected with respect to the control value (Table 1). The mean salinity of the lagoon water that was measured from different sites adjacent to individual plants used to measure the salt secretion, during the experimental period was 26.2 ± 4.41ppt.

The mean values of salt secretion by the four species are given in Figure 1. According to that variations, *Av. marina* showed highest salt secretion that is significantly different from all the others whilst the salt secretion by *Ac. ilicifolius* and *Ae. corniculatum* was the lowest and not significantly different each other. Salt secretion by *Av. officinalis* was at the moderate level.

3.2. Variations of salt secretion with the variations of soil salinity

The variations of the salt secretion by each species with the variations in soil salinity are given in Figure 2 and the relationships between the two parameters relevant to each of the four species are given in Table 2. It shows a positive relationship between the salt secretion by each species and the soil salinity. Figure 2 clearly shows that all the four species secrete salts even under fresh water condition, although the magnitude is lowest. Moreover it shows that the salt secretion by *Av. marina* and *Av. officinalis* increase with the increase of soil salinity up to 35 ppt, but the salt secretion by *Ac. ilicifolius* and *Ae. corniculatum* increase only up to 25 ppt and 15 ppt in soil salinity respectively.

Table 1 Results of the in situ measurement of Salt secretion by true mangroves in Rekawa lagoon. Values were corrected with respect to the control experiment and given as mean ± standard deviation.

Mangrove species	Mean Salt secretion (mg salt cm^{-2} day^{-1})
Acanthus ilicifolius	47.2 ±18.3
Aegiceras corniculatum	35.1±16.0
Avicennia marina	149.3± 45.9
Avicennia officinalis	81.6± 30.5
Bruguiera gymnorrhiza	0.0
Bruguiera sexangula	0.0
Ceriops tagal	0.0
Excoecaria agallocha	0.0012 ± 0.0018
Heritiera littoralis	0.0
Lumnitzera racemosa	0.0
Rhizophora mucronata	-0.05 ± 0.07

Table 2 Relationship between salt secretion ('Y' mg salt cm^{-2} day^{-1}) by each species and the soil salinity ('X' ppt).

Species	Relationship	r	SE of intercept	SE of slope
Acanthus ilicifolius	$Y = 25.51 + 1.17X$	0.86*	3.32	0.16
Aeigiceras corniculatum	$Y = 28.46 + 1.12X$	0.80*	4.09	0.20
Avicennia marina	$Y = 47.00 + 4.39X$	0.92*	9.08	0.44
Avicennia officinalis	$Y = 47.17 + 1.82X$	0.84*	5.61	0.27

3.3. Salt secretion under fluctuating salinities

Salt secretion by *Av. marina* was increased significantly when the plants were transferred from moderate soil salinity to higher soil salinity. But the salt secretions by the other three species, *Ac. ilicifolius*, *Ae. corniculatum* and *Av. officinalis*, were not significantly changed when the soil salinity was increased from moderate to higher level. Salt secretions by all the four species were increased significantly when the soil salinity was lowered, but only for a short period. The increased salt secretion was again reduced after the first 24 hour period under the reduced soil salinity (Figure 3).

4. Discussion

Salt tolerance of mangroves basically depends on physiological mechanisms they have for the salt and water balance and the efficiency of those mechanisms (Kathiresan and Bingham,2001; Tomlinson, 1988; Ye et. al. 2005). Salt secretion is one of the remarkable mechanism take place in some mangroves as a way of balancing water and salt in the plant body. However, it is reported that all the mangrove species do not possess this mechanisms in the same order. This study also revealed that only four species, *Ac. ilicifolius*, *Ae. coniculatum*; *Av. marina*, and *Av. officinalis*, out of

