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Climate and intertidal zonation drive variability in the carbon stocks of Sri Lankan mangrove forests

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ABSTRACT

Sri Lanka is at the forefront of global mangrove conservation. It is the first country to officially protect all its remaining mangrove forests and has embarked on an ambitious plan to restore 10,000 ha of wetland during the United Nations Decade of Ecosystem Restoration. One incentive for this conservation effort is a recognition, based on research mostly done elsewhere, of the importance of mangroves for carbon sequestration and storage. However, a lack of data on Sri Lankan mangrove carbon pools, especially on soil organic carbon, has been recognized as a major impediment to national climate change mitigation strategies. The current work examined both above and below-ground carbon stocks of five important mangrove forests in Sri Lanka (Rekawa, Puttalam-Kalpitiya, Pambala-Chilaw, Batticaloa and Negombo) which are situated in the three major climate zones (dry, intermediate and wet) and therefore sample the main climatic drivers of spatial variability. Above-ground carbon, below-ground root carbon and soil carbon stocks of mangroves in Sri Lanka ranged from 75.5 to 189.1 Mg C ha^{-1}, 7.9 to 14.3 Mg C ha^{-1} and 643.6 to 1253.6 Mg C ha^{-1}, respectively. The highest total mangrove carbon stock was recorded from the Rekawa lagoon which is in the intermediate climate zone (1455.4 Mg C ha^{-1}) while the lowest was found in the Batticaloa lagoon in the dry zone (734.7 Mg C ha^{-1}). Soil carbon stocks were substantially higher in the places where vegetation biomass and stand densities are high. Soil comprised 83–90% of the total mangrove carbon stocks at all sites, highlighting the large potential for release into the atmosphere as carbon dioxide if these habitats are disturbed. Overall, our study contributes important data that broadens our current understanding of how mangrove organic carbon pools vary spatially and with climatic zone.

1. Introduction

Mangroves are unique coastal ecosystems that occur within the intertidal zone of tropical and subtropical regions of the world (Mukherjee et al., 2014). They support an array of ecosystem services such as nutrient cycling, the provision of nursery, breeding and feeding grounds for fish and crustaceans, including many of economic importance, shoreline defense against storm surges and erosion and the trapping of sediments that could damage reefs and seagrass (Dahdouh-Guebas et al., 2005; Donato et al., 2011; Hilmi et al., 2017; Satyanarayana et al., 2017). Mangroves frequently underpin livelihoods for local communities through their provision of forest products including food (fish, crabs, and prawns), firewood, timber, waxes, honey and charcoal (Ron and Padilla, 1999; Walters et al., 2008).

Mangrove forests are also ranked amongst the most carbon rich of all ecosystems (Donato et al., 2011), often storing 4–8 times the carbon

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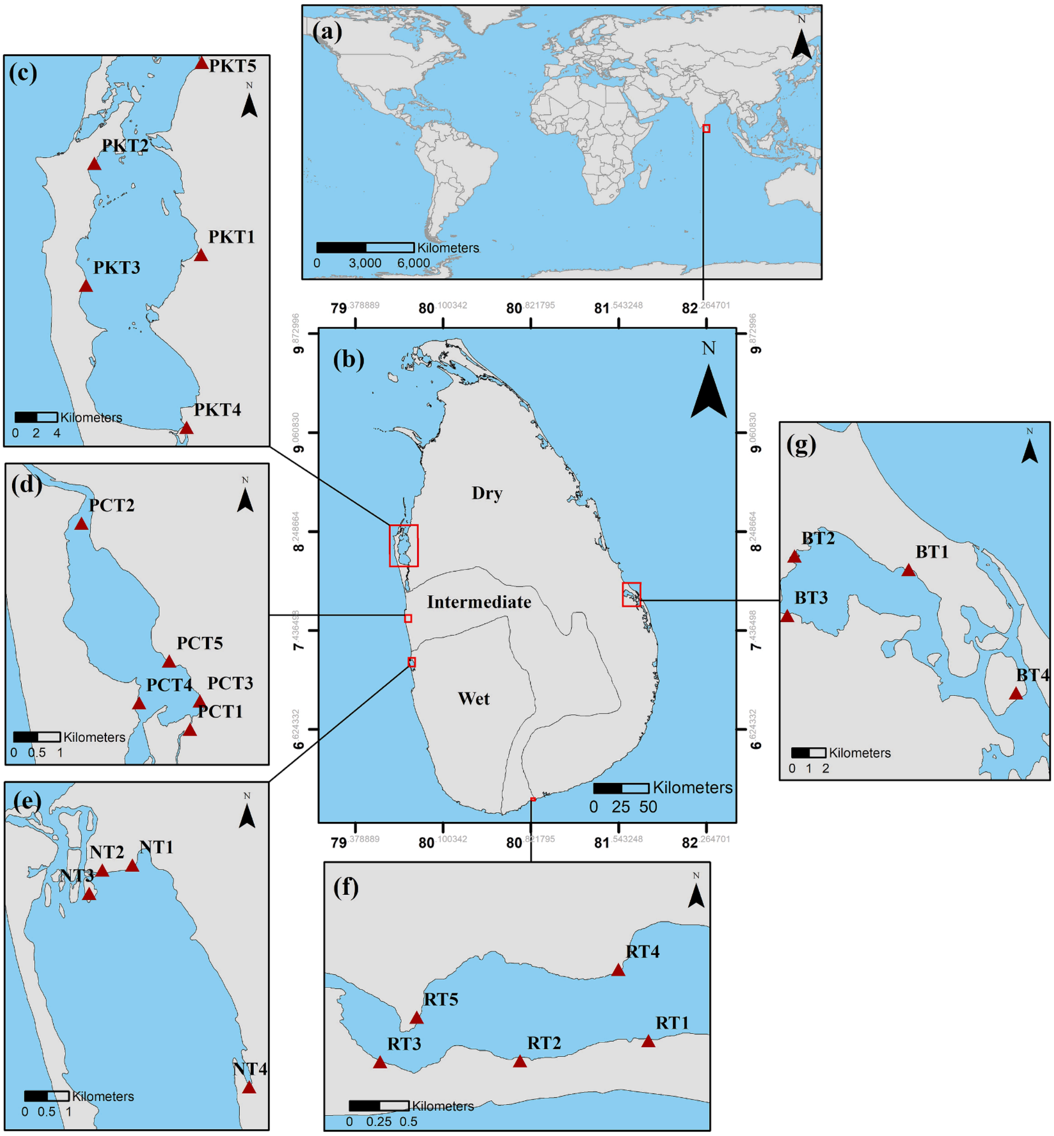

Fig. 1. Map showing the study locations and replicate transects (triangles) used for the study: where, (a) Sri Lanka's location in world, (b) distribution of study locations across the three major climate zones in Sri Lanka, (c) Puttalam-Kalpitiya lagoon, (d) Pambala-Chilaw lagoon, (e) Negombo lagoon, (f) Rekawa lagoon and (g) Batticaloa lagoon.

found in terrestrial forests (Lugo and Snedaker, 1974; Gress et al., 2017). Assuming a global mangrove coverage of 152, 361 km^2 (Spalding et al., 2010), the annual carbon burial in mangrove soils has been estimated at 34.4 Mg C Yr^{-1} with an average burial rate of 2.26 ± 0.39 Mg C ha^{-1} yr^{-1} (McLeod et al., 2011); this contrasts with many terrestrial forests that become saturated with carbon at maturity. Nevertheless, when disturbed by human activities mangroves can release greenhouse gasses, thereby shifting from a sink to a source of carbon (Kauffman et al., 2017; Adame et al., 2018) with estimates suggesting that approximately 316,996,250 Mg of CO_2 was released to the atmosphere as a result of global mangrove deforestation between 2000 and 2012 (Hamilton and Friess, 2018). It is estimated that mangrove conversion to shrimp ponds or pastures leads to emissions of between 1067 and 3003 Mg CO_2e per hectare (Kauffman et al., 2017). This is particularly disturbing given that mangrove forests continue to decline in many areas (Polidoro et al., 2010), although it is encouraging that recent research in Asia has shown rates of loss reducing to 0.18% yr^{-1} (Richards and Friess, 2016). Whilst international climate policy on nature-based solutions has focused mostly on terrestrial ecosystems, mangroves are now receiving enhanced interest as candidates for instruments such as Reducing Emissions from Deforestation and Forest Degradation (REDD +) and Enhancing Forest Carbon Stocks in Developing Countries and for inclusion within Nationally Determined Contributions under the Paris Agreement (Kauffman and Donato, 2012; Aziz et al., 2015; Ahmed and Glaser, 2016). Accurate quantification of existing total carbon stock (above-ground and below-ground pools) is required for the application of such policy tools (Boone Kauffman et al., 2017). Over the past 20 years blue carbon research has grown considerably and is expected to continue to do so in the future (Macreadie et al., 2019; Friess et al., 2020).

