



Driving forces of organic carbon spatial distribution in the tropical seascape



L.G. Gillis^{a,b,*}, F.E. Belshe^a, A.D. Ziegler^c, T.J. Bouma^b

^a Leibniz-Zentrum für Marine Tropenökologie GmbH, Bremen, Germany

^b The Royal Netherlands Institute for Sea Research, Yerseke, Netherlands

^c National University of Singapore, Singapore

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ABSTRACT

An important ecosystem service of tropical coastal vegetation including seagrass beds and mangrove forests is their ability to accumulate carbon. Here we attempt to establish the driving forces for the accumulation of surface organic carbon in southern Thailand coastal systems. Across 12 sites we found that in line with expectations, seagrass beds ($0.6 \pm 0.09\%$) and mangrove forests ($0.9 \pm 0.3\%$) had higher organic carbon in the surface (top 5 cm) sediment than un-vegetated mudflats ($0.4 \pm 0.04\%$). Unexpectedly, however, mangrove forests in this region retained organic carbon, rather than outwell it, under normal tidal conditions. No relationship was found between organic carbon and substrate grain size. The most interesting finding of our study was that climax and pioneer seagrass species retained more carbon than mixed-species meadows, suggesting that plant morphology and meadow characteristics can be important factors in organic carbon accumulation. Insights such as these are important in developing carbon management strategies involving coastal ecosystems such as offsetting of carbon emissions. The ability of tropical coastal vegetation to sequester carbon is an important aspect for valuing the ecosystems. Our results provide some initial insight into the factors affecting carbon sequestration in these ecosystems, but also highlight the need for further research on a global scale.

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1. Introduction

The ability of coastal vegetation to sequester carbon has been established as a keystone aspect in coastal zone management (Nellemann et al., 2009; Smith, 1981). In particular, connected tropical ecosystems such as mangrove forests and seagrass beds can accumulate 70% of organic carbon (OC) available in their local marine and terrestrial areas (Macreadie et al., 2014; Nellemann et al., 2009). There are three main processes that control how plants/trees and their associated ecosystems can sequester carbon. Firstly, mangrove trees and seagrass plants photosynthesize to acquire carbon from the atmosphere; seagrass plants can also sequester carbon from the water (Alongi, 2014; Lee et al., 2007). Secondly, organisms within the ecosystems such as macroalgae and microalgae can also assimilate carbon (Alongi, 2014; Lavery et al., 2013). Lastly, the ecosystems can sequester carbon via the transport and deposition of particulate organic material (POM) transported from within and between ecosystems and the catchment area (Alongi, 2014; Gillis et al., 2014b). Here we concentrate on how seagrass beds and mangroves forests sequester particulate carbon.

Sequestration rates for mangrove forests ($174 \text{ g C m}^{-2} \text{ y}^{-1}$) and seagrass beds ($138 \text{ g C m}^{-2} \text{ y}^{-1}$) are generally high compared to non-vegetated estuary and shelf areas ($17\text{--}45 \text{ g C m}^{-2} \text{ y}^{-1}$), making this a important topic for greater understanding (Alongi, 2014; McLeod et al., 2011).

Seagrass beds can receive carbon from both the sea and the land. For example, up to 50% of OC found in seagrass beds is from allochthonous sources (Kennedy et al., 2010). Seagrasses can also be a significant source of nutrients to other environments in the tropical seascape (Gillis et al., 2014b). Due to seagrass bed ability to reduce the water current and accumulate POM they can sequester sequester carbon 35 times faster than terrestrial systems, such as rainforests (Kennedy et al., 2010; Macreadie et al., 2014). Mangrove forests also reduce the current velocities, facilitating sedimentation of carbon rich POM both from within and outside the forest (Bouillon et al., 2008). As these systems are typically located where streams, channels and rivers drain upland environments, they potentially receive nutrients from a variety of terrestrial sources (Kristensen et al., 2008). As such, mangrove forest sediments have the potential to accumulate very large carbon pools. Approximately 75% of the total sediment pool in mangrove forests is carbon (Alongi, 2014).

