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Research Paper

Interspecific Variations in Responses of Mangrove Seedlings to Two Contrasting Salinities

key words: salinity, growth, vivipary, Sri Lanka

Abstract

The growth performance of seedlings of seven species of true mangroves (*Avicennia marina, A. officinalis, Bruguiera gymnorrhiza, B. sexangula, Rhizophora apiculata, R. mucronata,* and *Sonneratia caseolaris*) in response to two contrasting salinity regimes, low (*i.e.*, 3–5) and medium (i.*e.*, 25–27), was studied. Species represented all categories relevant to vivipary (*i.e.*, true viviparous species, cryptoviviparous species and non-viviparous species), and included closely related pairs as well as species commonly used in replanting in Sri Lanka. Species could be ranked in descending order of salinity tolerance as *A. marina* > *R. mucronata* > *R. apiculata* >*B. gymnorrhiza* > *A. officinalis* > *B. sexangula* > *S. caseolaris*, hence taxonomically similar species and those sharing vivipary characteristics may be distant in salinity tolerance.

1. Introduction

Mangroves are woody shrubs and trees that are salt and flood tolerant and hence dominate the intertidal areas of lagoons, estuaries and sheltered bays along tropical and subtropical coastlines (Tomlinson, 1986; Tuffers *et al.*, 2001; Ball, 2002). These tidal forests are of enormous ecological and economic importance (Walters *et al.*, 2008), providing ecosystem goods (food, medicines and timber) and services (such as fisheries nurseries and erosion control) to local communities living behind and within them. Despite this they are suffering high rates of destruction; currently between 1–2% of total forest area is lost per year (Duke *et al.*, 2007). Hence the conservation and restoration of mangrove ecosystems deserves high priority.

The tsunami that hit South-East Asia on December 26th 2004, killing over 270,000 people and leaving millions homeless, was a dramatic and tragic reminder of the coastal protection function of mangroves. In the aftermath of the tsunami, the common-sense view that mangroves can act as living dykes against ocean surges received empirical support (Dahdouh-

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GUEBAS *et al.*, 2005b; DANIELSEN *et al.*, 2005; LIU *et al.*, 2005). As a result, governments across the Indian Ocean have announced a plethora of new schemes to protect and replant mangroves and thereby attempt to rectify the widespread losses of mangroves that have occurred during the last few decades.

Careful consideration of site characteristics and species ecology is needed before attempting to restore degraded mangrove sites. Salinity and hydrology (*i.e.*, period and frequency of flooding) in selected habitats are two of the primary factors that determine the survival and growth of replanted mangroves (and hence the success of the replanting projects) because different true mangrove species vary in tolerance to such ecological factors (ALLEN *et al.*, 2003; HWANG and CHEN, 2001; YE *et al.* 2005; BOSIRE *et al.*, 2008). FIELD (1998) identifies the natural occurrence of a species in the vicinity of a proposed replanting site as the most important factor in determining its suitability for use in restoration efforts. This is sensible advice, but the presence of mature trees nearby does not necessarily ensure their suitability for a particular site, for three reasons. First, degraded sites often experience large changes in physical and chemical conditions, hence the former presence of a species (or its presence nearby) does not guarantee it is still appropriate (FIELD, 1998). Second, distributional patterns of mature trees may not correspond closely with early life history traits, including salinity tolerance (CLARKE *et al.*, 2001). Third, there may be large environmental heterogeneity even at small scales; this is particularly the case in Sri Lanka where distributional patterns can be very complex and dynamic (DAHDOUH-GUEBAS *et al.*, 2000; JAYATISSA *et al.*, 2002; DAHDOUH-GUEBAS *et al.*, 2005a). Hence measuring key environmental variables, such as salinity, at a small scale within the proposed site, and matching these variables to the appropriate early life history traits of local species is advisable.

Although salinity is often considered as a ‘stress’, NaCl may also be a resource for halophytic species (TUFFERS *et al.*, 2001; BALL, 2002). The classic growth response of halophytes, including most mangroves, to increasing salt concentration is similar to that shown for nutrients, with variation in the shape of the response curve reflecting concentrations which are deficient, saturating and toxic to growth (BALL, 2002; Krauss *et al.*, 2008). However, the degree of tolerance varies depending on the species, with some mangroves facultative halophytes and most performing best at salinities 50% or less of sea water (TOMLINSON, 1986; YE *et al.*, 2005; HOGARTH, 2007). This range of degrees of tolerance to salinity is one of the factors thought to generate zonation patterns in mangrove communities in the intertidal zone (MACNAE, 1968).

