Evaluation of Relationships Between Cover Estimates and Biomass in Subtropical Seagrass Meadows and Application to Landscape Estimates of Carbon Storage

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Seagrass habitats provide invaluable ecosystem services, including the ability to sequester carbon through primary production. In the absence of significant grazing pressure, changes in seagrass biomass reflect net photosynthetic activity in response to the light environment. We developed linear models to convert a commonly measured parameter, percent cover, into above- and belowground biomass for three tropical seagrass species, Thalassia testudinum, Halodule wrightii *and* Syringodium filiforme. *Linear models were estimated from the analysis of 126 biomass cores collected at five levels of percent cover from three coastal bays in Texas. The models showed an increase in aboveground biomass with increased percent cover ($R^2 = 0.52–0.77$), but belowground biomass displayed greater variability with respect to percent cover ($R^2 = 0.15–0.63$). Such linear biomass models can provide valuable estimates of carbon storage potential in living seagrass tissues using monitoring data collected across large spatial scales within the Gulf of Mexico.*

Resumen: *Los hábitats de hierba marina proporcionan servicios inestimables de los ecosistemas, incluyendo la capacidad de secuestrar el carbono a través de la producción primaria. En ausencia de una presión de pastoreo significativa, los cambios en la biomasa de los pastos marinos reflejan la actividad fotosintética neta en respuesta a la luz ambiental. Se desarrollaron modelos lineales para convertir un parámetro comúnmente medido, por ciento de cobertura, en biomasa subterránea y subterránea para tres especies de pasto marino tropical, Thalassia testudinum, Halodule wrightii y Syringodium filiforme. Los modelos lineales se estimaron a partir del análisis de 126 núcleos de biomasa recolectados en cinco niveles de cobertura porcentual de tres bahías costeras en Texas. Los modelos mostraron un aumento de la biomasa aérea con mayor cobertura porcentual ($R^2 = 0,52–0,77$), pero la biomasa subterránea mostró mayor variabilidad con respecto al porcentaje de cobertura ($R^2 = 0,15–0,63$). Tales* *modelos de biomasa lineal pueden proporcionar valiosas estimaciones del potencial de almacenamiento de carbono en los tejidos vivos de los pastos marinos usando datos de monitoreo recolectados a través de grandes escalas espaciales dentro del Golfo de México.*

KEYWORDS: *Halodule wrightii*, *Thalassia testudinum*, *Syringodium filiforme*, abundance, distribution

PALABRAS CLAVE: Halodule wrightii, Thalassia testudinum, Syringodium filiforme, abundancia, distribución

INTRODUCTION

Seagrass meadows are among the most productive habitats in the world (Duarte and Chiscano 1999), and provide a variety of economically and ecologically important services (Costanza et al. 1997; Barbier et al. 2011). Despite the plethora of ecosystem services that seagrasses provide, these critical habitats are facing unprecedented rates of decline worldwide due to anthropogenic and natural stressors (Orth et al. 2006; Waycott et al. 2009). To reverse this trend, numerous long-term monitoring programs throughout the world collect and analyze a variety of seagrass condition indicator data (Marbà et al. 2013; Roca et al. 2016). Various seagrass indicators and metrics are used to assess seagrass ecosystem status and provide early detection of changes in ecosystem condition. Of these, seagrass abundance measures are commonly collected to better understand the relationships between environmental and anthropogenic stressors and seagrass response. Seagrass abundance is measured using a suite of parameters such as percent cover, biomass, shoot density and canopy height (Duarte and Kirkman 2001), parameters clearly responsive to the plant's light environment (Dennison and Alberte 1985; Dunton 1994; Dennison et al. 1993; Abal et al. 1994).

Percent cover is frequently used in rapid assessments of seagrass distribution and abundance because it is both cost and time efficient (Neckles et al. 2012), and is widely collected throughout the Gulf unlike other measures of abundance. Seagrass percent cover is defined as the proportion of substrate obscured by vegetation and is used to estimate biomass by acquiring a small number of destructive samples and performing linear regressions (Duarte and Kirkman 2001). Unfortunately, biomass sampling involves the extraction of plants, which are severed and removed, and physically disturbs the meadow. Additionally, biomass collection and processing is very labor intensive and requires time and access to substantial resources. To address considerable resource requirements, seagrass biomass was reasonably estimated using quick and non-destructive techniques such as percent cover, cover classes and blade counts (Orth and Moore 1988; Mellors 1991; Heidelbaugh and Nelson 1996).

