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A Growing Threat to Tidal Forests: Incursion of Mangrove Ecosystems by Invasive Alien Species *Acacia auriculiformis* A. Cunn. ex Benth. (Fabaceae)

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Abstract—Mangrove forests are reported to be invaded by invasive alien species (IAS). This study was therefore aimed at studying the level of distribution of the IAS, *Acacia auriculiformis* A. Cunn. ex Benth. in mangrove ecosystems in the southern coast of Sri Lanka and assessing the risk to periphery of mangrove forest by considering the Rekawa mangrove forest as a model site. Growth performances of two mangrove species; *Rhizophora mucronata* and *Avicennia marina* in the presence of *Acacia* plants were also tested under three different competition levels; low, moderate and high. According to the results, infestation of *Acacia* plants was significant in the southern coast of Sri Lanka, particularly in Matara and Hambantota districts ($p < 0.05$). Species diversity determined as the Simpson diversity index was high (0.77) in the periphery of the Rekawa mangrove forest. Four true mangroves and two associates co-occurring with *A. auriculiformis* in the periphery could be observed during the field validation experiment. The highest seedling (15.4 ± 2.2 m^{-2}) and sapling (11.2 ± 2.8 m^{-2}) densities were reported for *A. auriculiformis* plants. Dominance, calculated as the importance value index of different species in the mangrove periphery varied from 18.0–120.6 and the latter highest was recorded for *Acacia* which has the highest relative density (42.1%) and the relative dominance (52.5%). The total leaf area of the *Rhizophora* plants grown in the high-competition level was significantly lower than that of the control plants, while the dry weights at three different competition levels were significantly higher ($p <$ 0.05) than the control. This could be due to the higher root biomass allocation. In *Avicennia* plants, cumulative shoot height, total leaf area and dry weight of the plants grown at the high-competition level were significantly lower than that of the control plants ($p < 0.05$). *A. auriculiformis* plants grown with these true mangrove species better performed and did not show any significant deviation from the respective control plants. The level of survival of *Acacia* was significantly reduced at 25 psu ($p < 0.05$). Early intervention and serious scrutiny are much needed to reverse the possible impacts of IAS on mangrove forests and the need for forest conservation is emphasized.

Keywords: inter-specific competition, mangrove periphery, invasion, relative dominance, relative density, Important Value Index (IVI), threats

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INTRODUCTION

Mangrove forests are unique intertidal plant communities that grow in hyperhaline, poikilohaline and other extreme environmental conditions including frequent inundation with associated hypoxia, anoxia, low air humidity and high temperatures. Mangrove ecosystems are restricted to the intertidal area of estuaries, creeks, sheltered bays and coastlines in tropical and sub-tropical areas worldwide (Mukherjee et al., 2014; Tomlinson, 2016). These tidal forests provide an array of ecosystem services such as the provision of nursery, breeding and feeding grounds for fish crustaceans and other various marine biota, nutrient cycling, including many of economic importance, shoreline defense against storm surges and erosion (Donato et al., 2011; Hilmi et al., 2017; Satyanarayana et al., 2017; Dahdouh-Guebas et al., 2021). Mangroves also frequently underpin the livelihoods of local communities through their provision of timber and non-timber forest products including food (fish, crabs, and prawns), firewood, timber, waxes, honey and charcoal (Ron and Padilla, 1999; Walters et al., 2008; Zu Ermgassen et al., 2020). With all the tangible and intangible benefits of mangrove forests, it seems a paradox that mangrove cover rapidly declines due to human action even though the current situation is better than 2–3 decades ago (Friess et al., 2020). Among them, overexploitation of the resources, land reclamation for settlement/industrial development, urbanization, eutrophication, pollution and modification of watersheds have created serious threats to the mangrove ecosystems in many parts of the world (Mukherjee et al., 2014; Richards and Friess, 2016; Okello et al., 2019; Goldberg et al., 2020). Similarly, incursion by invasive alien species (IAS) has been identified as a growing threat to mangroves in past decades (Biswas et al., 2007; Madarasinghe et al., 2015; Biswas et al., 2018). Nevertheless, in-depth studies on IAS in mangrove forests are scarce.

Biological invasion i.e. immigration of invasive species such as plants, organisms or microbes into a new environment which adversely affect the functionality of that environment (Valery et al., 2008) is not uncommon. In plant invasion, penetration of a plant to a new environment, followed by invasion could commonly be observed (Dahdouh-Guebas et al., 2004). Moreover, an IAS acquires competitive advantage to increase its cover and to spread rapidly becoming the dominant species/population in the recipient environment (Valery et al., 2008). Many studies have reported different types of invasive species that could be observed in various environments (UNEP, 2005; Donnelly et al., 2007; Gaertner et al., 2009; Hejda et al., 2009; Madarasinghe et al., 2015; Biswas et al., 2018). According to biological invasion theory, invasive plant species can spread only into disturbed natural environment/vegetation through succession (Houston and Smith, 1987; Ameen, 1999). When an ecosystem is disturbed that alters the physical environment and associated community which in turn, leads to incursion of IAS (Fox, M.D. and Fox, J.B. 1986; Biswas, 2007). However, at the start of growing, they are considered as alien species and become invasive in the long run. With reference to mangrove forests, plant species like aquatic weeds, climbers, ferns and trees; *Acrosticum aureum* L., *Clerodendrum inerme* (L.) Gaertn, *Eichhornia crassipes*, *Eupatorium odoratum* L., *Micania scandens* Willd, *Hibiscus tilliaceus* L. etc. have been recorded as invasive plant species in Sundarbans mangrove forest and were further classified as highly invasive, invasive and potentially invasive (Biswas et al., 2007). Similarly, *Nypa* palm species has also been identified as an invasive species after being introduced from the Indo-West Pacific into the Atlantic-East Pacific Niger River delta, Nigeria (Numbere, 2018) whereas *Sonneratia apetala* Buch. Ham has been confirmed as an invasive species in China (Ren et al., 2009). Apparently, many of the reported invasive species are either true mangroves or mangrove associates and only few terrestrial mesophytes were listed. The reason could be that saline environments and frequent inundation conditions are inhospitable for many terrestrial mesophytes and freshwater species (Biswas et al., 2018). However, even under these inhospitable conditions, *Acacia auriculiformis* A. Cunn. ex Benth. was observed to be a threat to mangrove forests, particularly in the southern coast of Sri Lanka (Madarasinghe et al., 2015). To the best of our knowledge, this species has not been recorded as a mangrove invasive plant anywhere.