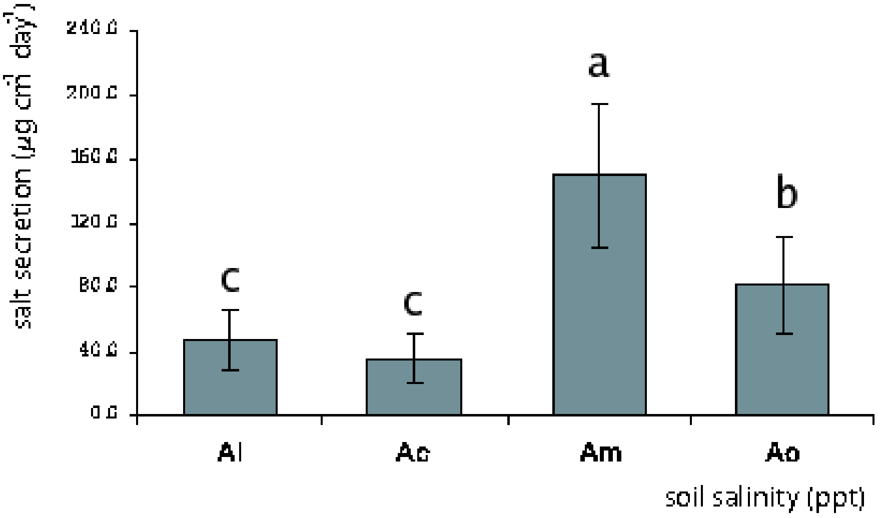

Figure 1 Mean values of the salt secretion by different mangrove species.(Ai, *Acanthus ilicifolius*; Ac, *Aegiceras coniculatum*; Am, *Avicennia marina*: Ao, *Avicennia officinalis*).

Note. (Longitudinal bars indicate standard deviations. Bars with different superscripts, indicate salt secretion values which are significantly different at $p < 0.05$).

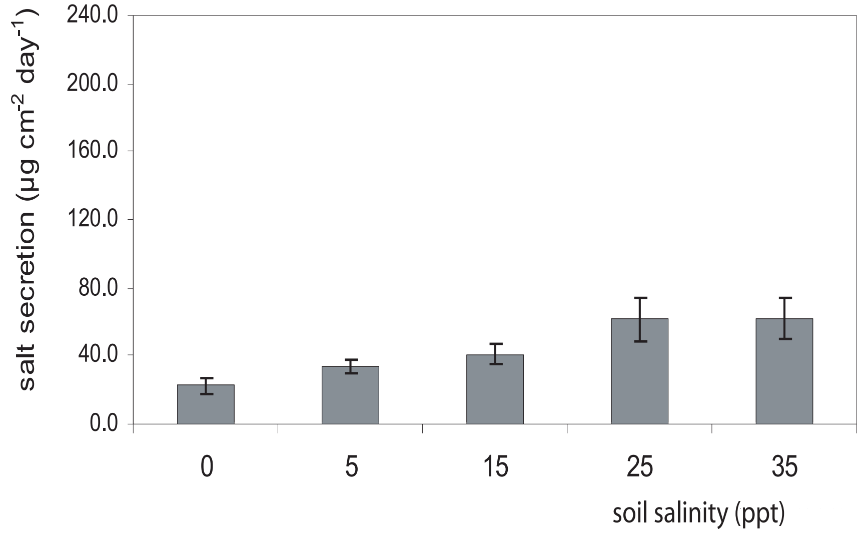

Figure 2 Variation of salt secretion (mean ± standard deviation) by *Ac. illicifolius* leaves, with the variation of soil salinity.

