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Response of mangrove plant species to a saline gradient: Implications for ecological restoration

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ABSTRACT

Mangroves are salt tolerant plants that occur in tropical and sub-tropical sheltered coasts. Saltwater intrusions into terrestrial landscapes often occur due to either anthropogenic reasons or natural calamities such as tsunamis. We investigated the potential of using mangrove species for rehabilitation of high saline environments by revealing the capacities of species to remove salt from sediment. We established the salt retention capacity of common mangrove species in Sri Lanka *i.e.*, *Rhizophora apiculata, Rhizophora mucronata, Ceriops tagal,* and *Avicennia marina* through *ex-situ* and *in-situ* measurements of NaCl content in plant tissue and soil samples, by titrating with 0.01 N $AgNO_3$. The results revealed *A. marina* to be the most efficient in retaining salt within plant tissues while *C. tagal* is superior to *R. mucronata* but inferior to *A. marina* in performing this function. These findings were further confirmed by measuring salt uptake rates of hydroponically grown seedlings of the same species. Although *R. mucronata* is the most popular species used for restoration, *A. marina* appears the most suitable mangrove species not only for coastal mangrove restoration but also for rehabilitating salinity affected landscapes.

Keywords: *Avicennia marina*, *ex-situ* experiments, growth performance, hydroponics, mangroves, Sri Lanka

Introduction

Natural and anthropogenic impacts, coupled with human population increases, in coastal areas of Sri Lanka have drawn considerable interest because of increasing soil salinity in the hinterland over time. Salinization of coastal ecosystems is a major emerging environmental problem since it leads to land degradation in coastal areas (Storey *et al.* 2003). Soil salinity of coastal areas is the cumulative result of interactions between the frequency of tidal flooding, evapotranspiration rates, hydrology, and coastal topography (Tanji 2002; Karunathilake 2003). Increases in salinity are due to sea-level rise and increasing tidal flooding, along with escalating evapotranspiration and increasing incidence of storm surges, through associated changes in global atmospheric temperature (Almeida & Mostafavi 2016). Moreover, unsustainable coastal aquaculture practices evidently contribute to exacerbating soil salinities in coastal lands (Tanji 2002; Karunathilake 2003).

Large-scale shrimp farms emerged in the late 1980s along coastal areas associated with Chilaw and Puttalam lagoons in the Northwestern region of Sri Lanka (Harkes *et al.* 2015). Extensive areas of mangroves and salt marshes were cleared to install culture ponds, resulting loss of a significant extent of healthy mangrove forests, effecting on ecosystem services (Harkes *et al.* 2015; Perera *et al.* 2018). Clearing mangrove forests, therefore, negatively affects

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important ecological functions and services such as carbon sequestration, primary production, coastal protection, and the provisioning of habitats (Jakovac *et al.* 2020). However, due to unsustainable culture practices that led to disease outbreaks in shrimp cultures, large scale shrimp farming was abandoned in the late 1990s, with most of the abandoned shrimp ponds now containing highly saline and acidic soils (Stevenson *et al.* 1999 ; Tho *et al.* 2008). By 2018, areas with abandoned ponds near the Chilaw lagoon have turned into barren lands. Low rainfall in these coastal areas also contributes to increased soil salinity as the flushing of salt in the soil is negligible.

Although natural regeneration of mangroves has been observed in some abandoned ponds, particularly around the Chilaw lagoon where the salinity is lower than in other shrimp farming areas on the northwestern coast, salinity in the majority of abandoned ponds is high and the soils are degraded. Rehabilitation of such areas has not been attempted thus far. The use of salt-tolerant plants could be a possible sustainable solution to improve the physiological characteristics of the soil (Pessarakli & Szabolcs 1999). The ecological success of mangroves living under harsh conditions is explained by several morphological, anatomical, physiological, biochemical, and molecular features (Aziz & Khan 2001a; Saenger 2002; Ridd & Sam 1996; Koyro & Lieth 2008; Parida & Jha 2010; Srikanth *et al*. 2016; Vinoth *et al.* 2019). The shade produced by mangrove tree canopies may contribute to reducing the loss of soil moisture through evapotranspiration, and therefore leads to less salt accumulation within soils (Ridd & Sam 1996). Besides, the presence of crab burrows in mangrove sediment may allow mangrove soils to retain more water and, thus, facilitate the movement of saline water out of the soil column. As such, mangroves might serve as a measure to rehabilitate saline areas, by planting the propagules of the most efficient species under high saline edaphic conditions. Since the tidal amplitude is very low in Sri Lanka, where spring tide does not exceed 0.7 m and neap tide falls to 0.05 m, the distribution of mangrove forests is confined to a narrow intertidal belt around lagoons (Jayatissa *et al.* 2002). Therefore, the restoration of these degraded habitats deserves attention to re-establish the ecosystem services lost due to anthropogenic changes.

Exposure to high salinities causes physiological and morphological changes in plants, depending on saline conditions, even in salt-tolerant plants. Physico-chemical properties of the substrate, such as salinity, pH, organic matter, and nutrients, determine the structure and composition of mangrove vegetation. Thus, we investigated how salinity affects the growth performance of mangrove seedlings of *Rhizophora mucronata*., *Rhizophora apiculata*, *Avicennia marina*, and *Ceriops tagal*, with the primary objective of identifying suitable species for use in rehabilitating degraded mangrove areas.