Although the salinity tolerances of most mangrove species have been studied, much information on salt tolerance that would be of use to restoration efforts remains to be discovered. The salinity tolerance or water use characteristics of the same species may vary depending on climatic and edaphic factors (YOUSSEF and SAENGER, 1998). Hence field studies of mangrove distribution and growth correlated with salinity will often be confounded by many other pertinent variables. Early growth and mortality in the field is likely to be controlled by the most severe conditions the seedling experiences. In the present study, the performances of seedlings of seven true mangrove species, including species commonly used in replanting, were tested under controlled conditions representing naturally occurring salinity levels.

It has been suggested that vivipary will affect the salinity tolerance of mangrove saplings (YE *et al.*, 2005). Sri Lanka, a small island with one third of the world’s true mangrove species (JAYATISSA *et al.*, 2002), shows complex patterns of mangrove distribution. Whilst species within the same genus do grow sympatrically, such co-occurrence is uncommon; hence closely related species may show different tolerance levels for edaphic factors, despite shared characteristics such as vivipary. In the current work, mangrove genera from three different categories of vivipary, with replicate species within genera where possible, were selected for study in order to explore any general effects of vivipary.

1.1. Objectives

The main aim of the current work was to study the interspecific variations in the salinity tolerance of common mangroves in Sri Lanka, in their early growth stage (*i.e.*, as seedlings). Specific objectives were to examine the differences between species in the same genera, because such variations are apparently neglected in many replanting programs leading to failures, and to compare tolerances in species with the full range of vivipary characteristics; in particular, to examine the suggestion that vivipary enhances salinity tolerance.

2. Materials and Methods

2.1. Selection of Species

The mangrove communities along the coastline of Sri Lanka contain 20 species of true mangrove in fourteen genera; four of these genera include more than one species (JAYATISSA *et al*., 2002). These genera cover the range of vivipary observed in mangroves. Hence seven common species were initially selected: four species from viviparous genera, *viz*. *Bruguiera gymnorrhiza* (L.) LAMK., *B. sexangula* (LOUR.) POIR., *Rhizophora mucronata* LAMK. and *R. apiculata* BL., two species from a cryptoviviparous genus, *Avicennia marina* (FORSK.) VIERH., and *Avicennia officinalis* L., and one species from a non-viviparous genus, *Sonneratia caseolaris* (L.) ENGLER.

2.2. Culture and Experimental Design

Mature propagules or seeds of the selected species were collected from natural mangrove sites and used as planting materials. A sandy soil was prepared by mixing sieved loam soil with sand and organic matter (degraded mangrove litter) in 1:1:1 proportions by volume. Initially propagules and seeds of all the species were planted in plastic pots (5 cm diameter and 15 cm height) filled with the prepared soil mixture and kept in a nursery irrigated with freshwater until the establishment of seedlings. Seedlings with the first two leaves unfurled were considered as established seedlings; eight seedlings from each species, all of similar size, were transferred individually to larger plastic pots (15 cm diameter and 40 cm height) filled with the same mixture of soil. Pots with seedlings were placed individually *(i.e.*, one per tray) on 7 cm deep plastic trays and four replicate pots from each species were randomly assigned to each salinity treatment. The experiment was started with these established seedlings in order to minimize masking of salinity effects by other effects (*i.e.*, effects of seed or propagule quality).

Two salinity regimes, ‘low saline’ (salinity of 3–5) and ‘medium saline’ (salinity of 25–27), were selected for the experiment (here and throughout salinity is given as practical salinity units). Low saline and medium saline water was prepared by mixing seawater and tap water, and used to irrigate seedlings in pots twice a day with the appropriate salinity treatment. Unfortunately distilled water was not available, hence it is possible that toxins were present in the tap water. However this is unlikely given that potable water from plastic pipes was used. Excess water accumulated in trays was returned to tanks every other day and the salinity of the water in tanks was checked using a hand refractometer (ATAGO S/Mill-E, Japan) and adjusted by adding tap water when necessary once every four days. Commercially available fertilizer (‘Nitrophoska’ GMBH, Belgium, with 12% N and 12% P) was also applied once a month by dressing the top of the soil with 1g per pot before irrigation. Seedlings in pots were distributed on benches set outside (hence exposed to ambient temperature and irradiance but protected from rainfall by a glazed roof) according to a completely randomized design.