Currently, very limited information is available on the total carbon storage of mangroves in Sri Lanka, with only a few studies having quantified above-ground carbon (AGC) and below-ground root carbon (BRC) pools using allometric models for biomass estimation (see, Amarasinghe and Balasubramaniam, 1992; Gunawardena et al., 2016; Perera and Amarasinghe, 2017, 2018; Cooray et al., 2018). However, these allometric biomass estimations, particularly for below-ground root biomass (BRB), can involve large errors when applied to sites where the environmental conditions differ from those where the models were originally developed, resulting in significant uncertainty in local

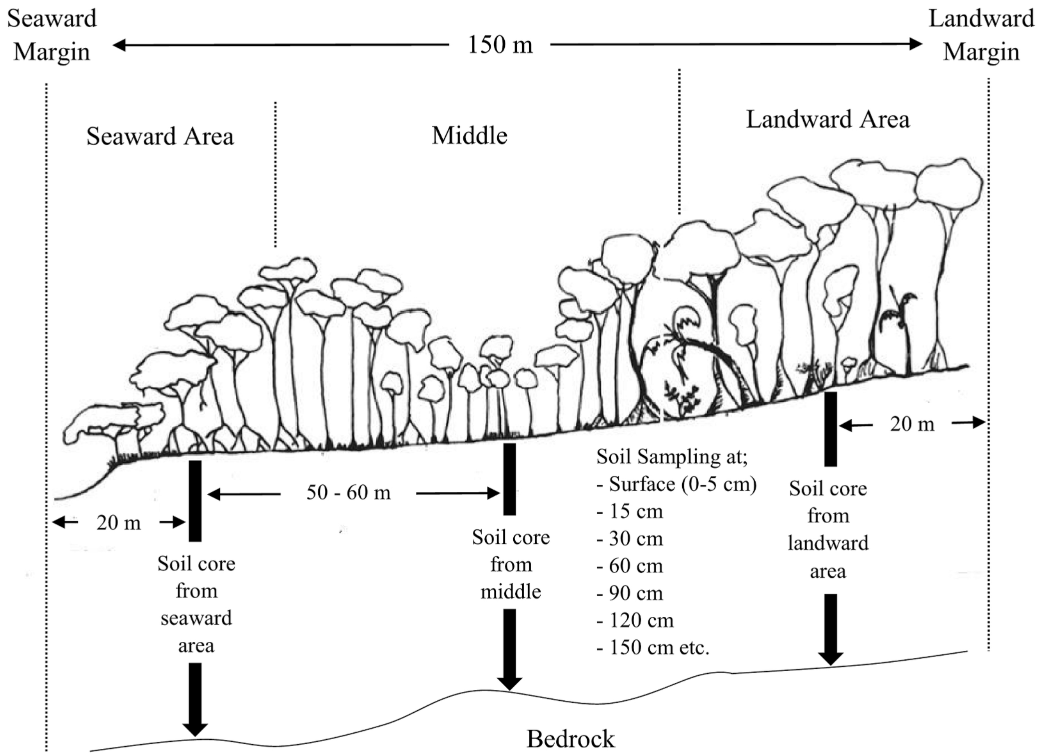

Fig. 2. A schematic diagram showing the sampling for root biomass and soil carbon along a 150 m long belt transect. On each transect, a core was taken from each of the three distinct vegetation assemblages, a) seaward, b) middle assemblage c) landward assemblage. Here, illustrative distances with respect to a 150 m long transect. These distances varied on the length of transect or the distance from the seaward to landward margin and the length of the different mangrove areas (seaward, middle and landward) along transect.

mangrove carbon assessments (Adame et al., 2017). Further, the data available for deep soil carbon pools of mangroves in Sri Lanka remains scarce, with a recent study revealing that soil carbon in the top 45 cm of the soil profile can range from 316.29 Mg ha^{-1} to 580.84 Mg ha^{-1} (Perera and Amarasinghe, 2019). Since mangroves are known to have carbon rich soils with organic horizons that may extend down to >600 cm depths (Ellison, 2008), these estimates are based on only a small fraction of the total carbon pool. Mangrove removal and degradation may quickly influence soil carbon dynamics even beyond 1 m in depth (e.g. Lang'at et al., 2014). Therefore, where mangrove soils exceed 1 m in depth, it is recommended to sample at least the top 100 cm of the soil profile to account for this potential variability (Kauffman and Donato, 2012).

The aim of the current study was to quantify the structure and total carbon stocks of mangrove forests spanning the three major climatic zones (dry, intermediate and wet zone) in Sri Lanka. We determined the above-ground vegetation attributes (stand densities, stand basal area and above-ground biomass) and the above-ground and the below-ground carbon pools of five large and important mangrove forests in the country. The following research questions were addressed: a) How is the total carbon storage of mangrove forests influenced by forest structure? b) How do other forest characteristics relate to total soil carbon stocks? c) How do the carbon stocks of mangrove forests in Sri Lanka differ across different climate zones? d) How do mangrove carbon pool estimates from Sri Lanka compare with available global mangrove carbon data? We address some of the knowledge gaps in the current understanding of mangrove carbon dynamics in Sri Lanka to support policy development and climate change mitigation.

2. Methodology

2.1. Study sites

Sri Lanka is an island located in the Indian Ocean, southwest of the Bay of Bengal, between latitudes of 5.55° and 9.51° N and longitudes of 079.41° and 081.54° E. The coastline extends for 1738 km and encompasses an area of 65,610 km^2 (Kodikara et al., 2017). The country is divided into three major climate zones based on annual rainfall and its distribution, namely the dry, intermediate and wet zones, with annual rainfall of <1750 mm, 1750–2500 mm and > 2500 mm, respectively. For this study, five large and important mangrove forests were selected covering all three climate zones (Fig. 1). Rekawa and Pambala-Chilaw are located in the intermediate zone while Puttalam-Kalpitiya and Batticaloa lagoons represented the dry zone. Wet zone mangroves were represented by Negombo lagoon.

2.2. Mangrove species richness, tree enumeration and vegetation structure

A minimum of four belt transects of 5 m width but of varying lengths (25–225 m) were established between the seaward and landward margins of the mangrove belt of each lagoon to include known differences in mangrove assemblages. Each belt transect was divided into 25 m^2 plots for sampling. All the mangrove trees with GBH $\geq$ 8.0 cm in each plot were enumerated (English et al., 1997; Dahdouh-Guebas and Koedam, 2006) and the species were recorded (Tomlinson, 1986). The number of mangrove saplings (GBH $<$ 8.0 cm and/or height $>$ 40 cm $<$ 130 cm) and seedlings (height $\leq$ 40 cm; Kairo et al., 2002) in each plot were counted and the species were recorded. Subsequently, the above-ground vegetation attributes stand densities (stem density, sapling density and seedling density) and stand basal area were estimated for each plot.

2.3. Estimation of total carbon stocks

2.3.1. Estimation of mangrove wood density

At least three wood samples were extracted from the trunks and mature branches of each mangrove species. These wood samples were cut into sub-samples comprising of wooden cubes. These were dried in an oven to a constant weight recorded to the nearest 0.01 g. Then oven-dried sub-samples were dipped in water for 30 min and subsequently, the volume of each sub-sample was measured following the water displacement method of Beets et al. (2007). The density (g/cm^3) of each wood type was calculated from weight/volume for each sub-sample of wood (Table A). Lastly, the average wood density for each mangrove species was calculated according to the following equation.

$$Wooddensity = \mathrm{Sampleweight(g)/Samplevolume(cm^3)} \tag{1}$$

2.3.2. Above-ground biomass and above-ground biomass carbon

Mangrove above-ground biomass was estimated using the following common allometric equation (Eq. (2a)) for mangroves (Komiyama et al., 2005) and above-ground carbon content was calculated using the Eq. (2b).

$$\mathrm{AGB} = 0.251.\rho.\mathrm{D}^{2.46} \tag{2a}$$

$$\mathrm{AGC} = \mathrm{AGB}.0.48 \tag{2b}$$

Where, AGB = above-ground biomass (kg), ρ = wood density (g $\mathrm{cm^{-3}}$), D = diameter at breast height/DBH (cm) and AGC = above-ground carbon content.

