Model-based approach for estimating biomass and organic carbon in tropical seagrass ecosystems

Milica Stankovic[1], Naruemon Tantipisanuh[2], Ekkalak Rattanachot[3], Anchana Prathep[1,3,*]

[1]**Seaweed and Seagrass Research Unit, Department of Biology, Faculty of Science, Prince of Songkla University, Hat Yai, Songkhla 90110, Thailand**
[2]**Conservation Ecology Program, King Mongkut's University of Technology Thonburi, 10150 Bangkok, Thailand**
[3]**Excellence Center for Biodiversity of Peninsula Thailand, Faculty of Science, Prince of Songkla University, Hat Yai, Songkhla 90110, Thailand**

ABSTRACT: Seagrass ecosystems play a vital role in climate change mitigation as they are globally significant carbon sinks and are responsible for 18% of marine carbon sequestration. However, their increasingly high rates of loss and degradation over the last decade have necessitated the development of effective and non-destructive ways to estimate biomass and, consequentially, stored organic carbon. In this study, we explore cost-effective ways to estimate total organic carbon storage in monospecific (*Enhalus acoroides*) and mixed (*E. acoroides* and *Thalassia hemprichii* or *Cymodocea serrulata*) seagrass ecosystems of Southeast Asia using a modeling approach. The model can be divided into 3 units: (1) biomass prediction, (2) carbon in living vegetation prediction, and (3) carbon in sediment prediction. A series of linear regression relationships linking the units, in which the results of the previous unit represent the predictor for the subsequent unit, was used to obtain information about seagrass biomass (above- and belowground), organic carbon in the living vegetation, and organic carbon in the sediment. All of the modeling units of monospecific patches had higher and more significant correlations between the predictor and response variables compared to those of mixed patches. Following the linked units, the predicted organic carbon on a landscape scale had a small margin of error for both monospecific and mixed patches. Although the models are applicable only for certain species, they improve the cost effectiveness of the data collection and can be easily applied over a larger spatial scale. The models provide the essential knowledge required to better understand and manage seagrass ecosystems and to more effectively address climate change.

KEY WORDS: Blue carbon · Carbon sink · Stepwise structural model · Marine vegetation · Non-destructive method

INTRODUCTION

Seagrass meadows provide a variety of ecosystem services, including a high capacity to store organic carbon in their sediments (Fourqurean et al. 2012a). The estimated carbon burial in seagrass meadows is 48.0–112 Mt yr^{-1} (Duarte et al. 2013a), making them responsible for 20% of marine carbon sequestration despite occupying less than 0.2% of the ocean surface (Kennedy et al. 2010, Duarte et al. 2013a). The trapped carbon can be stored for centuries and millennia (Duarte et al. 2005, Macreadie et al. 2014, Rozaimi et al. 2016); however, degradation and/or loss of meadows triggers the release of the trapped carbon (Marbà et al. 2015) and its re-emission into the atmosphere (Macreadie et al. 2014), thereby increasing the atmospheric inorganic carbon concentration. The 7% loss of global seagrass meadows since 1990 (Orth et al. 2006, Waycott et al. 2009) is mainly due to increased river runoff from coastal development (Halpern et al. 2007),

while in the Indo-Pacific region, overexploitation of fisheries was identified as a major threat (Fortes 1990, Tomascik et al. 1997, Nordlund 2007). The high loss of these ecosystems and their important role in climate change mitigation necessitate the development of non-destructive, rapid ways of estimating carbon over a range of meadow types, especially in the high-diversity areas of Southeast Asia.

Organic carbon in seagrass ecosystems is stored in living and dead above- and belowground seagrass vegetation, as well as in the sediment. To assess total carbon storage, it is necessary to develop approaches of estimating above- and belowground biomass of the living seagrass vegetation and to quantify stored carbon. Traditional measurements of the seagrass biomass include destructive, time-consuming, physical removal of the seagrass material from the field, which is undesirable (Downing & Anderson 1985, Duarte & Kirkman 2001). Thus, more efficient and non-destructive methods have been developed using visual techniques (Mellors 1991, Mumby et al. 1997a), photographs (Long et al. 1994, Kutser et al. 2007), percentage of seagrass cover (Heidelbaugh & Nelson 1996, Carstensen et al. 2016), and a combination of remote sensing and percentage of seagrass cover correlations (Armstrong 1993, Mumby et al. 1997b, Phinn et al. 2008, Knudby & Nordlund 2011, Lyons et al. 2015). Only the last approach can be applied over a large areal extent, using the generated relationship between percentage of seagrass cover and aboveground biomass and applying it over the whole area of the seagrass meadow. The problem with this approach is the low accuracy of biomass prediction within the meadows of several seagrass species (Knudby & Nordlund 2011). On the other hand, estimations of belowground biomass have been limited, with the few successful estimations using a correlation with blade counts (Heidelbaugh & Nelson 1996) and the strong positive relationship between above- and belowground biomass on a global scale (Duarte & Chiscano 1999). While the prediction from aboveground biomass using a linear model was not suitable for temperate species in Australia (Lyons et al. 2015) and tropical species in Kenya (Githaiga et al. 2017), belowground biomass predictions with low prediction error have been made for mangrove tree species (Njana et al. 2015) using an allometric modeling technique. Therefore, novel models should be tested on seagrass meadows.