2.3. Data Collection

The length of the epicotyl or shoot height of each sapling was measured once a week. Seedlings were harvested after three months of growth. The plastic pots were removed, and the soil carefully washed away to reveal the intact root system. Cleaned plants were blotted dry and separated into roots, hypocotyls ('propagules'), stems and leaves. The fresh weights of these four parts of each plant were measured and leaf area was quantified manually using millimeter paper. All parts were then oven dried at 60 °C for dry weight; pilot work showed 48 hours was sufficient for leaves and roots, whilst three days was needed to obtain constant weights for stems. The difference between the dry weight and fresh weight of individual plants was taken as the water content. Shoot/root ratios were calculated for each plant by dividing total shoot and leaf dry weight (*i.e.*, excluding hypocotyls) by root dry weight.

2.4. Data Analysis

Means and standard deviations of total dry weight, dry weight excluding hypocotyl, mean leaf size, percentage water content, shoot height and shoot/root ratio were calculated separately for each species grown under each salinity level, using the data collected after three months growth. Data were tested for homogeneity of variances; no transformations were necessary. Two-way ANOVA tests were then used to examine the effects of the factors salinity and species on all response variables among the six mangrove species (*S. caseolaris* was not used in ANOVA analyses since no medium salinity data were available). *Post hoc* comparisons were made with Tukey-Kramer tests, with further one-way tests made when significant interaction terms were found. For clarity of interpretation and presentation, two sample t-tests (Zar, 1984) were also carried out between means at each salinity level for each species.

3. Results

There were highly significant differences between species and salinity levels for three of the five response variables measured (Table 1). The strong general trends were for lower weight, smaller leaf size and lower water content in medium salinity treatments. The pattern of differences for dry weight was the same with or without the inclusion of the hypocotyl (although absolute values were very different for the propagule species), hence only data for total dry weights are presented. There was a significant interaction between species and salinity for leaf size showing the effects of salinity on this response varied between species. Leaf size was reduced at medium salinity for all species except *A. marina* (Fig. 1). *A. marina* and *R. mucronata* differed from the other species in showing no significant reduction in dry weight at medium salinity (Fig. 1).

Table 1. Results of two way ANOVA tests. In all cases, salinity and species were fixed factors with 1 and 5 *d.f.* respectively.

Response	Factor	*F*	*P*
Weight	Salinity	24	<0.001
	Species	110	<0.001
	Salinity × species	4.8	0.2
Leaf size	Salinity	93	<0.001
	Species	90	<0.001
	Salinity × species	4.8	0.002
% water	Salinity	42	<0.001
	Species	121	<0.001
	Salinity × species	2.0	0.1
Shoot/root	Salinity	0.21	0.65
	Species	1.43	0.24
	Salinity × species	2.7	0.07
Shoot length	Salinity	1.2	0.6
	Species	0.05	0.8
	Salinity × species	0.9	0.7