However, *A. auriculiformis* is recorded as invasive to non-mangrove ecosystems in several countries and regions around the globe, including Comoros, Mayotte, Bangladesh, Sabah, Singapore, Bahamas, Florida (USA), Cook Island, Federated States of Micronesia, Guam, Marshall Islands, Northern Mariana Islands, Palau, Solomon Islands and Brazil (Vélez-Gavilán, 2016; Heringer et al., 2020). British people started rapidly introducing economically important plants around the world for agroforestry, commercial forestry, landscaping or erosion control in the 19th century (Hossain, 2008). By continuing the same trend in the 20th century, *A. auriculiformis*, which is native to Australia, Indonesia and Papua New Guinea was introduced to tropical and sub-tropical countries, including Asia, Africa, North and Central America, Brazil, Oceania, Hawaii, Caribbean (Bahamas), Pacific and West Indian Oceanic islands (Joker, 2000; Starr et al., 2003; Kull Christian et al., 2008; Vélez-Gavilán, 2016). The first *Acacia* species was introduced to Sri Lanka in the 1860s and later in the 1980s, *A. auriculiformis* was initiated as a new species through a project embarked on by the Forest Department. They were mainly planted in the highlands to meet the requirements for fuelwood for the tea industry and railway and also as windbreaks, ornamentals and swan timber (Vivekanandan, 1993). Extensive plantations together with Eucalyptus in the dry zone and the dry intermediate zone have proven their promising performances in reforestation (Munasinghe, 2003). *Acacia* was also established in gravel and low-quality sites of abandoned and barren lands in tea and rubber estates with the involvement of the private sector (Weerawardane, 2008). Until this date, *A. auriculiformis* was not listed as an invasive species in Sri Lanka (Wijesundara, 2010).

Several studies reported that this species has invaded and altered the natural diversity of the native species in most of its introduced habitats. Terrestrial managed forests, plantations, disturbed areas, rail or roadsides, terrestrial natural forests, riverbanks, scrub or shrublands, coastal areas, coastal dunes and oligotrophic sandy, Savanna (Mussununga) ecosystems are reported to be threatened by *A. auriculiformis* (Heringer et al., 2020). Current evidence indicates that this *Acacia* species has a wide distribution range (i.e. high ecological hardness) and its invasion increases gradually resulting in damaging outcomes (Heringer et al., 2019a; Minteer et al., 2020; Vicente et al., 2020). The approach to manage IAS has been highly fragmented and uncoordinated, leading the spread of IAS has increased remarkably in recent decades to become insufficiently managed (Caffrey et al., 2014; Kodikara et al., 2018). Yet, IAS invasion necessitates early intervention and serious scrutiny to reverse the possible impacts. Therefore, this study was aimed at assessing the level of distribution and the risk of invasion to the periphery of the mangrove ecosystems along the southern coast of Sri Lanka. In addition, this attempt was to study the interspecific variations in the growth performances of *R. mucronata*, *A. marina* and *A. auriculiformis* under saline conditions. The working hypotheses of the investigation were (i) mangrove forests in the southern coast of Sri Lanka are invaded by *Acacia auriculiformis*; (ii) the periphery of mangrove forest of Rekawa lagoon is highly vulnerable to invasion of *Acacia auriculiformis*; (iii) *Acacia* plants can establish in saline conditions and compete with true mangrove species.

MATERIALS AND METHODS

Study Area

This study was comprised of three phases (a) initial field survey (b) green-house experiment and (c) field validation. The initial field survey was carried out along the coastal belt from Kalutara to Hambantota (210 km) as it represents three main climate zones of Sri Lanka, i.e. wet [Mean Annual Rainfall: (MAR) >2500 mm; Average Annual Temperature (AAT): 28.5°C)], dry [(MAR <1750 mm); AAT: 31.5°C] and intermediate [(MAR: 1750–2500 mm); AAT: 30.0°C) (Figs. 1, 2). The country is divided into four major climatic zones namely wet, dry, intermediate, and arid zones (Pemadasa, 1996). The wet zone is mainly confined to the southwestern region and the dry zone to the northern and the eastern part of the country (Fig. 2). These two zones are separated by the intermediate zone. The arid zone on the other hand is confined in the northwestern and the southern parts of the country. When considering the above categorization, the study belt covers three main climate zones despite the fact that the arid zone is restricted to small areas (Adapted from Kodikara et al., 2017a). Green-house experiments were conducted at the University of Ruhuna, Matara, Sri Lanka which is located approximately centrally in the aforementioned coastal stretch. The field validation survey was carried out in the mangrove ecosystem of Rekawa Lagoon, Hambantota district, Sri Lanka.

Initial Field Survey

All the mangrove ecosystems along the coastal stretch from Kalutara to Hambantota were investigated. In each site a belt transect of 20 m wide was placed along the landward periphery of the mangrove forests, 10 m into the mangrove forest and 10 m out of the forest. Within this belt transect, the presence/absence status of *Acacia auriculiformis* was carefully recorded. In addition, the abundance of *Acacia* plants was assessed semi-quantitatively by placing them into three categories: 'absent,' 'rare' (i.e. less than 10) and 'common' (i.e. more than 10) irrespective of size and age class of the individuals.

Green-House Experiment

The objective of the green-house experiment was to study the ability of *A. auriculiformis* to compete with some selected true mangrove species under saline condition. Two species, namely *Rhizophora mucronata* Lam. and *Avicennia marina* (Forssk.) Vierh. were selected for the study to represent true mangrove species in Sri Lanka (De Silva, K.H.G.M. and De Silva, P.K., 1998; Jayatissa et al., 2002; Jayatissa, 2012). The salinity level of 12–15 psu was selected to be used as it is the moderate salinity level for many of the mangrove ecosystems in Sri Lanka (Kodikara et al., 2017b). The defining of moderate salinity level in this work was based on the naturally occurring salinity range in lagoons in Sri Lanka whereas salinities higher than 40 psu in Sri Lankan lagoons even in drought periods, are very rare (pers. obs.).

Mature propagules of *R. mucronata* and *A. marina* were collected from natural mangrove sites in the southern coast. The seeds of *A. auriculiformis* were collected from the southern region and used as planning materials. A sandy soil was prepared by mixing sieved loam soil with sand and organic matter (Compost) in 1 : 1 : 1 (v/v) proportion. Collected propagules of mangrove species and seeds of *A. auriculiformis* were initially planted in small polythene pots (with 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 unfurled leaves were considered as established seedlings and transferred to larger pots (30 cm diameter and 40 cm height) filled with the same soil mixture. In transferring seedlings, always four seedlings were planted in the same pot to get nine treatments (Fig. 3).