Percent cover data sets provided by long-term monitoring programs can produce large-scale biomass estimates using simple regression analyses with minimal destructive sampling. Although percent cover is a useful measure of seagrass abundance, it cannot provide information on carbon stores in seagrass beds. Biomass measurements are used to derive carbon pool estimates in living biomass when the dried weight and carbon content of the tissue are known (McLeod et al. 2011;

Fourqurean et al. 2012). Large-scale assessments of the carbon storage capacity of seagrass meadows will be useful in the face of climate change, as changes in various environmental and anthropogenic drivers continue to stress seagrass populations that result in changes in their distribution and abundance (McLeod et al. 2011; Fourqurean et al. 2012; Duarte et al. 2013b).

The focus of this study was to translate seagrass percent cover into aboveground and belowground biomass for three common tropical seagrass species – *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme*. Recent studies produced biomass estimates using percent cover observations for temperate species such as *Zostera marina* (Carstensen et al. 2016) and a variety of tropical Indo-Pacific and Australian species (Lyons et al. 2015). However, to our knowledge, no connection between cover and biomass has been developed for all three predominant species within the Gulf of Mexico. Moreover, the relationship between percent cover and belowground biomass is relatively unexplored, specifically for these three species. Lastly, the equations produced from this study were used to construct distributional patterns of living biomass carbon stocks across a large geographic extent utilizing percent cover estimates collected by a seagrass monitoring program in Texas.

MATERIALS AND METHODS

Study location

Seagrass meadows in Texas extend 862 km^2, with 94 percent of the seagrasses distributed along the central and southeast coast (Dunton et al. 2011) in three major bay systems – the Coastal Bend, Upper Laguna Madre and Lower Laguna Madre. We focused on the seagrass beds within the Coastal Bend and Upper Laguna Madre, which are composed of monospecific and mixed seagrass beds of *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*, *Ruppia maritima* and *Halophila engelmannii*. Redfish Bay and East Flats of the Texas Coastal Bend are well flushed due to their connectivity with the Gulf of Mexico through Corpus Christi Pass and Aransas Pass ship channels, and support all five seagrass species. Relatively stable conditions, coupled with the protection from prevailing southeasterly winds by saltmarsh islands and shoals (Redfish Bay), and Mustang Island (East Flats), support lush seagrass communities (Dunton et al. 2011; Figure 1). Oceanic exchange also occurs through Packery Channel in Upper Laguna Madre, which supports dense stands of *S. filiforme* and *H. wrightii*.

Biomass and cover measurements

Seagrass percent cover and biomass were sampled near the peak of the growth season (August and September 2016) in monotypic stands of *T. testudinum* (Redfish Bay: RB), *H. wrightii* (East Flats: EF) and *S. filiforme* (Upper Laguna Madre: UL; Figure 1). Although seagrasses can grow in water depths up to 2 m in Texas, samples for this study were collected in water depths of < 1.2 m. Percent cover observations and above- and belowground biomass samples by species were collected at five cover levels: 20, 40, 60, 80 and 100 percent. For each species, two to three cover observations were visually estimated using a 0.25 m^2 quadrat at each cover level.