Note. Longitudinal bars indicate standard deviations.

the twelve common mangroves of Sri Lanka, can secrete salts. This corroborates the

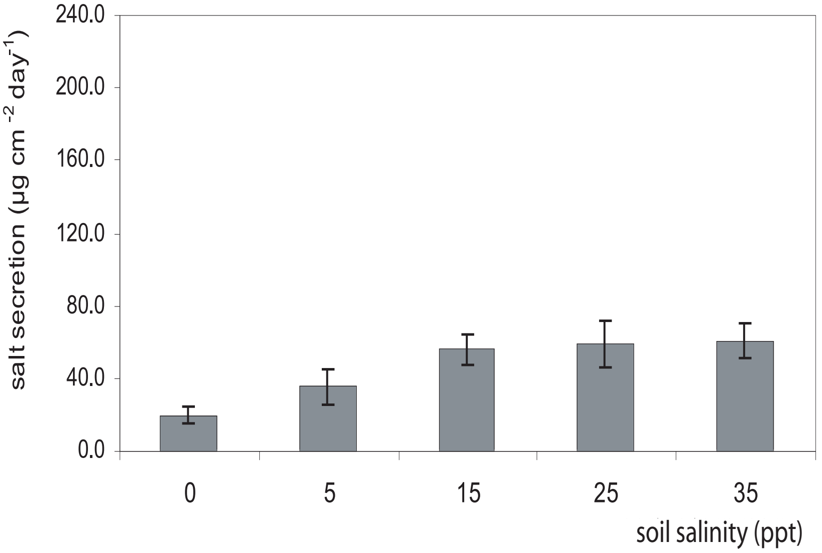

Figure 3 Variation of salt secretion (mean ± standard deviation) by *Ae. corniculatum* leaves, with the variation of soil salinity.

Note. Longitudinal bars indicate standard deviations.

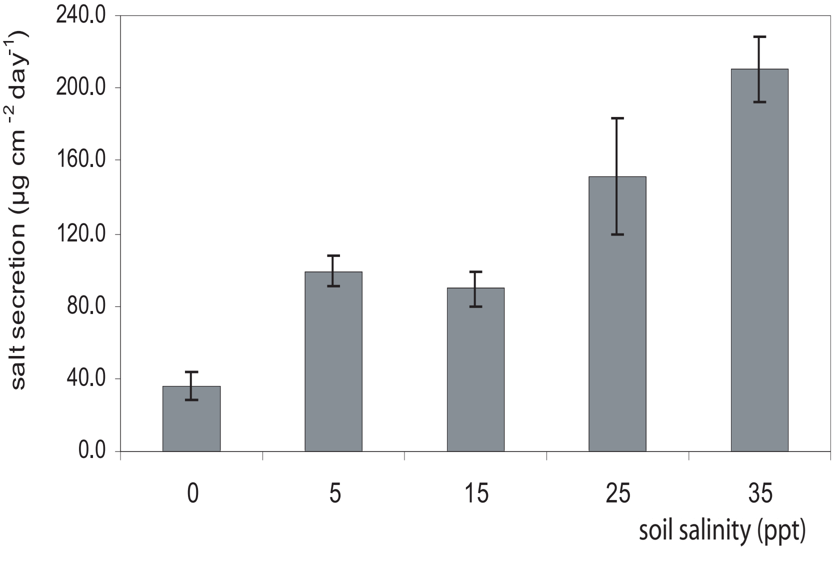

Figure 4 Variation of salt secretion (mean ± standard deviation) by *Av. marina leaves*, with the variation of soil salinity.

Note. Longitudinal bars indicate standard deviations.

published records and, hence validates the technique used in this study to measure salt secretion.