To quantify the carbon stored in living vegetation, similar methods as those used for sediment have been suggested, including a C, H, N elemental analyzer and loss on ignition (LOI) (Fourqurean et al.

2014). However, if the budget is limited and no extra equipment is available, the estimation of the carbon content can be performed using a carbon conversion value of 0.34 (Duarte 1990). This conversion value is the average of the carbon content of the leaves of 27 seagrass species on a global extent (Duarte 1990), with a few replications for the tropical Indo-Pacific species (*Cymodocea serrulata*, *Enhalus acoroides*, *Halodule uninervis*, *Halophila ovalis*, *Halophila stipulacea*, *Syringodium isoetifolium*, *Thalassia hemprichii*). However, the average values of the carbon in above- and belowground living vegetation for tropical species is lower than the global average for most species (Supriadi et al. 2014, Phang et al. 2015). Recently, Stankovic et al. (2017) indicated a significant correlation (p < 0.01, R^2 = 0.9763) between the aboveground biomass and carbon content of 3 tropical species using a simple linear model. Therefore, novel approaches are required that can link non-destructive, time efficient ways of data collection for several types of seagrass meadows and the carbon storage within the ecosystem.

In contrast to mangrove and terrestrial ecosystems, which store half of the carbon in living biomass (Fourqurean et al. 2012a), most of the organic carbon in seagrass ecosystems is stored in the sediment within the meadow, with twice the amount of organic carbon storage per hectare compared to terrestrial soils (Duarte et al. 2005, Kennedy & Björk 2009, Fourqurean et al. 2012a). The average estimates of global stocks of organic carbon in the sediment are 9.8 to 19.8 Pg C (Fourqurean et al. 2012a), which is roughly equal to the combined amount of organic carbon stored in marine tidal marshes and mangrove forests (Fourqurean et al. 2012a). Many factors influence the amount of stored organic carbon in the sediment of seagrass ecosystems (Mateo et al. 2006, Mcleod et al. 2011). Samper-Villarreal et al. (2016) suggested that higher structural canopy complexity, higher turbidity, and shallower and lower wave action sites have higher carbon content, which corresponds with the significant but weak correlation of canopy complexity and organic matter in Tang Khen Bay, Phuket (J. Panyawai unpubl. data). Ricart et al. (2017) determined that sedimentary organic carbon is influenced by the landscape configuration as well due to its greater capacity to retain autochthonous carbon and to accumulate higher portions of finer sediments (Miyajima et al. 2017).

To predict organic carbon content in seagrass sediment, several methods have been attempted. Githaiga et al. (2017) determined that aboveground biomass is not a suitable proxy for organic carbon in the

sediment prediction. Armitage & Fourqurean (2016) reported that sedimentary organic carbon can be successfully estimated from above- and below-ground carbon in *T. testudinum* tissues as the link between plants' productivity and soil carbon storage is already established in terrestrial ecosystems (Kirwan & Mudd 2012). Serrano et al. (2016) and Dahl et al. (2016) found that grain size was associated with the organic carbon content, where finer-size particles, <16 μm fractions (Secrieru & Oaie 2009) and <0.074 mm (Dahl et al. 2016), could be used to predict total organic carbon (%); however, Gillis et al. (2017) and Samper-Villarreal et al. (2016) did not find any correlation. Serrano et al. (2016) also concluded that mud content (<63 μm) is a good predictor for organic carbon for smaller species such as *Halodule*, *Halophila*, and *Zostera* spp., while it was a poor predictor for larger, long-living seagrass species, suggesting that the size of the species and its biomass has a positive correlation with organic carbon in the sediment. Gullström et al. (2018) found that organic carbon was strongly negatively linked to sediment density, where higher storage is found in the less compacted sediments due to microbial activity, which can be suppressed by the lack of oxygen (Belshe et al. 2017). Furthermore, Fourqurean et al. (2012b) reported that organic carbon (%) in the sediment has a positive relationship with the organic matter from LOI, and they developed a model for predicting sedimentary organic carbon on a global set of data with high R^2. However, R^2 of this model varies regionally (Fourqurean et al. 2012b, Phang et al. 2015, Samper-Villarreal et al. 2016), as the meadow structure and sediment in ecosystems have different properties.