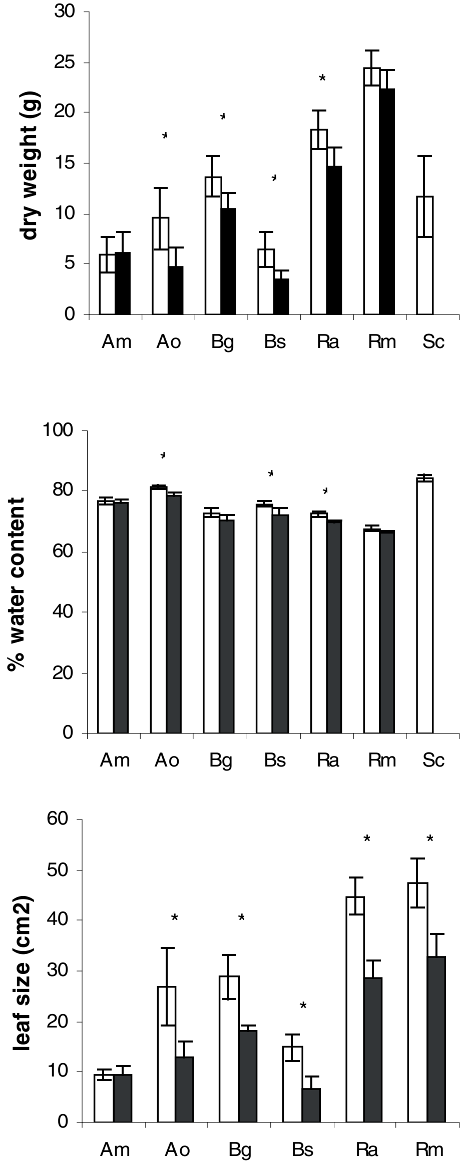

Figure 1. Mean (± *S.D.*) values of three different variables measured in 94 day old saplings of seven mangrove species (Am, *Avicennia marina*; Ao, *Avicennia officinalis;* Bg, *Bruguiera gymnorrhiza*; Bs, *Bruguiera sexangula*; Ra, *Rhizophora apiculata*; Rm, *Rhizophora mucronata*; Sc, *Sonneratia caseolaris*) grown under two different salinity regimes (low saline = 4–5, open bars; medium saline = 25–26, shaded bars). * indicates significant ($P < 0.05$) difference within a species between salinity treatments.

3.1. Interspecific Variations Irrespective of Salinity Effects

The comparison of the seven mangrove species for interspecific variations in dry weight, percentage water content and mean leaf size revealed that *R. mucronata* was significantly different from all the other species showing the highest values in dry weight and mean leaf size, and the lowest value in percentage water content (Table 2). The higher values of percentage water contents were recorded under low saline conditions and the highest water content was recorded from *S. caseolaris* under low saline conditions. When differences between the two species in each of the same genus are considered, *R. apiculata* and *R. mucronata* showed significant differences in dry matter accumulation and percentage water content. The two species in the genus *Avicennia, i.e.*, *A. marina* and *A. officinalis*, showed a significant difference only in percentage water content (Table 2). *B. gymnorrhiza* and *B. sexangula* were not significantly different in percentage water content, but differed significantly in mean dry weight and mean leaf size. Table 2 shows mean values for species pooled across salinity treatments. For those variables that showed significant interactions between salinity and species, separate one-way ANOVAs were performed on data taken from low and medium salinity treatments (since interactions may confuse the interpretation of the effects of the main factors). However the patterns of interspecific differences remained the same under both conditions (Table 2).

The growth rate as measured by the increment of shoot height also showed interspecific variation. The lowest and highest growth rates were recorded from *B. sexangula* and *S. caseolaris* respectively. The growth rates of the rest of the species were at intermediate levels (Fig. 2). Data for *S. caseolaris* were not included in ANOVA tests, since this would have led to non-factorial design given the absence of medium saline results. However, there were non-overlapping 95% confidence intervals for final mean shoot length between *S. caseolaris* and the low salinity means of *B. gymnorrhiza, B. sexangula* and *R. mucronata* suggesting significant differences for these contrasts (Fig. 2).

Table 2. Mean dry weight, leaf size, % water content, shoot/root ratio and shoot length of seven mangrove species. Means represent data pooled for both salinity levels. Different superscripts denote significantly different ($P < 0.05$) groupings according to Tukey-Kramer HSD test (The data from *S. caseolaris* was not included in the ANOVA as the available data were from plants grown under low salinity level only.).

Species	Dry weight (g)	Leaf size (cm^2)	Water (%)	Shoot/root ratio	Shoot length (cm)
A. marina	5.97 ^{d}	9.39 ^{c}	76.31 ^{b}	3.36^{a}	57.0^{a}
A. officinalis	7.09 ^{d}	20.02 $^{b\ c}$	79.99 ^{e}	3.06^{a}	42.5^{a}
B. gymnorrhiza	12.09 ^{c}	23.39 ^{b}	71.75 $^{c\ d}$	2.97^{a}	23.5^{a}
B. sexangula	5.01 ^{d}	10.70 ^{c}	73.93 $^{c\ d}$	2.88^{a}	14.9^{a}
R. apiculata	16.49 ^{b}	36.58 ^{a}	71.20 ^{d}	2.58^{a}	40.4^{a}
R. mucronata	23.39 ^{a}	40.10 ^{a}	66.86 ^{a}	3.49^{a}	22.0^{a}
S. caseolaris	11.65	16.8	84.32	0.37	81.0

3.2. Interspecific Variations in Response to Salinity

The negative effect of salinity on the growth of saplings was most pronounced for *S. caseolaris* as all the individuals under medium saline conditions died within the first two week period. However the growth curve of *S. caseolaris* saplings under low saline conditions shows the highest growth rate over the first five weeks (Fig. 2g). The growth of seedlings

