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Ecological connectivity of seagrasses with mangroves increases the carbon storage of tropical seagrass meadows of an island ecosystem

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Ecological connectivity of seagrasses with mangroves increases the carbon storage of tropical seagrass meadows of an island ecosystem

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Ecologically connected ecosystems are considered more resilient to climate change mitigation by storing increased amounts of carbon than individual ecosystems. This study quantified the carbon storage capacity of seagrass (*Thalassia hemprichii*) meadows that are adjacent to mangroves (MG; *Rhizophora apiculate*) and without mangroves (WMG) at three locations in tropical Andaman and Nicobar Islands (ANI) of India. The sediment organic matter (OM) carbon (C_{org}) content was 2-fold higher at the MG sites than WMG sites of all three locations within the top 10 cm. The C_{org} in the total biomass was higher at MG sites than the biomass at WMG sites. The sediment grain size positively influenced the sediment OM and C_{org} content. The canopy height of *T. hemprichii* showed a better relationship with sediment OM and C_{org} at MG sites. In contrast, the shoot density of *T. hemprichii* showed a better relationship with sediment OM and C_{org} at WMG sites. The total carbon in 144 ha of *T. hemprichii* meadows of all three MG sites was 11031± 5223 Mg C, whereas the carbon in 148 ha of WMG sites was 4921±3725 Mg C. These *T. hemprichii* meadows of ANI store around 40487±19171 ton of CO_2 in the MG sites and 18036 ±13672 ton of CO_2 at WMG sites. The social cost of these carbon stored in these *T. hemprichii* meadows is around US$ 34.82 and 1.5 million at the MG and WMG sites, respectively. This study points out the efficiency of seagrass ecosystems of ANI as carbon sinks and the potential of these connected seascapes in increasing the efficiency of seagrass carbon storage. Therefore, this connectivity approach should be further explored to include these connected ecosystems of India as a nature-based solution for climate change mitigation and adaptation plans.

Keywords: Seagrass, Blue carbon, Tropical islands, Nature-based solution, Ecological connectivity, Mangroves

Introduction

Seagrasses are keystone coastal ecosystems that act as natural carbon sinks by sequestering atmospheric CO_2 and storing it in their sediments. Together with saltmarsh and mangroves, seagrass ecosystems account for the storage of 50% of oceanic organic carbon in their sediments (Duarte et al. 2005). Blue carbon refers to the organic carbon (Corg) stored in these ecosystems that has a high potential for offsetting global carbon emissions derived from anthropogenic activities (Macreadie et al. 2019). As long as these ecosystems are conserved or protected from anthropogenic disturbances, the blue carbon stored in their sediments can be stored safely for millenniums (Duarte et al. 2005; Macreadie et al. 2014). However, once destroyed, these ecosystems act as the source of carbon rather than sinks (Salinas et al. 2020; Serrano et al. 2020; Stankovic et al. 2021). As a result, globally, the importance of blue carbon stored in seagrass ecosystems (19.9 Pg of Corg) has gained attention, and their utilization as a nature-based solution for climate change mitigation is gaining momentum (Stankovic et al., 2021; Macreadie et al., 2019; UNEP, 2020). Global research on the blue carbon storage potential of seagrass ecosystems has emphasized the lack of data at local/regional scale studies (Fourqurean et al. 2012a; Howard et al. 2014; Macreadie et al. 2019). Within this framework, India is the least represented in terms of carbon storage in seagrass ecosystems as there is few (n=4) studies providing carbon storage data of the seagrass ecosystems of India considering its vast seagrass ecosystems (Ghosh et al. 2016; Ganguly et al. 2018; Kaladharan et al. 2020; Stankovic et al. 2021).

Seagrass ecosystems of India consist of 16 seagrass species that covers an area of 517 km2 along the east and the west coast of India, including the islands of Andaman and Nicobar and Lakshadweep up to a depth limit of 21 m (Geevarghese et al. 2018; Bayyana et al. 2020). As mentioned above, the carbon storage potential of these seagrass ecosystems is limited to only a few studies and five species, i.e., *Halophila ovalis* and *Halodule uninervis* from the Chilika lagoon, *Cymodocea serrulata*, *Syringodium isoetifolium,* and *Thalassia hemprichii* from Palk Bay and Gulf of Mannar region and *H. ovalis* and *T. hemprichii* from the Andaman and Nicobar Islands (Ghosh et al. 2016; Ganguly et al. 2018; Kaladharan et al. 2020; Stankovic et al. 2021). Interestingly, Stankovic et al. (2021) observed that an area of 200 hectares of *H. ovalis* and *T. hemprichii* meadows from the Andaman and Nicobar Islands could reduce around 3% of the carbon emissions of India, suggesting the massive potential of the seagrass ecosystems of India as a natural carbon sink and its role in offsetting carbon emissions.

Considering the vast area of seagrass ecosystems in India, the present study aims to quantify the carbon storage capacity of the Andaman and Nicobar Islands (ANI). The ANI in the Andaman Sea is home to 13 of the 16 seagrass species found in India, covering 29.3 km2 (Jagtap et al., 2003; Ragavan et al., 2016). *Thalassia hemprichii* is one of the keystone seagrass species of ANI found in the sandy intertidal habitats and amidst coral rubbles up to a depth of 15 m (Jagtap et al., 2003). *Thalassia hemprichii* is also found associated with other seagrass species such as *H. ovalis* and *C. rotundata* or with mangrove ecosystems (Mishra and Mohanraju 2018; Mishra and Apte 2020; Mishra and Kumar 2020). The association of *T. hemprichii* with mangroves has increased population dynamics, whereas, in areas without mangroves, the population was declining (Mishra and Apte 2020). However, how this connectivity influences the carbon storage capacity of the seagrass meadows of ANI has never been attempted.

Therefore, this study aims to assess the carbon storage capacity of *T. hemprichii* meadows adjacent to mangroves and without mangroves. Similarly, the study will quantify carbon storage of *T. hemprichii* meadows associated with other seagrasses such as *H. ovalis* and *C. rotundata.* We hypothesize that seagrass areas adjacent to mangroves can accumulate and store higher organic carbon than the individual or mixed seagrass meadows. This study aims to evaluate the economic gains of the carbon stored in these seagrass ecosystems and how these carbon sinks can benefit India's carbon reduction plans through Intended Nationally Determined Contribution (INDC) under the Paris Climate Agreement 2015. This study proposes leveraging the monetary values of this blue carbon potential for better conservation and management of seagrass ecosystems in these islands and across India.

2.Methods

2.1. Study sites

The Andaman and Nicobar Islands (ANI) are situated in the southeast of India in the Andaman Sea (Fig.1). These islands are rich in seagrass and mangroves due to their tropical settings. These islands are part of the global bioregion model five for seagrasses (Short et al., 2007) and have 13 species of seagrasses that are found in the Indian subcontinent (Mishra and Apte, 2021). The proposed study surveyed three locations of ANI; Saheed Dweep (hereafter called as Neil Island), Swaraj Dweep (hereafter called as Havelock Island) and Burmanallah situated in the southeast side of ANI (Fig.1). This survey was carried in the summer/dry season (Feb-March 2019) of these islands. Sampling was carried out in the coastal ecosystems of the above mentioned three locations where patches of seagrasses (*Thalassia hemprichii*) and mangroves (*Rhizophora apiculate*) co-existed. At each location two sites were selected, one where seagrasses are adjacent to mangrove ecosystems (MG) and another without mangroves (WMG). In these study locations a tidal amplitude of 2.45m, a temperature range of 26.28 to 31.67°C, and a salinity range 32 to 35 existed. Being an island ecosystem, these study areas exhibited a matrix of ecosystems, where coral reefs (dead or live) were present towards the seaward side, seagrasses in the middle and mangroves towards landward side (Mishra and Mohanraju 2018; Mishra and Apte 2020; Mishra et al. 2021)

Havelock island

Havelock Island is also situated in the southeast of ANI and north of Neil Island (Fig.1a). The two sites here were 900-1000 m apart and each site was surrounded by dead coral patches. The *T. hemprichii* population was found in mono-specific patches at both sites. *Thallsia hemprichii* population was sampled within a depth of 0.5 m during low tide from meadows adjacent to mangroves (MG;1008 m x 500 m) and without mangroves (WMG ; 886 m x 978 m).

Neil Island

Neil Island is situated in the southeast region of ANI (Fig.1b) The two sites selected here were 1000 m apart and were separated by dead coral patches. *Thalassia hemprichii* population was sampled at both MG (250m x 900 m) and WMG (200 m x100 m) sites within a depth of 0.5 m during low tide.

Burmanallah

Burmanallah is situated in the southeast region of ANI (Fig.1c). This location has rocky intertidal beaches and human-made coastal concrete walls. The study sites with mangroves have an outlet that discharges land run-off into the mangrove area. The *T. hemprichii* meadows within the mangrove area were monospecific. The sites here were 1000 m apart from each other. *T. hemprichii* population was sampled within a depth of 0.3m during low tide from the MG (800 m x 900 m) and WMG (750 m x 800 m) areas.