2.3.3. Below-ground root biomass and root carbon

Sri Lankan mangroves typically display three ecological zones: a) a seaward assemblage of pure mangrove stands of *Rhizophoraceae* species; b) a middle assemblage which consists of mixed mangrove stands (e.g. *Avicennia* sp. *Aegiceras corniculatum*, *Excoecarea agallocha*); c) a landward assemblage which is composed of true mangroves and mangrove associates (Abeywickrema, 1960). Each belt transect was therefore divided into three sections namely seaward, middle and landward zones. Three soil cores were obtained from each belt transect representing all three zones (Fig. 2) giving a total n = 15 per site, apart from n = 12 for Batticaloa and Negombo lagoons. A soil core sampler of 20.4 cm internal diameter and 75.0 cm length with a sharpened edge was used to excavate soil containing roots down to a depth of 60 cm. Subsequently, each soil core was sectioned into four 15 cm sub-samples. Each sub-sample was washed through a 1 mm sieve and all live and dead roots were extracted. Roots were oven-dried at 60 °C temperature to obtain a constant weight. Oven-dried weights of mangrove roots were multiplied by a factor of 0.39 (Kauffman and Donato, 2012) to obtain corresponding root carbon values. Note that only the below-ground roots were considered in determining the root carbon and above-ground roots were taken under above-ground carbon estimations.

$$\mathrm{BRC} = \mathrm{OvenWMR}^{*}0.39 \tag{3}$$

Where, BRC = below-ground root carbon, OvenWMR = oven-dried weight of mangrove root and multiplication factor: 0.39

2.3.4. Soil carbon contents, soil sampling and analyses

In addition to the soil cores used for the estimation of below-ground root biomass and root carbon, another three soil cores were obtained from each belt transect representing the three major mangrove zones (seaward, middle and landward), from the surface down to bedrock (or maximum depth, whichever came first; Fig. 2) using an extendable soil core sampler with an internal diameter of 3.8 cm. The maximum depth to which the soil core sampler was able to operate was restricted to 390 cm. Prior to the collection of the soil core, the litter layer was removed to expose the soil surface.

All soil was carefully removed and a sub-sample was collected at different depths i.e. 0–5 cm (surface), 15 cm, 30 cm, 60 cm then at every 30 cm interval down to the bed rock or maximum depth. Each sub-sample was immediately transferred into labelled polythene bags, air tightened and transported to the laboratory.

Soil sub-samples were oven-dried at 105 °C to a constant weight and the bulk density was estimated as the mass of the oven-dried soil per volume of bulk soil. Oven-dried soil sub samples were homogenized and the organic matter content was determined using loss on ignition (LOI) (Benson et al., 2017; Shaltout et al., 2019) whereby 5.0 g of homogenized oven-dried sub-samples were heated at 550 °C for 4 h in a muffle furnace (Heiri et al., 2001; Ratnayake et al., 2007). Organic matter contents were divided by a factor of 1.72 to estimate the organic carbon contents of soils, and estimates of total soil organic carbon per ha, based on pooled data from cores, were calculated according to Eqs. (4)–(7) (Allen et al., 1974; Connor et al., 2001)

Estimating soil carbon content per core; for example, a core which included three soil slices (A, B and C) of 15 cm thickness of each. The sample calculation of soil carbon content per slice is only shown for slice ‘A’.

$$OMC_{sub} = \frac{(Initialweightofovendriedsoil - finalweightofignitedsoil)}{Initialweightofoven - driedsoil} \tag{4}$$

Where, $\mathrm{OMC_{sub}}$ = organic matter content of 5 g-sub-sample

$$OMC_{slice} = OMC_{sub} \times thicknessofsliceA(cm) \times meanDBD(gcm - 3) \tag{5}$$

Where, OMC slice = organic matter content of the slice ‘A’

$$SCC_{core} = \frac{OMC_{slice}A + OMC_{slice}B + OMC_{slice}C}{1.72} \tag{6}$$

Where, SCC core = soil carbon content of the core (soil organic matter content is now converted to soil organic carbon)

Assume that the surface area of the core is C $\mathrm{cm^2}$

$$\text{Soil carbon stock } \left(\mathrm{Mg\ C\ ha^{-1}}\right) = \left[\mathrm{SCC_{core}/C\ cm^2}\right]^{*}10^{-6}{}^{*}10^{8}\mathrm{Mg\ C\ ha^{-1}} \tag{7}$$

During the soil sampling (for root carbon and soil carbon estimation), soil compression was negligible and thus was not considered further in our study.

Because soil depth varied between sites, we calculated both total soil carbon stocks and carbon concentration values defined according to a standard depth for all sites. This latter depth was the most shallow depth recorded at any site in the study (90 cm), and soil carbon values corresponding to this (and hence directly comparable between sites as reflecting carbon concentrations) were termed ‘corrected soil carbon stocks’; subsequently where this term is not used, all soil carbon figures refer to maximum-depth based soil carbon (DelVecchia et al., 2014). These corrected soil carbon stocks were used only for correlation and regression analyses. where soil carbon and “core length” were considered.

2.4. Data analyses

Above-ground vegetation attributes (stand densities, stand basal area and above-ground biomass), below-ground root biomass, root carbon and total soil carbon stocks were treated as continuous variables while individual mangrove forests, climate zones, mangrove areas and soil depths were considered as fixed factors. Prior to all the analyses, Shapiro–Wilk’s and Levene’s tests were used to examine the data for normality and homogeneity of variance, respectively. When necessary, data were transformed into natural log and/or square root values in order to meet the assumptions of parametric statistics. However, when the data violated the assumptions of parametric statistics, Welch’s ANOVA or non-parametric Kruskal-Wallis test were employed accordingly (Liu, 2015). Total mangrove carbon contents (above-ground carbon and below-ground carbon) were compared among the fixed factors ‘mangrove forests’ and ‘soil depths’ using two-way ANOVA. Further, differences of soil carbon content and total carbon stocks in mangrove forests among the predictor variables: climate zone, mangrove forest, soil depth of sampling, and vegetation biomass with random effect of mangrove areas of sampling (seaward, middle, landward), were checked using Generalized Linear Mixed Models (GLMMs) that included crossed effect (i.e. interaction terms).

The relationships between soil carbon stock and core length were determined using correlation analysis followed by a simple regression. The relationships between corrected soil carbon stocks and above-ground vegetation attributes (stand densities, stand basal area and

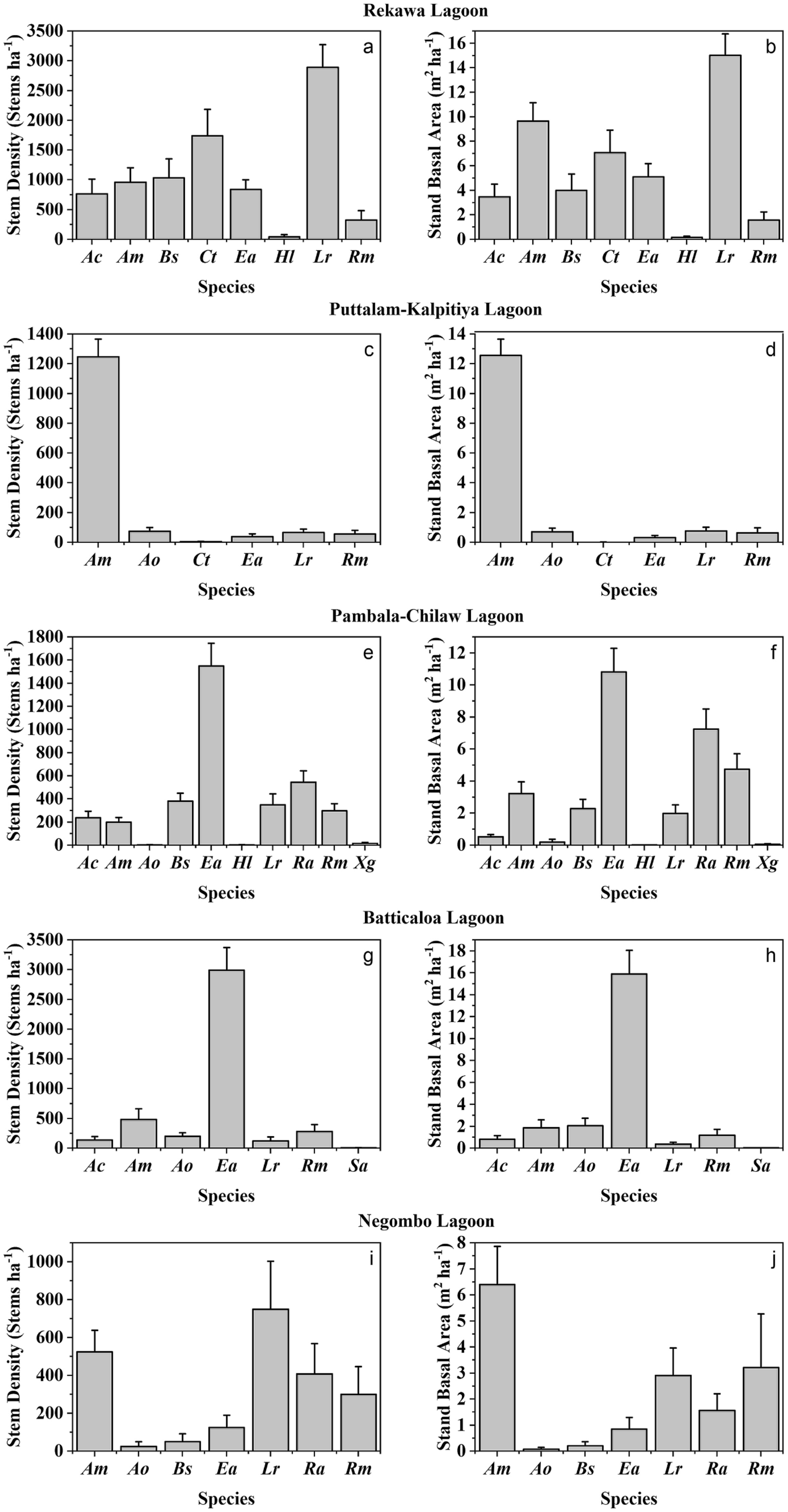

Fig. 3. Mean (±SE) stem density (a,c,e,g,i) and stand basal area (b,d,f,h,j) of mangroves studied: where, *Ac*: *Aegiceras corniculatum*; *Am*: *Avicennia marina*; *Ao*: *Avicennia officinalis*; *Bs*: *Bruguiera sexangula*; *Ct*: *Ceriops tagal*; *Ea*: *Excoecaria agallocha*; *Hl*: *Heritiera littoralis*; *Lr*: *Lumnitzera racemosa*; *Ra*: *Rhizophora apiculata*; *Rm*: *Rhizophora mucronata*; *Sa*: *Sonneratia alba*; *Xg*: *Xylocarpus granatum*.