There are many factors that determine the amount, availability and composition of organic carbon content in the soils within seagrass

* Corresponding author at: Leibniz-Zentrum für Marine Tropenökologie GmbH, Bremen, Germany.

E-mail address: lucy.gillis@zmt-bremen.de (L.G. Gillis).

meadows and mangrove forests (Mateo et al., 2006; McLeod et al., 2011). Seagrass beds and mangrove forests are depository environments where the roots or leaves reduce the water flow to allow for fine sediment deposition (Kristensen et al., 2000; Papadimitriou et al., 2005; Tue et al., 2012). Therefore sedimentological characteristics such as grain size are likely correlated with the organic carbon content. Previous work has indicated that finer sediments have higher OC content because of greater surface area, relative to coarse sediments (Krishna Prasad and Ramanathan, 2008; Ranjan et al., 2010).

The supply of organic carbon from allochthonous sources, such as connected ecosystems in the coastal environment and upper catchment terrestrial areas, are essential to consider for accumulation rates. Investigating the connectivity between seagrass beds and mangrove forests is especially important because these systems are dominated by ecosystem engineers (mangrove trees and seagrass plants) that both donate/export and trap organic material (Gillis et al., 2014b). Movement of OM can be altered by tidal inundation; therefore, the spatial distribution of mangroves forests and seagrass beds in the seascape and their location within the bay will also affect the movement. The physical aspects

(length, breadth, area) of the bay in which the ecosystems are located will also influence tidal inundation, which in turn affects OC movement.

Only recently has research concentrated on determining which are the most important driving factors in controlling OC accumulation within tropical vegetation (Duarte et al., 2013; Lavery et al., 2013; McLeod et al., 2011). For seagrasses, inundation depth, external supply of OC, and productivity has been found to be an important consideration (Duarte et al., 2013; Lavery et al., 2013). Mangrove forest accumulation of carbon will also be influenced by external POM supply, tidal depth, as well as tidal extent and period. The few studies that have investigated sedimentation rates in mangrove forests (Alongi, 2014; McLeod et al., 2011), all emphasize the need for data from connected ecosystems in other global regions. To our knowledge, there have been no studies conducted that investigate the spatial variability of surface carbon between and within connected mangrove forests and seagrass beds. Given that these ecosystems are highly connected depository environments which both potentially donate OC to each other (Gillis et al., 2014b), establishing the driving forces and the spatial patterns of surface OC between ecosystems should be a research priority.