Materials and methods

Ex-situ experiment on assessing salt absorption potential

Hydroponic experiments were carried out to investigate the salt tolerance capacity of mangrove seedlings in different salinity conditions. We collected mature and healthy propagules/seedlings of common Sri Lankan mangrove species *R. mucronata* Lam., *R. apiculata* Blum., *A. marina*(Forsk) Vierh., and *C. tagal* (Perr.) C.B.Rob. from wild stands on the western and southern coasts of Sri Lanka. The seedlings/propagules were then planted in plastic pots with coir dust and kept in containers with water of four different salinities prepared by mixing seawater and de-ionized freshwater: 0 PSU (Practical Salinity Unit), 15–17 PSU, 25–27 PSU, and 34–36 PSU. Fifteen replicates were used for each treatment. We replenished each medium every month with a commercially available water-soluble fertilizer to supply the nutrients required for seedling growth. The salinity of the water in the containers was monitored once a day using a hand-held refractometer (MA886, Milwaukee). Salinity conditions in each container were maintained by daily addition of de-ionized water, and the culture medium was replaced with freshly prepared culture solution to avoid fouling. All plants were grown in the greenhouse at the University of Kelaniya in Sri Lanka under natural temperature and light for a period of nine months.

Seedling growth measurements

The appearance of the first two leaves was considered as seedling establishment. The number of established seedlings was recorded to obtain the germination percentage of seeds of each species. We measured growth performance in terms of shoot height, total number of leaves produced, leaf area, and seedling dry weight. Shoot height was measured (in cm) from epigeal cotyledons to the base of the apical leaf pair every seven days during the study period (Pinzon *et al.* 2003). Leaf length and width were measured to calculate leaf area. After nine months, leaves at different stages of maturity of each seedling were sampled, measured for length and width and used to calculate mean leaf area (DELTA-T leaf area meter). Seedling dry weight was determined by measuring the dry weight of leaves and roots separately. For this, triplicate samples of leaves and roots of nine-month-old seedlings were dried at 80 °C (±1 °C) to constant weight.

In-situ experiments

Sampling of mangrove leaves and soil

Mangrove leaves and soil were sampled from mangrove areas of Kirinda (6°13'36" N, 81°20'38" E), Rekawa (6°2'52" N, 80°50'51" E) Kalametiya (6°5'23" N, 80°57'1" E), and Negombo

(7°11’48” N, 79°50’42” E), representing the gradient of dry to wet climatic zones located on the western and southern coasts of Sri Lanka (Fig. 1). Mature and young leaves of the studied mangrove species were collected using six 10 m × 10 m plots placed parallel to the shoreline. Trees of 3 to 4 meters in height were selected to sample mature and young leaves from the upper and lower portions of the crown. A total of six mature leaves and six young leaves were collected from each *R. apilculata* and *R. mucronata* tree, while a total of ten mature leaves and ten young leaves were collected from each *C. tagal* and *A. marina* tree. Thus, a total of 45 trees of *C. tagal* and 57 trees of each of *R. apilculata, R. mucronata,* and *A. marina* were sampled. In addition, three soil samples were taken at 0 m, 0.5 m, and 1 m from each tree from which leaf samples were obtained to make a composite sample for the locality.

Determination of NaCl content of leaves and roots

To determine NaCl content of leaves and roots, seedling samples were washed to remove foreign material, allowed to air dry, and then oven-dried at 70–80 °C for 12 to 24 hours. Leaf and root samples were individually ground and passed through a 1 mm sieve. One gram of the ground leaf or root sample was then weighed in a crucible, to which 0.25 g of CaO was added. Six aliquots of 0.25 g of CaO were placed in separate recipient to represent the blank sample. Leaf, root and the blank samples were placed in a muffle furnace at 550 °C for 90 min, after which 15 mL of hot water was added to each mixture and then poured through filter paper into a 250 ml Erlenmeyer flask. The residue in the filter was washed with five 10 mL portions of hot water and the final volume brought up to the 100 mL mark with water. The extraction was cooled to air temperature and then 25 % acetic acid was added drop by drop until the pH reached 6 – 7. The samples and blanks were titrated with standard 0.01N $AgNO_3$, in the presence of potassium chromate as an indicator, until a persistent light orange-red color appeared (Clemson University 2009).

Determination of NaCl in soil

To determine NaCl in the soil, a soil suspension was prepared by dissolving 20 g of soil in 100 mL of distilled water using finely crushed, air-dried soil of the composite sample collected from each study site. The soil suspension was allowed to settle for one hour with intermittent swirling, after which it was filtered. Next, 25 mL of the clear extract was pipetted into an Erlenmeyer flask. The pH of the extract was adjusted to the range of 4–8, followed by titration with 0.01 N $AgNO_3$ solution, in the presence of the potassium chromate as an indicator. Three replicates were measured for each composite soil sample while three replicates of 25 mL distilled water were measured as controls (Raiment & Higginson 1992).

Data analysis

Analysis of variance (R Development Core Team 2019) was performed to assess whether growth performance, in terms of shoot height, dry weight, leaf area, and NaCl content, of the mangrove seedlings varied significantly among the different salinity conditions. Tukey HSD pairwise comparison was used to test the significance of differences between pairs of treatments (different salinity conditions). Pearson’s correlation analysis was performed to determine whether there was an association between growth performance and NaCl content of leaves and roots of the hydroponically grown seedlings. Pearson’s correlation was also used to evaluate the correlation between soil NaCl content and internal NaCl content of young and mature leaf samples (R Development Core Team 2019).