2.2. Seagrass sampling and analysis

Ten quadrats were collected randomly from a transect of 30 m perpendicular to the beach at both sites within a depth of 0.5m during low tide. We used a quadrat of 20 cm x 20 cm and a hand shovel to dig out seagrass samples up to 10 cm in depth. The density (individual m-2), biomass (g DWm^{-2}) and canopy height (cm) values were obtained from Mishra and Apte, (2020; See Supplementary Table 2). The separated and dried biomass of 0.2 mg was combusted using a CHNS analyser (Elementar, UNICUBE) to determine the total organic carbon (C_{org}). The biomass (g DWm^{-2}) was converted to Mg C DW ha^{-1} after multiplying by the carbon content (%C) in the above-ground and below-ground biomass.

2.3. Sediment sampling and analysis

Sediment cores (n=10) were collected from each quadrat where seagrass was sampled using 5cm diameter and 10 cm long plastic core. It was not possible to collect sediment cores higher than 10 cm depth because of the habitat structure, which is mostly made of coral reefs or rocks of volcanic origin. The collected sediment cores were stored in plastic zip-lock bags and brought to the laboratory. In the laboratory, the sediment samples were oven-dried at 60°C for 72 hours before being sieved for grain size fractions. The sediment samples were homogenized using a disc mill (Retsch, RS 200, USA) after the removal of large stones or twigs.

Then the dry bulk density (DBD g/cm^3) of the sediment was calculated as

$$DBD = \frac{weight\ of\ dry\ soil}{volume\ of\ the\ core} \ldots\ldots\ldots\ldots\ldots\ldots..(1)$$

Following the loss on ignition (LOI) method, five grams of homogenized sediment samples was heated to combustion at 450º C for 4 hours using a muffle furnace (Heiri et al., 2001). The LOI (%) was calculated as

$$LOI\ (\%) = \left[\frac{A-B}{A}\right] * 100 \ldots\ldots\ldots\ldots\ldots\ldots.. (2)$$

Where A is the initial weight of sediment in grams and B is the final weight of sediment after combustion.

From the remaining fraction of the homogenized sediment, 1gm of sediment was acid treated with 10% HCl for 24 hours, washed with distilled water and dried again at 60º C for 24 hours (Howard et al., 2014). From this acid treated sediment samples 0.2 mg was combusted using CHNS analyser (Elementar, UNICUBE) to determine the total C. A regional relationship between organic matter (%LOI) and carbon (%C) content in the sediment was calculated using sediment samples (n=18) from seagrass meadows with mangroves and without mangroves (Fig.2). The fraction of organic carbon (%C_{org}) was then calculated using the following relationship:

$$\%Corg = -0.406 + (0.512 * \%LOI) \ldots\ldots\ldots\ldots (\text{MG; } R^2 = 0.94) \ldots\ldots\ldots. (3)$$

$$\%Corg = -1.117 + (0.496 * \%LOI) \ldots\ldots\ldots\ldots. (\text{WMG; } R^2 = 0.89) \ldots\ldots.. (4)$$

The total carbon (Mg ha^{-1}) was calculated by adding the total carbon in the sediment and the seagrass biomass (Howard et al., 2014). The total areas of all seagrass meadows included in this study (Table1) were multiplied by the quantified carbon present in the seagrass biomass (Mg C ha^{-1}) and in the sediment (Mg C ha^{-1}) to calculate the total carbon stored in these seagrass meadows of three locations of ANI. The carbon dioxide (CO_2) equivalent emission/storage per hectare (Mg CO_2 ha^{-1}) was calculated by multiplying the CO_2 conversion factor (3.67) by the mean carbon stock of the seagrass ecosystem (Howard et al., 2014).

2.4. Valuation of carbon sequestration and storage

The social cost of carbon (SCC) represents the economic cost associated with climate chage related damage (or benefit) due to emission of one ton of CO_2 or its equivalent (Nordhaus 2017; Ricke et al. 2018). We used the regional approach to estimate SCC, than the global approach, as country level (regional) estimates allow better understanding of regional impacts and are important for better adaptation and compensation measures (Ricke et al., 2018). We used the recent estimate of SCC for India, which is US$86 per ton CO_2 (Ricke et al., 2018). Recent US$ to Indian Rupees (INR) conversion was used to estimate the price of CO_2 in rupees.

Statistics

Pearson Correlation was used to test the effects of plant height and density in trapping higher or lower organic matter/carbon content in the meadows. Similarly, a correlation between sediment grain size and organic matter/organic carbon was tested to check the influence of sediment grain size in storing higher or lower organic matter/carbon. Two-way ANOVA was used to test the significant differences between *T. hemprichii* density and biomass estimates with sites (with mangroves (MG) and without mangroves (WMG)) and locations of ANI (Neil, Havelock, and Burmanallah) as fixed factors. All data was pre-checked for normality and homogeneity of variance. When variances were not homogenous, data were ln (x+1) transformed. When there were significant effects, the Holm-Sidak test was performed for a posteriori comparison among factor levels. All statistical tests were conducted at a significance level of $p < 0.05$ (Sokal and Rohlf, 2012), and data are presented as mean and standard error (S.E.). Sigmaplot (ver. 11.01.102) software was used for all statistical analyses.

3.Results

The sediment dry bulk density of *T. hemprichii* meadows was significantly different ($p<0.001$) between the three locations than among the MG and WMG sites of each location (Table 1). In general, the dry bulk density was 1-fold higher among the *T. hemprichii* meadows associated without mangroves (0.84 ± 0.13 g cm^{-3}) than the meadows with mangroves (0.75±0.23 g cm^{-3}) (Table 1). The mean organic matter (52.55±16.49 % DW) and C_{org} (26.51±8.44 % DW) in the sediment of *T. hemprichii* meadows associated with MG sites was 1.3-fold and 1.4-fold higher than the meadows of WMG areas (Table 1). The relationship between the sediment organic matter and C_{org} were significant for both MG (R^2=0.94) and WMG (R^2=0.89) locations, with a better relationship at *T. hemprichii* meadows within the MG than WMG areas at all three locations (Fig.2).

The mean AB-and BG-biomass were significant and different between the locations and sites (Fig.3). The AB-biomass (1.99 ± 0.48 Mg DW ha^{-1}) of *T. hemprichii* at the MG sites was 2.4-fold higher than the biomass at WMG sites (0.82 ± 0.31 Mg DW ha^{-1}). The BG-biomass of *T. hemprichii* followed a similar pattern and was 1.5-fold higher at MG (3.94 ± 0.89 Mg DW ha^{-1}) than WMG (2.55 ± 0.76 Mg DW ha^{-1}) sites. The total biomass (AB+BG biomass) was higher between the three locations at Neil Island MG sites than at Havelock and Burmanallah locations (Fig.3). In general, the carbon content in AB-biomass (leaves) of *T. hemprichii* was higher than the BG-biomass (rhizomes + roots), which resulted in higher Corg in the AB-biomass than the BG-biomass (Table 1). The carbon content in AB-biomass was 1.4-fold higher at the MG sites (49.12 ±17.12 % DW) than at the WMG sites (35.1± 5.32 % DW). Similarly, the carbon content in BG-biomass of *T. hemprichii* at the MG sites (43.37± 12.26 % DW) was 1.2-fold higher than WMG sites (34.86± 5.25 C %DW) (Table 1). These higher carbon content resulted in higher C_{org} in AB-biomass than BG-biomass at MG sites than WMG sites (Fig.1). The C_{org} in AB-biomass of *T. hemprichii* at the MG sites (90.78± 70.7 Mg C DW ha^{-1}) was 3.2-fold higher than WMG sites (27.74 ± 9.01 Mg C DW ha^{-1}). In contrast, the C_{org} in BG-biomass of *T. hemprichii* at the MG sites (141.89 ± 83.7 Mg C DW ha^{-1}) was 1.8-fold higher than WMG sites (78.23± 45.38 Mg C DW ha^{-1}) (Table 1). Between the three locations, following the total biomass patterns, the C_{org} in *T. hemprichii* meadows was higher in the total biomass of the Neil Island than the other two locations (Fig.1).

In general, the carbon content in the sediment was lower than that of carbon in the biomass of *T. hemprichii* meadows at both MG and WMG sites (Table 1). The carbon content in the sediment of *T. hemprichii* meadows at the MG sites (26.51 ± 8.44 % DW) was 1.4-fold higher than the meadows at WMG sites (18.49 ± 6.63 % DW). Among the three locations, the sediments of *T. hemprichii* meadows at the Burmanallah MG site was recorded with the highest carbon content in the sediment, followed by the Havelock MG site (See Supplementary Table 1). A similar pattern was observed for the carbon content in the sediment of *T. hemprichii* meadows at the WMG sites.

Higher carbon content in the sediment at MG sites resulted in higher Corg in *T. hemprichii* meadows associated with MG sites than WMG sites (Table 1). The mean Corg in the sediment of *T. hemprichii* meadows at the MG sites (21.87 ±11.53 Mg C ha^{-1}) was 1.4-fold higher than the WMG sites (15.62 ± 6.50 Mg C ha^{-1}) (Fig.4). Interestingly owing to the low sediment dry bulk density of *T. hemprichii* meadows at the MG site of Neil Island, the sediment Corg was 1.2-fold lower at the MG site than the WMG site (Fig.4a). However, among the three locations, the Corg in the sediment of *T. hemprichii* meadows at Burmanallah was the highest, followed by the MG site of Havelock (Fig.4a). The total Corg in the sediment between the three locations was higher at MG sites (1265.35 ± 1010 Mg C) than at the WMG sites (839.07± 641.05 Mg C) (Table 1). Between the three locations, the highest total Corg in the sediment was recorded in the *T. hemprichii* meadows of Burmanallah location, followed by Havelock and Neil Islands (See Supplementary Table 1).