Table 1
Above-ground attributes of the mangroves studied. (Mean ± Standard error of mean. Superscripted letters compare values down in a column. Values followed by different superscripted letters are significantly different at 0.05 significance level).

Lagoon	Stem Density (Stems ha^{-1})	Sapling Density (Saplings ha^{-1})	Seedling Density (Seedlings ha^{-1})	Stand Basal Area (m^{2} ha^{-1})	Above-ground Biomass (Mg ha^{-1})	Above-ground Carbon Stock (Mg C ha^{-1})
Rekawa	8594 ± 576^{a}	4364 ± 813^{a}	11022 ± 1909^{a}	46.02 ± 2.45^{a}	393.97 ± 21.36^{a}	189.11 ± 10.25^{a}
Puttalam-Kalpitiya	1484 ± 112^{b}	1238 ± 239^{ab}	4574 ± 1154^{a}	14.98 ± 1.05^{b}	160.16 ± 19.71^{b}	76.88 ± 9.46^{b}
Pambala-Chilaw	3582 ± 216^{c}	359 ± 125^{c}	15505 ± 2731^{a}	31.12 ± 1.53^{c}	327.17 ± 29.44^{a}	157.04 ± 14.13^{a}
Batticaloa	4225 ± 402 ^{cd}	1557 ± 365^{b}	211 ± 64^{b}	22.17 ± 2.28^{b}	173.46 ± 40.52^{b}	83.26 ± 19.45^{b}
Negombo	2183 ± 285^{bd}	3733 ± 1187^{ab}	17317 ± 5147^{a}	15.20 ± 2.50^{b}	157.21 ± 38.27^{b}	75.46 ± 18.37^{b}

Table 2
Below-ground root carbon stock of mangroves studied. (Mean ± Standard error of mean. Superscripted uppercase letters compare vales across rows and lowercase letters compare values down in a column. Values followed by different superscripted letters are significantly different at 0.05 significance level).

Zone	Soil Depth (cm)	Below-ground Root Carbon Storage (Mg C ha^{-1})				
		Rekawa	Puttalam-Kalpitiya	Pambala-Chilaw	Batticaloa	Negombo
Landward	0–15	7.56 ± 1.31	6.71 ± 2.16	7.01 ± 1.34	4.81 ± 1.89	8.16 ± 0.50
	15–30	4.00 ± 0.91	2.43 ± 0.84	2.82 ± 0.42	1.55 ± 0.71	2.77 ± 0.46
	30–55	1.51 ± 0.61	1.30 ± 0.31	1.78 ± 0.68	0.70 ± 0.30	1.41 ± 0.25
	45–60	1.01 ± 0.27	0.68 ± 0.10	1.89 ± 1.06	0.52 ± 0.22	0.95 ± 0.21
	Total	14.07 ± 2.41^{a}	11.13 ± 3.02^{a}	13.50 ± 1.32^{a}	7.58 ± 2.69^{a}	13.28 ± 0.73^{a}
Middle	0–15	9.14 ± 1.71	5.30 ± 1.34	6.05 ± 1.66	2.65 ± 0.66	7.38 ± 0.49
	15–30	2.00 ± 0.61	3.37 ± 0.83	2.72 ± 0.69	1.24 ± 0.23	2.28 ± 0.23
	30–55	0.75 ± 0.32	0.93 ± 0.22	1.37 ± 0.38	0.60 ± 0.04	1.37 ± 0.25
	45–60	0.61 ± 0.24	0.54 ± 0.14	0.59 ± 0.16	0.35 ± 0.05	0.72 ± 0.20
	Total	12.50 ± 2.40^{a}	10.14 ± 2.27^{a}	10.72 ± 2.62^{a}	4.83 ± 0.91^{a}	11.75 ± 0.43^{a}
Seaward	0–15	8.07 ± 1.41	7.95 ± 1.67	5.92 ± 0.84	6.67 ± 1.80	11.57 ± 2.34
	15–30	2.43 ± 1.02	4.56 ± 1.45	4.07 ± 0.42	1.45 ± 0.42	2.86 ± 0.49
	30–55	0.59 ± 0.10	1.95 ± 0.94	2.42 ± 0.24	2.42 ± 0.70	2.03 ± 0.41
	45–60	0.47 ± 0.13	1.17 ± 0.49	1.30 ± 0.23	0.66 ± 0.20	1.44 ± 0.24
	Total	11.57 ± 2.45^{a}	15.63 ± 3.88^{a}	13.70 ± 0.93^{a}	11.19 ± 2.63^{a}	17.90 ± 1.60^{a}
Average		12.71 ± 0.73^{A}	12.30 ± 1.69^{A}	12.64 ± 0.96^{A}	7.87 ± 1.84^{A}	14.31 ± 1.85^{A}

above-ground biomass) and root carbon stocks were evaluated following correlation analysis. Finally, the interrelation of two parameter groups of below-ground carbon pool and above-ground vegetation attributes was identified with canonical correlation analysis (Eni et al., 2012). All the statistical tests were performed using IBM SPSS Statistics for Windows, Version 20.0.

3. Results

3.1. Mangrove species richness and vegetation structure

The highest mangrove species richness (S) was recorded in Pambala-Chilaw lagoon (S = 10) while Rekawa, Puttalam-Kalpitiya, Batticaloa and Negombo lagoons recorded 8, 6, 7 and 7 species respectively. Rekawa lagoon was co-dominated by *Lumnitzera racemosa* (32.6%)*, Avicennia marina* (21.0%)*, Ceriops tagal* (15.4%) and *Excoecaria agallocha* (11.1%), while *Excoecaria agallocha* (34.7%), *Rhizophora apiculata* (23.3%) and *Rhizophora mucronata* (15.2%) were the co-dominant species present in Pambala-Chilaw lagoon (Fig. 3). Puttalam-Kalpitiya lagoon was dominated by *Avicennia marina* (83.8%), and *Excoecaria agallocha* (71.7%) was found to be the dominant species in Batticaloa lagoon. Negombo lagoon was co-dominated by *Avicennia marina* (42.1%), *Rhizophora mucronata* (21.1%) and *Lumnitzera racemosa* (19.2%).

Mean stem density ($F = 14.01$, $p < 0.001$), sapling density ($F = 2.98$, $p = 0.047$), seedling density ($F = 7.25$, $p = 0.001$), stand basal area ($F = 12.63$, $p < 0.001$) and above-ground biomass ($F = 9.94$, $p < 0.001$) all varied significantly among sites (Table 1). The highest stem density, of 8594 ± 576 stems ha^{-1}, and the highest sapling density, of 4364 ± 813 saplings ha^{-1}, were found in Rekawa lagoon, whilst the highest seedling density of 17317 ± 5147 seedlings ha^{-1} was recorded in Negombo lagoon. The stand basal area at Rekawa, of 46.02 ± 2.45 m^{2} ha^{-1}, was significantly higher than that at all other sites ($p < 0.05$); the basal area of 15.20 ± 2.50 m^{2} ha^{-1} was recorded in Negombo lagoon.

3.2. Total mangrove forest carbon stocks

3.2.1. Above-ground biomass and above-ground carbon stock

Above-ground biomass (AGB) of mangrove forests ranged from 157.21 ± 38.27 Mg ha^{-1} to 393.97 ± 21.36 Mg ha^{-1} ($p < 0.05$; Table 1). Above-ground carbon (AGC) stock of mangroves showed a significant variation in distribution among the five sites studied ($F = 9.94$, $p < 0.001$) and ranged from 75.46 ± 18.37 Mg C ha^{-1} in Negombo lagoon to 189.11 ± 10.25 Mg C ha^{-1} in Rekawa lagoon. We also found a significant variation in AGC stock of mangroves based on climate zone ($F = 7.83$, $p = 0.003$), where the AGC stock of mangroves in the intermediate zone (189.11 Mg C ha^{-1}) was significantly higher than that of the dry (107.33 Mg C ha^{-1}) and wet (75.46 Mg C ha^{-1}) zones.