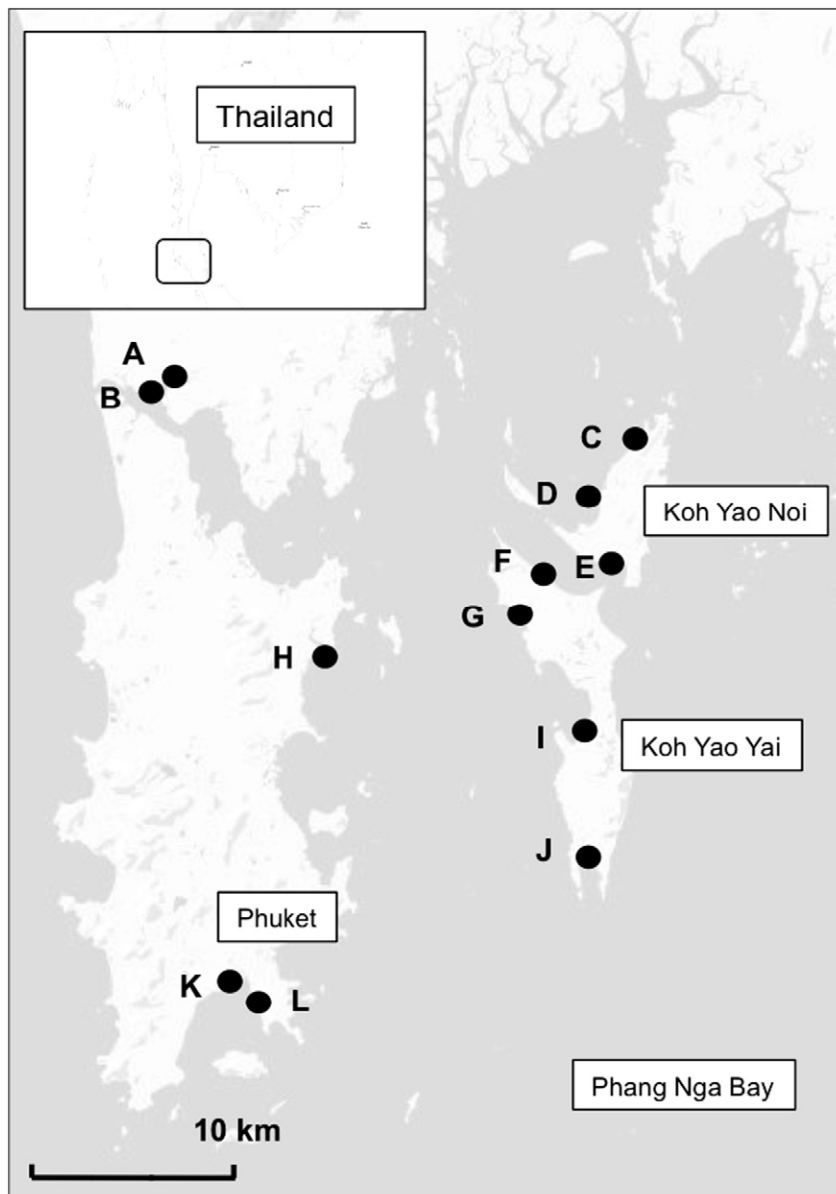


Fig. 1. Map showing location of 12 sites in Phang Nga Bay, Southern Thailand.

Here we establish spatial distribution of organic carbon in mangrove and seagrass sediments in Southern Thailand, a region that is understudied in regard to this respect. We focus on surface OC (i.e., 5 cm cores), which represents recent storage. This approach allows us to investigate what influences the deposition of POM in different ecosystem engineering vegetation types along a fully connected natural depth gradient. The purpose of this study is to answer five main questions regarding connected tropical ecosystems: *i*) Does surface sediment from vegetated coastlines accumulate greater amounts of OC than sediment from adjacent un-vegetated mudflats; *ii*) Do areas (bare or seagrass) nearby mangrove forests have enhanced OC as an indication of outwelling; *iii*) How do species of seagrass beds affect OC content in the surface sediment; *iv*) Is organic carbon content associated with grain size; and *v*) how do physical variables of the bay, mangrove forests and seagrass beds change the OC content.

2. Material and methods

The sampling sites were located in Phang-nga Bay, Phuket (68 km × 82 km; area of 3000 km²; Fig. 1). Mean tidal range is 1.8 m; mean annual rainfall is ~2300 mm; and mean temperature is 28 °C (Chansang, 1984). Samples were collected from fully accessible mangrove sites (12 sites in total) located in the middle and west of Phang-nga Bay in March 2011 (Fig. 1). All seagrass beds were fully exposed at low tide and the depth of the seagrass beds at high tide ranged between 1 and 10 m.

At each site we established transects beginning at the edge of the mangrove, extending through the mudflat and continuing across an adjacent intertidal seagrass patch. Sampling points were established at

distances of 0 (seaward edge of mangrove forest), 50, 100, 200, 300, 400, 500, 1000, 1500 and 2000 m along the transect. At each of these distances, three core samples of surface sediment were taken at points 50 m apart using a 5-cm length hand-held PVC corer that extracted a volume of 90 cm³.