Our objective in this study was to explore a rapid, non-destructive approach to predict carbon storage in the seagrass ecosystem with limited resources, which can help to estimate blue carbon. This can be achieved by a series of linked equations, in a stepwise structure, where the predictor for the first unit (% coverage of the plant) is necessary and the output is used as the predictor for the next unit.

MATERIALS AND METHODS

Study site

The study was conducted along the west coast of southern Thailand in Phuket, Trang and Krabi Provinces (Fig. 1). In total, 5 of the largest seagrass meadows (>2.5 km^2) with the highest seagrass diversity were located and selected as study areas. In each study area, the type of patch was distinguished as monospecific (*Enhalus acoroides*) and mixed species (*E. acoroides* and *Thalassia hemprichii* or *Cymodocea serrulata*). These species were selected, as Stankovic et al. (2017) found that large (*E. acoroides*) and medium-sized (*T. hemprichii* and *C. serrulata*) species store more carbon in the plants as well as in the sediment, compared to smaller species. In total, we sampled 48 patches (6 replicates per patch type from each study area). Field collection was carried out from April 2015 to December 2016 to cover 2 seasons, which led to 96 samples in total. The south of Thailand has 2 seasons, rainy (May–October) and summer (December–April), that are based on the southwest monsoon occurrence (from mid-May to mid-October) (Thai Meteorological Department, https://www.tmd.go.th/en/).

Field collection

In each study area, 6 replicates per patch type of biomass and sediment samples were taken. Quadrats (50 × 50 cm^2) were randomly placed in each replicate, with a distance of at least 100 m. The percent coverage within the quadrats was recorded following McKenzie & Campbell (2002). All living vegetation from a quadrat was collected and placed in pre-labeled bags
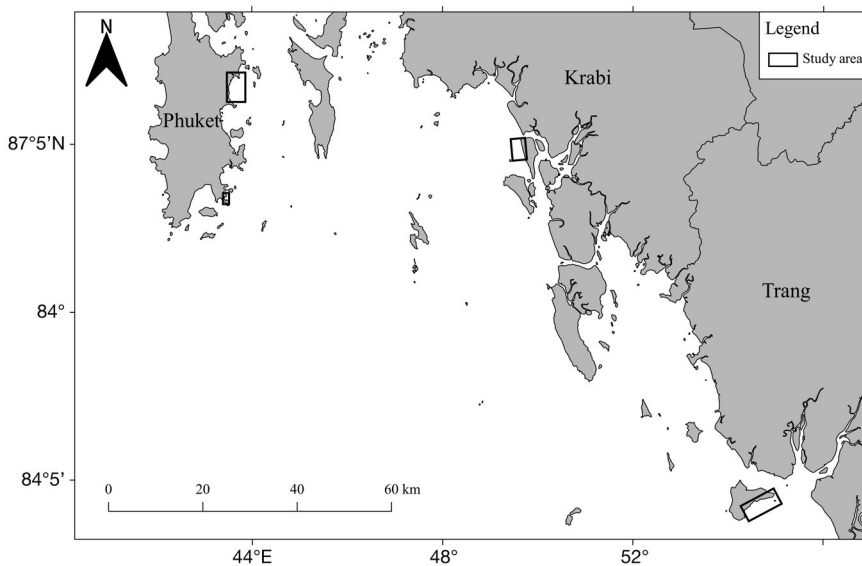

Fig. 1. Study sites along the west coast of Thailand

and kept at 4°C until a laboratory was reached. Sediment samples were collected using stainless steel cores (5 cm diameter × 1 m length), which were placed in the same area of the quadrats. Cores were covered with duct tape before being hammered into the sediment. As a core was removed from the sediment, the bottom and top parts of the core were covered using rubber stoppers so that the oxygen intrusion to the deepest layers was minimal. Sediment samples were cut off at 3 cm intervals (Fourqurean et al. 2012b) by peeling duct tape from top to bottom (n = 2679 sediment subsamples). Each subsample was packed in pre-labeled bags and kept at 4°C until a laboratory was reached.