3.2.2. Below-ground root carbon stock

Carbon stock estimates for below-ground root biomass of mangroves (BRC) ranged from 0.99 Mg C ha^{-1} in Batticaloa to 27.20 Mg C ha^{-1} in Puttalam-Kalpitiya lagoons ($F = 2.19$, $p = 0.079$) (Table 2). BRC did not vary significantly between the three climate zones and with distance from the seaward margin. However, BRC stock distribution varied significantly in a vertical direction from superficial to deeper sediments, with the top 0–15 cm sediment layer containing the highest mean BRC stock of 7.01 ± 0.47 Mg C ha^{-1} ($F = 121.05$, $p < 0.001$), which corresponds to 58.91 ± 1.93% of the total mean root carbon percentage (Table 2). This trend was common for all the mangrove forests studied.

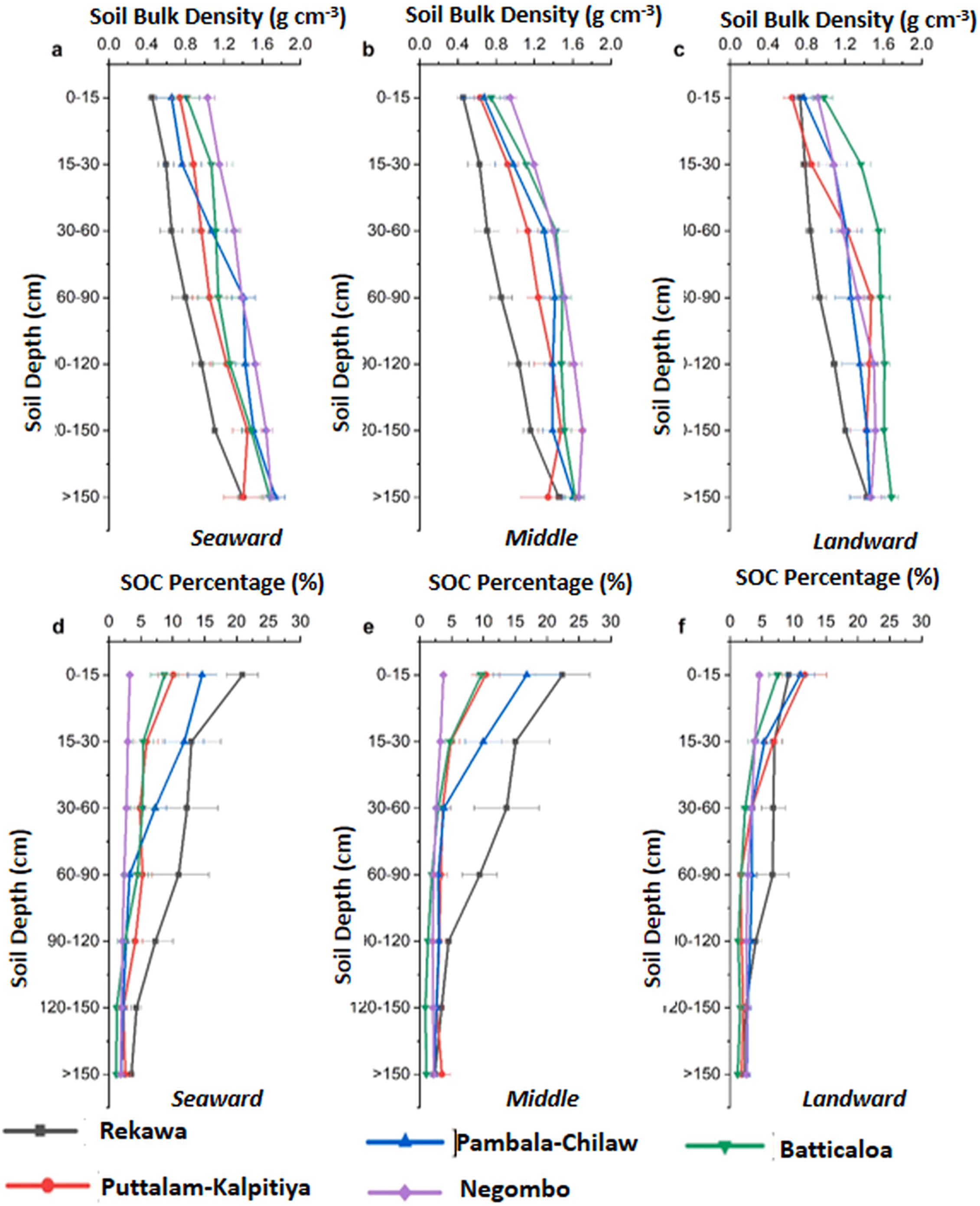

Fig. 4. The graphs show the variation of soil bulk density (gcm^{-3}) (a–c) and soil organic carbon percentage (%) (d–f) from seaward to landward (horizontal variation) as well as from top to down soil layers (vertical variation). Error bars indicate standard error of mean.

3.2.3. Soil carbon content and soil properties

The maximum possible sampling depth in different lagoons, and at different places of the same lagoon system, varied greatly, from 205 ± 20 cm in Puttalam-Kalpitiya lagoon to 271 ± 17 cm in Rekawa lagoon. Pambala-Chilaw, Batticaloa and Negombo lagoons had average sampling depths of 226 ± 12 cm, 269 ± 28 cm and 231 ± 10 cm, respectively. Out of 69 sampling locations, 15 had a soil depth of >300 cm (21.74%) while the remainder showed values that were <300 cm in depth with respect the bedrock. In all the lagoons sampled, soil depth decreased with the distance from the seaward margin.

In general, soil bulk density (SBD) increased and soil carbon percentage decreased with the soil depth at all the sites (Fig. 4). These variations in vertical distribution of SBD and soil carbon percentage were significantly different across the depth profile ($F = 19.04$, $p < 0.001$). Mean SBD ranged from 0.45 ± 0.05 g cm^{-3} in Rekawa lagoon to 1.74 ± 0.10 g cm^{-3} in Pambala-Chilaw lagoon. The Lowest average SBD for the entire depth profile (0.85 ± 0.06 g cm^{-3}) recorded at the seaward zone of the Rekawa lagoon while the highest (1.47 ± 0.05 g cm^{-3}) was found at the landward zone of Batticaloa lagoon. All mangrove forests contained a relatively high mean of soil carbon percentage in the top sediment layer (0–15 cm), ranging from 3.26 ± 0.23% in Negombo to 22.41 ± 4.28% in Rekawa, while soil layers > 150 cm varied from 1.07 ± 0.16% carbon in Batticaloa to 3.51 ± 0.34% in Rekawa lagoons. The highest and lowest mean soil carbon percentages across the entire depth

Table 3
Soil carbon stocks of mangroves studied. (Mean ± Standard error of mean. Superscripted uppercase letters compare vales across rows and lowercase letters compare values down in a column. Values followed by different superscripted letters are significantly different at 0.05 significance level).