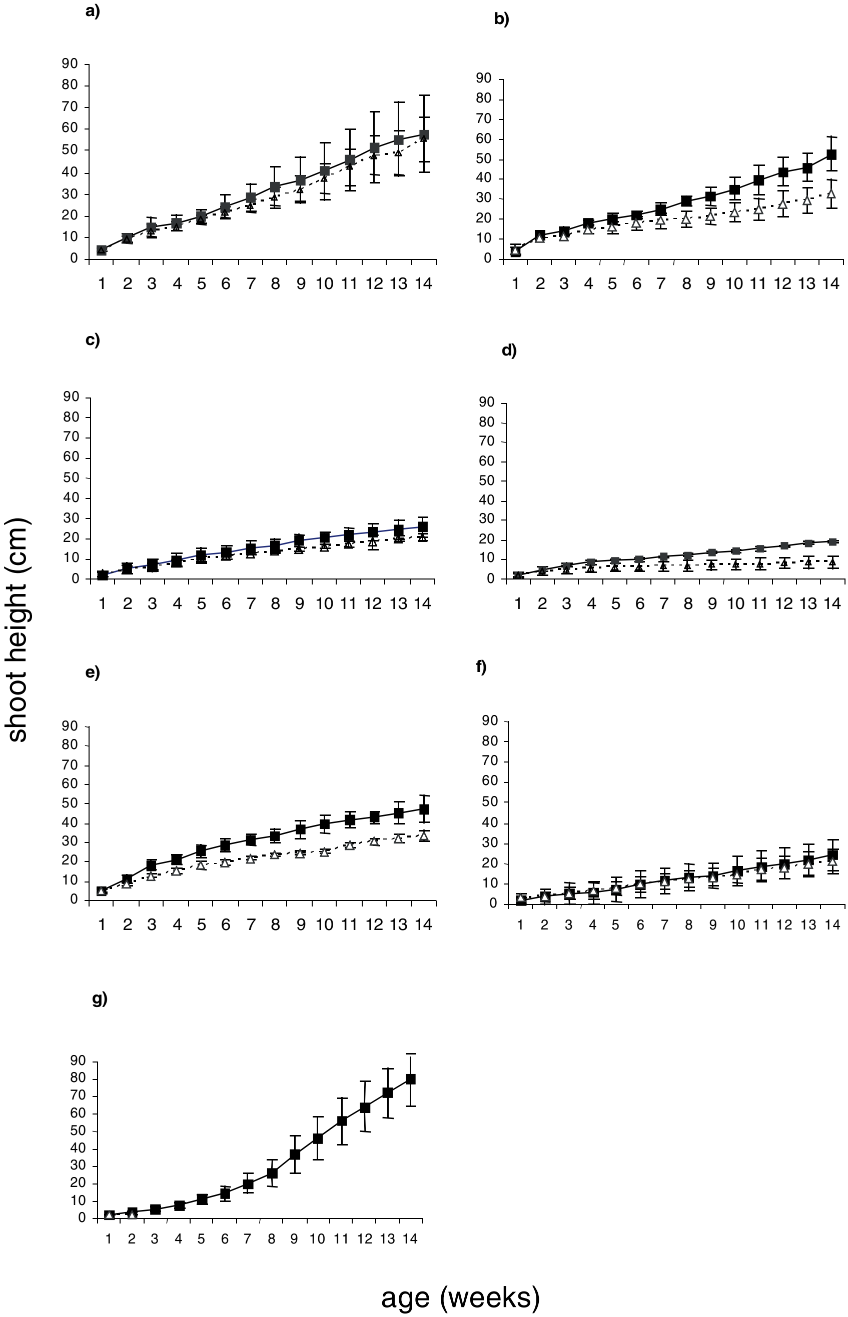

Figure 2. Mean (± *S.D.*) shoot growth *(i.e.*, stem height) of mangrove saplings of seven species grown under two different salinity regimes (Low saline = 4–5, full line and squares; Medium saline = 25–26, broken line and triangles) over 14 weeks. Species are: a) *Avicennia marina*, b) *Avicennia officinalis,* c) *Bruguiera gymnorrhiza*, d) *Bruguiera sexangula*, e) *Rhizophora apiculata*, f) *Rhizophora mucronata* g) *Sonneratia caseolaris.* $n = 4$ for each treatment × species combination.