Laboratory study

Biomass samples from each patch type were separated into above- (leaves) and belowground (roots and rhizomes) parts (n = 288). Leaf blades were manually scraped to remove epiphytes, and cleaned material was dried in an oven at 60°C until a constant weight was achieved. The dry weights of the above- and belowground parts were recorded. Since there is little variation in organic carbon content in living vegetation (Duarte 1990), only a small number of samples (n = 48), including roots, rhizomes, and leaves, were used for organic carbon analysis. Between 20 and 30 mg of each vegetative part was crushed into powder using a mortar and pestle, and 10 mg of subsamples were used for carbon analysis (% carbon) as determined by a CHNS/O Analyzer (Thermo Quest, Flash EA 1112 Series) at the Central Equipment Division, Faculty of Science, Prince of Songkla University (PSU). Carbon content, as particulate organic carbon from above- and belowground parts for each patch type, was calculated as:

$$\text{Carbon content (g)} = \text{carbon (\%)} \times \text{dry weight of sample (g)} \quad (1)$$

Sediment subsamples were oven-dried at 60°C until their weights were constant. Approximately 15 g from each subsample (n = 240) was ground into fine powder, and 20 mg of the ground subsample was used for organic carbon (C_{org}) analysis, which was performed using the same method mentioned above for plant parts. Particulate organic carbon content (g) in each sediment subsample was calculated using Eq. (1). Inorganic carbon analysis was performed with ~5 g of fine ground powder, using acidification with 1 N HCl. The rest of the fine ground subsample powder was weighed and used

for %LOI analysis. The samples were heated in a furnace at 450°C and kept for 4–8 h (Heiri et al. 2001). %LOI was calculated as:

$$\%\text{LOI} = [(\text{dry mass before combustion} - \text{dry mass after combustion}) / \text{dry mass before combustion}] \times 100 \quad (2)$$

Model structure and analyses

To predict carbon estimates in the seagrass ecosystem, the whole model is divided into 3 units: (1) biomass prediction, (2) carbon in the living vegetation prediction, and (3) carbon in the sediment prediction (Fig. 2). Both monospecific and mixed patch types were explored separately. All statistical analyses were performed using the open source language R (R Studio Team 2015). All relationship models between 2 variables were tested using linear regression analysis. For each model, both untransformed and transformed data (log and square-root transformations) were tested. The model with the lowest Akaike's information criterion (AIC) value was selected. When several models had ΔAIC <2, the simpler model was chosen as a prediction model.

In the first unit, biomass values (for both above- and belowground, 'AG' and 'BG') were predicted using 2 models: 'cover-AG' and 'AG-BG' models (Fig. 2). In the first model (cover-AG), aboveground biomass (in g dry weight [DW] m^{-2}) was predicted from seagrass coverage (i.e. cover, %). In the second model (AG-BG), belowground biomass (g DW m^{-2}) was predicted from aboveground biomass. For both models, data from 45 quadrats per patch type were tested.

For the second unit, carbon in the living vegetation was predicted from the biomass value. Two methods were tested using 20 samples per patch type (Fig. 2). The first method created a conversion factor following procedures described in detail by Howard et al. (2014). Average values of organic carbon for above- and belowground biomass for each patch type were calculated separately and used as the conversion factor. The second method was the model to predict carbon in the living vegetation (Mg ha^{-1}) from total biomass (g DW m^{-2}) ('biomass-carbon' model).