Zone	Soil Depth (cm)	Soil Carbon Storage (t C ha^{-1})									
		Rekawa		Puttalam-Kalpitiya		Pambala-Chilaw		Batticaloa		Negombo	
Seaward	0–15	119.89 ± 4.18	(7.55)	86.82 ± 11.25	(9.41)	105.44 ± 4.87	(10.60)	70.94 ± 8.22	(10.40)	51.07 ± 6.02	(6.63)
	15–30	87.96 ± 12.72	(5.54)	64.43 ± 11.77	(6.98)	91.53 ± 8.42	(9.20)	56.80 ± 8.37	(8.33)	50.37 ± 2.89	(6.54)
	30–60	169.76 ± 29.75	(10.69)	118.35 ± 17.26	(12.83)	149.70 ± 16.28	(15.05)	104.55 ± 19.99	(15.33)	106.21 ± 9.86	(13.79)
	60–90	170.71 ± 34.88	(10.75)	131.64 ± 30.39	(14.27)	129.43 ± 8.84	(13.01)	81.39 ± 20.35	(11.93)	101.58 ± 12.75	(13.18)
	90–120	148.34 ± 29.54	(9.34)	117.43 ± 24.31	(12.73)	111.36 ± 9.27	(11.20)	61.95 ± 15.08	(9.08)	97.38 ± 10.10	(12.64)
	120–150	140.57 ± 26.50	(8.85)	84.77 ± 15.05	(9.19)	96.64 ± 11.55	(9.72)	35.05 ± 9.71	(5.14)	95.99 ± 8.66	(12.46)
	>150	750.79 ± 145.16	(47.28)	319.24 ± 159.95	(34.60)	310.54 ± 104.77	(31.22)	271.40 ± 71.47	(39.79)	267.86 ± 65.44	(34.77)
	Total	1588.03 ± 85.89^{a}		922.69 ± 247.59^{a}		994.64 ± 133.95^{a}		682.08 ± 79.10^{a}		770.46 ± 80.71^{a}	
Middle	0–15	116.65 ± 16.29	(9.61)	80.90 ± 14.56	(11.46)	91.64 ± 6.06	(10.78)	94.46 ± 12.22	(14.67)	53.81 ± 5.56	(6.98)
	15–30	98.91 ± 23.87	(8.14)	56.02 ± 13.42	(7.93)	70.97 ± 8.28	(8.35)	67.80 ± 5.10	(10.53)	57.58 ± 4.62	(7.47)
	30–60	195.85 ± 44.91	(16.13)	105.98 ± 27.60	(15.01)	117.11 ± 13.27	(13.78)	107.21 ± 20.40	(16.65)	109.74 ± 13.44	(14.23)
	60–90	173.05 ± 19.12	(14.25)	106.72 ± 22.70	(15.12)	117.92 ± 13.27	(13.87)	78.71 ± 14.94	(12.22)	100.92 ± 6.77	(13.09)
	90–120	136.97 ± 14.82	(11.28)	83.46 ± 26.87	(11.82)	118.80 ± 15.38	(13.98)	54.59 ± 9.72	(8.48)	100.89 ± 9.46	(13.08)
	120–150	115.56 ± 15.51	(9.52)	71.44 ± 28.19	(10.12)	103.98 ± 11.56	(12.23)	30.13 ± 8.71	(4.68)	110.13 ± 10.43	(14.28)
	>150	377.42 ± 138.66	(31.08)	201.51 ± 125.13	(28.54)	229.52 ± 63.57	(27.00)	211.14 ± 74.01	(32.78)	237.96 ± 30.30	(30.86)
	Total	1214.41 ± 52.48^{b}		706.03 ± 230.02^{a}		849.94 ± 119.98^{a}		644.04 ± 100.15^{a}		771.04 ± 62.70^{a}	
Landward	0–15	98.79 ± 17.57	(10.31)	85.49 ± 14.34	(16.51)	98.73 ± 6.87	(12.04)	94.92 ± 11.86	(15.70)	56.45 ± 3.55	(6.37)
	15–30	80.02 ± 16.61	(8.35)	75.34 ± 11.32	(14.55)	74.59 ± 4.69	(9.10)	65.14 ± 13.31	(10.77)	58.71 ± 4.22	(6.63)
	30–60	159.17 ± 36.08	(16.61)	108.63 ± 8.75	(20.98)	116.11 ± 9.63	(14.16)	98.42 ± 16.49	(16.27)	119.79 ± 7.77	(13.53)
	60–90	164.68 ± 41.93	(17.18)	71.67 ± 9.41	(13.84)	112.56 ± 13.97	(13.73)	75.01 ± 12.46	(12.40)	109.88 ± 10.97	(12.41)
	90–120	118.30 ± 17.12	(12.34)	73.35 ± 6.72	(14.16)	106.14 ± 14.20	(12.94)	62.05 ± 8.68	(10.26)	114.47 ± 18.33	(12.93)
	120–150	88.78 ± 9.71	(9.26)	49.51 ± 19.11	(9.56)	105.61 ± 10.66	(12.88)	76.59 ± 22.11	(12.66)	123.02 ± 17.39	(13.89)
	>150	248.54 ± 52.99	(25.94)	53.90 ± 19.99	(10.41)	206.31 ± 51.99	(25.16)	132.61 ± 22.11	(21.93)	303.31 ± 57.53	(34.25)
	Total	958.28 ± 95.68^{b}		517.88 ± 69.74^{a}		820.05 ± 78.12^{a}		604.74 ± 65.04^{a}		885.62 ± 109.36^{a}	
Average		1253.57 ± 81.24^{A}		715.53 ± 122.70^{B}		888.21 ± 68.26^{B}		643.62 ± 54.15^{B}		809.04 ± 57.93^{B}	

profile were recorded in the seaward zones of Rekawa (10.31 ± 1.59%) and Negombo lagoons (2.46 ± 0.14%), respectively (Fig. 4). The study revealed an inverse relationship between the two soil parameters, soil bulk density and soil carbon percentage.

The mean total soil carbon stock of mangroves ranged from 1253.57 ± 81.24 Mg C ha^{-1} in Rekawa lagoon to 643.62 ± 54.15 Mg C ha^{-1} in Batticaloa lagoon ($F = 7.79$, $p < 0.001$) and Rekawa stored significantly larger amounts of soil carbon when compared to other lagoons studied ($p < 0.05$; Table 3). In general, mangroves within the intermediate climate zone stored relatively more soil carbon when compared to dry and wet zone mangroves ($p < 0.05$). In all the lagoons except for Negombo, soil carbon stocks decreased with increasing distance from the seaward to landward margin (Fig. 5). Rekawa contained a large proportion of the total soil carbon stock at the seaward area ($p < 0.05$) while for the rest of the locations there was no statistically significant variation in soil carbon stocks along the seaward to landward margin. The GLMM best-fit model results showed that there was no significant random effect of the mangrove areas that were used for below-ground carbon contents.

However, when corrected carbon stocks (to compare the sites and mangrove areas without the complicating effect of varying core lengths) were used, all sites were shown to be homogenous in the distribution of soil carbon stock from the seaward to landward margin (hence differences were driven by soil stocks rather than by different carbon concentrations). Comparing the soil carbon pool with depth profile, the deeper sediment layers (>150 cm) stored a considerable proportion of total soil carbon stock (10.41%–47.28%) (Table 3).

Combining all sampled sites, soil depth was shown to be a highly significant predictor of total soil carbon stock ($r = 0.56$; $p = 0.003$). Corrected soil carbon stocks positively related to root carbon stock ($r = 0.36$), SBA ($r = 0.49$), AGB ($r = 0.47$), stem density ($r = 0.54$), sapling density ($r = 0.57$) and seedling density ($r = 0.31$) (Fig. 6). The results of correlating below-ground carbon pools with above-ground vegetation attributes are shown in Table 4. Only the first canonical variate was significant ($p = 0.010$) with a canonical correlation coefficient of 0.8074. Redundancy coefficient of the first canonical variate for below-ground carbon pools showed that 42% of the variance in below-ground carbon pools were accounted for by the variability in above-ground vegetation attributes. The first linear combination for below-ground carbon pools strongly and positively loaded on soil carbon stocks (0.9993), while that of above-ground vegetation attributes showed a heavy loading on sapling density (0.7615).

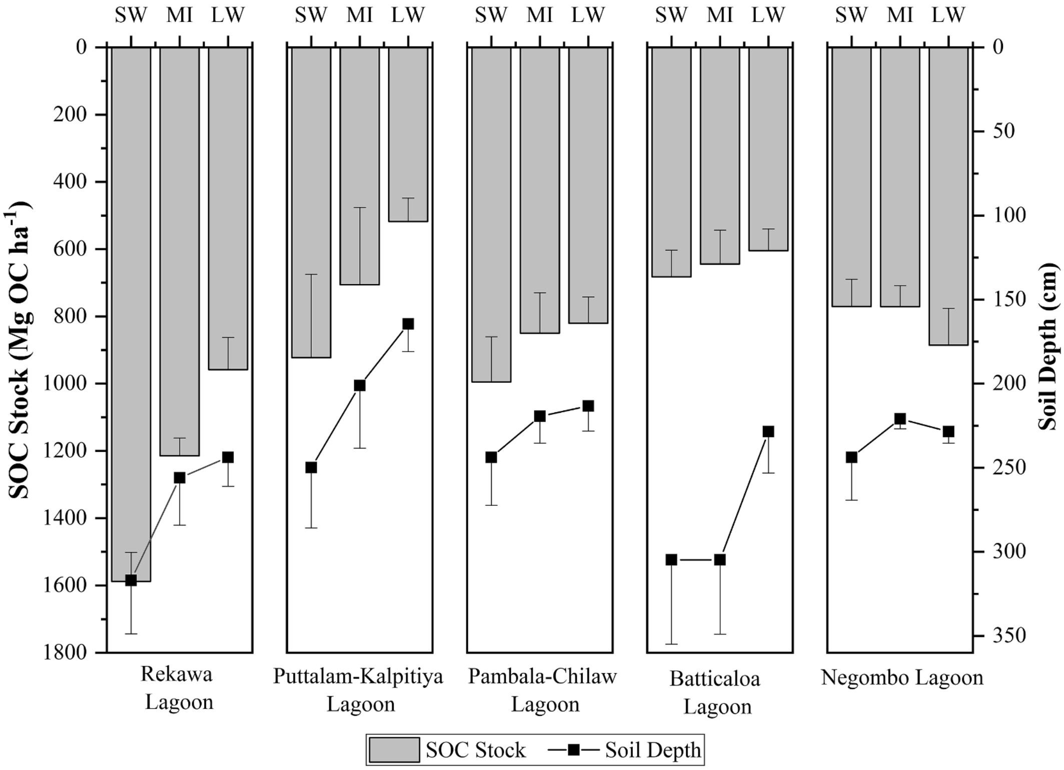

Fig. 5. Variation of soil organic carbon stock (Mg OC ha^{-1}) with soil depth across the three major mangrove areas of sites studied: where, SW: Seaward area; MI: Middle area; LW: Landward area (error bars indicate standard error of mean).