Results

The germination percentage for *R. mucronata* and *C. tagal* was 100 % for 15–17 PSU while for *A. marina* it was 80 %. In contrast, the highest germination percentage for *R. apiculata* was for 0 PSU (Fig. 2). Trend analyses revealed that the seed germination capacity of the studied mangrove species trended negatively with increasing salinity. The seed germination capacity of *R. apiculata* however, had the strongest negative correlation with salinity (R^2 =0.99) (Fig. 2). Furthermore, *R. mucronata*, *A. marina,* and *C. tagal* had their best growth performance at 15–17 PSU whereas that for *R. apiculata* was at 0 PSU (Fig. 3). Plant growth and salt accumulation were significantly affected by salinity. One–way ANOVA revealed that performance of shoot height for *R. apiculata, R. mucronata* and *C. tagal* ($p < 0.001$) was significantly affected by salinity (Tab. 1). In addition, plant biomass (in dry weight) also differed significantly among salinities ($p < 0.05$; Tab. 1). Furthermore, salinity had a significant effect on shoot height and dry weight of *A. marina*. The greatest shoot height for *R. apiculata* (*i.e.*, 25.1 cm) was observed with 0 PSU while shoot height declined significantly with increasing salinity. Leaf area for *R. apiculata, R. mucronata* and *C. tagal*, and *A. marina* differed significantly among salinities (Tab. 1). The highest growth performances, in terms of shoot height and dry weight, for *R. mucronata, C. tagal,* and *A. marina* were observed at 15–17 PSU. All four species had their lowest growth performance at 34–36 PSU (Fig. 3 and Tab. 1).

Root and leaf NaCl content for the studied mangrove species varied among salinities (Tab. 2). NaCl accumulation increased dramatically with maturity and increasing salinity. Leaf NaCl content for six-month-old and nine-month-old seedlings grown at 15–17 PSU was 1081.33±2.9μmolg^{-1} and 1784±19.44 μmolg^{-1}, respectively, for *A. marina*, while for *R. mucronata* it was 492±9.24 μmolg^{-1} and 522 ± 18.1μmolg^{-1}, respectively (Fig. 4 and Tab. 2). Moreover, the maximum NaCl content in leaves of nine-month-old seedlings of *R. apiculata*, *R. mucronata*, *C. tagal*, and *A. marina* was 712 μmolg^{-1}, 840 μmolg^{-1}, 1502 μmolg^{-1}, and 2042 μmolg, $^{-1}$ respectively, while the maximum NaCl content in

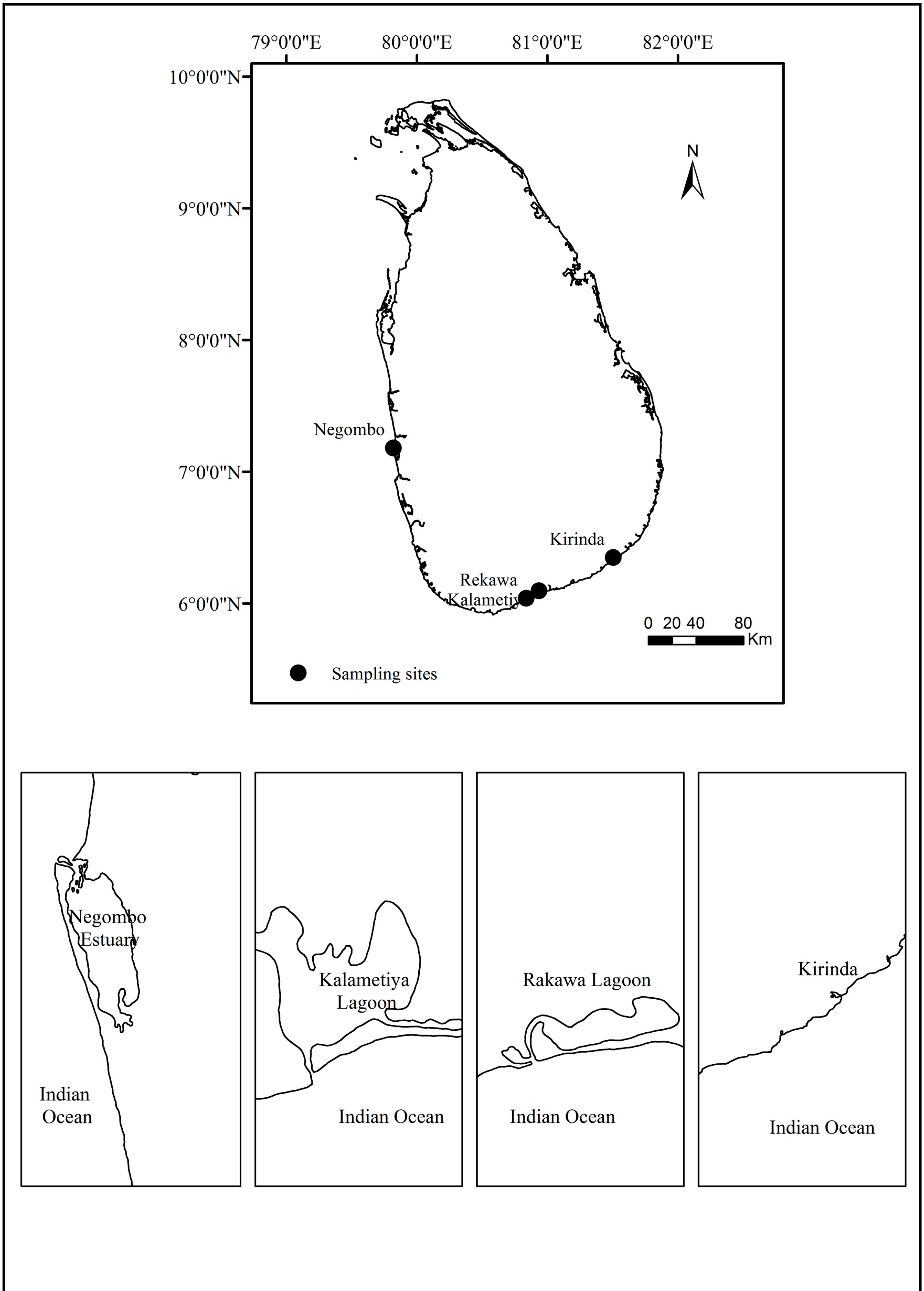

Figure 1. Mangrove leaves, seeds/propagules and soil sampling areas in Sri Lanka.