In the last unit, organic carbon in sediment (C_{org}) was predicted. Two models were tested: 'LOI-C_{org}' and 'plant-C_{org}': (Fig. 2). The first model (LOI-C_{org}) predicted organic carbon in sediment per sample based on organic matter from the LOI technique from 100 sediment samples per patch type. The results of C_{org} (%) from the C, H, N analyzer and the LOI (%)
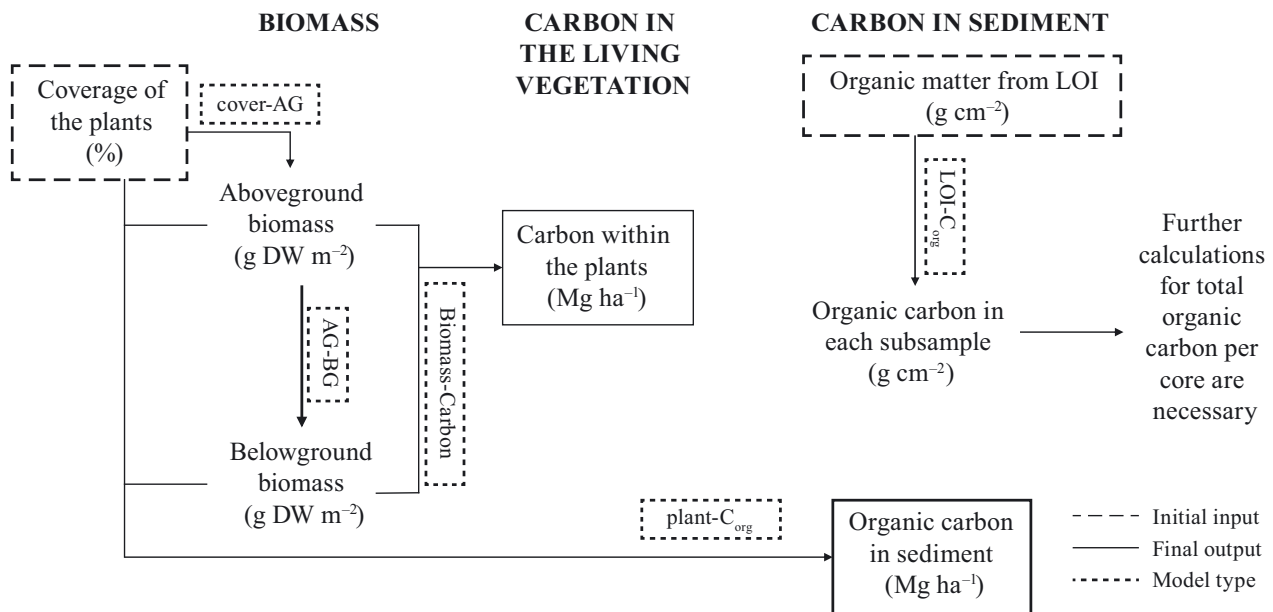
Fig. 2. Model structure with 3 units: biomass prediction, carbon in living vegetation prediction, carbon in sediment prediction. DW: dry weight; LOI: loss on ignition; AG: aboveground biomass, BG: belowground biomass

data were transformed to g cm^{-2}. In the second model (plant-C$_{org}$), organic carbon in sediment (Mg ha^{-1}) per core was predicted from plant attributes (e.g. seagrass coverage, above- and belowground biomass) from ~45 samples per patch type. The key difference between these 2 models is that the LOI-C$_{org}$ model requires field data collection for calculating LOI and uses it as a predictor variable, while the second model can use plant attributes such as % cover and above- and belowground biomass, which can be easily calculated using the previously mentioned units. Moreover, the first model predicts the organic carbon per subsample, so further calculations of the total carbon pool in the sediment are necessary, while the plant-C$_{org}$ model predicts the organic carbon per sample (core), which is the amount of carbon stored in 1 m of sediment.

Model evaluation

To provide the expected prediction error and predictive performance of the selected models, the models were evaluated using overall RMSE, R^2, and 95% CI of beta-coefficients of predictor variables. Between 3 and 20 samples were used for RMSE calculations for each model. Moreover, residual plots of the selected model were tested.

To demonstrate predictive performance of the selected models on the landscape scale, data were gathered from Tha Rai Island in Nakhon Si Thammarat Province in July 2017. Middle and lower intertidal areas were selected for data collection, as there were similar species compositions for mixed (*E. acoroides, T. hemprichii*, and *Halodule uninervis*) and monospecific (*E. acoroides* with few patches of *H. uninervis*) patches. Eleven replicates of the coverage data and 1 replicate of sediment to 60 cm depth were obtained per patch type. Sediment data were later extrapolated up to 1 m depth, as the model predicts organic carbon in sediment up to 1 m depth.

RESULTS

Modeling units

For the biomass prediction unit (cover-AG and AG-BG models), a linear model with untransformed data was chosen as the model predictor for both monospecific and mixed species patches (Table S1a−d in the Supplement at www.int-res.com/articles/suppl/m596p061_supp.pdf). All predicted equations are shown in Table 1.