All sediment samples were placed in separate sample bags, stored in a cooling box and transported immediately to the field laboratory where they were dried at 60 °C for 48 h. Samples were then packed in an airtight container and transported to the laboratory of Royal Netherlands Institute for Sea Research (NIOZ) for elemental analysis. The sediment core samples were first split into two equal proportions. Half were analyzed for grain size; the other for OC. To analyze grain size we used the Malvern 2000 particle size analyzer which uses the angle and intensity of scattered light to determine the particle size for coarse (0.5–1 mm), medium (0.25–0.5 mm), fine (0.062–0.25 mm) and silt (<0.062 mm). Material in the other sub-sample was ground for homogenization and then acidified to remove carbonates (Nieuwenhuize et al., 1994). All samples were analyzed for organic carbon (OC) by means of elemental analysis isotope ratio mass spectrometry (EA-IRMS) using a Thermo Finnigan Flash 1112.

Using a generalized linear model (GLM) we determined organic carbon distribution across the seascape versus descriptive parameters. We explored linear trends of OC versus distance from mangrove forest and compared OC content among types of vegetation (mangrove forest, un-vegetated mudflat, seagrass bed), seagrass species and grain size (coarse, medium fine and silt). We completed a step-wise regression to determine the extent that physical variables of the bays (mangrove forest area, seagrass bed area, mangrove forest width, bay area and the ratio of the length/breadth of the bay) had a relationship with the

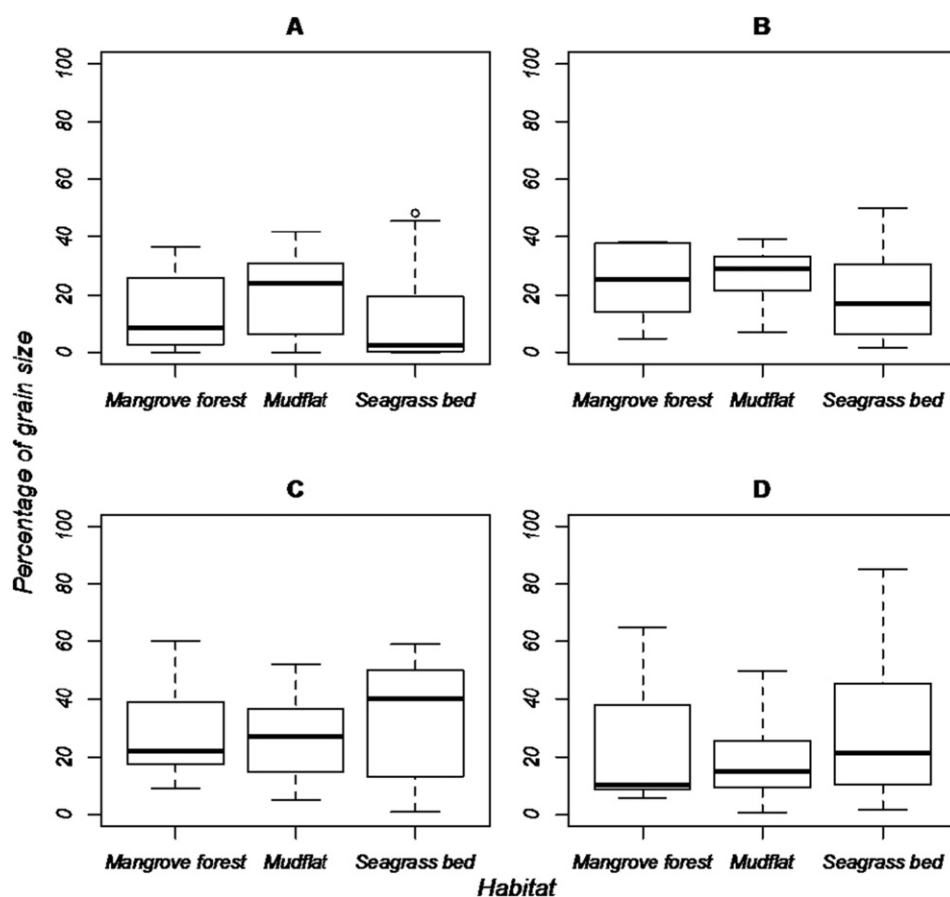


Fig. 2. Sediment grain size in 5-cm surface sediment cores values against the different habitats we monitored in mangrove forests, un-vegetated mudflats and seagrass beds. Panel A indicates coarse grain sediment (0.5–1 mm); panel B depicts medium grain sediment (0.25–0.5 mm); panel C shows fine grain sediment (0.062–0.25 mm); and panel D indicates silt (<0.063 mm). No significant difference was seen between sites (mangrove forests, un-vegetated mudflats and seagrass beds) and grain size (coarse, medium, fine and silt). Thick black lines in the center of the boxes indicate means of the data, the whiskers indicate the variability of the grain sizes outside the upper and lower quartiles.