The carbon storage as CO_2 equivalent in the *T. hemprichii* meadows ranged between 147-10400 Mg CO_2 at the MG sites and between 28-6529 Mg CO_2 at the WMG sites (Fig.4b). The CO_2 equivalent storage followed the same pattern as total C_{org} in the sediment. The average price of this carbon is around 0.39 million US$ for MG sites and 0.26 million US$ for WMG sites, while the price of this carbon in Indian Rupees (INR) was 29.69 and 19.69 million for MG and WMG sites, respectively. The total carbon in the ecosystem (carbon in total biomass+ sediment) was 2-fold higher at the MG sites (272.54±164 Mg C ha^{-1}) compared to the WMG sites (128.79 ± 55.89 Mg C ha-1) (Table 1). Due to the higher total biomass of *T. hemprichii* meadows of Neil Island, the total carbon in the ecosystem was higher at the Neil Island MG site, followed by Havelock and Burmanallah locations (Fig.4c). The total C_{org} for the studied area of *T. hemprichii* meadows was 2.2-fold higher at MG sites (11031 ± 5223 Mg C) than WMG sites (4921±3725 Mg C). Similarly, the mean carbon equivalent of CO_2 storage in the entire ecosystem was higher at MG sites (40487 ± 19171 Mg CO_2) than at WMG sites (18036 ± 13672 Mg CO_2) (Fig.4d). Among the locations, the MG sites of Neil Island stored the highest CO_2 equivalent, followed by Havelock and Burmanallah (Fig.4). The mean price of the carbon stored in the entire ecosystem of *T. hemprichii* meadows of ANI at MG sites

(34.82 ±16.48 million US$) and WMG sites (1.55 ±1.17 million US$). The price in INR for MG sites is 2589 million INR, and that of WMG sites is 115.52 million INR (Table 1).

The relationship between sediment silt content with organic matter/Corg was significant for both MG and WMG sites, with higher significance at MG sites (Fig.5). The morphometrics of *T. hemprichii*, such as canopy height and shoot density, positively influenced the sediment organic matter/C_{org} content at both MG and WMG sites (Fig.6). The canopy height of *T. hemprichii* showed a better relationship with sediment organic matter/C_{org} at MG sites of all three locations (Fig.6a & b). In contrast, the shoot density of *T. hemprichii* showed better relationships at WMG sites of all three locations (Fig.6c & d).

4.Discussion

Ecological connectivity between seagrass and mangroves is a multifaceted process and plays an important role in the ecological functioning of coastal ecosystems (Berkström et al. 2020; Mishra and Apte 2020; Carlson et al. 2021). This connectivity between seagrass and mangrove ecosystems positively influences the carbon storage capacity in the seagrass ecosystems (Juma et al. 2020; Asplund et al. 2021). The present study quantified the carbon storage in ecologically connected seagrass and mangrove ecosystems in a tropical island (ANI) ecosystem and observed that seagrass meadows adjacent to mangrove ecosystems store a higher amount of carbon in their sediment and biomass compared to seagrass ecosystems without mangroves. This influence of ecological connectivity with mangroves on seagrass (*T. hemprichii*) population dynamics has been previously studied in ANI, India (Mishra and Apte, 2020). However, to our knowledge, this is the first time the influence of mangroves on seagrass carbon storage has been quantified in ANI and India.

4.1. Carbon stored in the sediment

Sediment grain size (<63 µm) plays an important role in carbon accumulation and storage in seagrass meadows across biogeographical regions (Mazarrasa et al. 2018; Ricart et al. 2020; Potouroglou et al. 2021; Santos et al. 2021). The dry bulk density observed in our study was within the global range of sediment density (1.03±0.02 g DW cm3) observed for seagrass meadows ((Fourqurean et al. 2012b). In the present study, the fine fraction of sediment (mostly silt) distribution in *T. hemprichii* meadows associated with mangroves was low at the Neil and Havelock islands. This is because the *T. hemprichii* meadows were growing on sandy substrates with coral rubbles, and the *Rhizophora apiculate* mangrove ecosystems of both the islands do not receive land-based run-off, whereas the *T. hemprichii* meadows at Burmanallah received such input (Mishra and Apte, 2020; Nobi et al., 2010; Savurirajan et al., 2018). Mangrove ecosystems of these islands play an essential role in out-welling nutrients to the surrounding ecosystems, which includes organic matter and organic carbon content (Jha et al. 2013, 2015; Sahu et al. 2013; Mishra and Kumar 2020).

Seagrass meadows are efficient in trapping sediment and organic matter from the water column that comes their way from the mangrove ecosystem through daily receding tides (Miyajima et al. 2017). Seagrasses utilize the height of their leaves (canopy height) and dense rhizome network to trap the inflowing particles and organic matter (Samper-Villarreal et al. 2016; Potouroglou et al. 2017; Barcelona et al. 2021). This mechanism is evident in our study, as there is a better correlation between the canopy height of *T. hemprichii* with organic matter content at MG sites (Fig.6). Similar correlations are observed for shoot density and organic matter content in MG sites (Fig.6). However, it is essential to notice here that the *T. hemprichii* meadows at the WMG sites exhibited better correlations of organic matter with shoot density than the MG sites. This is probably because the WMG sites in our study locations are exposed to high wave dynamics that make them prone to leaf breakage resulting in reduced canopy height (Fig.7b, Mishra and Apte, 2020). As a result, the plant invests in better below ground structures to withstand the wave dynamics, resulting in higher organic matter trapping. Secondly, the ecosystem matrix of Neil and Havelock islands are such that the *T. hemprichii* meadows at WMG sites are exposed to high intertidal temperatures resulting in leaf damage and leaf reddening (Fig.7a). Similar mechanisms of hydrodynamic setting and its influence on seagrass ecosystems have been observed elsewhere (Beaufort et al., 1998; Saenger & Funge-Smith, 2012). Furthermore, the influence of local hydrodynamic settings, sediment grain size, canopy height and shoot density having a positive effect on various seagrass species and connected mangrove seascapes have also been observed for *T. hemprichii*, *Cymodocea rotundata*, *Enhalus acoroides* and *Thalassodendron ciliatum* from the coast of Madagascar (Asplund et al., 2021) and Gazi Bay of Kenya on *C. rotundata*, *C. serrulata*, *E. acoroides*, *T. ciliatum* (Juma et al., 2020).

The sediment C_{org} in our present study is significantly higher (~9-13 times) than other studies of seagrass meadows from the east coast of India (Ghosh et al. 2016; Ganguly et al. 2017a; Kaladharan et al. 2020, 2021). The sediment C_{org} in our study is also higher than the global average (5.7 ± 0.3 % C DW) but was within the range (0-100 %C DW) reported for various seagrass ecosystems (Fourqurean et al., 2012). However, this global study lacked data points for India, including ANI. Higher C_{org} in the sediment of ANI could be possible for two reasons, 1) the previous authors have mainly studied seagrass ecosystems that are not connected to mangroves. As a result, the sediment organic carbon is not influenced by mangrove based out-welling and 2) being an island ecosystem and oligotrophic, the *T. hemprichii* meadows have adapted to store a higher amount of carbon within their sediment. However, other than mangroves, seaweed and macroalgal communities associated with dead and live corals may have contributed to the sediment organic carbon fraction (Ricart et al. 2015; Liu et al. 2020; Mazarrasa et al. 2021). Higher sediment C_{org} than the seagrass meadows of the mainland coast of India has also been observed by Sachithanandanam et al. (2020) at Burmanallah and Havelock Island of ANI previously. This indicates that the seagrass ecosystem of ANI stores a higher amount of Corg in their sediment, and the presence or absence of mangroves directly influences this organic carbon storage. In general, it is thought that the seagrass ecosystems contribute 98% of the autochthonous C_{org} in the sediment (Lavery et al. 2013; Serrano et al. 2018). However, 50% of this autochthonous C_{org} is buried in the seagrass meadows, and the rest is transferred to surrounding ecosystems (Duarte and Krause-Jensen, 2017). However, our results suggest that in tropical island ecosystems and adjacent to mangroves, this contribution and storage can change, as seagrass can accumulate and develop organic-rich soil consisting of autochthonous and allochthonous carbon (Kennedy et al. 2010; Duarte et al. 2013) if its remains sheltered and less disturbed compared to disturbed conditions at WMG sites. A similar influence of mangroves on seagrass sediment C_{org} has been observed for *T. hemprichii* from the Western Indian Ocean region (Asplund et al., 2021).