For the carbon in the living vegetation prediction unit, monospecific patches had average carbon values of 32% for aboveground parts and 30% for belowground parts, suggesting conversion factors of 0.32 and 0.30, respectively. For mixed-species patches, average carbon values were 34 and 32%,

Table 1. Summary table for all of the selected models. For all models, p < 0.01. Cover: plant coverage (%); AG (BG): above-ground (belowground) biomass (g dry weight [DW] m^{-2}); biomass: AG + BG biomass (g DW m^{-2}); carbon: carbon content in plants (Mg ha^{-1}); LOI: loss on ignition (g cm^{-2}): C_{org}: organic C in sediment (g cm^{-2})

Model	Equation	95 % CI	R^2 (%)	Overall RMSE
Cover-AG	Monospecific: AG = 1.90157 + 1.02125 × cover	0.8715–1.1710	83	10.99
	Mixed: AG = 9.033 + 0.771 × cover	0.5709–0.9711	60	20.29
AG-BG	Monospecific: BG = 29.419 + 5.125 × AG	4.5568–5.7461	89	20.86
	Mixed: BG = 26.5542 + 2.8491 × AG	1.8899–3.8083	45	27.00
Biomass-Carbon	Monospecific: Carbon = −0.1016756 + 0.0144978 × Biomass	0.0137–0.0153	99	1.59
	Mixed: Carbon = −0.0606922 + 0.0139800 × Biomass	0.0134–0.0145	99	1.83
LOI-C_{org}	Monospecific: C_{org} = 10.1740 + 0.1714 × LOI	0.1276–0.2151	41	1.95
	Mixed: C_{org} = 10.21697 + 0.13441 × LOI	0.0804–0.1884	32	8.79
Plant[a]- C_{org}	Monospecific: C_{org} = −139.53 + 122.96 × log(BG)	122.85–123.06	87	22.81
	Mixed: C_{org} = −112.46 + 102.28 × log(BG)	102.37–112.36	79	22.50

[a]Various plant attributes

respectively, suggesting conversion factors of 0.34 and 0.32. Similarly to the first unit, a linear model with untransformed data was chosen as the model predictor for both patch types in the biomass-carbon unit (Table S1e,f). The predicted equations for both patch types are shown in Table 1.

For the sedimentary carbon prediction unit, similarly to the first 2 units, a linear model with untransformed data was chosen for the LOI-C_{org} model as the model predictor for both patch types (Table S1g,h). In contrast, for the plant-C_{org} model, a linear model with log-transformed data was chosen as the model predictor for both patch types (Table S1i,j). All predicted equations are shown in Table 1.

Model performance and evaluation

Models of monospecific patches with R^2 values of 83, 89, 41, and 87 had higher R^2 values than models of mixed patches, with R^2 values of 60, 45, 32, and 79 for cover-AG, AG-BG, LOI-C_{org}, and plant-C_{org} models, respectively (Table 1). However, R^2 values had the same value (99%) in both patch types for the biomass-carbon model. The overall RMSE of monospecific patch models was lower than that for mixed patches for cover-AG, AG-BG, biomass-carbon, and LOI-C_{org} models as well, while it was higher for monospecific conversion factor and plant-C_{org} models (Table 1).

On the landscape scale (at Tha Rai Island), coverage of the seagrass varied between 10 and 65% in monospecific meadows and between 50 and 80% in mixed meadows. Collected sedimentary organic car-

bon was 65.39 and 66.29 Mg ha^{-1} in monospecific and mixed species meadows, respectively. When carbon was extrapolated to 1 m depth, carbon estimations were 130.78 Mg ha^{-1} in monospecific and 132.58 Mg ha^{-1} in mixed species meadows. Following a stepwise structure of the models (Fig. 3), predicted average organic carbon in sediment was (mean ± SD) 149.95 ± 21.68 and 124.32 ± 5.38 Mg ha^{-1} in monospecific and mixed species meadows, respectively. Overall RMSE was 27.91 in monospecific and 6.31 in mixed meadows.

DISCUSSION

Biomass prediction (cover-AG and AG-BG models)

The biomass prediction unit was built up on the already established knowledge of the relationships between coverage and above- and belowground biomass (Armstrong 1993, Heidelbaugh & Nelson 1996, Mumby et al. 1997b, Duarte & Chiscano 1999). In the case of the cover-AG model, the relationship between plant coverage and the aboveground biomass has been established for several years (Armstrong 1993, Heidelbaugh & Nelson 1996, Mumby et al. 1997b, Fonseca et al. 2002, Knudby & Nordlund 2011, Lyons et al. 2015, Carstensen et al. 2016). However, our model, which separates monospecific species from the mixed-species patches, has higher R^2 values and smaller marginal error values, while the other models of total biomass (Phinn et al. 2008, Knudby & Nordlund 2011, Lyons et al. 2015) reported medium and low R^2 values with an overall RMSE > 26.