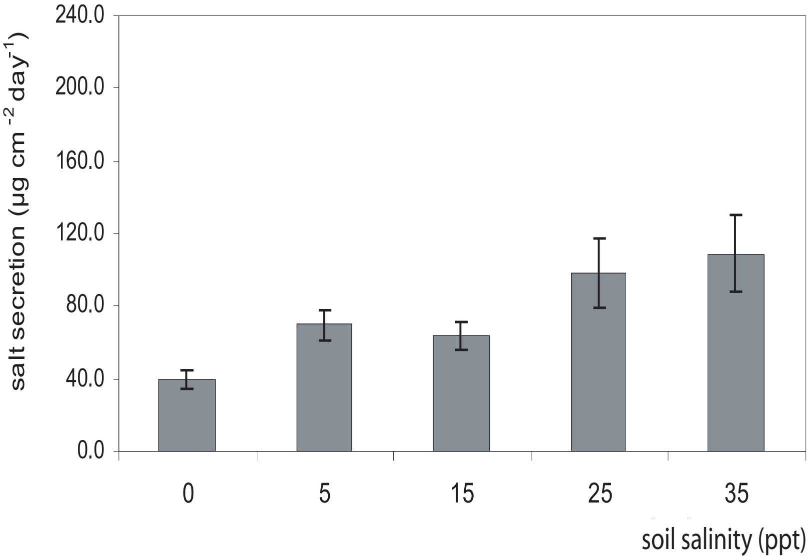

Figure 5 Variation of salt secretion (mean ± standard deviation) by *Av. officinalis* leaves, with the variation of soil salinity.

Note. Longitudinal bars indicate standard deviations.

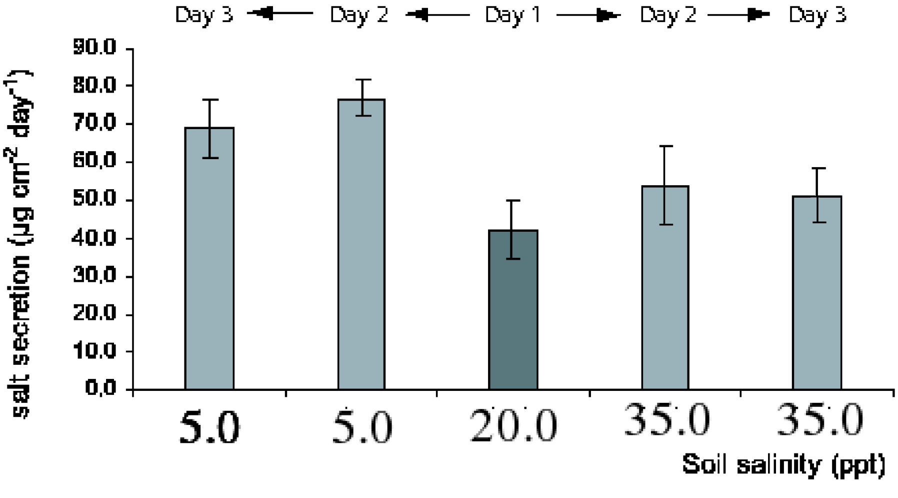

Figure 6 Variation of the salt secretion (mean ± standard deviation) by *Ac. illicifolius*, under fluctuating soil salinity.

Note. Longitudinal bars indicate standard deviations. Different superscripts with bars, indicate salt secretion values which are significantly different at $p < 0.05$.

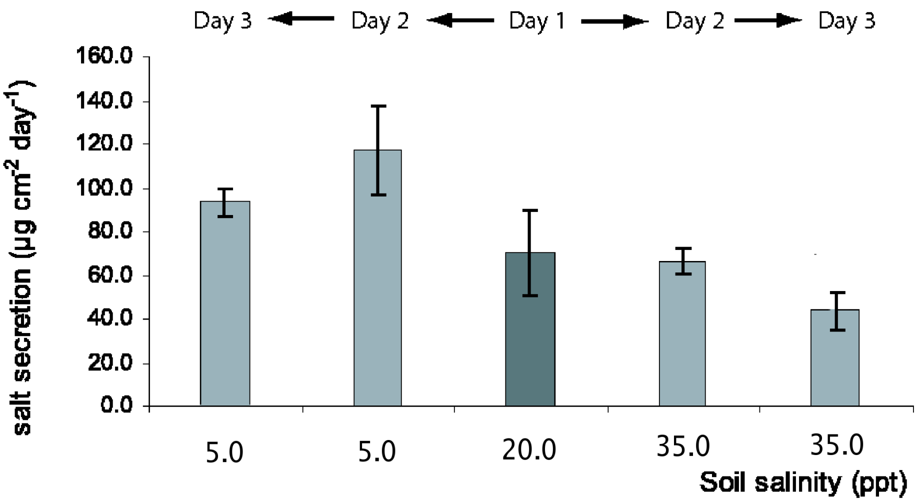

Figure 7 Variation of the salt secretion (mean ± standard deviation) by *Ae. corniculatum*, under fluctuating soil salinity.