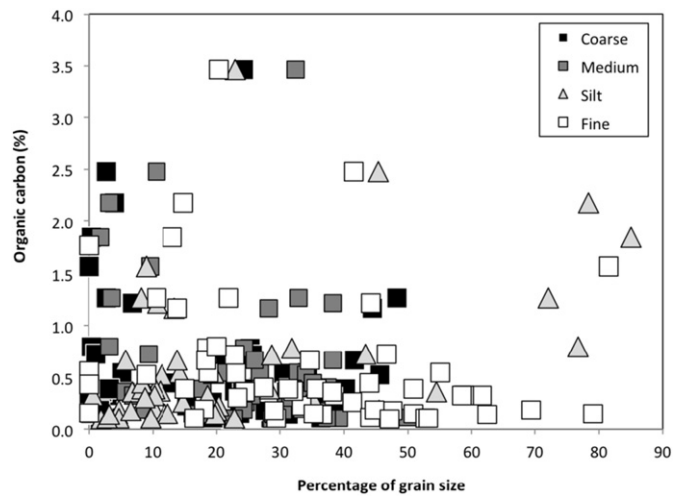


Fig. 3. Organic carbon (%) in 5-cm surface sediment cores versus percentage of sediment grain size. Black squares indicate coarse grain sediment (0.5–1 mm), grey squares depict medium grain sediment (0.25–0.5 mm), non-filled squares show fine grained sediment (0.062–0.25 mm) and black triangles indicate silt (<0.063 mm). No significant difference was seen between grain size (coarse, medium, fine grained sediment and silt) and OC (Table 1; GLM test).

organic carbon distribution. All tests were performed in the R programming platform (R Development Core Team, 2012) and were considered significant at the level of $p < 0.05$.

3. Results

Fine grain sizes were the dominant sediment grain size across seagrass beds, un-vegetated mudflats and mangrove forests with the highest amount being found in seagrass beds (mean \pm SE = $39.8 \pm 3.9\%$) compared to un-vegetated mudflats ($34.2 \pm 2.7\%$) or mangrove forests ($37.8 \pm 5.7\%$) (Fig. 2 and SI Table 1). However, overall no difference could be shown between the sites and grain size (Fig. 2).

None of the grain sizes were correlated with organic carbon (Fig. 3 and Table 1; GLM test).

Further, no significant difference was seen in changes of OC content with distance from the mangrove forest through the mudflat and into the seagrass bed (Fig. 4 and Table 1; GLM test). When all data are pooled across seagrass types, organic carbon in seagrass beds ($0.6 \pm 0.09\%$) was higher than in un-vegetated mudflats ($0.4 \pm 0.04\%$); and it was significantly lower than in mangrove forests ($0.9 \pm 0.3\%$) (Fig. 4 and Table 1; GLM test).

Table 1
Statistical summary of the i) general linear model (GLM); organic carbon vs. descriptive parameters (distance from mangrove vegetation, type of vegetation, species of seagrass, grain size) and ii) organic carbon vs. physical variables of the bay (mangrove forest area, seagrass bed area, mangrove forest width, bay area and length/width ratio). All tests were considered significant at the level of $p < 0.05$.