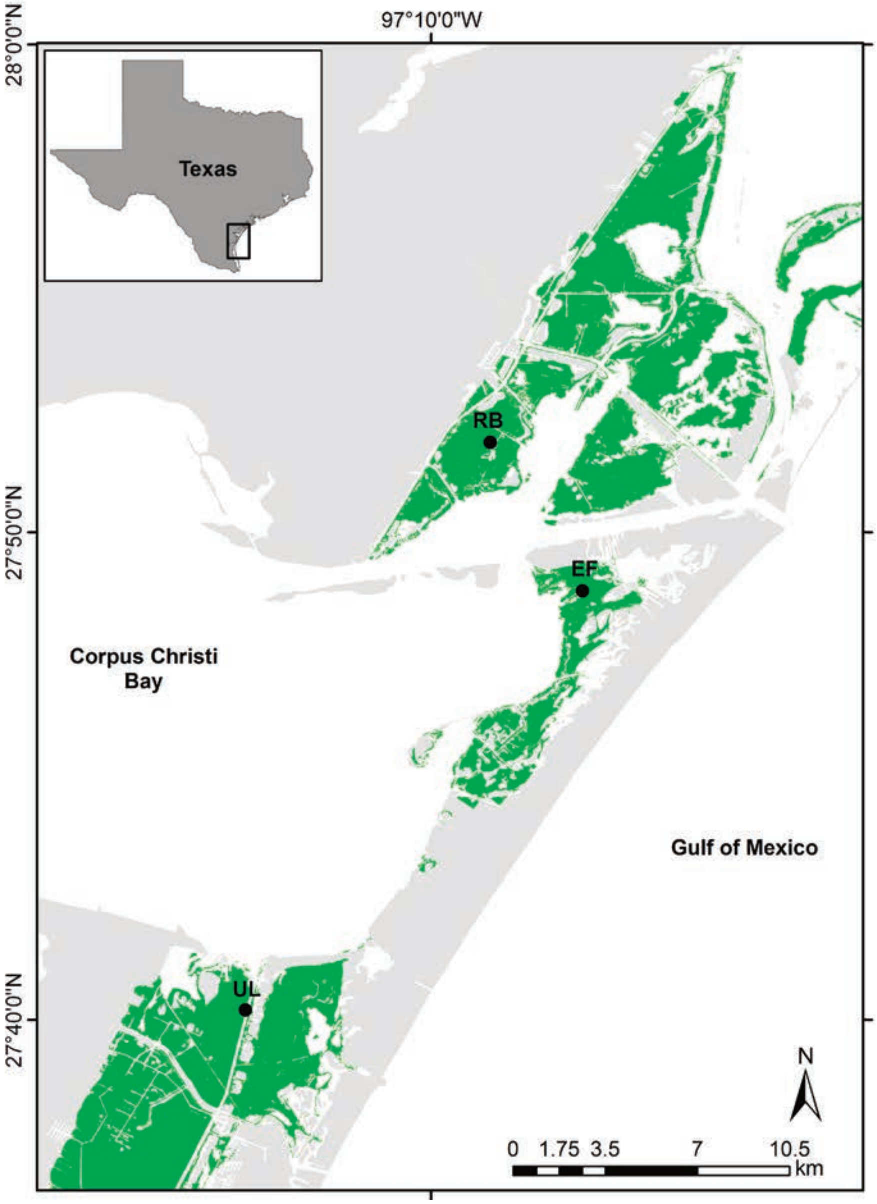

Figure 1. Location of study sites. Dark gray represents continuous seagrass cover using the NOAA 2004/2007 Benthic Habitat Mapping data set. Seagrass biomass samples were collected from monospecific beds of Thalassia testudinum *in Redfish Bay (RB),* Halodule wrightii *in East Flats (EF) and* Syringodium filiforme *in the Upper Laguna Madre (UL).*

Following each percent cover observation, above- and belowground biomass were harvested using a 0.0079 m^2 (10 cm diameter) core sampler inserted up to 18 cm into the sediment. Three biomass cores were extracted from within each quadrat since shoot density can be highly clumped and non-homogeneously distributed. Biomass cores were carefully sieved (1 mm mesh) to keep meristems intact and then placed on ice for subsequent processing, usually within 72 h. During preparation, only intact meristems were processed for living biomass measurements, and broken shoots, debris and dead plant material were discarded. We identified living biomass from senescent material by placing the sieved biomass samples in a shallow tray with water. Buoyant plant material was retained for living biomass measurements, and detached dead leaves and roots/rhizomes were removed using forceps and discarded prior to analyses. Seagrass blades were scraped manually to remove epiphytes. Samples were separated into aboveground (photosynthetic) and belowground (roots + rhizomes + leaf sheaths) biomass and rinsed with milli-Q water. Above- and belowground tissues were dried to a constant weight at 60°C and dried plant material was used to determine seagrass biomass in grams of dry weight (g DW). Seagrass biomass was estimated by extrapolating the dry weight of the sample to one square meter and expressed as g DW m^{-2}. The three core subsamples were used to determine the mean dry weight for each quadrat.