There were four replicates for each treatment and they were distributed and maintained in the greenhouse according to a completely randomized design (CRD). Each pot was kept individually in a plastic tray (40 × 35 × 15 cm) with moderately saline water (i.e., 12–15 psu) up to a level of 10 cm and irrigated twice a day with the same water. The salinity of the water in the tanks was measured by a hand refractometer (ATAGO S/Mill-E, Japan) once a week and adjusted when required. Commercially available fertilizer was applied once a month to each pot (Jayatissa et al., 2008; Dissanayake et al., 2014; Kodikara et al., 2017b; Dissanayake et al., 2018). The number of surviving

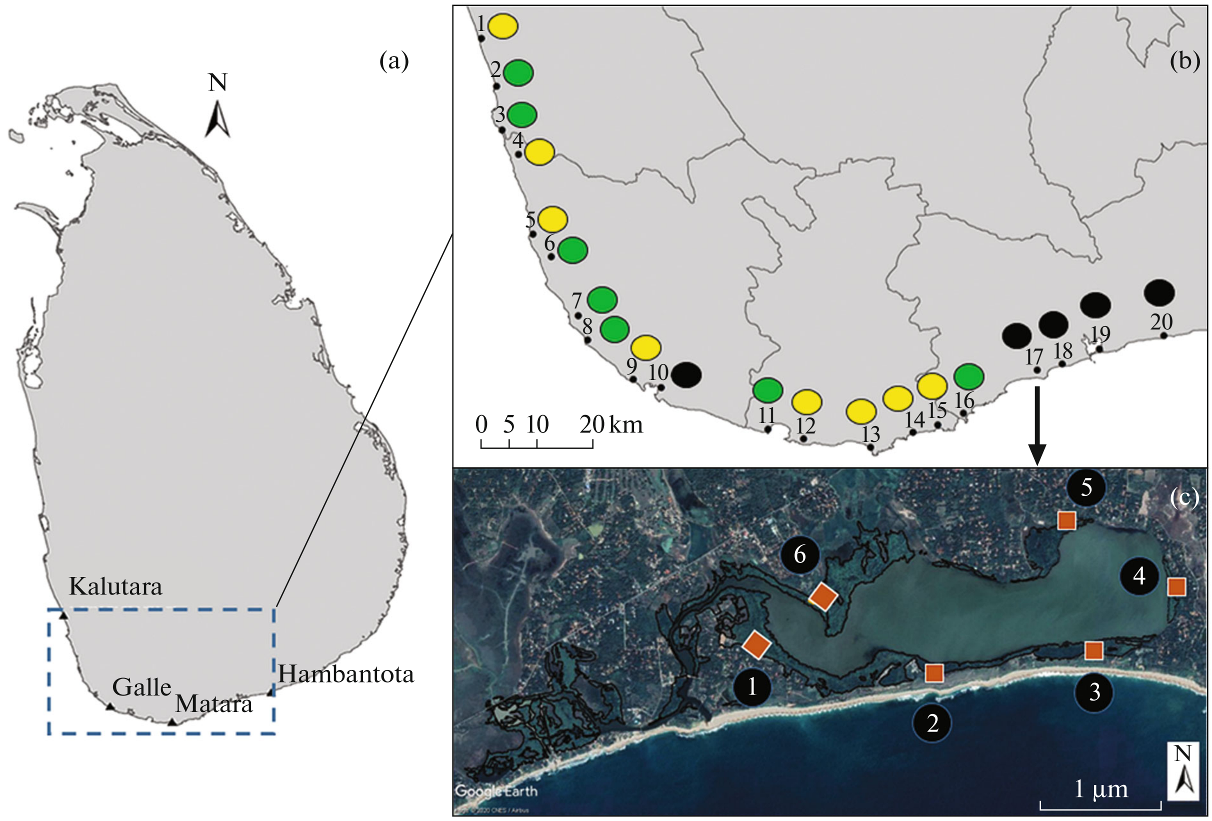

Fig. 1. Maps showing the study area (a) map of Sri Lanka; (b) presence and absence of *Acacia auriculiformis* along the coatal strip from Kalutara to Hambantota (green colour: none; yellow colour: rare; black: common); (c) Google Earth satellite image of Rekawa lagoon (14.04.2019; Maxar Technologies) showing the mangrove cover outlined in black and the study plots in brown squares.

seedlings in all the treatments and controls were counted at the end of the study.

The shoot height of each seedling to the top of the epicotyl was measured once a fortnight. Lengths of all branches were also measured and added to the height of the main stem to get the 'cumulative shoot height' of each seedling/sapling. At the end of the study, total leaf area of each seedling/sapling was quantified manually using millimeter paper method on which the exact size and shape of leaves were marked for all plant leaves. After six months of growth, saplings were harvested by using the following procedure. The plastic pots were removed and soil was carefully washed away to get the intact root system. Cleaned plants were blotted dry and were separated into roots, hypocotyls and shoot (stem and leaves). The fresh weights of shoots (excluding the hypocotyls of *R. mucronata*) and roots of each plant were measured. Then all parts were oven dried at 80°C until obtained constant value for dry weight. In addition, level of survival of *Acacia auriculiformis* under different salinity levels (~5, ~10, ~15 and ~25 psu) was studied by using 25 *Acacia* plants for each salinity level and the experiment was carried out for 30 weeks.

Field Validation

In order to study the negative impacts of *A. auriculiformis* on mangrove forests, particularly the risk to peripheries of mangrove forests, a detailed field study was carried out in Rekawa Lagoon (06°03′ N–080°50′ E) which is situated in the intermediate climate zone of Sri Lanka. The surface area of the lagoon is 250 ha and it has wide basin of 3.3 km in length, 0.9 km in width and 1.4 m in depth. The lagoon's long axis is running parallel to the ocean. There is inflow of several small freshwater sources that significantly account to change the salinity of the lagoon. The discharge of the lagoon is blocked by a sand bar that is frequently removed by local inhabitants facilitating the discharging. The salinity ranges from 0 to 35 psu (annual average of 15 psu) at the lagoon mouth, and from 5 to 16 psu in the middle and upper parts of the lagoon (annual average of 7.5 psu). The fringe mangrove forest is composed of true mangrove species such as *Avicennia marina*, *A. officinalis* L., *Aegiceras corniculatum* (L.) Blanco, *Bruguiera gymnorrhiza* (L.) Lamk., *B. sexangula* (Lour.) Poir., *Excoecaria agallocha* L., *Rhizophora mucronata*, *R. apiculata* Blume, *Ceriops tagal* (Perr.) C.B. Rob., *Lumnitzera racemosa* Willd., *Nypa fruticans* Wurmb. and mangrove associates such as