roots of nine-month-old seedlings of these species was 720 μmolg^{-1} 1828 μmolg^{-1} 1746 μmolg^{-1} and, 2152 μmolg^{-1}, respectively. All species exhibited retarded growth with high salinity. Growth parameters for *R. apiculata* and *R. mucronata* were negatively correlated with internal NaCl content of both roots and leaves (Tab. 3), suggesting that the growth performances of seedlings of both species were strongly affected by substrate NaCl salinity. Internal NaCl content of leaves and roots of nine-month-old seedlings of *R. mucronata*, *A. marina,* and *C. tagal* under different salinities performed in a similar pattern, implying NaCl of internal tissues of roots and leaves increased with increasing

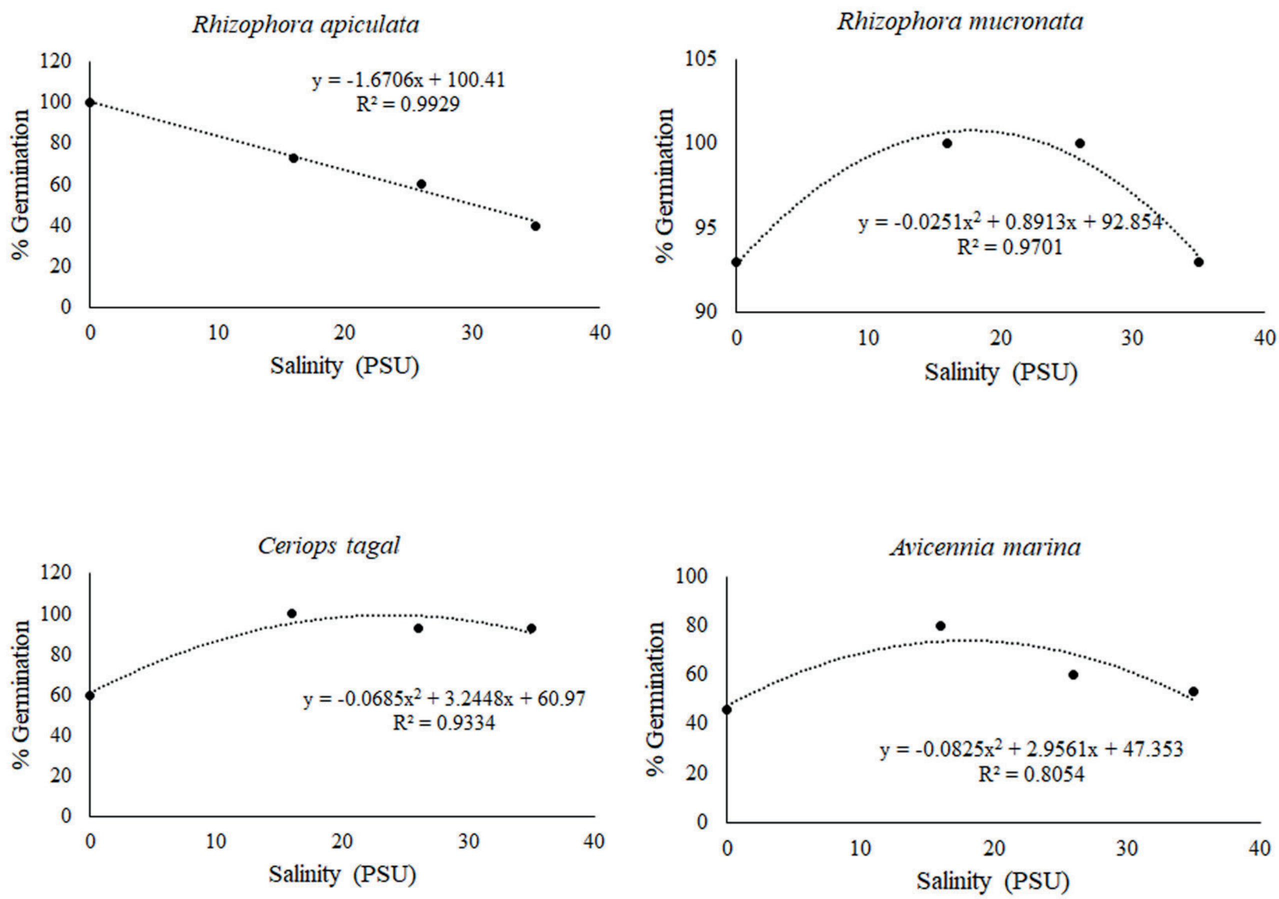

Figure 2. Germination trends of seeds/propagules of Rhizophora apiculata, *Rhizophora mucronat*a, *Ceriops tagal*, and *Avicennia marina* grown under salinity conditions of 0 PSU, 15-17 PSU, 25-27 PSU and 34-36 PSU.