Analysis		Statistic	p value	Other	Number
i)					
Organic carbon	vs. distance	General linear model	0.28	df = 60	72
	vs. type of vegetation	General linear model	0.0005	df = 60	72
	vs. species of seagrass	General linear model	0.02	df = 60	34
	vs. grain size; coarse	General linear model	0.45	df = 60	61
	vs. grain size; medium	General linear model	0.54	df = 60	61
	vs. grain size; fine	General linear model	0.46	df = 60	61
	vs. grain size; silt	General linear model	0.06	df = 60	61
	ii)				
Organic carbon	vs. mangrove forest area	Stepwise regression	0.59	Coefficient = 1.05, $r^2 = 0.094$	72
	vs. seagrass bed area	Stepwise regression	0.66	Coefficient = 1.08, $r^2 = 0.094$	72
	vs. mangrove forest width	Stepwise regression	0.05	Coefficient = 1.54, $r^2 = 0.094$	72
	vs. bay area	Stepwise regression	0.20	Coefficient = -9.12, $r^2 = 0.094$	72
	vs. length/width ratio	Stepwise regression	0.53	Coefficient = 9.92, $r^2 = 0.094$	72

Within different types of seagrass beds, organic carbon content varied and was significantly different (Fig. 5 and Table 1; GLM test).

Further investigation of the means showed that OC in both *Enhalus acoroides* ($0.7 \pm 0.2\%$) and *Halophila beccarii* ($0.8 \pm 0.2\%$) were significantly higher than in the mixed meadows containing *Enhalus acoroides*, *Halophila beccarii*, *Cymodocea serrulata* and *Halodule pinifolia* ($0.4 \pm 0.1\%$) (Fig. 5, Table 1; GLM test and SI Table 1).

Stepwise regression did not indicate a significant relationship between OC content and bay area, ratio of length/breadth of the bay, seagrass bed area and mangrove forest area (Table 1). Importantly a significant difference was found for higher OC content with increasing width of the mangrove forest (Table 1; stepwise regression).

4. Discussion

Seagrass beds and mangroves sediments as expected had significantly higher OC content than un-vegetated mudflats. The high values of OC in the mangrove forests provide support that mangroves are depository environments where their physical structure reduces water flow allowing for OM to be deposited (Ranjan et al., 2010; Tue et al., 2012). These forests are located at the mouth of catchments where the various upstream land uses drain; they are also affected by oceanic tidal inundation. Collectively, these processes allow for the deposition of particulate matter (Valiela and Cole, 2002). Seagrass beds and un-vegetated mudflats receive carbon from both terrestrial and oceanic sources (Burkholder et al., 2007; Gillis et al., 2014b). Seagrass beds may also accumulate particulate matter and associated nutrients flowing into them by altering the hydrodynamics causing organic material from oceanic and terrestrial sources to be deposited (Koch, 2001; Wilkie et al., 2012).

The abundance of fine grain sizes in seagrass beds and mangrove forests provides further evidence of them being depository environments (Fig. 1). To our surprise there was not a significant difference between the locations in the bays and grain size, which we expected from previous studies (Krishna Prasad and Ramanathan, 2008; Papadimitriou et al., 2005).

Also un-expected was no relationship between fine sediment and OC content. This may be because the amount of OC reflects local production, making it decoupled from the sediment trapping ability of the seagrass bed or mangrove forest. In general, fine grain sediment is associated with fluvial processes (Ranjan et al., 2010). In this region we can see that the three different ecosystems (mangrove forests, un-vegetated mudflats, seagrass beds) receive and are dominated by terrestrial sediment.

Prior work found that the supply of organic material may affect the accumulation rates of OC (Alongi, 2014; Mateo et al., 2006). In our data we did not find a significant (inverse) relationship between OC and distance from the mangroves, through the un-vegetated mudflat