Note. Longitudinal bars indicate standard deviations. Different superscripts with bars, indicate salt secretion values which are significantly different at $p < 0.05$.

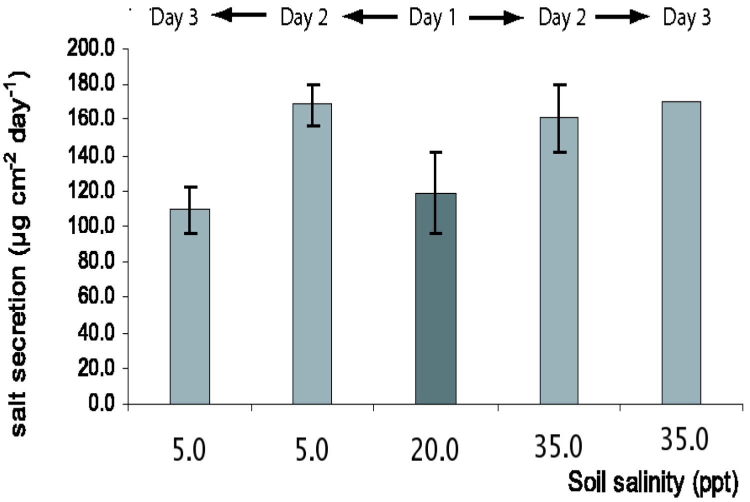

Figure 8 Variation of the salt secretion (mean ± standard deviation) by *Av. marina*, under fluctuating soil salinity.

Note. Longitudinal bars indicate standard deviations. Different superscripts with bars, indicate salt secretion values which are significantly different at $p < 0.05$.

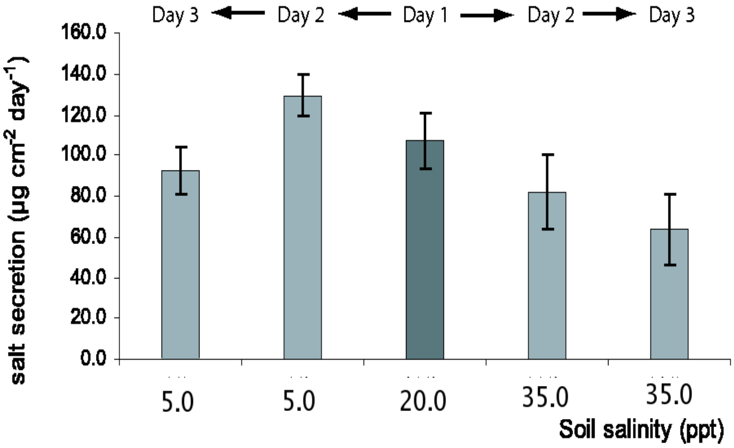

Figure 9 Variation of the salt secretion (mean ± standard deviation) by *Av. officinalis*, under fluctuating soil salinity.

Note. Longitudinal bars indicate standard deviations. Different superscripts with bars, indicate salt secretion values which are significantly different at $p < 0.05$.