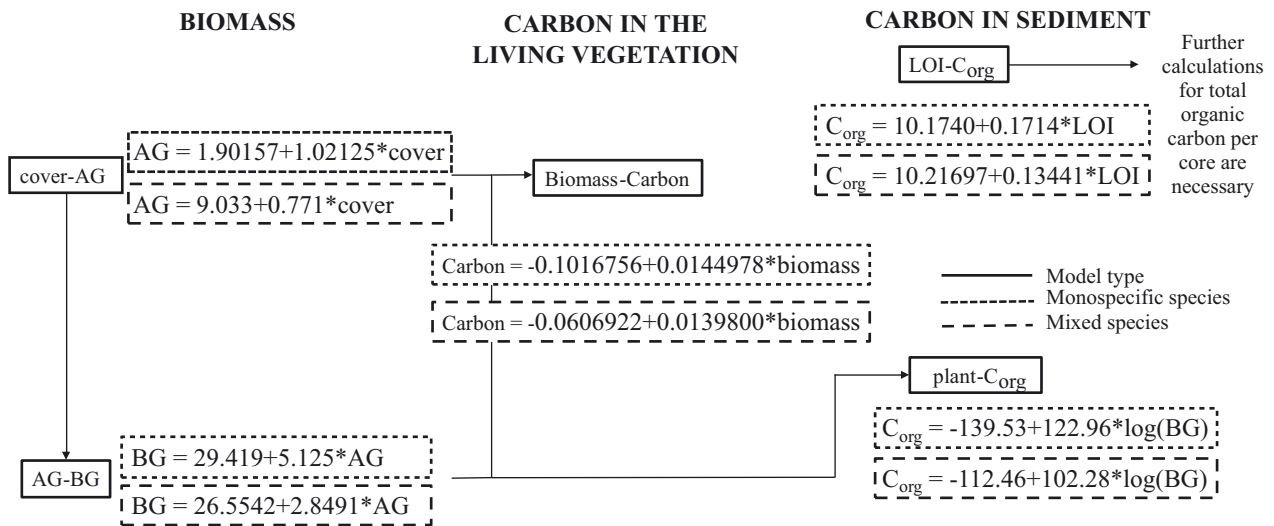BIOMASS CARBON IN THE LIVING VEGETATION CARBON IN SEDIMENT

Fig. 3. Model structure with results for all 3 units: biomass prediction, carbon in living vegetation prediction, carbon in sediment prediction. See Table 1 for abbreviations

The second biomass model, AG-BG, is the model that successfully and with a small margin of error predicted belowground biomass from the aboveground biomass. This result is supported by the model of Githaiga et al. (2017) that also successfully predicted belowground biomass from aboveground biomass (only for *Enhalus acoroides* meadows). Likewise, Congdon et al. (2017) successfully predicted belowground biomass from coverage of the plants for *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme*. However, Lyons et al. (2015) suggested that the prediction is not appropriate using a simple linear model, due to the plants' variability in phenology (Maxwell et al. 2014).

The existing relationship between above- and belowground biomass (Duarte & Chiscano 1999) was based on the global data set, with monospecific and mixed species pooled together, resulting in a high variation of the above- and belowground ratio (0.005–8.56), and thus a lower correlation. Similarly, our results in both models (cover-AG and AG-BG) resulted in better performance of monospecific species models than for mixed species. These same patterns of lower model performance in the mixed species patch might suggest that mixed species patches are more complex and that more input information for the model is necessary. Since Lyons et al. (2015) observed a reduction in the margin of error of the aboveground biomass prediction in the 'species' and 'dominant species' models in the mixed patches, it could be suggested that each species component of the biomass should be separated for future modeling.

Carbon in the living vegetation prediction (conversion factor and biomass-carbon model)

We suggested 2 methods of predicting organic carbon within the seagrass tissues. The first included creating conversion factors, while the second tested the relationship between organic carbon and biomass. While the global average value of organic carbon is assumed to be approx. 35% (Duarte 1990, Fourqurean et al. 2012a), the average value of the Southeast Asian region was lower at 27.5% (Phang et al. 2015). The difference of the average carbon content in seagrass tissues between global averages and the Southeast Asian region created the need for a specific carbon conversion factor for the region.

Although the conversion factor is very useful in carbon calculations, the linear regression model between organic carbon within the plants and biomass (biomass-carbon model) provides better results with a very strong correlation and a low error margin. The results from Stankovic et al. (2017) showed a very strong correlation ($p < 0.01$) as well, which suggests a linear increase in carbon within the tissues of the plants based on their structural components, form, and role in the ecosystem (Duarte 1990, Wirachwong & Holmer 2010, Rustam et al. 2017). However, when the data are separated between patch types, results show smaller errors and stronger relationships. Since both methods provided satisfactory results, in our study we can conclude that the relationship between biomass and organic carbon within the plants is not species-specific and is not influenced by the type and structure of the seagrass patch.