4.2. Carbon stored in Total Biomass

The mean AB-biomass and BG-biomass at the MG and WMG sites of ANI were within the range limit (AB;2.15 and BG; 5.08 Mg DW ha^{-1}) for the global seagrass ecosystem (Fourqurean et al., 2012). The carbon stored in seagrass BG-biomass is generally 2-fold higher than the AB-biomass (Fourqurean et al., 2012), and our results showed a similar pattern (See Supplementary Table 2). The differences in C_{org} in AB-and BG-biomass was more evident at the WMG sites (2.8-fold) than at the MG sites (1.5-fold) because the AB-biomass of the WMG sites were more prone to breakage and loss than at MG sites. As compensation for this breakage of leaves, *T. hemprichii* involves most of its stored energy in leaf growth, vertical rhizome growth and below-ground roots (Mishra and Apte, 2020). This resulted in an almost 3-fold higher C_{org} in the BG-biomass of *T. hemprichii* at the WMG sites than the AB-biomass. This higher biomass at MG sites of the three locations enhanced the capacity of *T. hemprichii* meadows to store higher autochthonous C_{org} in their meadows. The meadow size also facilitated this higher carbon storage, the density, rhizomes, roots, seagrass necromass and dissolved organic carbon are that are higher at MG than WMG sites of the three locations, that contribute significantly to the primary production of these meadows (Mishra and Apte, 2020; Mishra and Kumar, 2020), resulting in higher carbon in the biomass. Higher productivity leading to higher carbon storage in the biomass has been observed for *T. hemprichii* mixed meadows at the Palk Bay and Gulf of Mannar region of Tamil Nadu in India (Ganguly et al., 2017; Singh et al., 2015).

4.3. Total carbon in the seagrass ecosystem

The total carbon stored in the seagrass ecosystem (sediment + biomass) at the MG and WMG sites showed a high standard deviation (Table 1) because of differences in habitat configuration of each study location. Secondly, the total meadow size (in hectares) for each of the MG and

WMG sites at all three locations were different. For example, the total biomass of *T. hemprichii* meadows was higher at the MG site of Neil Island than the other two locations, but due to the small area, the total carbon in the ecosystem was on the lower side (Fig.4). Similarly, with a smaller size at the WMG site, the carbon in the ecosystem was the lowest at Neil Island. Consequently, even though the biomass of *T. hemprichii* at Burmanallah MG and WMG sites were lower than the other two locations, due to the higher meadow area, the meadows of *T. hemprichii* had the second-highest carbon in the entire ecosystem (Fig.4). This suggests that seagrass meadow size plays an important role in determining the total carbon storage in the ecosystem. A similar impact of meadow size affecting seagrass carbon storage has been observed for seagrass ecosystems of India at Chilika lake of Odisha, Pulicat lake, Gulf of Mannar and Palk Bay of Tamil Naidu (Ghosh et al. 2016; Ganguly et al. 2017a; Kaladharan et al. 2020, 2021).

Previous studies have shown that the total carbon in the seagrass meadows of ANI (184.24 ± 23.84 Mg C ha^{-1}) is higher than in other southeast Asian countries (Stankovic et al. 2021). Our findings agree with the previous studies and show that seagrass meadows of ANI have 66% higher carbon storage capacity at MG sites (272.54 ± 164 Mg C ha^{-1}) and low at WMG sites (128.79 ± 55.89 Mg C ha^{-1}). These differences in our study from Stankovic et al. (2021) is probably because the authors derived the total carbon in the ecosystem through a model-based approach, whereas in our study, we have used the traditional methods of quantification recommended for blue carbon research (Howard et al., 2014). The total carbon stock in the *T. hemprichii* meadows at the MG sites (144ha; 11031 ± 5223 Mg C) was 2-fold higher than the WMG sites (148 ha; 4921 ± 3725 Mg C) of ANI. This indicates that *T. hemprichii* meadows associated with mangroves can store a higher amount of carbon in the ecosystem than individual seagrass ecosystems. These islands of ANI are oligotrophic; as a result, even though the total meadow size at WMG sites were higher, it did not result in higher carbon storage in the ecosystem.

Consequently, with a small meadow size, the MG sites were able to accumulate higher carbon stocks. Because at the MG sites, there is a flow of nutrients and organic matter from the mangrove ecosystem (Mishra and Kumar, 2020; Jha et al., 2015; Sahu et al., 2013) that helps the *T. hemprichii* meadows in meeting their nutrient demands and increasing productivity (Mishra and Apte, 2020). The total carbon stock in our studies is limited to the upper 10 cm of the sediment depth as dead corals made it challenging to collect increased depth cores. So, the standard extrapolation of sediment depth to 1m was avoided. Similarly, from the seagrass meadow perspective, we estimated the carbon stock in a total of 292 ha for both MG and WMG sites and have avoided the extrapolation to the total seagrass area of ANI. Avoiding the extrapolation was necessary because, in India, previous seagrass carbons storage research has measured carbon storage in a single species and have extrapolated that data to the total seagrass coverage, which have mixed species of seagrass (Kaladharan et al. 2020, 2021; Ghosh et al. 2018). This has resulted in biased carbon storage values because seagrass carbon storage capacity is species-specific, and the local abiotic factors such as hydrodynamics, land run-off, anthropogenic pollution and habitat disturbances play an important role in determining this capacity (Howard et al., 2014; Duarte and Krause-Jensen, 2017; Macreadie et al., 2019). Based on the International Panel for Climate Change (IPCC, 2014) Tier 1 assessment, the MG sites can prevent the emission of 40487 Mg CO_2, while the WMG sites can prevent 18036 Mg CO_2 (Howard et al., 2014). Based on the amount of carbon stored in the MG and WMG site of ANI, the price of this CO_2 storage is around 34.82 million US$ for MG sites and 1.55 million US$ for WMG sites. However, our values differ from the previously reported pricing values of Stankovic et al. (2021) for ANI because the previous authors use carbon pricing for ANI based on (Nurdianto and Resosudarmo, 2016) for ASEAN countries, where the price of one ton of CO_2 was priced at US$10. Whereas we used the recent price for one ton of CO_2 for India by Ricke et al. (2018) at US$86. However, ANI is part of India and not ASEAN countries, which seemed appropriate for estimating the social cost of carbon using the recent price by Ricke et al. (2018).

4.4. Contribution of seagrass ecosystems for India's Intended Nationally Determined Carbon (INDC) Plans

In its INDC commitments under Paris Climate Agreement (UNFCC, 2015), India has pledged to reduce 33-35% of its carbon emissions by 2030. The foundation in achieving this target is laid in the National Environmental Policy, 2006, which promotes sustainable development while protecting and conserving the various ecosystems. The National Action Plan on Climate Change (NAPCC) further sustains the idea of ecosystem management through national missions, which outlines priorities for climate change mitigation and adaptation measures. The present studied seagrass ecosystems of ANI can store 0.17 Mg ton (0.007%) of the total CO_2 emissions of India (2300 Mg ton; Karstensen et al., 2020). However, this fraction is very small considering the huge emissions of India. However, the total seagrass area of ANI was not considered in this study which can reflect different carbon storage scenarios.

Furthermore, the blue carbon storage potential of seagrass ecosystems of India needs more detailed studies considering species-specific carbon storage potential. Secondly, seagrass ecosystems of India are missing in any of the climate change mitigation plans (Koshy et al.

2018; Ramesh et al. 2018), whereas mangroves are included. However, through this carbon storage study of ecologically connected seagrass and mangrove ecosystems of ANI, this study emphasizes on the importance of seagrass ecosystems. Secondly, as these seagrass ecosystems are adjacent to mangrove ecosystems of ANI, these ecosystems can be considered along the Mangroves for the Future (MFF) and Island Protection Zones (IPZ) programs of the NAPCC for initiating conservation and management practices for seagrass ecosystems of India that are under decline from various anthropogenic activities (Mishra and Apte, 2020; Mishra et al., 2021a, 2021b). Loss of seagrass ecosystems of India will make these ecosystems as source of carbon emission than storehouse and can release various other greenhouse gases (Banerjee et al., 2018).

5.Conclusion

Seascape connectivity across blue carbon habitats results in higher carbon storage than individual ecosystems (Huxham et al. 2018; Macreadie et al. 2019) and our results agree showcase this increased carbon storage in seagrass meadows associated with mangroves. This present study adds new data and knowledge to the growing importance of connected ecosystems across coastal seascapes and their role in increased carbon storage in the ecosystem. To our knowledge, this is for the first-time carbon storage of connected ecosystems is reported from India. This study observed a 2-fold increase in carbon storage capacity of seagrass meadows associated with mangroves than without mangroves, probably due to organic matter and carbon input from the mangrove ecosystems. The positive influence of this cross-habitat connectivity on blue carbon storage potential within the coastal seascape of ANI and other parts of India needs further exploration as nature-based solutions for climate change mitigation plans of India. This ecosystem service of seagrasses of India needs to be integrated with NAPCC for better management of seagrass ecosystems of India (UNEP, 2020).