Results of this study shows that the capacity to secrete salts at any given salinity was different between four species, following an order of *Av. marina* > *Av. officinalis* > *Ac. ilicifolius*, and *Ae. corniculatum*. *Av. marina* proved to be the species with the highest tolerance to high saline conditions among the true mangrove species in Rekawa lagoon (Jayatissa and Wickramasinghe 2006). Many other studies have also shown that *Av. marina* has a better salinity tolerance (Clough, 1984; Downton, 1982; Ye et al, 2005). The order of the capacity to secrete salts by the other three species also parallel to the order of their salinity tolerance. (Jayatissa and Wickramasinghe 2006; Ye et. al. 2005). This indicates that salt secretion by mangroves is related to their salt tolerance. Thus, it can be predicted that *Av. marina* could grow in high saline conditions as it proved to be the most efficient salt secreting species. Similarly, *Ac. ilicifolius*, *Ae. corniculatum* and *Av. officinalis* mostly grow in less saline habitats.

In the present study, all the four species exhibited increase in salt secretion with increases in soil salinity, consistent with previous reports (Ball, 1988; Sorbrado, 2002; Boon and Allaway, 1982; Ye et al., 2005). However, the two Avicennia species, *Av. marina* and *Av. officinalis*, showed better correlation between the salt secretion and soil salinity as their salt secretions increased continuously up to the maximum level of soil salinity. Conversely, the salt secretion of the other two species, which are known to have a lower salinity tolerance compared to Avicennia species, was reached to a maximum before reaching to the maximum level of soil salinity. These variations also indicate that the salt secretion by mangroves is strongly related to their salt tolerance.

It is reported that the salt secretions by mangroves are stimulated by salts in soil (Boon and Allaway, 1986; Drennan and Pammenter, 1992; Ball, 1988; Sobrado, 2002). However, a salt secretion by all the four species even under fresh water condition was recorded in this study. This little secretion can be expected as plants were kept under moderate salinity before transferring them to the fresh water condition and hence at least a lower content of salts could be left in the plant body as well as in soil when the salt secretion was measured. Increases of the salt secretion by mangroves with the increasing soil salinity can be expected as salinity is often considered as a "stress" and the salt secretion is a physiological adaptation developed to overcome the stress. But this study revealed that the salt secretion by all the four species immediate after reducing the soil salinity was increased significantly. This increased salt secretion gradually comes back to normal if the plants were remained under the same lower level of soil salinity. This could be an opportunistic removal of salts which was accumulated in the plant body under high saline condition. There are some reports for similar opportunistic actions by mangroves. Kathiresan and Bingham (2001) reports that mangrove species, particularly those that are less tolerant to high saline conditions, opportunistically absorb and store more water when they are exposed to low saline conditions. Lin and Sternberg (1994) also reports that the fine root biomass of mangroves increases in the wet season, as a response to decreased salinity of the surface waters, directly enhancing the uptake of low-salinity water.

This study reveals that a mangrove species cannot tolerate higher salinities just becoming a salt secreting species. The salt tolerance appeared to be depends mainly on the capability of the species to increase its salt secretion with the increase of soil salinity. Relevant to that capability, the four of the salt secreting species can be arranged in order as *Av. marina* > *Av. officinalis* > *Ac. ilicifolius*, and *Ae. corniculatum*. As an active physiological process, the salt secretion may be affected by many other physiological processes and environmental factors. Therefore the effects of such factors on salt secretion of mangroves should be studied further under the green house condition as well as natural field condition, in order to understand the mechanism fully.

References

Allen JA, Krauss KW, Hauf, RD. 2003. Factors limiting intertidal distribu-tion of the mangrove species Xylocarpus granatum. Oecologia 135:110-121.

Ball MC. 1988. Salinity tolerance of the mangroves, Aegiceras corniculatum and Avicennia marina, Part 1. Water use in relation to growth, carbon partitioning and salt balance. Australian Journal of Plant Physiology 13: 689-698.

Ball MC. 1996. Comparative ecophysiology of mangrove forest and tropical lowland moist forest. In "Tropical forest plant ecophysiology" (SS Mulkey, RL Chazdon and AO Smith, eds), pp.461-469. Chapman and Hall, New York.

Ball MC. 2002. Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradient. Trees 16:126-139.