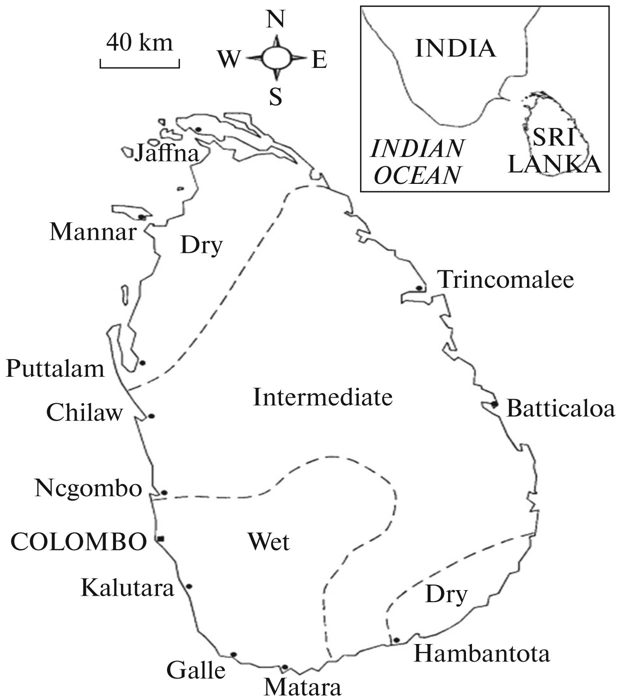

Fig. 2. Map of Sri Lanka showing the major climate zones (Adapted from Dahdouh-Guebas et al., 2000).

Acrostichum aureum L. Moreover, almost all the species that are reported as common mangrove species in Sri Lanka occur in the Rekawa mangrove forest. The mangrove belt is surrounded by localized grassy planes, scrub forests, paddy fields and homesteads at the leeward side and by coconut plantations at the seaward side. The intermediate zone along the south coast of Sri Lanka consists of intermediate climatic conditions. These conditions are intermediate to the dry and wet zones of Sri Lanka and have a short and less prominent dry season which runs from August to October. The annual average precipitation ranges between 1900–2500 mm which is predominantly influenced by two monsoons: the north-east monsoon (November to February) and south-west monsoon (May to August) and subsidiary influenced by the first inter monsoon and the inter monsoon. Temperature varies from 24 to 26°C determined by the cold breeze wind coming from the sea and blowing towards the land.

Periphery of the lagoon which includes outer margin of true mangrove zone, buffer zone and terrestrial zone (mesophytes) was the target study belt. The study plots were selected in the region of periphery of the mangrove forest. In total, six plots of 40 × 40 m were randomly selected using a grid map of the mangrove

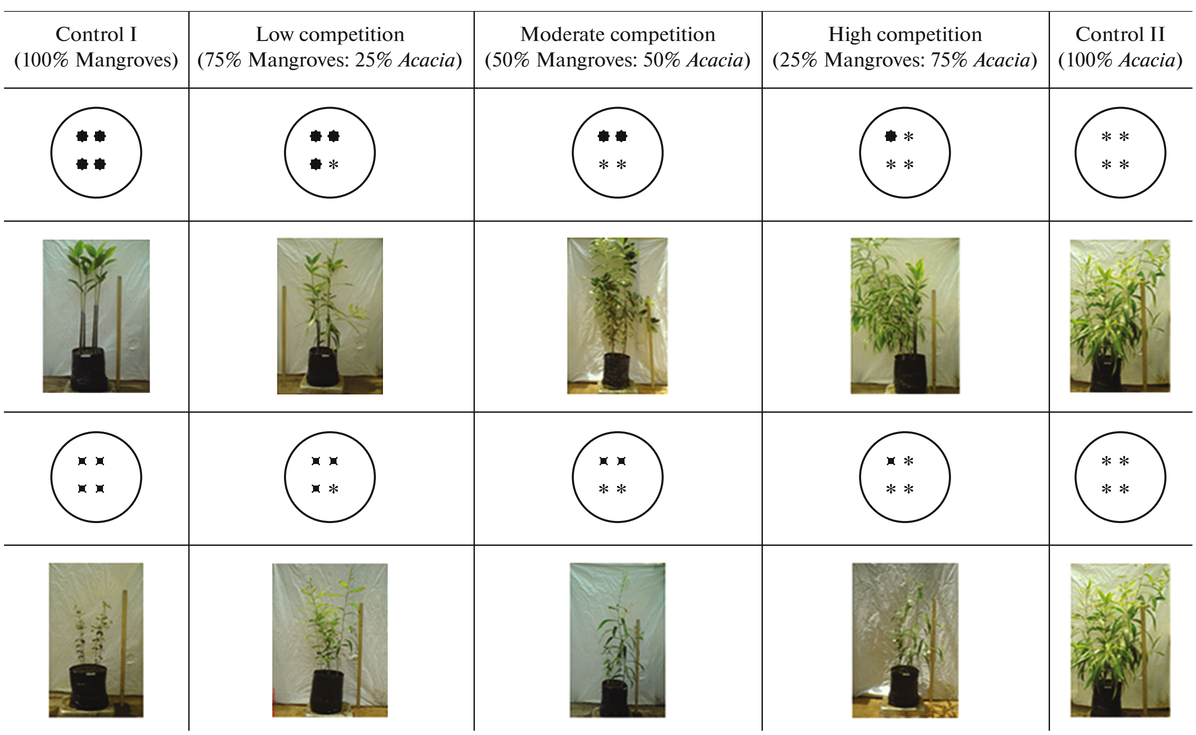

Fig. 3. Illustration depicting the experimental design of treatments under plant-house conditions and the levels of competition with the controls. Control I (first row: *Rhizophora mucronata*) (second row: *Avicennia marina*) consist of only true mangroves while control II is composed of only *Acacia auriculiformis*. In low competition level, a combination; 75% of true mangroves while 25% of *Acacia* plants is included. In moderate and high competition levels, 50 : 50 and 25 : 75% of true mangroves to *Acacia* plants are incorporated respectively. In both rows: 5 arms-star: *Acacia*; in the top row: black-filled symbol: *Rhizophora*; in the second row: four-pointed symbol: *Avicennia*.

ecosystem and a random number table. In view of that, a total area of 9600 m^2 (6 plots × 1600 m^2) was sampled and studied qualitatively (i.e. species composition, growth forms) and quantitatively (tree density, stem diameter, dominance, frequency and diversity and soil parameters like pH, redox and salinity). In each plot, species composition was first studied and recorded. The plants with >20 cm diameter at 130 cm (D_{130}) height were considered as trees and the plants which collar circumference at the base is lower than 10 cm were taken as seedlings while 10–20 cm collar circumference at the base were considered saplings (Bhuyan et al., 2003). Within each plot, all trees (mature plants in case of shrubs) were counted and identified.

In addition, the girth at height of 130 cm (G_{130}) of tree species was measured and the seedling bank was studied. The vegetation data collected from the mangrove ecosystems were quantitatively analyzed for density, dominance and frequency and relative values of the respective variables: relative density (RD), relative dominance (RDo) and relative frequency (RF) as described by (Mishra, 1968).