3.2.4. *Total carbon stock*

The highest total carbon stock of mangroves was reported in Rekawa lagoon (1455.39 ± 45.16 Mg C ha^{-1}) while the lowest was found in Batticaloa lagoon (734.75 ± 57.68 Mg C ha^{-1}) (Fig. 7). The total carbon stocks of Puttalam-Kalpitiya, Pambala-Chilaw and Negombo lagoons were recorded as 804.71 ± 183.16 Mg C ha^{-1}, 1057.90 ± 107.82 Mg C ha^{-1} and 898.81 ± 57.97 Mg C ha^{-1}, respectively. Soils dominated in their contribution to total carbon stocks, with 83.24 ± 1.96% to 90.06 ± 1.72% of the total ecosystem carbon pool of the sampled mangrove sites, while the contribution of above-ground and root carbon pools ranged from 8.33 ± 1.78% to 15.52 ± 1.95% and from 0.86 ± 0.14% to 2.02 ± 0.48%, respectively. According to the GLMM results climate zone, mangrove forest, vegetation biomass and soil depth all had significant effects on the total carbon stocks. The best-fit model indicated that climate zone, mangrove forest, vegetation biomass and soil depth of sampling and the interactive effects of climate zone and soil depth were the best determinants of total carbon contents (AIC: 304.2; df: 69; REML: 870.4). About 70% of the variation was explained by the above determinants.

4. Discussion

4.1. *A comparison of above-ground and below-ground mangrove carbon stocks across the globe*

The AGC stocks of studied mangrove sites are within the wide range of 11.80 Mg C ha^{-1} (Murdiyarso et al., 2009) to 226 Mg C ha^{-1} (Kirui et al., 2008) recorded for the world's mangrove ecosystems. Global AGC estimates vary depending on differences in mangrove species composition, forest structure, climate, geomorphology, hydrology and disturbances (Fromard et al., 1998; Cohen et al., 2013; Stringer et al., 2015) and also vary with sampling designs and the availability of localized allometric equations for AGB estimations (Stringer et al., 2015).

The BRC stocks of mangroves in Sri Lanka are at the lower end of those reported for mangroves across the globe. However, BRC estimates derived using allometric equations for mangroves appear to yield comparatively higher results (Kauffman et al., 2011; Adame et al., 2013) than those from destructive sampling methods such as the soil coring used in the current work (Murdiyarso et al., 2009; Chalermchatwilai et al., 2011; Adame et al., 2014; Cormier et al., 2015; Robertson and Alongi, 2016). A recent study comprehensively summarizes the BGB estimates of mangroves obtained through destructive techniques (soil cores, felled trees and trenches) across the world, where the ratio between BRB and AGB (root:shoot ratio) ranges from 0.02 to 10.69 (Adame et al., 2017) and our value of 0.10 for root:shoot ratio is well placed within this global range. BRB allocation of halophytes like mangroves can be highly sensitive to salinity variations, where high salinity encourages greater proportional biomass allocation to below-ground components in order to compensate the increasing need for water and nutrients (Komiyama et al., 2000, 2008; Bernstein and Kafkafi, 2002). Sri Lankan mangroves typically show low levels of salinity and our root:shoot ratios are correspondingly low. The results of our study concur well with previous observations that BRB generally decreases with soil depth (Adame et al., 2017).

Globally, total soil carbon stocks within mangrove forests vary from 316.29 Mg C ha^{-1} to 1485.5 Mg C ha^{-1} (Gress et al., 2017; Boone Kauffman et al., 2017; Perera and Amarasinghe, 2019) and our values, with the exception of Rekawa lagoon, are well placed within this more general range. The total mangrove soil carbon stock in Rekawa lagoon (i.e. 1253.57 Mg C ha^{-1}) is close to the maximum of the above range and sets a new maximum in the Sri Lankan context. These variations in carbon estimates reflect not only the differences in species composition, stand maturity, tidal inundation, climate and geomorphology (Bouillon et al., 2008; Alongi, 2014), but also the contrasting sampling approaches and data reporting techniques employed (Stringer et al., 2015). Crucially, the sampling depth of soil is one of the most important factors driving variability in mangrove carbon assessments, with values ranging from 45 cm (Perera and Amarasinghe, 2017, 2019) to >300 cm

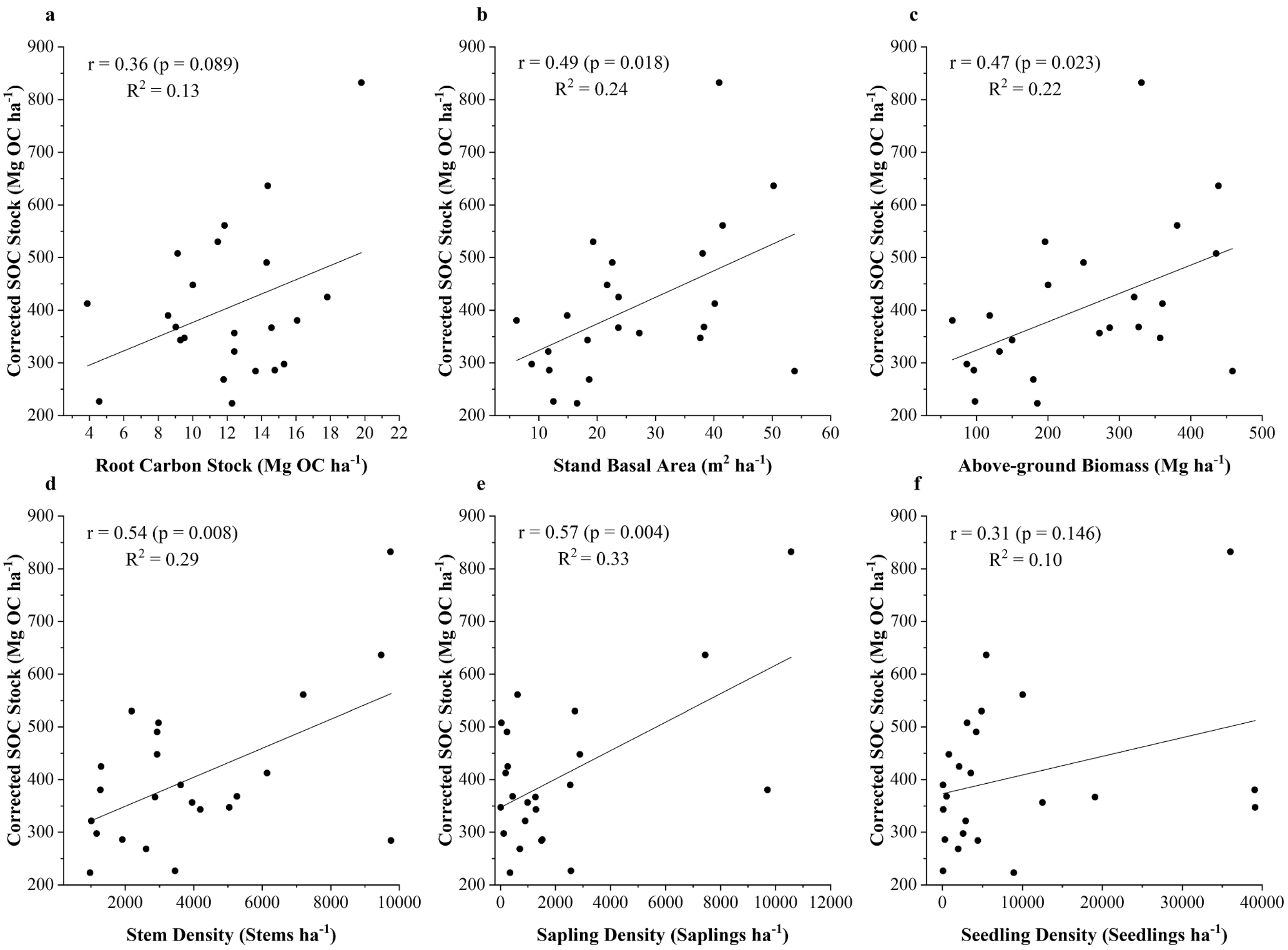

Fig. 6. Relationships of standardized soil organic carbon stock with above-ground and below-ground attributes.

Table 4
Results of canonical correlation analysis between two variable groups of below-ground carbon pools and above-ground attributes of mangroves.