Table 1. Growth performance of nine-month-old mangrove seedlings, *Rhizophora apiculata, Rhizophora mucronata, Ceriops tagal,* and *Avicennia marina* cultivated in different salinity conditions/ seawater concentrations. The standard error (±standard error), from the average values from replicates shows after the average value. Different superscripts in each row mention significantly different of growth parameters at different salinity conditions according to ANOVA Tukey statistical test. Bold means higher comparative.

Parameter	Plant species	Salinity (PSU)			
		0	15-17	25-27	34-37
Shoot Height (cm)	*Rhizophora apiculata*	**25.1 ±0.2**^{a}	23.9± 0.6^{a}	13.7 ±0.4^{b}	11.2± 0.3^{c}
	Rhizophora mucronata	23.1 ±0.3^{a}	**28.6± 0.4**^{b}	18.1±0.3^{c}	14.5± 0.1^{d}
	Ceriops tagal	4.1 ±0.1^{a}	**4.7± 0.1**^{a}	2.9 ±0.3^{b}	1.4 ±0.0^{c}
	Avicennia marina	18.8±1.1^{a}	**28.6** ±1.9^{b}	21.4 ±0.9^{b}	17± 1.7^{a}
Dry weight (g)	*Rhizophora apiculata*	3.12 ±0.7^{a}	**3.3 ±0.2**^{a}	1.41±0.4^{b}	1.19± 0.1^{b}
	Rhizophora mucronata	6.53 ±0.8^{a}	**7.09** ±0.7^{a}	4.35 ±0.7^{ab}	2.91 ±0.4^{b}
	Ceriops tagal	1.92 ±0.0^{ab}	**3.3** ±0.1^{a}	2.27 ±0.2^{ab}	1.21 ±0.6^{b}
	Avicennia marina	0.87±0.1 ^{a}	**2.02** ±0.3^{b}	1.67 ±0.1^{a}	0.68 ±0.15^{a}
Leaf area	*Rhizophora apiculata*	16.8±0.03^{a}	**23.9**±0.0^{b}	11.9±0.1^{c}	11.3±0.2^{d}
	Rhizophora mucronata	**32.2**±0.2^{a}	27.2±0.0^{b}	13.9±0.0^{c}	8.9±0.0^{d}
	Ceriops tagal	5.5±0.1^{a}	**16.2**±0.0^{b}	12.7±0.0^{c}	4.9±0.1^{d}
	Avicennia marina	4.5±0.0^{ab}	**5**±0.0^{a}	4.5±0.0^{ab}	4.1±0.2^{b}

salinity and that salt accumulation was significantly affected ($p < 0.001$; Tab. 2). Plant growth for *C. tagal*, in terms of shoot height, was negatively correlated with root salinity (Tab. 3). Root and shoot NaCl content showed a strong positive correlation for the studied mangrove species (Tab. 3). Growth performance for *A. marina* was weakly correlated with root and leaf NaCl content (Tab. 3), suggesting that the growth performance of seedlings of this species is marginally affected by internal (tissue) NaCl content in seedlings.

The *in-situ* experiments of the present study revealed that mature mangrove leaves of almost all tested species had more NaCl content than did young leaves (Tab. 4).