of *A. officinalis* and *B. sexangula* was greatly reduced under medium saline conditions whilst that of *B. gymnorrhiza* and *R. apiculata* was moderately reduced. Salinity effects on the growth of shoots of *A. marina* and *R. mucronata* were negligible (Fig. 2). Dry weights of saplings of each of *A. marina* and *R. mucronata* grown under low and medium saline conditions were not significantly different whilst those of the other species were significantly decreased (Fig. 1). In the medium saline condition, decreases in mean dry weight (compared with low saline means) of *A. officinalis, B. gymnorrhiza, B. sexangula* and *R. apiculata* were 51%, 23%, 45% and 20% respectively.

The percentage water content in three month old saplings of each of *A. officinalis, B. sexangula* and *R. apiculata* grown under low saline conditions were significantly different from those grown under medium saline conditions. Saplings of *A. marina*, *B. gymnorrhiza*, and *R. mucronata* did not show such a difference in their water content (Fig. 1).

Apart from *A. marina*, in which leaf size under low saline conditions and medium saline conditions was not significantly different, leaves produced by all the other species under medium saline conditions were significantly smaller than those produced under low saline conditions (Fig. 1).

4. Discussion

In planning the rehabilitation and reconstruction efforts after the tsunami that hit South-East Asia on December 26th, 2004, many countries gave a high priority to the re-establishment of natural barriers against tsunamis and other ocean surges, focusing interest on the potential for mangroves to act as such barriers (Dahdouh-Guebas *et al.*, 2005b; Danielsen *et al.*, 2005; Liu *et al.*, 2005). Mangrove replanting programs were initiated and supported with the help of governments and non-governmental organizations. However, the success of such programs depends on the selection of suitable species based on the prevailing edaphic and hydrological conditions at the planting site. True mangrove species are characterised by adaptations to harsh environmental conditions. However, most species show optimum growth only under a rather narrow range of conditions, and whilst they may be capable of growth under suboptimal conditions for a few variables, multiple sources of stress will lead to high mortality (Allen *et al.*, 2003; Hwang and Chen, 2001; Ye *et al.*, 2005). Mangroves are likely to show particular sensitivity during the initial establishment and early growth of saplings. The effects of salinity on seedling establishment were not considered in the present study, since most replanting programs in Sri Lanka are started with seedlings established in a nursery where fresh water or low saline water is used for irrigation.

The current study considered responses of mangrove seedlings under low and medium saline conditions over only 14 weeks. Such a short period may be insufficient to reveal slowly developing responses (Ball *et al.*, 1997). Nevertheless, rapid responses to soil salinity during the early growth of seedlings may be important determinants of their survival. As an example, *B. sexangula* showed a severe inhibition (*i.e.*, 45%) of its dry mass under medium compared with low salinity conditions after three months of growth, hence further growth and development is also likely to be impaired, particularly once the initial food reserves in the propagule are exhausted. It has been reported that viviparous species perform better than non-viviparous species in seedling establishment, implying the beneficial effects of propagules in early growth (Ye *et al.*, 2005)

Out of the seven species tested in this study, *S. caseolaris* showed the lowest salinity tolerance, with all the seedlings under medium saline conditions dying within the first two weeks. Natural stands of *S. caseolaris* in Sri Lanka are mainly restricted to river estuaries in the wet zone of the country (Jayatissa *et al.*, 2002; Jayatissa *et al.*, 2006). Hence its distribution is congruent with its status as a low saline species (although adult trees may show higher tolerance than seedlings and can be found in higher salinity areas; Bhosale, 1994).

Whilst the range of economic uses of *S. caseolaris* make it an attractive choice for replanting schemes (JAYATISSA *et al.*, 2006) the present results and its distribution suggest that it is not suitable for medium (or high) saline areas. *S. caseolaris* was the fastest growing species studied (Fig. 2g), supporting the idea of a physiological trade-off between speed of growth and salinity tolerance (HOGARTH, 2007).

The rest of the six species survived under medium saline conditions but showed some differences in growth performances, with the exception of *A. marina*. The relative tolerance of *A. marina* to medium salinity recorded here is consistent with many other studies (*e.g.*, DOWNTON, 1982; CLOUGH, 1984; YE *et al.*, 2005). For the remaining less salt tolerant species, a reduction in leaf size was the most sensitive indicator of salinity stress, with all species showing significant reductions. This represents a typical response to water stress, with smaller leaves produced in order to reduce transpirational losses (PARIDA and DAS, 2005).