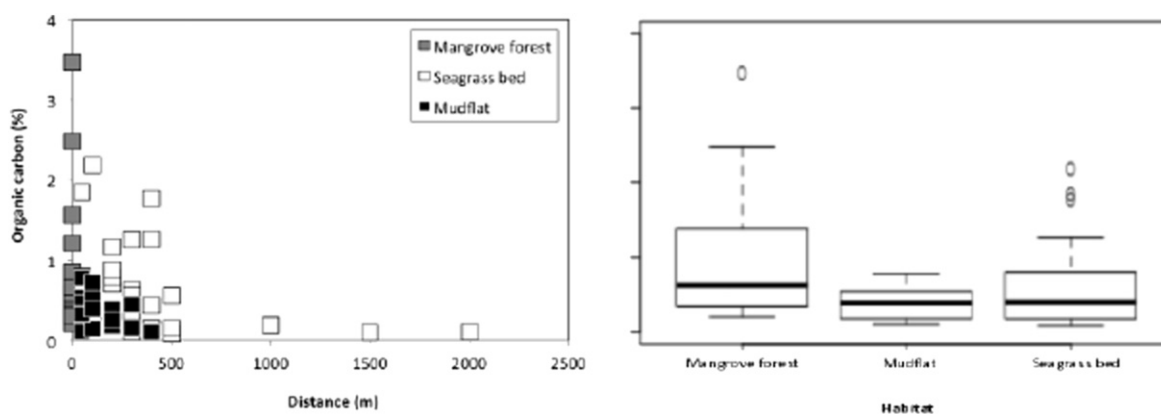


Fig. 4. The left panel shows organic carbon (%) in 5-cm surface sediment cores distributed along transects extending from the mangrove forest (0 m), through the un-vegetated mudflat and to the seagrass bed 500–2000 m seaward (data from 12 transects are shown). The right panel indicates a boxplot of the each different habitat (mangrove forest, mudflat, seagrass bed) and the organic carbon (%) found in 5-cm surface sediment cores. Thick black lines in the center of the boxes indicate means of the data, the whiskers indicate the variability of the OC outside the upper and lower quartiles (data from 12 transects are shown). A difference was seen between organic carbon found in the mangrove forest sediments which was significantly higher than in the, in the un-vegetated mudflat and in the seagrass bed sediments (Table 1; GLM test).

and to the seagrass beds. However the significantly higher carbon content in the mangrove forests and seagrass beds compared to un-vegetated mudflats indicates that OC originating from mangroves is highly likely to be deposited in seagrass beds, rather than nearby un-vegetated mudflats. This is because un-vegetated mudflats have lower organic carbon due to lack of vegetation to trap particulate organic material. Seagrass plants reduce the water velocity, which facilitates trapping of internal and external material. Therefore outwelled POM from the mangrove forest is more likely to be deposited within seagrass beds than at un-vegetated mudflats. The higher organic carbon values found in mangrove forests could also be because of the forests location, buffering the terrestrial and oceanic zone, which equates to the forests receiving material from the upper catchment areas.

Mangrove forests are believed to outwell nutrients (Lee, 1995), although this strongly depends on the physical conditions of the site