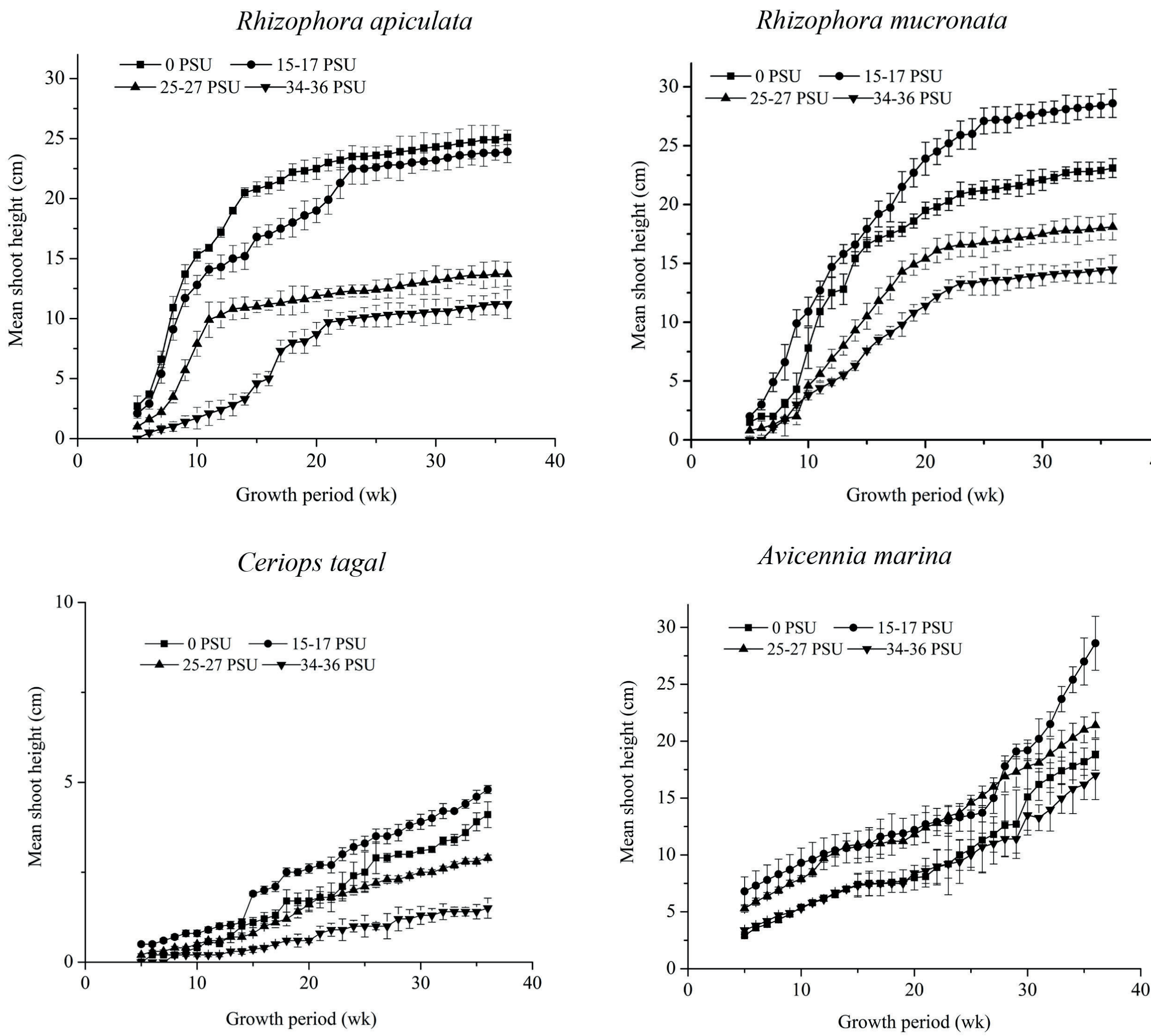

Figure 3. Growth performance expressed as shoot height of the nine-month-old seedlings of *Rhizophora apiculata*, *Rhizophora mucronata*, *Ceriops tagal* and *Avicennia marina* grown under salinity conditions of 0 PSU, 15-17 PSU, 25-27 PSU and 34-36 PSU.

Table 2. Internal NaCl content of roots and leaves of 9th-month–old mangrove seedlings grown at different salinity conditions.

Salinity (PSU)	Mangrove species							
	NaCl content of tissues of seedlings (µmol/g)							
	Rhizophora apiculata		*Rhizophora mucronata*		*Avicennia marina*		*Ceriops tagal*	
	Leaves	Roots	Leaves	Roots	Leaves	Roots	Leaves	Roots
0	291±3.5^{a}	264±3.5^{a}	420±4.7^{a}	370±6.4^{a}	1090±9.4^{a}	734±2.3^{a}	491±6.7^{a}	614±3.0^{a}
15-17	567±13.7^{b}	408±1.7^{b}	522±8.1^{b}	950±14.9^{b}	1784±19.4^{b}	1280±9.5^{b}	1180±1.3^{b}	1086±5.0^{b}
25-27	575±5.7^{b}	546±2.3^{c}	645±19.4^{c}	1190±16.7^{c}	1917±4.8^{c}	1690±7.5^{c}	1217±4.8^{c}	1400±7.5^{c}
34-36	705±3.5^{c}	707±6.4^{d}	826±6.7^{d}	1729±49.4^{d}	2037±2.9^{d}	2145±4.0^{d}	1496±4.2^{d}	1732±7.5^{d}

Note: Standard error (± standard error), from the average values from replicates shows after the average value. Different superscripts in each row mentions significantly different of NaCl retention capacity at different salinity conditions (ANOVA Tukey statistical test).

For instance, the NaCl content for young and mature *A. marina* was 1116.85±9.5 μmolg^{-1} and 1505.73± 12.7 μmolg^{-1}, respectively, and 1482.09±12.72 μmolg^{-1} and 1045.91 ±10.52 μmolg^{-1}, respectively, for *R. mucronata*. The results also found that the NaCl content of *A. marina* tissues was higher than that for the other species (Fig. 3).

Furthermore, the *in situ* experiments indicated that the internal NaCl content of young and mature leaves were positively correlated ($p < 0.001$) with that of soil, and it was conspicuously stronger between mature leaves of *A. marina* and that of soil collected from the vicinity of *A. marina* plants in the natural mangrove stands (Tab. 4).