Ball MC, Cochrane MJ and Rawson HM. 1997. Growth and water use of the mangroves Rhizophora apiculata and R. stylosa in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO2. Plant Cell and Environment 20:1158-1166.

Boon PI, Allaway WG. 1982. Assesment of leaf-washing techniques for measuring salt secretion in *Avicennia marina*, Vireh, Australian Journal of Plant Physiology, 9, 728-734.

Boon PI, Allaway WG. 1986. Rates and ionic specificity of salt secretion from excised leaves of the mangrove, Avicennia marina (Forsk.) Vierh. Aquatic Botany 26: 143-153.

Clough BF. 1984. Growth and salt balance of the mangrove Avicennia maraina (Forsk.) Vierh. and Rhizophora stylosa Griff. in relation to salinity Australian Journal of Plant Physiology 11: 419-430.

Dahdouh-Guebas F, LP Jayatissa D, Di Nitto JO, Bosire D, Lo Seen and Koedam N. 2005. How effective were mangroves as a defense against the recent tsunami? Current Biology 15(12): 443-447.

Downton, WJS. 1982. Growth and osmotic relations of the mangrove, Avicennia marina, as influenced by salinity. Australian Journal Plant physiology 9: 519-528.

Drennan PM, Berjak P and Pammenter NW. 1992. Ion gradients and adenosine triphosphatase localization in the salt glands of Avicennia marina (Forsk.) Vierh. South African Journal of Botany 58(6): 486-490.

Dschida W, Platt-Aloia K. and Thomson W. 1992. Epidermal peels of Avicennia germinans (L.) Stern: a useful system to study the function of salt glands. Annals of Botany 70(6): 501-509.

Fitzgerald MA, Orlovich DA and Allaway WG. 1992. Evidence that abaxial leaf glands are the sites of salt secretion in leaves of the mangrove Avicennia marina (Forsk.) Vierh. New Phytologist 120: 1-7.

Hong WC and Eong OJ 1984. Electron microscopy studies on the salt glands of Acanthus ilicifolius L. In: Soepadmo E, Rao AN and Macintosh DJ. (eds.) Proceedings of the Asian symposium on mangrove environment; Research and management. UNESCO. pp 827.

Jayatissa LP and Wickramasinghe WAADL. 2006. Guidance for mangrove replanting; 1. Interspecific variations in responses of mangrove saplings to two contrasting salinities. Ruhuna Journal of Science 1: 47-60

Kathiresan K and Bingham BL. 2001. Biology of mangroves and mangrove eosystems. Advances in Marine Biology 40: 81-251.

Lin, GH and Sternberg LDSL 1994. Utilization of surface water by red mangrove(Rhizophora mangle L.): An isotopic study. Bulletin of Marine Science 54 (1):94-102.

Naskar K and Mandal R. 1999. Ecology and biodiversity of Indian Mangroves, Part I - Global status. Daya Publishing House, Delhi, India. p359

Scholander P, Hammel HT, Hemmingsen EA and Cray W. 1962. Salt balance in angroves. Plant Physiology 37:722-729.

Sobrado M.2002. Effect of drought on leaf gland secretion of the mangrove Avicennia marina germinans L. Trees 16:1-4.

Tomlinson PB 1986. The botany of mangroves. The Cambridge University Press. London, UK.

Ye Y. Tam, NFY. Lu CY, Wong SH. 2005. Effects of salinity on germination, seedling growth and physiology of three salt secreting mangrove species. Aquatic Botany 83:193-205.

Youssef T and Saenger P. 1998. Photosynthetic gas exchange and accumulation of phytotoxins in mangrove seedlings in response to soil physico-chemical characteristics associated with water logging. Tree Physiology 18(5): 317-324.

Zar JH. 1984. Biostatistical analysis (Second edition). Prentice-Hall Inc. A Simon and Schuster company, Englewood Cliffs. New Jersey, pp718.