RD is defined as total number of individuals of a species in all quadrates to total number of quadrats in which the species occur while RDo means coverage value of a species with respect to the sum of coverage of the rest of the species in the area. The chance or probability of an individual of a given species to be present in randomly placed quadrat out of occurrence of all species is defined as RF. The importance value index (IVI) for each species was computed summing up the relative density, relative dominance and relative frequency (Curtis, 1959; Phillips, 1959). The IVIs were used to assess the dominance of *A. auriculiformis* plants in the studied plots. Phytographs were plotted and used for comparison of the different species. Simpson's diversity index was calculated for the studied plot area by using the following equation (Eq. 1).

$$\text{Simpson's diversity index} = 1 - [\Sigma(n_i/N)^2], \quad (1)$$

where, n_i = importance value of a species; N = sum of importance values of all the species.

In addition, six composite soil samples were taken from (the top 20 cm layer of) each plot and pH, redox and salinity were measured by using a bench top multimeter (Hach HQD, India).

Statistical Analyses

Growth parameters i.e. cumulative shoot height, total leaf area and dry weight of *Rhizophora mucronata*, *Avicennia marina* and *Acacia auriculiformis* were treated as continuous variables. Parametric tests (*t*-test for independent samples) were performed to check the significant differences for all variables examined under different competition levels and the tests were carried out separately for the three species with respect to their controls (Control-Ia, Control-Ib and Control-II). Also, levels of survival of *Avicennia marina*, *Rhizophora mucronata* and *Acacia auriculiformis* plants under the 15 PSU salinity level in the study were tested using binomial proportional test (2-sample test for equality of proportions with chi-squared (χ^2) values). Mann–Whitney *U* Test was performed to check the significant difference of *Acacia* infestation between Hambantota and Matara districts and Galle and Kalutara districts. All statistical analyses were performed using R-3.2.2 statistical software.

RESULTS

Initial Field Survey

The results showed that 65% (13 sites/20 sites) of the studied sites in the southern coast of Sri Lanka are infested by *A. auriculiformis* (Table 1). Further, 38% of the infested sites are highly invaded by *Acacia* plants. Interestingly, the sites located towards the south-eastern coast are more vulnerable to *Acacia* invasion as compared to the other sites. When comparing the infestation of *Acacia* in Matara and Hambantota districts with Galle and Kalutara districts, significant incursion could be observed in the first two districts [Mann–Whitney *U* Test, $(n_1, n_2) = (10, 10)$, $U < 23$, $p < 0.05$].

Green-House Experiment

In the green-house experiment, the two mangrove species and *A. auriculiformis* had 100% survival percentage at all competition levels. Growth performances of the mangrove species grown with the *Acacia* plants showed significant variations at different competition levels (Tables 2 and 3). Cumulative shoot heights of the *Rhizophora* plants grown with *Acacia* plants under different competition levels did not show significant differences as compared to the control plants (Control-Ia). Nevertheless, the total leaf area of the *Rhizophora* plants grown in the high-competition level was significantly lower than that of the control plants [$t(18) = -3.31$, $p < 0.05$] while, more interestingly, the dry weights at three different competition levels; low, moderate and high, were significantly higher [$t(26) = 4.54$, $t(22) = 5.22$, $t(18) = 4.02$, $p < 0.05$ respectively] (Table 2). On the other hand, *A. auriculiformis* plants performed at their best and did not significantly differ from the control plants (Control-II). Mentioning the *Avicennia* plants, cumulative shoot height, total leaf area and dry weight of the plants grown at the high-competition level were significantly lower [$t(18) = -6.12$, $t(18) = -8.92$, $t(18) = 9.33$, $p < 0.05$ respectively] than that of the control plants (Control-1b) (Table 3). The *Avicennia* plants grown under the low and moderate competition levels did not show any significance in growth parameters with the control plants. *A. auriculiformis* plants grown with the *Avicennia* plants performed at their maximum and did not show any significant deviation from the

Table 1. Abundance of *A. auriculiformis* at the periphery of mangrove forests along the coastal stretch from Kalutara to Hambantota ('rare' is the number of individuals in 10 m wide belt beyond the outer margin of the mangrove forest is less than 10; 'common' is the number of individuals in 10 m wide belt beyond the outer margin of the mangrove forest is more than 10); N/A = not applicable because it is absent)

Mangrove forest	Number in the map	Presence/Absence	Abundance of *Acacia auriculiformis*
Kalutara	1	Presence	Rare
Maggona	2	Absence	N/A
Kaluwamodara	3	Absence	N/A
Bentota	4	Presence	Rare
Madu Ganga	5	Presence	Rare
Ambalangoda (Madampe Lake)	6	Absence	N/A
Hikkaduwa	7	Absence	N/A
Dodanduwa	8	Absence	N/A
Galle (Mahamodara)	9	Presence	Rare
Galle (Dewata)	10	Presence	Common
Weligama	11	Absence	N/A
Mirissa	12	Presence	Rare
Dondra	13	Presence	Rare
Lunukalapuwa	14	Presence	Rare
Dickwella	15	Presence	Rare
Moraketiara	16	Absence	N/A
Rekawa	17	Presence	Common
Kalametiya-Lunama	19	Presence	Common
Kahandamodara	18	Presence	Common
Hambantota	20	Presence	Common

Table 2. *Rhizophora mucronata* with *Acacia auriculiformis*. Values are mean of four replicates of each treatment. Different letters next to values indicate statistically different means at $P \leq 0.05$. Level of significance was checked with the fixed factor "level of competition." N/A: not applicable

Plant species	*Rhizophora mucronata*			*Acacia auriculiformis*		
competition level	cumulative shoot height, cm	leaf area, cm^2/plant	dry weight, g	cumulative shoot height, cm	leaf area, cm^2/plant	dry weight, g
Control-Ia	77.8 ± 9.3^{a}	36.18 ± 2.15^{x}	9.87 ± 2.54^{a}	N/A	N/A	N/A
Control-II	N/A	N/A	N/A	127.2 ± 11.4^{x}	96.22 ± 14.31^{a}	30.16 ± 3.18^{x}
Low competition	66.2 ± 8.7^{a}	38.64 ± 3.34^{x}	$\mathbf{17.46 \pm 1.95^{b}}$	130.5 ± 14.1^{x}	87.62 ± 10.88^{a}	34.31 ± 5.23^{x}
Moderate competition	65.9 ± 5.1^{a}	37.82 ± 2.35^{x}	$\mathbf{16.96 \pm 2.42^{b}}$	129.7 ± 10.3^{x}	92.37 ± 16.26^{a}	29.91 ± 4.51^{x}
High competition	67.0 ± 4.4^{a}	$\mathbf{31.01 \pm 1.20^{y}}$	$\mathbf{16.86 \pm 1.37^{b}}$	133.4 ± 9.5^{x}	91.56 ± 12.39^{a}	28.75 ± 4.33^{x}

control plants (Control-II). The level of survival of *Acacia* plants after 30 weeks showed 100% under 5 psu salinity level, 96% when the salinity level was 10 psu, 92 and 44% under 15 and 25 psu levels respectively. Therefore, the level of survival of the *Acacia* plants grown under 25 psu was significantly low [$\chi^2 = 11.48$, df (1), $p < 0.05$] (Fig. 4).