Carbon in the sediment prediction (LOI-C_{org} and plant-C_{org} models)

The LOI-C_{org} model is a moderately good predictor of organic carbon in sediment, corresponding to the results of Phang et al. (2015). On the other hand, studies from temperate zones have reported much stronger relationships, with $R^2 \geq 0.80$ (Fourqurean et al. 2012a,b, Samper-Villarreal et al. 2016). Because results differ regionally, it is possible that sediments in tropical seagrass meadows experience mass loss during the LOI process even with no organic carbon present in the sediment, which could be due to the structural water and/or soluble salts in the sediment (EPA 1990).

The second model (plant-C_{org}) showed that the belowground biomass of the plants could be a moderately good predictor of organic carbon in the sediment. The large belowground biomass of the longer-living species such as *E. acoroides* and *T. hemprichii* (Duarte et al. 1998) produces a significant contribution to the total carbon pool (Supriadi et al. 2014), suggesting that belowground biomass has a positive correlation with organic carbon in the sediment (Serrano et al. 2016). While monospecific patches consist of a long-living single species, mixed patches consist of 2 species and are more structurally complex with 2 layers of canopy and roots. Rattanachot & Prathep (2015) reported that the redox potential and the organic carbon in the sediment were not different between monospecific and mixed-species patches, suggesting that root complexity has little influence on organic carbon in the sediment. However, Stankovic et al. (2017) concluded that monospecific patches of larger-sized species store more carbon within their sediments than smaller species. Samper-Villarreal et al. (2016) proposed that seagrass structural complexity of the canopy is the key driver in non-turbid waters that correlates with the organic carbon in the sediment, suggesting that carbon in the seagrass sediments increases as structural complexity increases. Canopy complexity is an important factor in water flow attenuation, as it limits resuspension of the organic particles to the water column (Koch 2001, Hendriks et al. 2008). The trapped carbon from external sources via canopy complexity is added to the overall carbon accumulation in the sediment (Kennedy et al. 2010, Duarte et al. 2013b). These results suggest that both patch types demonstrate a high possibility of carbon sequestration and accumulation in the sediment via larger biomass sizes in monospecific or via canopy complexity in mixed species patches. Further investigation of the correlation of the belowground biomass and structural complexity and organic carbon in the sediment should be made for more precise conclusions and more accurate models.

Landscape-scale model and its advantages

The stepwise structural model proposed in this study is the first model that can predict the organic carbon pool in seagrass ecosystems using only the coverage of plants. The lower values of the error margin on the landscape scale show that the series of the proposed linked relationships can successfully predict organic carbon, which can have several advantages compared to other approaches. Time and cost for the research can be greatly decreased. Field work for data collection can be reduced (for collecting information about species coverage), and post-field data processing in the laboratory (e.g. for organic carbon analysis) is not required. Time and cost can even be less if remote sensing imagery is applied, as field trips can be limited to ground-truth data collection. This advantage is especially important for many countries in Southeast Asia where research budgets are limited. Another key advantage is its applicability over a large area. Finally, although the model-based approach is assumed to provide less accurate results than visual/destructive sampling methods, the subjective estimates and human error during sampling cannot be quantified, while the model error is repeatable and quantifiable.

The models proposed in this study should be used with caution, as they are applicable only to a few species. Users should be aware of model errors and limitations and should apply mixed-species patches separately from monospecific species patches. Our proposed models address only autochthonous organic carbon sources, but in the seagrass ecosystems, allochthonous sources play important roles (Fourqurean et al. 2012a), so their contributions should not be neglected.

Although the models have certain limitations, they can be used in various situations. Managers can use them as a tool to promote and enhance seagrass health, conservation, and restoration, and to set conservation priorities. They can also be used by local people or government officers who want to promote seagrass meadows within national greenhouse gas schemes via carbon credits. As seagrass ecosystems contribute to climate change mitigation, the proposed models can be used for modeling of seagrass distribution in future climates and to develop efficient climate change mitigation strategies. However,

it is necessary to continue to test the relationships between coverage, biomass and organic carbon — especially in mixed-species patches — so that biomass and carbon storage can be as successfully predicted as in monospecific patches, and to improve the prediction of sedimentary organic carbon. We hope that this approach can be used as a stepping stone for future research studies within the SE Asian region, as this region is failing to match the pace of current blue carbon studies.

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