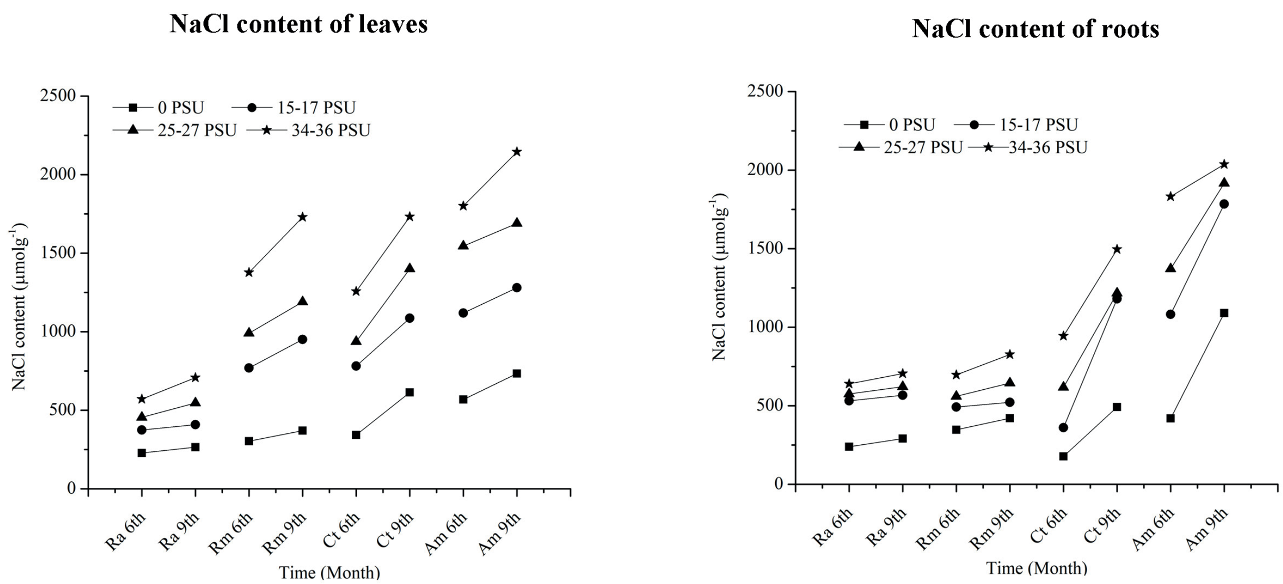

Figure 4. NaCl retention capacity of leaves and roots of 6th month old and 9th month old seedlings of species under studied; *Rhizophora apiculata* (Ra), *Rhizophora mucronata* (Rm), *Ceriops tagal* (Ct) and *Avicennia marina* (Am).

Table 3. Correlation coefficients (Pearson) of NaCl content of leaves, roots, and growth parameters of the mangrove species, *Rhizophora apiculata, Rhizophora mucronata, Ceriops tagal,* and *Avicennia marina.*

Mangrove species	Growth parameter	NaCl content of leaves	NaCl content of roots
Rhizophora apiculata	Dry weight	-0.58*	-0.76**
	Height	-0.77**	-0.94***
	No. of leaves	-0.76**	-0.95***
	Leaf area	-0.30	-0.63*
	NaCl content of leaves		0.92***
	NaCl content of roots	0.92***	
Rhizophora mucronata	Dry weight	-0.82**	-0.73**
	Height	-0.79**	-0.67*
	No. of leaves	-0.72**	-0.58*
	Leaf area	-0.96***	-0.94***
	NaCl content of leaves		0.97***
	NaCl content of roots	0.97***	
Ceriops tagal	Dry weight	-0.1	-0.32
	Height	-0.62*	-0.81**
	No. of leaves	-0.34	-0.57
	Leaf area	0.22	-0.03
	NaCl content of leaves		0.95***
	NaCl content of roots	0.95***	
Avicennia marina	Dry weight	0.22	-0.13
	Height	0.09	-0.24
	No. of leaves	-0.04	-0.24
	Leaf area	-0.18	-0.47
	NaCl content of leaves		0.93***
	NaCl content of roots	0.93***	

Note: *Correlation is significant at 0.01p < 0.05, ** correlation is significant at 0.001 p< 0.01 and ***correlation is significant at p < 0.001.

Table 4. Correlation coefficients (Pearson) of NaCl content of mature/young leaves and NaCl content of soil samples collected from the same tree from which leaf samples were collected (In-situ experiments). The standard error (±standard error), from the average values from replicates shows after the average value.

Mangrove species	Mature/young leaves	NaCl content of leaves (µmol/g)	NaCl content of soil (µmol/g)	Pearson correlation coefficients of NaCl content of leaves and soil
Rhizophora apiculata	Young leaves	960.42±6.1	242.24±3.3	0.64***
	Mature leaves	1105.96±6.4		0.46***
Rhizophora mucronata	Young leaves	1045.91±10.5	429.12±3.8	0.52***
	Mature leaves	1482.09±12.7		0.59***
Ceriops tagal	Young leaves	941.57±17.4	287.46±1.7	0.49***
	Mature leaves	1345.58±9.5		0.63***
Avicennia marina	Young leaves	1116.86±9.5	438.07±7.2	0.55***
	Mature leaves	1505.74±12.7		0.85***

Note: ***correlation is significant at p< 0.001.

Discussion

Depending on the salt tolerance capacity, mangrove species are distributed widely or confined to specific localities with tolerable soil salinities (Kodikara *et al.* 2017; Amarasinghe & Perera, 2017). Substrate salinity can impede the rehydration of cotyledons, endosperm and embryo (Wahid *et al.* 1999). Thus, the establishment of propagules/seeds in conditions of high salinity is lower than in areas of low salinity (Ye *et al*. 2005). The three species other than *R. apicula* had their highest germination percentage for seeds/propagules at 15–17 PSU, indicating their relative salt tolerance capacities, which contribute to their natural distribution pattern. Soil salinity, therefore, is crucial to sustaining the biodiversity of mangrove ecosystems.