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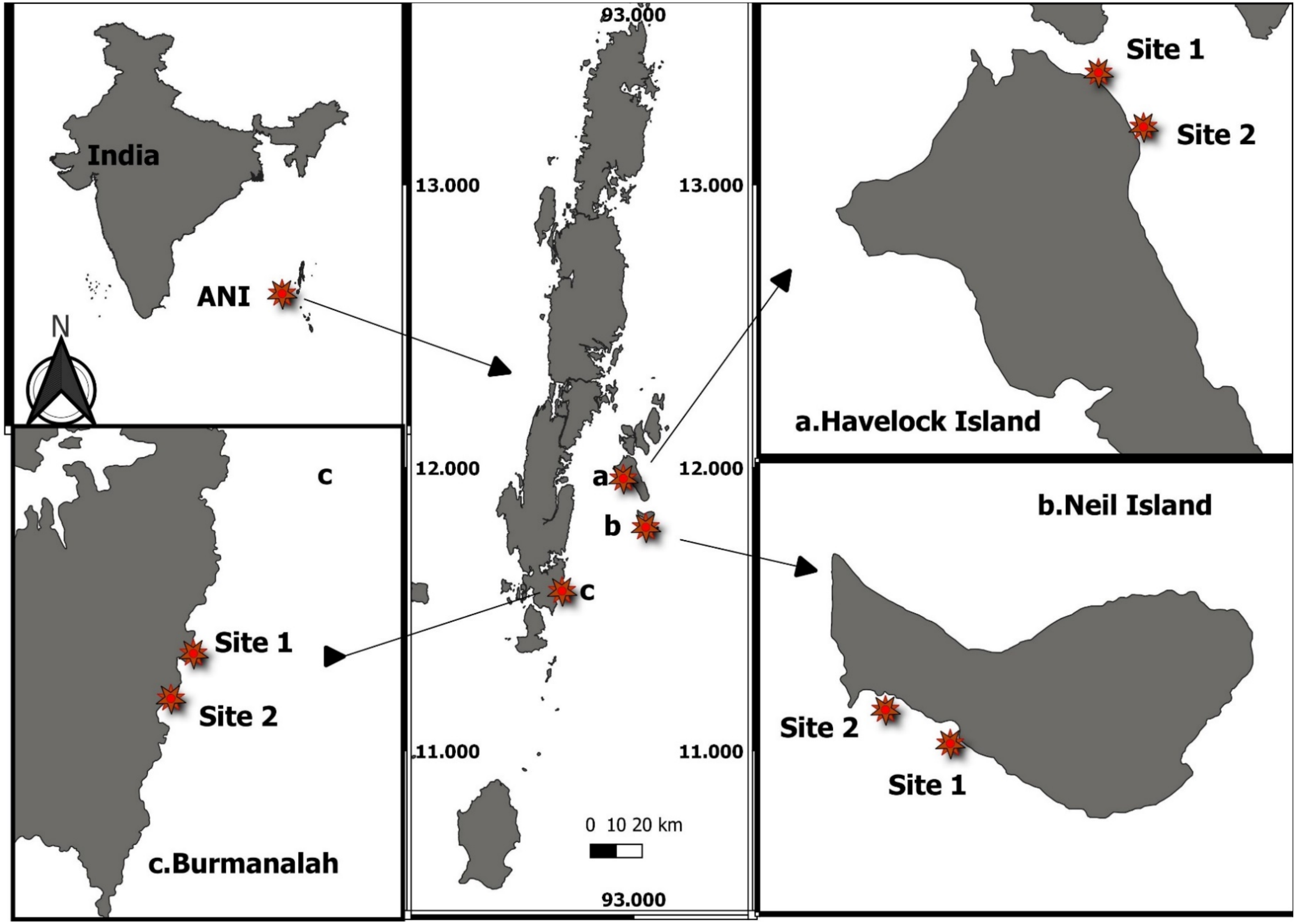

India
ANI
N
93.000
13.000
13.000
12.000
12.000
11.000
11.000
93.000
a
b
c
0 10 20 km
Site 1
Site 2
a.Havelock Island
b.Neil Island
Site 2
Site 1
c
Site 1
Site 2
c.Burmanalah

Fig.1. Map showing the study locations of a) Havelock Island, b) Neil Island and c) Burmanallah of ANI, India. Seagrass areas with mangroves are presented as Site 1 and without mangroves as Site 2

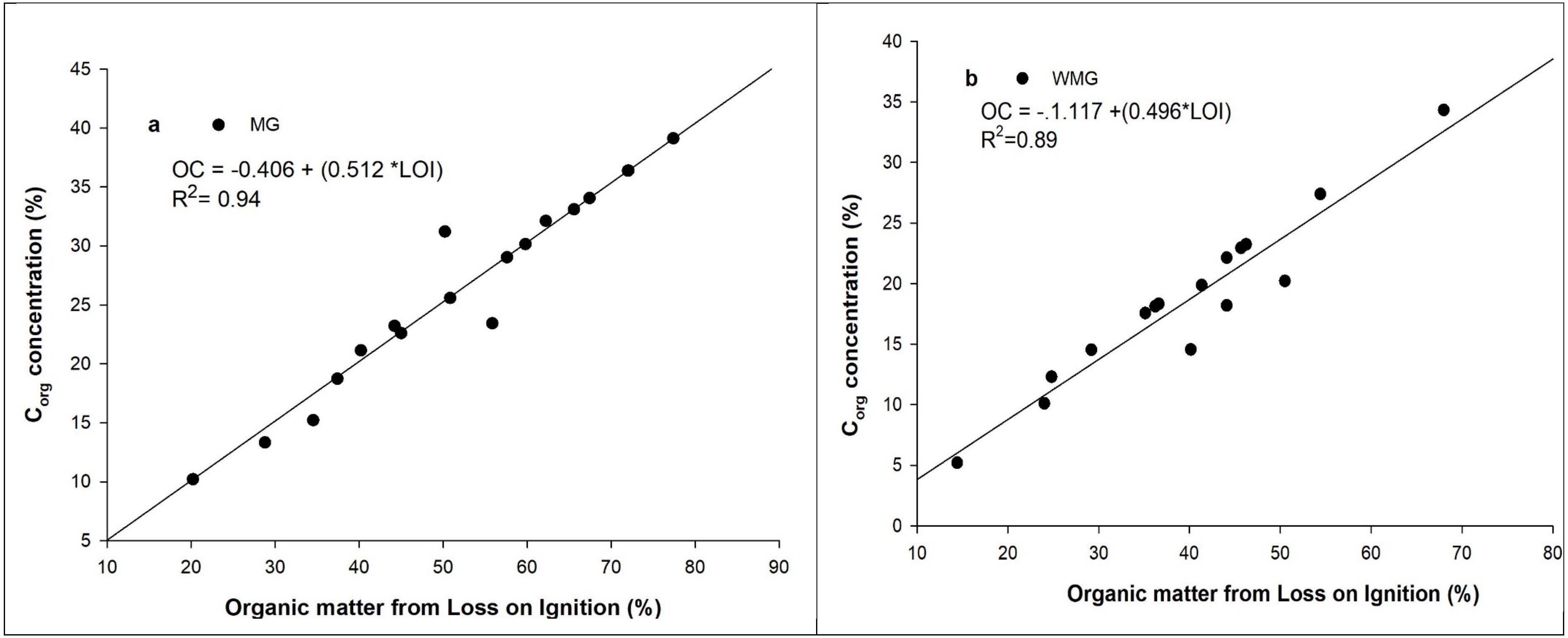

Fig. 2 The relationship of organic matter (%LOI) with organic carbon (%OC) for the seagrass ecosystems with mangroves (a) and without mangroves (b) of ANI, India.

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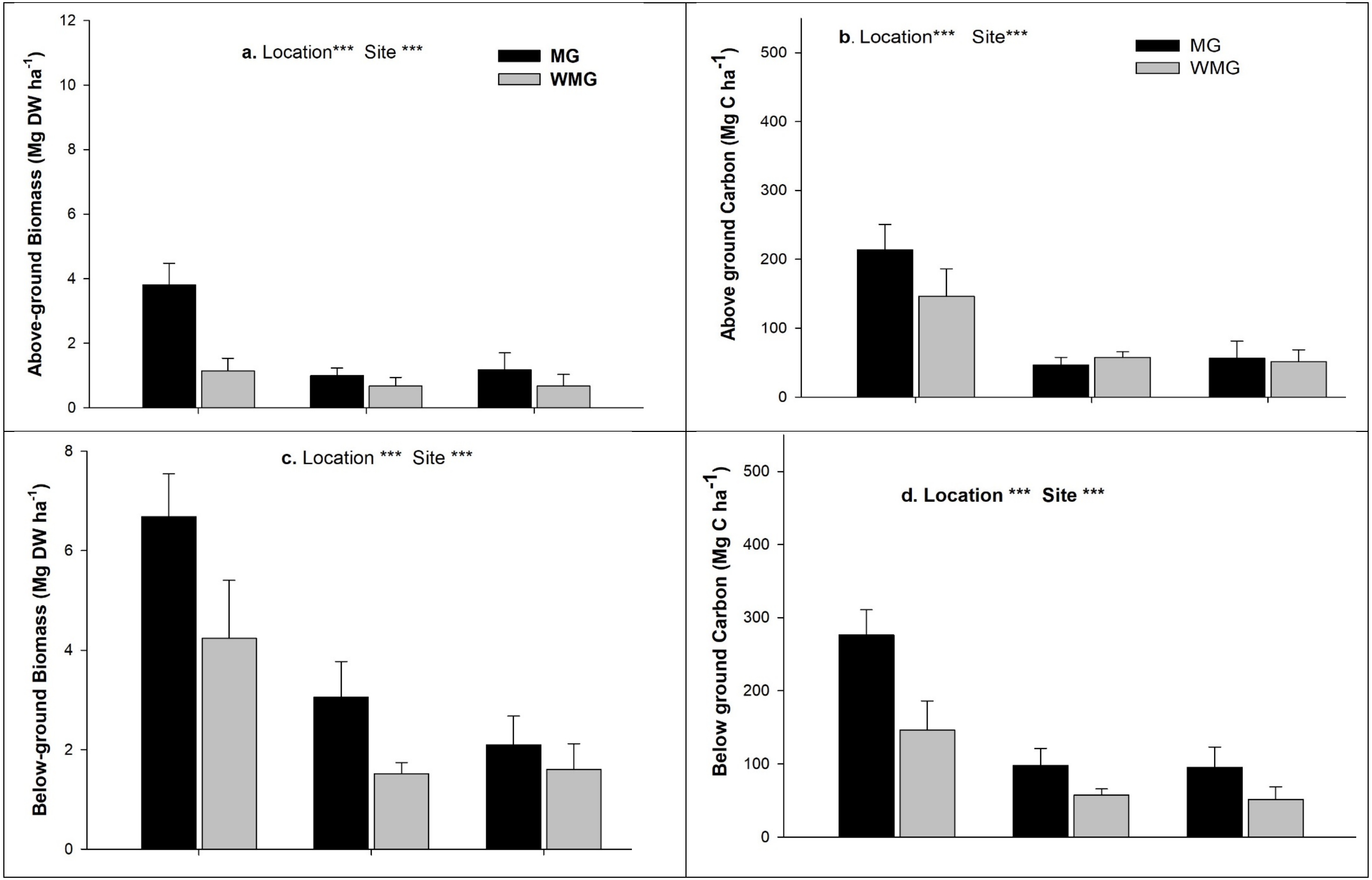