Field Validation Experiment

The species present in the plots are *Aegiceras corniculatum* (plot nos. 2 and 3 in Table 4), *Bruguiera gymnorrhiza* (plot nos. 1, 2 and 3 in Table 4), *Excoecaria agallocha* (plot nos. 2, 3 and 5 in Table 4), *Lumnitzera racemosa* (plot nos. 2, 3, 4 and 6) [True mangrove species], *Acrosticum aureum* (plot nos. 2, 3 and 5

Table 3. *Avicennia marina* with *Acacia auriculiformis*. Values are mean of four replicates of each treatment. Different letters next to values indicate statistically different means at $P \leq 0.05$. Level of significance was checked with the fixed factor "level of competition." N/A: not applicable

Plant species	*Avicennia marina*			*Acacia auriculiformis*		
competition level	cumulative shoot height length, cm	leaf area, cm^2/plant	dry weight, g	cumulative shoot height length, cm	leaf area, cm^2/plant	dry weight, g
Control-Ib	85.1 ± 8.8^a	12.24 ± 1.84^x	6.22 ± 1.1^a	N/A	N/A	N/A
Control-II	N/A	N/A	N/A	127.2 ± 11.4^x	96.22 ± 14.31^a	30.16 ± 3.18^x
Low competition	89.4 ± 6.2^a	10.49 ± 2.62^x	6.38 ± 1.4^a	126.9 ± 14.8^x	97.45 ± 12.77^a	29.33 ± 5.74^x
Moderate competition	78.0 ± 7.4^a	9.61 ± 1.43^x	5.59 ± 1.1^a	134.5 ± 14.7^x	90.34 ± 10.26^a	33.54 ± 6.32^x
High competition	$\mathbf{51.0 \pm 4.6^b}$	$\mathbf{6.72 \pm 0.78^y}$	$\mathbf{3.64 \pm 0.6^b}$	131.7 ± 10.8^x	91.47 ± 8.77^a	32.90 ± 2.97^x

Table 4. Floristic composition, vegetation attributes (frequency, density and dominance), and their relative data of six plots (9600 m^2) sampled in Rekawa lagoon. Vegetation data collected from different plots were separately compiled in calculating vegetation attributes. (Area coverage was considered instead of tree density, for *Acrostichum aureum* in calculating density and dominance)

Rekawa mangrove forest (Plot 01–06)							
species	frequency	relative frequency, %	tree density, m^{-2} ($\times 10^{-3}$)	relative density, %	dominance, m^2	relative dominance, %	IVI (/300)
Bruguiera gymnorrhiza	50.0	13.0	2.50	10.6	2.56	22.3	**45.9**
Excoecaria agallocha	50.0	13.0	3.75	16.0	0.37	3.2	**32.2**
Lumnitzera recemosa	66.6	17.4	4.16	17.7	0.58	5.0	**40.1**
Acrostichum aureum	50.0	13.0	0.37	1.6	0.72	6.3	**20.9**
Aegiceras corniculatum	33.3	8.8	1.10	4.7	1.02	8.8	**22.3**
Acacia auriculiformis	100.0	26.0	9.89	42.1	6.06	52.5	**120.6**
Hibiscus tiliaceus	33.3	8.8	1.72	7.3	0.22	1.9	**18.0**
Total	**383.2**	**100.0**	**23.49**	**100.0**	**11.53**	**100.0**	

in Table 4), *Hibiscus tiliaceus* (plot nos. 4 and 6 in Table 4) [mangrove associates] and *Acacia auriculiformis* (plot nos. 1–6) [Invasive alien species]. Periphery of the mangrove forest exhibits a multi-tiered stratification with a sub-canopy layer occupied by the species *B. gymnorrhiza*, *A. corniculatum*, and *L. racemosa* while shrub level by *E. agallocha*. Moreover, the understory is represented by *A. aureum*.

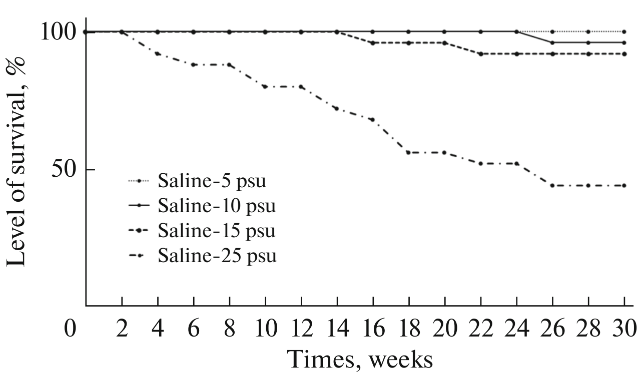

Fig. 4. Graph showing the level of survival of *Acacia auriculiformis* plants grown under different saline conditions; 5, 10, 15 and 25 psu.

Saplings and seedlings were only observed for *A. corniculatum*, *B. gymnorrhiza* and *A. auriculiformis.* Sapling and seedling densities (i.e. number of individuals of a particular species per square meter) of *A. corniculatum* and *B. gymnorrhiza* were 1.5 ± 0.5 and 5.1 ± 0.9 m^{-2} and 1.5 ± 0.3 and 4.5 ± 0.7 m^{-2} respectively. For *A. auriculiformis*, sapling density was 11.2 ± 1.4 m^{-2} while seedling density was 15.4 ± 1.5 m^{-2}. The results showed the highest seedling density of *Acacia* plants in the periphery of mangroves. Furthermore, all types of *Acacia* plants (seedlings, saplings and trees) co-occur with true mangrove species. The main girth class of *A. corniculatum* and *B. gymnorrhiza* was 31–44 cm and *L. racemosa*, *E. agallocha* and *Hibiscus tiliaceus* Linn. plants and *A. auriculiformis* were in the girth class of 17–30 cm.