Although mangroves can survive under a wide range of salinity, their growth is stimulated under low to moderate salinities, *i.e.*, 5–50 % seawater (Ball 1998; Aziz & Khan 2001b; Kathiresan & Bingham 2001; Ball 2002). The results of the present study corroborate this observation, as seedlings of *R. mucronata, C. tagal,* and *A. marina* showed their best growth performance at 15–17 PSU. Higher salinities than optimum (*i.e.*, 15–17 PSU) resulted in decreased growth for all the species studied. *R. apiculata*, however, had its best growth at a salinity of 0 PSU. Seedlings of *R. apiculata* have been reported to perform well in mangrove and non-mangrove soil mixtures (with low salinity) under nursery conditions (Silva & Amarasinghe 2010), suggesting that the species has an ability to thrive in soils of very low salinity. Besides, the accumulation of high amounts of sodium and chloride ions in plant tissues, and energy-consuming production of organic osmolytes such as proline and betaine to maintain the osmotic balance (required for plant water uptake), may result in lower seedling growth (Aziz & Khan 2001a; Singh & Sharma 2017). Cyclitols that serve as an osmolyte in response to salt stress are known to be present in *R. mucronata* (Aziz & Khan 2001b). The stunted growth observed in this study for *R. mucronata* at higher salinities may be the inevitable result of diverting energy to produce such organic solutes for osmoregulation. Our result revealed that *R. mucronata* is more salt-tolerant than *R. apiculata*. In the same direction, *R. mucronata* has been reported to tolerate drought periods (Duke 2006; Robert *et al.* 2015). Reduced leaf area of seedlings with increasing salinity, a trend that was observed with the four species studied here, confirms similar findings reported with other species (Ball 2002; Súarez & Medina 2005; Kathiresan 2007; Jayakody *et al*. 2008; Kodikara *et al.* 2017; Siddique *et al*. 2017).

Our results suggest that increased salinity of substrate causes significant negative effects on photosynthesis and growth performance of mangrove seedlings. *A. marina* performed best with respect to all growth parameters at the salinity of 15–17 PSU and its growth decreased with increasing salinity, an observation corroborates that reported for *A. marina* in mangroves of Bangladesh (Aziz & Khan 2001a). Growth rates for *A. marina* in salinities of 0 and 34–36 PSU did not differ significantly, suggesting that this species can tolerate (at least) a salinity range of 0–36 PSU (the range adopted in this study), as reported for the species in other mangrove areas (Khan & Aziz 2001; Kodikara *et al.* 2017).

NaCl content in both leaves and roots of *C. tagal* was comparatively higher than that in *R. mucronata* and *R. apiculata* while it was lower than that in *A. marina*. This confirms the observation of Khan & Aziz (2001) that *A. marina* has a greater capacity to tolerate high substrate salinity. *C. tagal* avoids salt damage by immobilizing the vacuoles in leaf cells (Aziz & Khan 2001a). This could be the reason for the relatively high content of NaCl in their leaves. The subsequent shedding of salt-laden leaves is another part of the salt regulation strategy of this mangrove species. It has been reported that the amount of proline present in cells becomes significantly high to balance high concentrations of sodium and chloride ions (Patel *et al.* 2010). Through the production and accumulation of cyclitols along with Na^+ and Cl^-, *C. tagal* maintains cellular osmotic balance (Aziz & Khan 2001a). This adaptation probably allows *C. tagal* to perform well, in terms of leaf area and dry weight, despite high internal NaCl content in seedlings. Corroborating this, the highest shoot length of *C. tagal* seedlings after nine months was at the salinity of

15–17 PSU, which is 12 % higher than non-saline water. Compartmentalization of salt and exclusion of salt through ultra-filtration mechanisms in roots of *Rhizophora* spp. (Khan & Aziz 2001) may have caused the comparatively low NaCl content in leaves of seedlings of both the *Rhizophora* species of the present study.

NaCl content in tissues of the seedlings continued to be affected by time and increasing substrate salinity (Fig. 3). This result was further confirmed by the comparison of measurements of mature and young leaves of plants grown *in-situ*. Cram *et al.* (2002) reported that NaCl is accumulated in leaves and the quantity increases with increasing leaf area (time/age of leaf) during growth due to the production of new cells and tissues that can contain salt. This mechanism is more prominent in *A. marina* and *C. tagal*.

The weak correlation found between internal NaCl salt content in tissues of *A. marina* and growth performance of seedlings (Tab. 3) sufficiently confirms past records (Manea *et al.* 2019) that *A. marina* seedlings can grow well under a wide range of substrate salinities and accumulate salt within their tissues. Low availability of freshwater significantly affects plant growth performance (Wesemael *et al.* 2019). Therefore, mangroves should essentially maintain high salt content in their tissues to sustain water flow from the root to the shoots (Aslam *et al.* 2011). Salt in the rhizosphere moves into root tissues and builds up root salt content. The present study found high salt content in the roots of seedlings grown in highly saline substrates. As a result, low salt conditions are maintained in the rhizosphere, supporting the growth of these salt-tolerant plants on saline soils.

Soils of the abandoned shrimp ponds on the northwest coast of Sri Lanka are of various degrees of salinity, depending on local hydrological regimes (Silva *et al.* 2013; Jil *et al.* 2015). Restoring abandoned shrimp ponds with suitable mangrove species, therefore, could provide a pragmatic strategy to rehabilitate them and resume the lost processes and functions that supported a variety of species. The success of rehabilitation will depend on the selection of mangrove species to suit the soil salinity regimes. The results of this study confirm the ability of *A. marina* as a promising candidate species for replanting the abandoned shrimp ponds with varying soil salinities due to its capacity to maintain growth without being affected by salt in soils. *R. mucronata* is the most commonly used mangrove species for the restoration/rehabilitation of mangroves in Sri Lanka because of the wide availability of seedlings/propagules throughout the year and for the ease with which the propagules can be reared in the nursery or planted directly in the field. The present study revealed *A. marina* and *C. tagal* to be more suitable for replanting, particularly in soils with high salinities, nevertheless they are rarely used for the purpose. Development and popularizing nursery techniques and protocols for rearing seedlings of *A. marina* and *C. tagal* is needed to encourage interested parties to use these species for reforestation of hypersaline coastal areas. *R. nucronata* is more appropriate for moderately saline soils while *R. apiculata* qualifies to be a more successful candidate mangrove species to rehabilitate coastal soils with low salinity.

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