a. Location*** Site ***
MG
WMG
Above-ground Biomass (Mg DW ha-1)
0
2
4
6
8
10
12
b. Location*** Site***
MG
WMG
Above ground Carbon (Mg C ha-1)
0
100
200
300
400
500
c. Location *** Site ***
Below-ground Biomass (Mg DW ha-1)
0
2
4
6
8
d. Location *** Site ***
Below ground Carbon (Mg C ha-1)
0
100
200
300
400
500

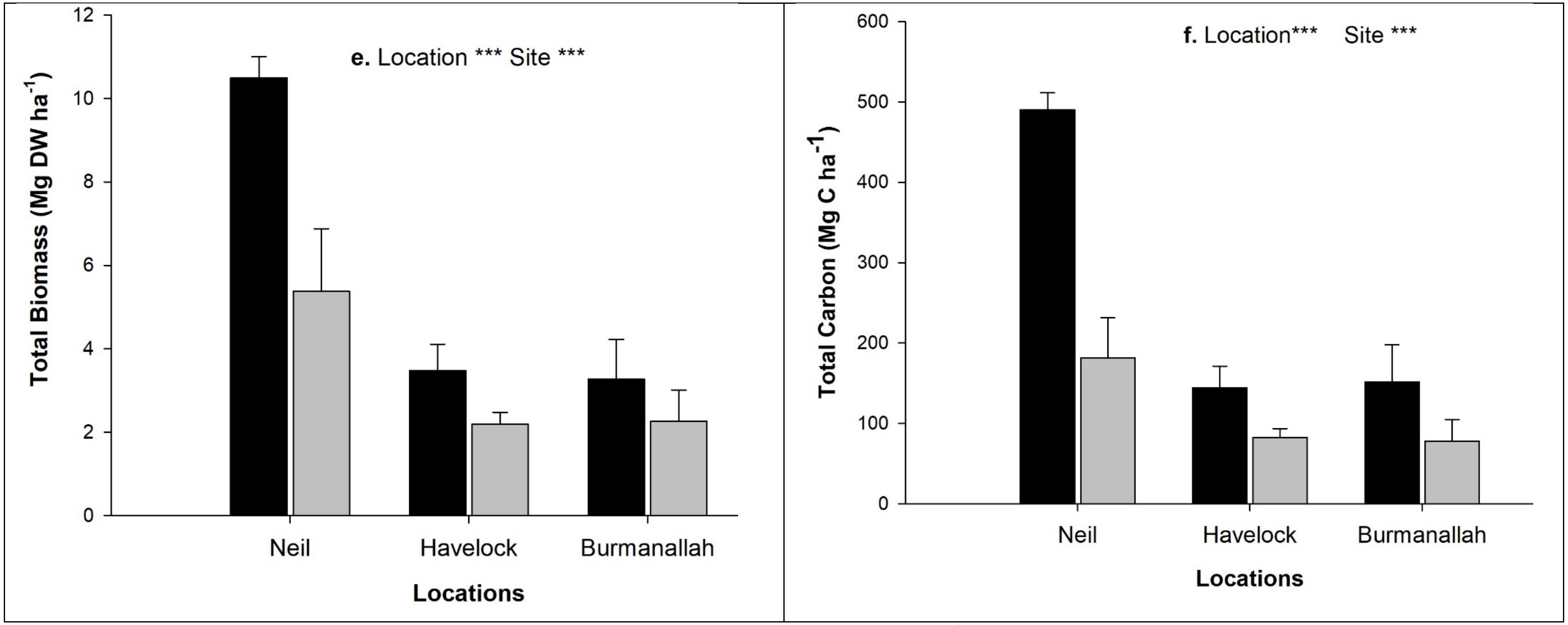


Fig. 3. Average values (mean ± SD) of biomass (Mg DW ha-1) and the carbon (Mg C ha^{-1}) stored in the respective biomass of *T. hemprichii* in the sites with and without mangroves of Neil, Havelock and Burmanallah location of ANI, India. Significant differences were derived from two-way ANOVA analysis using location and site as fixed factors. (p<0.001***, p<0.01**).

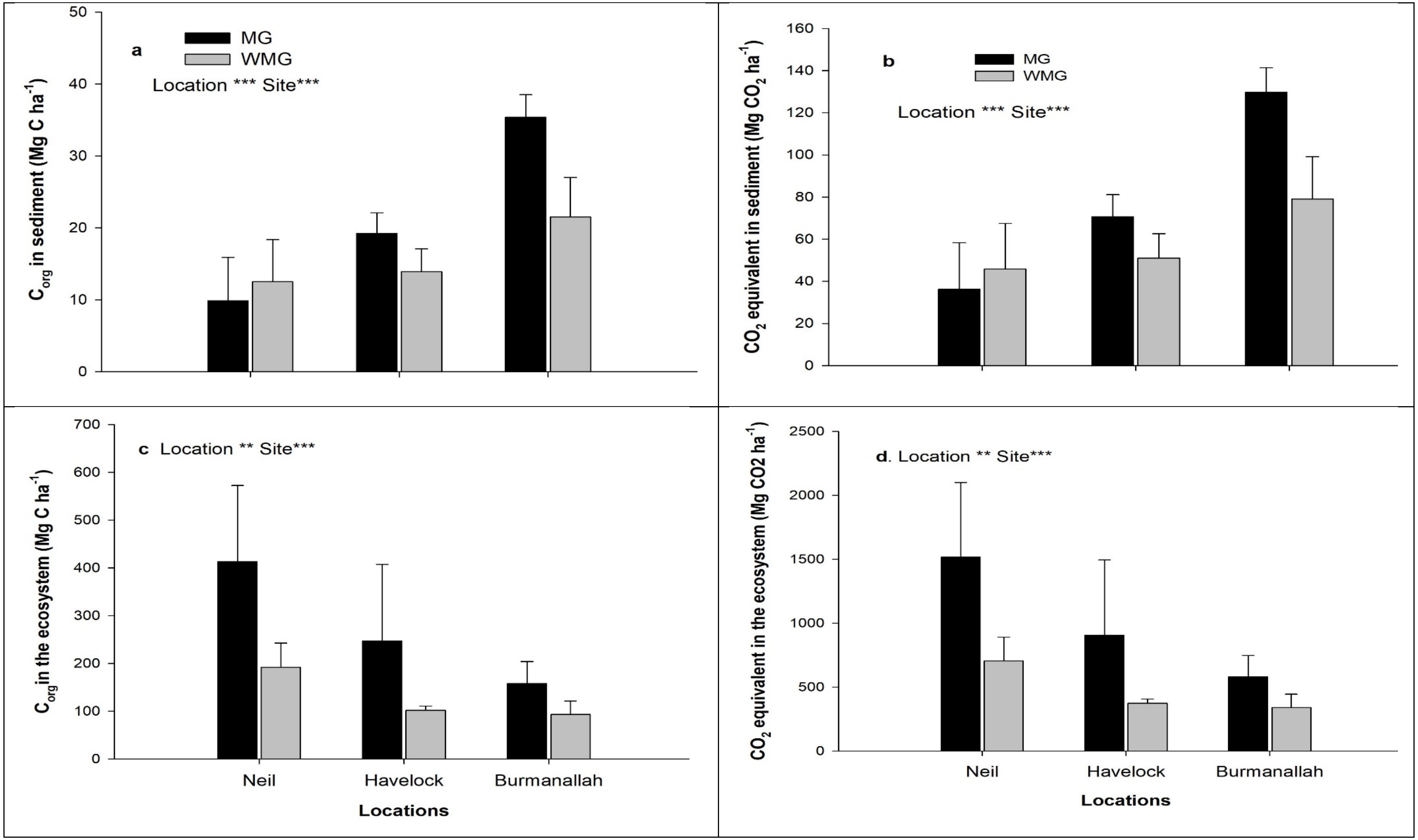

a
MG
WMG
Location *** Site***
C_{org} in sediment (Mg C ha^{-1})
b
Location *** Site***
CO_2 equivalent in sediment (Mg CO_2 ha^{-1})
c Location ** Site***
C_{org} in the ecosystem (Mg C ha^{-1})
d. Location ** Site***
CO_2 equivalent in the ecosystem (Mg CO2 ha^{-1})
Neil
Havelock
Burmanallah
Locations

Fig.4. Average values (mean ± SD) of the carbon (Mg C ha^{-1}) stored in the sediment and seagrass ecosystem (sediment+ seagrass biomass) and their CO_2 equivalent of *T. hemprichii* meadows in the sites with and without mangroves of Neil, Havelock and Burmanallah location of ANI, India. Significant differences were derived from two-way ANOVA analysis using location and site as fixed factors. (p<0.001***, p<0.01**).