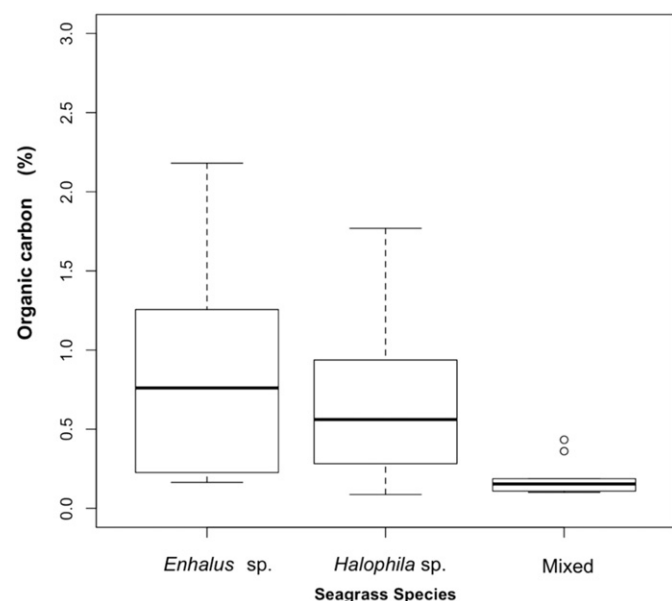


Fig. 5. Boxplot showing organic carbon (%) in surface (5 cm) sediment cores taken within seagrass beds of different species composition—either dominated by *Enhalus acoroides* (clear squares) or *Halophila beccarii* (grey squares) or mixed with *Halophila beccarii*, *Cymodocea serrulata* and *Halodule pinifolia* (black squares). Organic carbon in mixed seagrass beds was significantly lower than in *Enhalus acoroides* or *Halophila beccarii* beds (Table 1; GLM test). Thick black lines in the center of the boxes indicate means of the data, the whiskers indicate the variability of the OC outside the upper and lower quartiles (data from 12 transects are shown).

(Adame and Lovelock, 2010; Lee, 1995). We found a positive relationship between carbon content and sea-facing width of the mangrove forest—and this implies a relationship between OC and the extent that the forest is exposed to waves. Here, we recognize that waves may decrease the ability of mangrove roots to trap organic matter, and therefore, increase the transport of OC from the mangrove forest to adjacent ecosystems such as seagrass beds (Gillis et al., 2014a; McLeod et al., 2011).

An important finding in our study was that seagrass species were not equal in relation to their ability to accumulate carbon within their sediments. Pioneer and climax species (*Halophila beccarii* and *Enhalus acoroides*) both had greater OC in surface sediments, compared with mixed species meadows. This difference could result from the morphology of the seagrass plants and the meadow characteristics of the seagrass beds. For example, the spatial patterning and morphology of *Halophila ovalis* rhizomes (similar in morphology to *Halophila beccarii*) have been shown to facilitate OC accumulation by trapping particulate material (sediments and associated organic matter) and limiting its resuspension (Lavery et al., 2013). In comparison, *Enhalus acoroides* creates tall and dense mono-specific meadows (141 shoots m^{-2}) (Ooi et al., 2011; Rattanachot and Prathep, 2011; Torres-Pratts and Schizas, 2007). The high-densities and tall homogeneous meadow heights associated with this species, allows for a ‘skimming flow’, causing slow flow inside the meadow, an effect that directs particulate matter into its beds (Lavery et al., 2013), thereby facilitating OC accumulation.

We hypothesize that the mixed meadows mentioned above did not have this effect because the difference in seagrass species leaf length reduced the ‘skimming flow’ effect (Adhitya et al., 2014). Lavery et al. (2013) found that differences in OC accumulation for different species in Australia were only significant at deeper sites and not at intertidal beds such as those we examined in Thailand. The observed regional differences between Thailand and Australia in OC accumulation of seagrass species supports the need for further work to understand how these mechanisms manifest around the globe.

If managers want to develop protocols for using the restoration or preservation of seagrass beds for carbon offsetting and valuing ecosystems, then regional information about the carbon accumulation potential is required. It is especially important to quantify the OC accumulation potential of specific species, and the dependence on species traits and the bed composition to enable local carbon management. This is important if the communities’ primary ecosystem service requirement is offsetting carbon for valuing. At the global scale, regional information is also vital to validate models of carbon stock estimation around the world.

5. Conclusion

Our study provides initial evidence that species composition may affect OC accumulation in seagrass beds in intertidal areas. In this sense, dense homogenous seagrass beds or species with rhizomes that trap sediments are better at accumulating carbon than mixed meadows. Although we only analyzed near-surface (upper 5 cm) OC, the observed spatial trends likely reflect those below the surface unless drastic physical changes to the depositional environment have occurred (Lavery et al., 2013; McLeod et al., 2011). We also found for our sites that mangrove forests retained organic carbon rather than outwelled it, and this was probably related to the mangrove forest exposure to hydrodynamic processes. Our study provides some basic insights on which aspects are of key importance when deciding which ecosystem under which environmental conditions and which seagrass species to restore if carbon accumulation is a target ecosystem service to be achieved to offset carbon use of other industries (Camino-Serrano et al., 2014; Greiner et al., 2013; Troxler, 2013).

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.seares.2016.12.006>.

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