	Canonical loading	
	Variate I	Variate II
Below-ground carbon pools		
Soil carbon stock	0.9663	−0.2573
Root carbon stock	0.5906	0.8069
Redundancy coefficient (%)	41.81	7.88
Above-ground attributes		
Stand basal area	0.5137	−0.7343
Above-ground biomass	0.5121	−0.5930
Stem density	0.5859	−0.6841
Sapling density	0.7615	0.1929
Seedling density	0.4661	0.4209
Redundancy coefficient (%)	21.73	6.91
Canonical correlation coefficient	0.8074	0.4688
Squared canonical correlation	0.6520	0.2197
p-value	0.010	0.348

(Murdiyarso et al., 2009). Since this study and results from elsewhere reveal that core length can be a significant predictor of total soil carbon stock (DelVecchia et al., 2014) and soil dominates the carbon pool (Adame et al., 2013; Boone Kauffman et al., 2017; Perera and Amarasinghe, 2019), inconsistency in sampling depth may have a large and significant impact on estimating total ecosystem carbon stocks accurately. As an example, a recent study sampling only the top 45 cm of mangrove sediment reported the soil carbon stock of Rekawa and Batticaloa lagoons as only 580.84 Mg C ha^{-1} and 316.29 Mg C ha^{-1}, respectively (Perera and Amarasinghe, 2019), <50% of the estimates from this study. Moreover, alluvial and riverine mangroves generally consist of deep soils (>300 cm) and any land use changes in these ecosystems may rapidly affect soil properties, including carbon concentrations, even at depths of below 100 cm (Kauffman et al., 2014, 2016; Lang'at et al., 2014). It is normal practice to report carbon stocks to a standardized depth of 100 cm. Whilst this avoids confusion when comparing carbon concentrations between sites, it will generally underestimate total mangrove soil stocks. We argue, therefore, that where possible total stocks should also be given, in order to accurately determine the potential impact of land use and climate change on ecosystem carbon dynamics (Boone Kauffman et al., 2017). It also shows the importance of taking freshwater flows/hydrology into account when deciding the soil depth of sampling in carbon estimation studies. We further suggest including predictor variables like stem density, species composition (Gress et al., 2017) and freshwater hydrology into mixed model effects that would be useful in extracting the variation (∼30%) not accounted for in the current model.

4.2. Factors affecting the variability of mangrove soil carbon

The soil carbon that accumulates in mangrove forests can be autochthonous, from local mangrove production, and/or allochthonous (imported from adjacent ecosystems via streams, rivers or tidal actions; Bouillon et al., 2003; Chen et al., 2012; Li et al., 2018). Both of these components are linked to vegetation biomass and net primary production (Ren et al., 2010). Numerous studies have shown positive

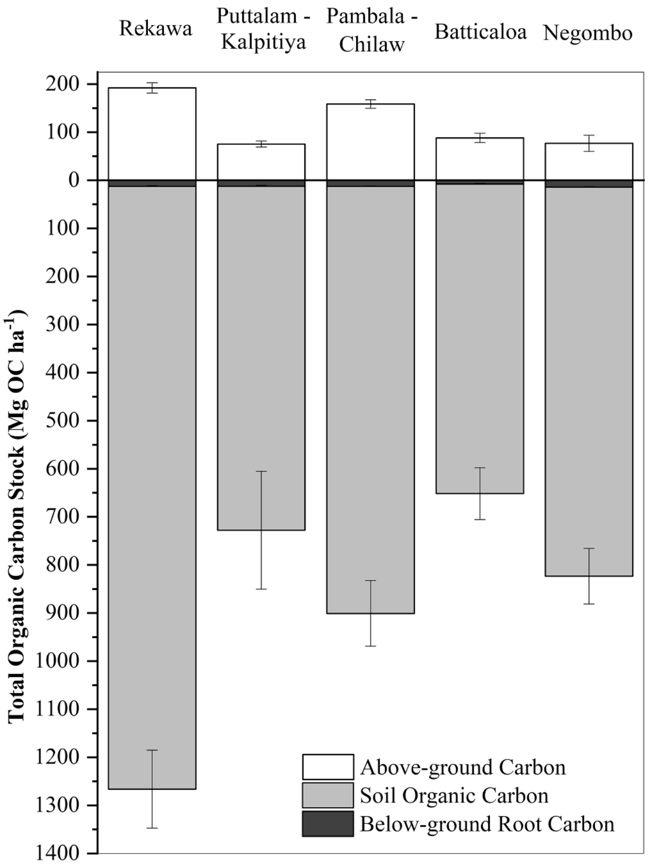

Fig. 7. Total organic carbon (TOC) stocks of mangroves studied.

relationships between soil carbon content and aboveground biomass in mangroves (e.g. Ren et al., 2010; Wang et al., 2013; Xin et al., 2018). Standing vegetation contributes to the soil carbon pool through litter production and the input of dead roots (Ren et al., 2010). The variations in litter production can be attributed to differences in mangrove species composition and geographical location (Woodroffe et al., 1988). Typically, the highest mangrove litter production is observed in tropical regions and decreases with increasing latitude (Hossain and Hoque, 2008). Mangrove litter production is also positively influenced by stand density (Mahmood and Saberi, 2005) and high stand density also helps to trap more debris and particles on the forest floor (Alongi, 2012). AGB is typically positively correlated with root biomass, which itself correlates with soil carbon (Gleason and Ewel, 2002). In addition, it has been found that the intertidal position of mangroves can also determine the level of carbon accumulation (Jacotot et al., 2018). Our study found vegetation biomass to be one of the best predictor variables in determining the total carbon stocks in mangroves.

4.3. Mangrove destruction and the implications for climate change mitigation

Throughout South-East Asia, >100,000 ha of mangroves were lost between 2000 and 2012 (Richards and Friess, 2016). During the same period net mangrove coverage in Bangladesh, India, Pakistan, and Sri Lanka decreased by 11,673 ha because of anthropogenic activities and natural causes as conversion of mangroves into aquaculture and settlements, over harvesting of mangroves, pollution, cyclones and tsunamis, limited freshwater inputs, reduced silt deposition and coastal erosion (Gunawardena and Rowan, 2005; Giri et al., 2015; Mathanraj and Kaleel, 2015). Whilst mangroves can be very resilient in the face of natural impacts such as flooding, storms and sea level fluctuations, climate change will exacerbate all of these stresses. Sri Lankan mangroves are located in micro-tidal settings which are more vulnerable to sea level rise than other mangrove forests (Lovelock et al., 2015; Ward et al., 2016), hence Sri Lankan mangroves will face increasing threats linked to climate change in the near future. According to Satyanarayana et al. (2017), 90% of the Sri Lankan coast is vulnerable to water-related impacts, including sea level rise, and mangrove forests found in the north, eastern and south-eastern coasts, e.g. Jaffna, Komari, Panama, Yala, are relatively highly vulnerable. Healthy mangrove forests, with good hydrological and ecological connectivity and high species richness are more resilient. Therefore, management action that enhances mangrove resilience through new policy enforcement or the strengthening of existing policies, execution of mangrove restoration where it is needed and the introduction of alternative green or physical barriers are highly recommended.

The climate change mitigation potential of mangrove ecosystems depends on their ability to store large quantities of carbon. However, when mangroves are disturbed by human activities (e.g. shrimp farming, development projects and garbage dumping), soil organic matter content can be oxidized, subsequently releasing CO_2 into the atmosphere (Strangmann et al., 2008; Lovelock et al., 2011; Arnaud et al., 2020). Considering the average soil carbon storage of the top 100 cm of mangroves studied (404.37 Mg C ha^{-1}), an amount of soil carbon dioxide equivalent (CO_2e) of 1484.04 Mg CO_2e could be released upon the deforestation of each hectare of mangroves, which is comparatively higher than that reported for estuarine mangrove sediments elsewhere (1060 Mg CO_2e ha^{-1}; Murray et al., 2011). Sri Lanka lost 242 ha of mangroves between 2000 and 2012, at a rate of 20.17 ha $year^{-1}$ (Giri et al., 2015). Whilst this is small on a global scale, it still amounts to the release of around 29,933.09 Mg CO_2e per year (i.e., equivalent to 3.4 million gallons of gasoline burnt). The current mangrove coverage in Sri Lanka is approximately 8000 ha (Kodikara et al., 2017) with the potential to release $\sim 12.72 \times 10^6$ Mg CO_2e, if disturbed. This is equivalent to approximately 70% of total annual emissions from Sri Lanka (Carbon Dioxide Information Analysis Center, 2014). However, given that the impacts of disturbance on mangrove ecosystems can affect not only the surface layers, but also the deep soil layers (Hooijer et al., 2006; Kauffman and Donato, 2012; Lang'at et al., 2014), these numbers may be an underestimate. At a conservative market value of US$ 15 per Mg of CO_2e (Tvinnereim and Røine, 2010), Sri Lankan mangroves (considering of a total emission of 1988.22 Mg CO_2e ha^{-1} accounting both above-ground and below-ground components) could hold an economic value of US$ 29,823.30 per hectare if the ecosystem service of carbon storage was monetized. This shows that the financial returns that could be achieved from mangrove afforestation and reforestation initiatives in the country could be very high.

5. Conclusion

Our results suggest that mangrove forests in Sri Lanka play a crucial role in storing carbon and are among the most carbon rich mangrove ecosystems in the world. The soil carbon fraction dominates the total mangrove ecosystem carbon storage with carbon-rich deep soil horizons. Soil depth is a key factor in the determination of total carbon standing stocks of mangrove soils. Above-ground forest structural attributes (stand densities, stand basal area and biomass) appear to have a direct influence on the magnitude of the ecosystem carbon stock. In conclusion, this study reveals the opportunities and potential for mangrove forests in Sri Lanka to contribute to carbon valuation schemes (e.g., REDD+) and initiatives that revolve around payments for ecosystem services (PES), as one route towards the conservation, protection and restoration of these vital ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2021.114929.

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