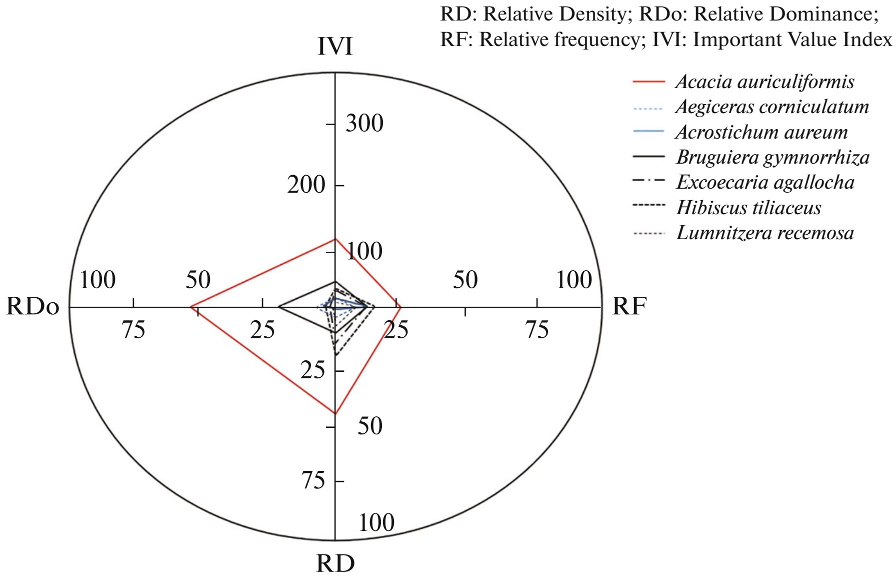

Fig. 5. Phytograph showing the important value indexes (IVIs) of the periphery of Rekawa mangrove forest. Relative values of species frequency, density and dominance are included in the phytographs and the total is given out of 300. IVIs of different species are shown in different colors and given in the legend. Exact IVIs are given in Table 4.

The IVI of the studied plots ranged between 18.0 and 120.6 with the highest value recorded for *A. auriculiformis* (see Fig. 5). The high relative density (42.1%) and relative dominance (52.5%) largely contributed for the IVI of *A. auriculiformis*. True mangrove species held IVI values in the range of 22.3 to 45.9 and the highest was recorded for *B. gymnorrhiza*. Moreover, mangrove associates like *A. aureum* and *H. tiliaceus* showed low IVI values (see Table 4 and Fig. 5). Simpson diversity index was 0.77 for the mangrove periphery of the lagoon. Average pH of the soil samples was 6.4 ± 0.3 and redox potential was shown to be -135 ± 23 mV. Mean soil salinity recorded was 9.5 ± 0.5 psu.

DISCUSSION

Ecological Interpretation

Apparently, invasive species have become a topmost threat to biodiversity of Sri Lanka (Kariyawasam et al., 2019). (Marambe et al., 2001) mentioned that these invasive species are introduced in two ways; i.e. intentionally and unintentionally (accidentally). According to the preliminary survey, it has been revealed that *Acacia* plants were distributed among the people in the Hambantota district as an ornamental and shelter plant in the early 2000s. Moreover, in view of the increased global warming, *Acacia* species established along with *Eucalyptus*, *Pinus*, teak and mahogany in several places in Sri Lanka including Matara and Hambantota to increase the carbon stocks of the mixed culture forest plantations aiming at regulating the carbon cycle (De Costa and Suranga, 2012). This could be the reason why Hambantota and Matara regions are highly affected by *Acacia* invasion. Furthermore, poor management and less scrutiny may have caused to widespread this species (Marambe et al., 2001; Kodikara et al., 2018). However, too little evidence exists to confirm that *A. auriculiformis* has been introduced to Kalutara and Galle. Therefore, it is assumed that *A. auriculiformis* dispersed naturally in these regions (Kariyawasam et al., 2019). Alejandro and Lohengrin (2008) reported that when an alien plant species is placed in a non-native habitat, there is a high possibility to increase their vegetation cover within a short period of time and different strategies are employed to do so. A wide range of adaptability of *A. auriculiformis* has made it a dominating invader in the vegetation (Islam et al., 2019). *Acacia* plants have rapid early growth rates and produce an excessive amount of seeds with a high dispersal capacity (Heringer et al., 2020). This facilitates their initial establishment in a non-native environment. Moreover, they produce long-lived flowers with early reproductive maturity and a greater probability of pollination (Minteer et al., 2020). Also, this invasive *Acacia* is responsible for the high water consumption and disturbed water balance in their invaded sites. Their strong massive root system penetrates and extends into the soil to reach ground water (de Moura et al., 2020). In many plantations, the established trees shade out their surrounding native flora threatening the growth of understory species (Minteer et al., 2020). Since *Acacia* plants are well armored with aforementioned different survival mechanisms, they are able to compete with native plants for space, water and nutrients. It is suggested that many of these adaptations must have been used in invading the periphery of the Rekawa mangrove forest.

According to the results, *A. auriculiformis* has become the dominant plant species in the back-mangroves of the Rekawa forest co-occurring with true mangroves. The recorded highest sapling and seedling densities and the highest IVI with a high contribution of relative densities and relative dominance further support the competitive domination of the *Acacia* plants over mangroves. This scenario is further facilitated by the significant changes that occur in the forest soil. Since the decomposition rates of the *Acacia* residues are slower it results in higher total biomass with lower diversity and different taxonomic compositions with significant changes in the soil microbial communities. This, in turn, modifies biogeochemical cycles, for example, the nitrogen cycle. Moreover, it can also drastically increase the carbon composition in the soil. Hence, this litter accumulation is responsible for the reduced soil fertility and the process of seed germination of mangrove species by reducing the viability of their seeds (de Moura et al., 2020; Minteer et al., 2020). Besides, *Acacia* creates a rhizomatous system with massive surface root development exploiting the soil density. On the contrary, the richness and abundance of the seeds of true mangroves and the mangrove associates in the understory are severely affected by the accumulation of *Acacia* seeds. The native seed diversity of the seed bank is drastically decreased. Mangroves are a rich reservoir of microbial diversity which harbors a unique accumulation of microorganisms. The modified chemical composition of the soil affects the structural and functional diversity of the mangrove microbiome hindering its supply of nutrients which in turn reduces the growth rates of the mangrove plants (Souza-Alonso et al., 2017).

Despite not being a halophyte, *A. auriculiformis,* has a remarkable survival rate in saline environments (up to 25 psu). With an average annual salinity of 15 psu in the lagoon mouth and 7.5 psu in the upper and middle parts of the lagoon, Rekawa Lagoon seems to be an environment facilitating growth and reproduction of this species invading the mangroves bordering the lagoon. Performance of maximum growth of *A. auriculiformis* with no significant difference with the control plants at all three competition levels revealed their greater potential in the competitive invasion. In contrast, the studied mangrove species demonstrated significant variations in their growth parameters when compared to the control plants, especially at the highest competition level. However, this ability to express higher growth performances can make *A. auriculiformis* to possibly replace the co-occurring true mangrove species from their native habitats, thereby influencing the dominance of the invasive plants and hindering the succession of the natives. Once *A. auriculiformis* is established through succession, it tends to shade the native understory of the disturbed mangrove habitat. In Rekawa lagoon, the understory is represented by the conventional mangrove associate *A. aureum*. It is reported that *A. aureum* is severely threatened and replaced by the invasive *A. auriculiformis* in the Rekawa lagoon exploiting its natural biodiversity (Madarasinghe et al., 2015). This is well depicted by the obtained low IVI values of *A. aureum* and *H. tiliaceus* in this study. These disruptions can alter the mangrove microsite conditions radically. Thus mangroves will lose its opportunity to compete with invasions and opens windows for *A. auriculiformis* to exploit the new environment. These changes will prevent the succession back to its original state resulting in a different ecosystem (Lugo, 1999).