Dry weight, shoot length, shoot/root ratio and water content of *R. mucronata* saplings grown under medium saline conditions were not significantly different from those grown under low saline conditions, with leaf size being the only variable to vary significantly. Therefore, out of the seven species studied, *R. mucronata* appeared to be the second highest in salinity tolerance.

When the relative differences in all response variables under medium compared with low saline conditions are considered, the species tested in this study can be arranged in descending order of salinity tolerance as *A. marina* > *R. mucronata* > *R. apiculata* > *B. gymnorrhiza* > *A. officinalis* > *B. sexangula* > *S. caseolaris*. For example, *B. sexangula* showed average changes in leaf size, % water content, and dry weight of −56, −5 and −46 percent respectively, under medium compared with low salinities. These compared with −38, −3 and −23 for *B. gymnorrhiza* and −52, −4 and −51 for *A. officinalis.* This ranking shows that closely related species *i.e.,* species in the same genera, may be distant in salinity tolerance, and hence that shared vivipary or cryptovivipary do not determine response to salinity. Laboratory studies such as the present work may not always suggest the same optimal conditions for mangrove growth as those recorded from field distributions (HWANG and CHEN, 2001). These discrepancies can result from numerous potential confounding variables, along with synergistic effects and fluctuating values, under field conditions. However, the field distributions of these species in Sri Lanka do reflect these relative tolerances; for example, the last three species of the above series are restricted to mangrove communities with more riverine influence (JAYATISSA *et al.*, 2002). The pairs of species that share the same genus but are distant in salinity tolerance rarely exist in the same immediate area (although all the species can occur in the same community, for example in the same lagoon). Even within a species (*Avicennia marina*), height, physiognomy, leaf size, *etc*. are known to be significantly different between landward and seaward zones where salinities are contrasting (DAHDOUH-GUEBAS *et al.*, 2004).

In general, plants growing in habitats with a deficit of water possess adaptations to store water. Mangrove plants have to face a physiological drought due to high soil salinity implying that mangroves growing under higher salinities should have higher water contents. In contrast, the present study found that the percentage water contents in saplings of species less tolerant of salinity, *i.e.*, *A. officinalis, B. sexangula*, *R. apiculata*, were higher when they were grown under low saline conditions. In a mangrove habitat, the soil salinity is not constant but fluctuates depending mainly on the fresh water inflow and, in the case of Sri Lanka, blocking of lagoonal mouths. Mangrove species, particularly those that are less tolerant of high saline conditions, could be opportunistically absorbing and storing more water when they are exposed to low saline conditions (KATHIRESAN and BINGHAM, 2001). Hence, lower water content in plants under medium or high saline conditions may be considered as a sign of salt stress. Water stressed plants are also likely to invest in means of obtaining more water and of reducing transpiration. The decrease in leaf size found in the more salt sensitive species can be explained in these terms. SAINTILAN (1997) showed a relationship between increasing sediment salinity and reducing shoot: root ratio in *A. marina* in the field – a similar effect may have been expected in the current work. However, this response became clear only at salinities in excess of 40, hence the medium levels used in the current study may have been insufficient to produce differences in shoot : root allocation.

Much previous work suggests that salinity is a key determinant of mangrove zonation and establishment success (*e.g.*, MACNAE, 1968; BALL and PIDSLEY, 1995; SAUREZ and MEDINA, 2005; YE *et al*., 2005; KRAUSS *et al.*, 2008). As an example, *A. marina* may occupy a wider range of intertidal habitats because of its high salinity tolerance (DAHDOUH-GUEBAS *et al*., 2004). The current study supports the vital importance of salinity in determining mangrove growth, and shows that salinity tolerance is a species-specific trait unrelated to vivparity. Many attempts to restore mangroves fail completely, as they are poorly planned and managed (ELSTER, 2000; ERFTEMEIJER and LEWIS III, 2000; LEWIS III, 2005), although examples also exist of careful restoration of mangrove flora with associated faunal recovery (*e.g.*, BOSIRE *et al.,* 2008; KIRUI *et al.*, 2008). A clear knowledge of the salinity tolerances of available species, along with the salinity regime at the proposed planting site, are essential for success.

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