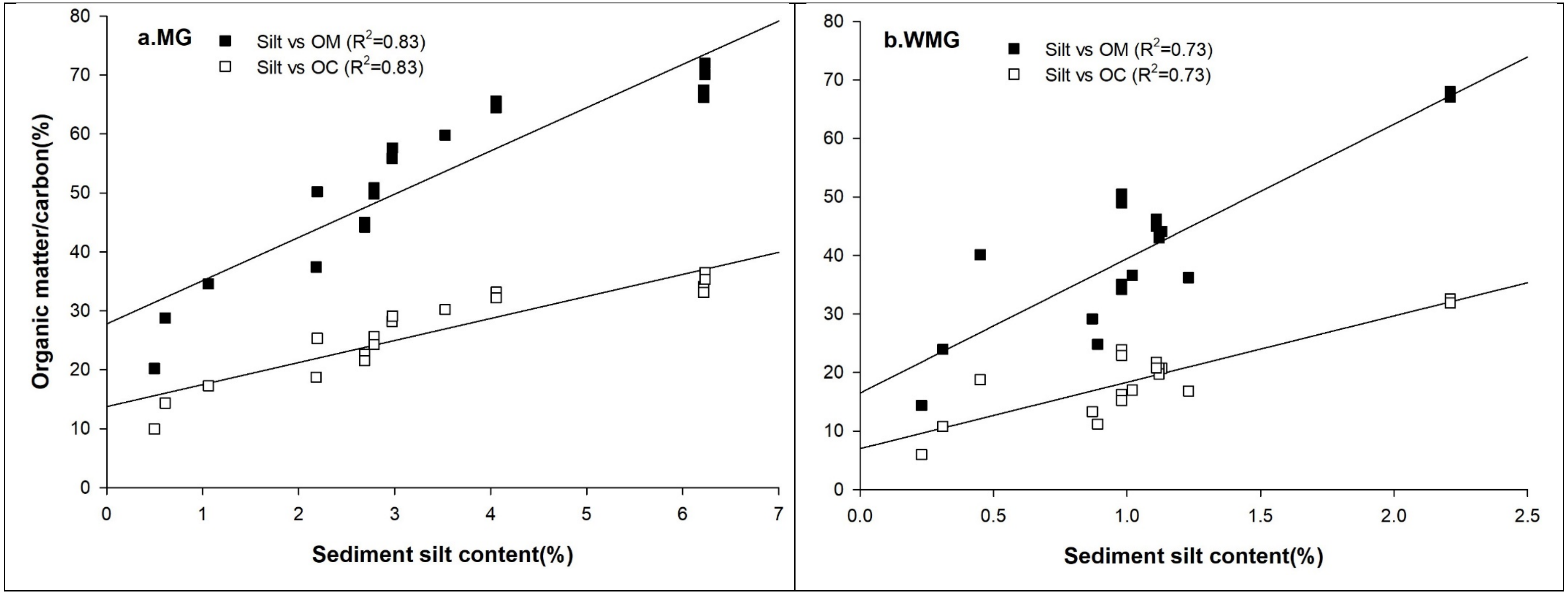
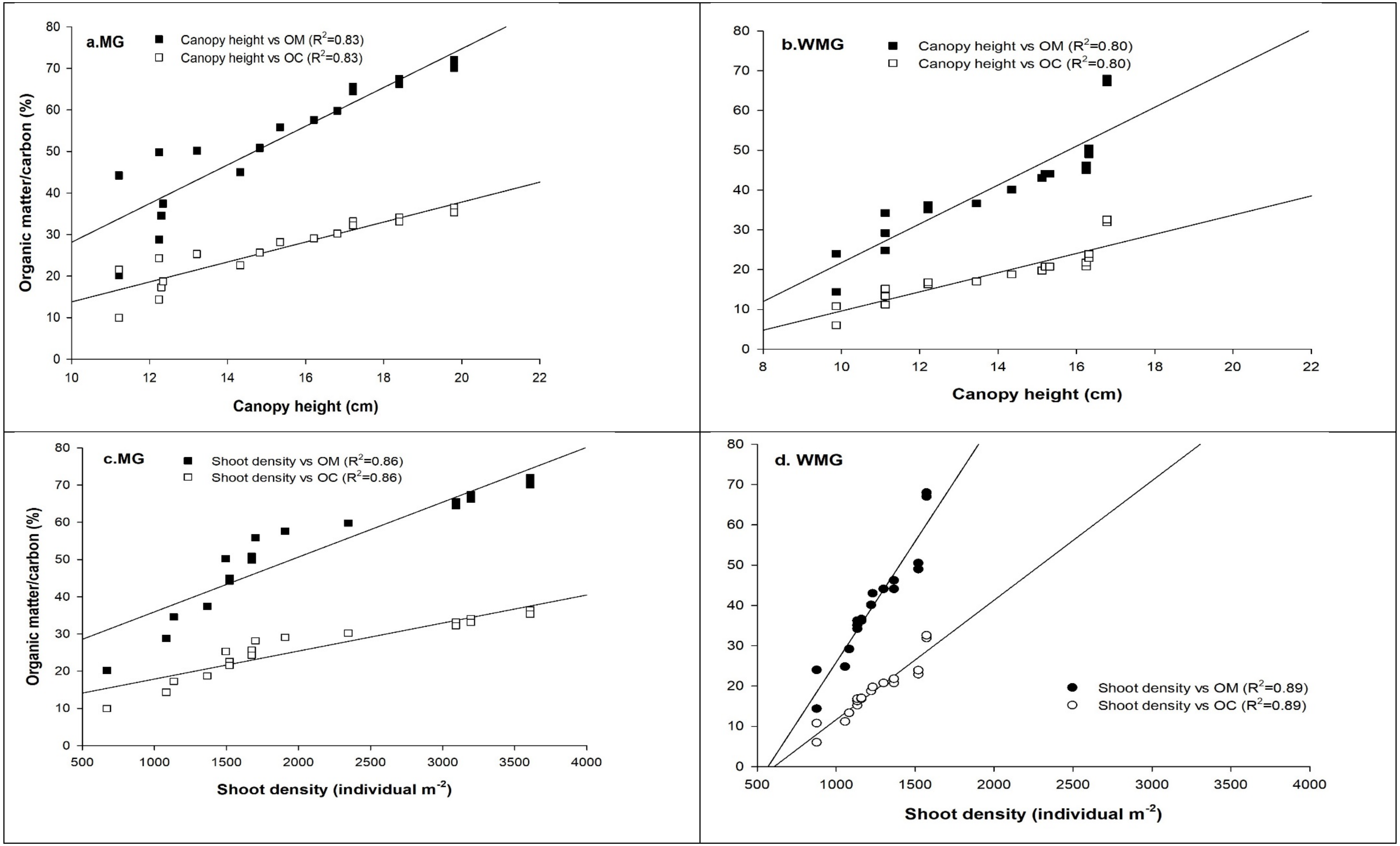
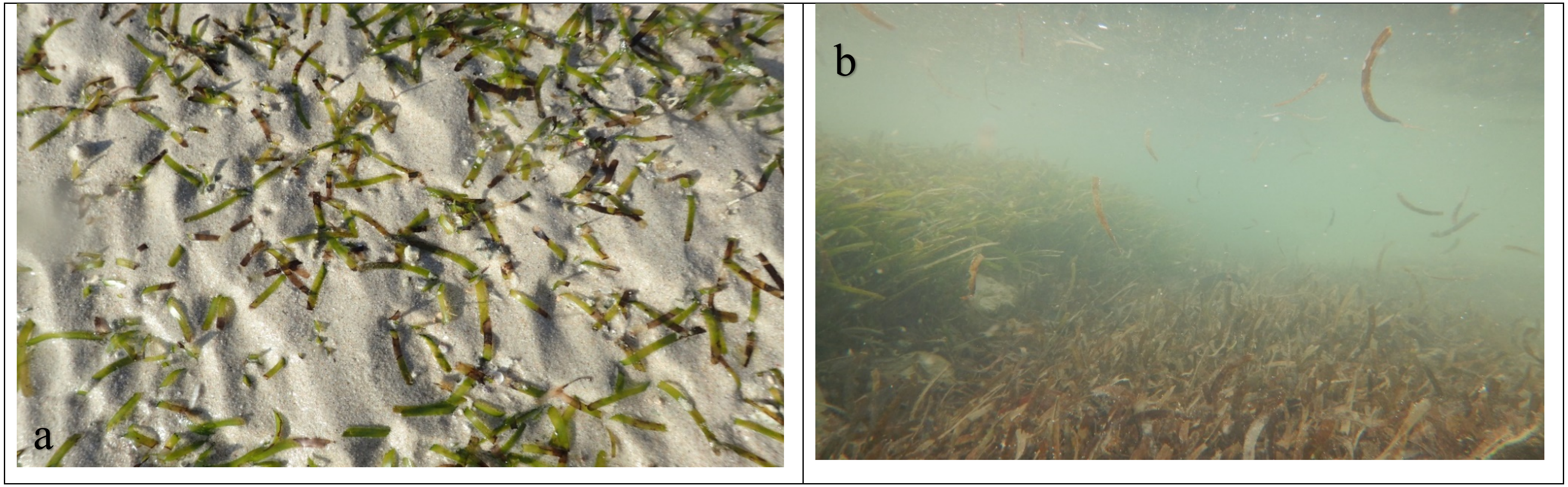