In addition to the aforementioned mechanisms, allelopathic effect of *Acacia* plants could have negatively affected the true mangroves (for example, *A. corniculatum*, *B. gymnorrhiza*, *L. racemosa* and *E. agallocha*). Minteer et al. (Minteer et al., 2020) has shown that the allelopathic properties of leaf leachates of *A. auriculiformis* give this invader a competitive advantage in their introduced habitats. It has been found that allelopathy can affect seed germination, seedling growth, root and shoot elongation, lateral roots, net photosynthetic and respiration rates and the biomass of the surrounding species (Souza-Alonso et al., 2017). More specifically, allelochemicals that are produced by IAS can cause immediate or aberrant effects on the development of native species favoring its invasion (Vijayan, 2015). The findings of this study indicate a reduction in the growth of *Rhizophora* at the high competition level suggesting the allelopathic effect might be increased and that may have caused to reduce the growth of *Rhizophora* plants. However, the level of tolerance of *Rhizophora* plants is satisfactory as the total leaf area was only affected by the high competition. Lorenzo (Lorenzo et al., 2010c) highlighted that *Acacia dealbata* releases allelochemicals mostly during its flowering seasons and affects targeted species. Accordingly, since this study was only carried out for six months and the plants did not reach its flowering season, the allelopathic effect on *Rhizophora* might be less and lead to the remarkable tolerance at moderate competition level only if *A. auriculiformis* allelochemicals interact similar to *A. dealbata*. However, allelopathy related bioassays are mostly conducted under controlled/optimum conditions in laboratories, thus when it is applied in the fields the results may vary due to soil conditions and the presence of soil microbes.

When considering the growth performances of *Avicennia marina* it had less competitiveness at high density of *Acacia* plants. Although genus *Avicennia* is known to have a wide range of tolerance as compared to genus *Rhizophora* (Robert et al., 2009), it has been proven that *Rhizophora* is a strong competitor in case of invasive plant species. Concerning the higher dry weights at all three competition levels of *Rhizophora,* it could be a mechanism to make them robust against the invasive plant and it would be interesting to experiment dry matter allocation among shoot and root systems under different competition levels in future studies.

Implication on Ecosystem Monitoring and Management

Vegetation is often monitored through remote sensing (Lucas et al., 2020; Madarasinghe et al., 2020a, 2020b) which in many cases is used as a quantitative tool to study total vegetation cover or to break the latter down into cover per species (Van et al., 2015). In some cases, remote sensing is used to quantify biomass (Hamdan et al., 2014; Lucas et al., 2021). However, decline of species richness has been shown to precede qualitative degradation in Sri Lanka (Koedam and Dahdouh-Guebas, 2008; Satyanarayana et al., 2011). Looking at qualitative composition of the vegetation such as proportion of vegetation is, therefore, not enough to understand the functional ecological implications of changing species compositions. Cryptic ecological degradation, a qualitative ecological and socio-economic degradation of one ecosystem component that is masked by an easily detectable quantitative status quo or even increase of another, has been found responsible for functional degradation of the mangrove (Dahdouh-Guebas et al., 2005). More particularly, the functional degradation involves a qualitative decline of typical, stenotopic, vulnerable, valuable and functional species that is masked by a quantitative increase of less typical, eurytopic, disturbance-resistant, less valuable and less functional species, overall resulting in a reduced functionality and resilience of a system (Dahdouh-Guebas et al., 2021). We emphasize the need of pinpointing *Acacia auriculiformis* trees in any remote sensing monitoring studies on the landward mangrove area to prevent erroneous conclusions on expanding "mangrove" species. Earlier studies performed by Jayatissa (Jayatissa et al., 2002) and Dahdouh-Guebas (Dahdouh-Guebas et al., 2005) showed that conservation and management decisions were indeed based on mangrove forest area, rather than on composition or functionality. Pinpointing invasive species or stratifying vegetation monitoring into canopy trees, understory trees and juvenile plants has been identified before as a tool for prediction and as an early-warning system for functional degradation (e.g. (Dahdouh-Guebas and Koedam, 2002; Dahdouh-Guebas et al., 2005; Satyanarayana et al., 2011).

Mitigation Measures

Sustained suppression of *A. auriculiformis* is challenging owing to the accumulation of abundant seed banks in the soil and the speedy growth of invasive *A. auriculiformis.* As a short term strategy, large scale herbicidal control combined with mechanical control can achieve potentially effective results against invasive plants (Wagner et al., 2017). Once the new seedlings emerge, follow up control programs should be carried out to successfully limit the growth. It is also expected to take several years for the ecosystem to recover and bring back the original diversity and functionality to the state prior to the invasions. As an efficient method, the accumulated large layer of litter should be simultaneously removed to facilitate the germination of mangrove seeds. Nevertheless, considering the secondary effects, adequate planning and proper management are necessary to enhance the fertility of the subsoil without leading to soil erosion and to maintain a native seed bank. Furthermore, ecosystem recovery can be facilitated by the rehabilitation of native mangroves with low demand for nutrients and can surpass the growth of remaining invasive *A. auriculiformis* seedlings.

The current conventional control methods and management practices are quite expensive, laborious and impractical at large scales. Therefore, biological control methods can be introduced to infested environments that can reduce the seed germination and damage saplings and seedlings of *A. auriculiformis.* Biological control methods integrated with conventional control methods will lead to viable long term results. Several arthropods and fungal species that are host specific and has the potential to act as damaging agents can be used as potential biological control agents (Souza-Alonso et al., 2017; Minteer et al., 2020). In addition, an ethnobotanical management approach would also help in eradicating invasive plant species (Kodikara et al., 2018, Vandebroek et al., 2020) and in case of *Acacia* plants, people can be encouraged to use these plants for firewood. If this is well executed, it may cause to reduce the vegetation cover of *Acacia* plants in the long-run. We encourage the relevant government institutions to take early action to remove yet another threat to mangrove functionality in the invasive species and recommend it should be done in close connection with the local communities living within and adjacent to the mangrove forest.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement of the welfare of animals. The article does not contain any studies involving animals in experiments performed by any of the authors.

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