Fig.5. Relationship between sediment silt (%) and organic matter/carbon (%) content in the seagrass meadows of ANI, India a) with mangroves (MG) and b) without mangroves (WMG). R^2 values derived from linear regression are provided.



a.MG
Canopy height vs OM (R2=0.83)
Canopy height vs OC (R2=0.83)
Organic matter/carbon (%)
Canopy height (cm)
b.WMG
Canopy height vs OM (R2=0.80)
Canopy height vs OC (R2=0.80)
Canopy height (cm)
c.MG
Shoot density vs OM (R2=0.86)
Shoot density vs OC (R2=0.86)
Organic matter/carbon (%)
Shoot density (individual m-2)
d. WMG
Shoot density vs OM (R2=0.89)
Shoot density vs OC (R2=0.89)
Shoot density (individual m-2)

Fig.6. Relationship between the seagrass canopy height (cm) and shoot density (individual m^{-2}) with organic matter/carbon (%) content in the seagrass meadows of ANI, India a & c) with mangroves (MG) and b & d) without mangroves (WMG). R^2 values derived from linear regression are provided.



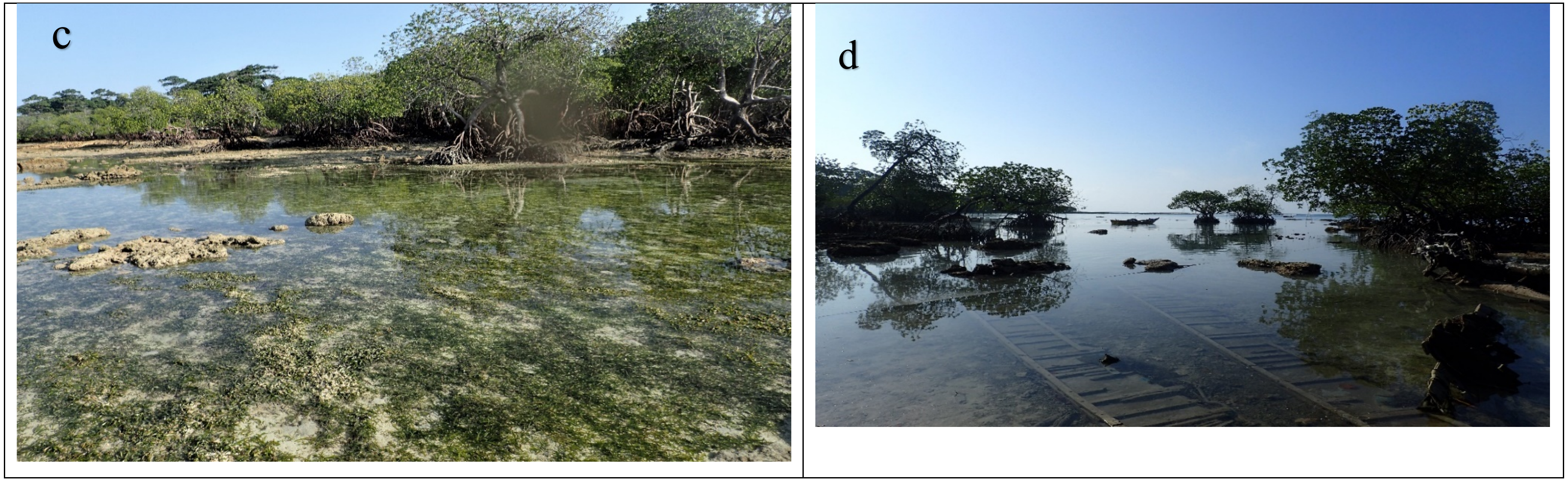


Fig.7. Pictures of *Thalassia hemprichii* meadows with a) leaf reddening and b) breakage of leaves during tidal inundation at WMG sites, and c) sheltered at mangrove sites during low tide and d) associated with mangrove ecosystems of Neil Islands.

Table 1. Summary of data for seagrass biomass and soil properties from the seagrass areas with mangroves (MG) and without mangroves (WMG) of ANI, India. Range and mean± standard deviation (SD) is presented. The social cost of carbon was adopted as US$86 (=6395.07 INR) per tonne of CO_2.

Seagrass/Variables	**Range**		**Mean ± SD**	
	MG	**WMG**	**MG**	**WMG**
Sediment dry bulk density (g cm^{-3})	0.18-1.11	0.64-1.09	0.75±0.23	0.84 ± 0.13
Sediment organic matter (% dry weight)	20.21-72.03	14.5-68	52.55±16.49	39.56 ± 13.39
Sediment C_{org} (% dry weight)	9.47-36.49	6.01-32.58	26.51±8.44	18.49 ± 6.63

Carbon content in above-ground biomass (%C)	30.63-79.53	25.70-39.38	49.12 ± 17.12	35.10± 5.33
Carbon content in below-ground biomass (%C)	19.42-68.12	28.72-44.09	43.73± 12.26	34.87 ± 5.27
Above-ground biomass (Mg C ha^{-1})	22.89-263.67	9.34-50.73	90.78±70.7	27.74±11.91
Below-ground biomass (Mg C ha^{-1})	52.37-301.26	22.95-187.52	141.89±83.7	78.23±45.38
Total biomass (Mg C ha^{-1})	86.54-526.70	34.83-224.51	232.68±155	105.98±52.42
Carbon content in the sediment (Mg C ha^{-1})	1.79-39.59	3.90-29.65	21.87±11.53	15.62 ± 6.50
Total Carbon in the sediment (Mg C) in total area, MG (144 ha); WMG (148 ha)	40.28-2883	7.80-1779	1265.35 ± 1010	839.07±641.05
CO_2 equivalent storage in sediment (Mg CO_2) in total area, MG (144 ha); WMG (148 ha)	147-10400	28.65-6529	4643.75 ± 3709	3079.41 ± 2352
Price in US$ and INR (Values expressed in million, i.e., 10^6)	0.012-0.89 ($) 0.94-66.51 (INR)	0.002-0.56 ($) 0.18-41.75 (INR)	0.39 ± 0.31 ($) 29.69± 23.72 (INR)	0.26 ± 0.20 ($) 19.69 ± 15.05 (INR)
Carbon in the ecosystem (Mg C ha^{-1})	93.02-530.78	48.79-240	272.54± 164	128.79± 55.89
Total carbon in the ecosystem (Mg C) in total area, MG (144 ha); WMG (148 ha)	2885-26751	226-9646	11031±5223	4921± 3725
CO_2 equivalent storage in the ecosystem (Mg CO_2); MG (144 ha); WMG (148 ha)	10591.46-98177	830-35402	40487 ± 19171	18036± 13672
Price in US$ and INR (Values expressed in million, i.e., 10^6)	9.11-84.3($) 677-6278 (INR)	0.07-3.04($) 5.31-226 (INR)	34.82± 16.48 ($) 2589 ± 1226 (INR)	1.55±1.17($) 115.52± 87(INR)

Table 2. Mean ± SD values are presented from literature review for various blue carbon studies in India using different seagrass species and the data from present study of *T. hemprichii* meadows with mangroves (MG) and without mangroves (WMG) of ANI.

Location	**Species**	**C_{org} (%DW)in sediment**	**Blue carbon stock (Mg C ha^{-1})**	**Reference**
Chilika lake, Odisha	Mixed seagrass	0.395	2.018± 0.67	(Kaladharan et al., 2021)
Pulicat lake, Tamil Nadu	Mixed seagrass	0.473	0.998±0.41	Kaladharan et al., 2021
Gulf of Mannar, Tamil Nadu	Mixed seagrass	0.09 ± 0.014	3.45	(Kaladharan et al., 2020)
Palk Bay, Tamil Nadu	Mixed seagrass	0.71±0.08	3.88	“
Gulf of Mannar, Tamil Nadu	*C. serrulata*	1.98	-	Ghosh et al., 2016
	H. ovalis	1.13	-	“
	T. hemprichii	1.07	-	“
Chilika lake, Odisha	*H. ovalis* + *H. uninervis*	0.68-0.93	127.08	(Ganguly et al., 2017)
Palk Bay, Tamil Nadu	*C. serrulata* + *T. hemprichii* +*S. isoetifolium*	0.97-1.01	159.53	“
Palk Bay, Tamil Nadu	*C. serrulata*+ *S. isoetifolium*	0.93-1.01		
Andaman and Nicobar Islands	***T. hemprichii* (MG)**	**26.51±8.44**	**272.54±164**	**Present study**

	***T. hemprichii* (WMG)**	**18.49±6.63**	**128.79±55.89**	“