Carbon content and storage

After the aboveground and belowground dried plant material was weighed, tissues were prepared for elemental (carbon content) analyses for *T. testudinum*, *H. wrightii* and *S. filiforme*. The three subsamples from within each quadrat were combined into one representative sample for each quadrat. Dried tissues were homogenized by grinding to a fine powder using a mortar and pestle. Tissue samples were analyzed for carbon content using a Carlo Erba 2500 elemental analyzer coupled to a Finnigan MAT DELTAplus isotope ratio mass spectrometer. Only the newest leaves in the leaf bundle were used for aboveground carbon content. Above- and belowground tissue carbon content was determined by averaging all biomass samples collected for each species.

Total carbon storage of living biomass was estimated using percent cover observations from the Texas Statewide Seagrass Monitoring Program (data available at www.texasseagrass.org). In 2015, percent cover observations were made at 634 stations that spanned from San Antonio Bay to Lower Laguna Madre. These data were used to estimate inventories of total seagrass biomass and carbon stores. The biomass estimates produced from these relationships were used to generate cumulative carbon storage values for above- and belowground tissues for each species using the carbon content percentages produced in this study. Briefly, above- and belowground biomass estimates by species were multiplied by their respective carbon content to derive g C m^{-2}. Geographic information system (GIS) analysis was used to illustrate the distribution of carbon stores in living seagrass biomass along the Texas coast (San Antonio Bay, Coastal Bend, and Upper and Lower Laguna Madre).

Data analysis

The relationship between percent cover and biomass for *T. testudinum*, *H. wrightii* and *S. filiforme were* modeled using linear regressions. Correlation coefficients were calculated using a least-squares fit between above- and belowground biomass for each species with percent cover. All statistical analyses were performed in R version 0.99.486 (R Core Team, Vienna, Austria, 2016).

For mapping visualizations of estimated carbon content, we used Inverse-Distance Weighting (IDW) interpolation to predict values between 634 sampling points. We identified 12 sampling stations from a variable search radius to generate a predicted value at each unknown point (100 m^2). Interpolations were spatially restricted to seagrass cover extent created during the 2004/2007 NOAA Benthic Habitat Assessment. The interpolations of carbon storage for above- and belowground biomass estimates from percent cover observations were bounded by seagrass extent. All spatial analyses were performed in ArcMap 10.1 (Environmental Systems Research Institute).

RESULTS

Biomass and cover measurements

Aboveground biomass measurements tended to increase with percent cover for *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme* (Figure 2A-C). Results indicated that percent cover significantly predicted aboveground biomass for *T. testudinum* ($p < 0.001$), *H. wrightii* ($p < 0.001$) and *S. filiforme* ($p < 0.01$; Table 1). Although cover was a significant predictor of aboveground biomass for all three species, it weakly predicted *H. wrightii* belowground biomass (Table 1; Figure 3B). However, percent cover explained more than 50 and 30 percent of the variation in *S. filiforme* and *T. testudinum* belowground biomass, respectively (Table 1;

Table 1. Summary of linear models and R^2 values for percent cover versus biomass relationships for Thalassia testudinum, Halodule wrightii *and* Syringodium filiforme. *Values are reported for both aboveground (AG) and belowground (BG) biomass in* T. testudinum *and* H. wrightii *(df = 13) and* S. filiforme *(df = 10). Bolded equations indicate an $R^2 > 0.50$ and significant p-values ($p < 0.01$).*

Linear model (response ~ predictor)	Equation	R^2	p-value
T. testudinum			
lm ($biomass_{AG}$ ~ cover)	**$y = 1.14x + 80.40$**	0.77	< 0.001
lm ($biomass_{BG}$ ~ cover)	$y = 4.95x + 331.45$	0.31	0.018
H. wrightii			
lm ($biomass_{AG}$ ~ cover)	**$y = 1.12x + 4.52$**	0.61	< 0.001
lm ($biomass_{BG}$ ~ cover)	$y = 1.00x + 90.57$	0.15	0.085
S. filiforme			
lm ($biomass_{AG}$ ~ cover)	**$y = 2.98x - 22.51$**	0.52	0.004
lm ($biomass_{BG}$ ~ cover)	**$y = 2.84x - 6.42$**	0.63	0.001

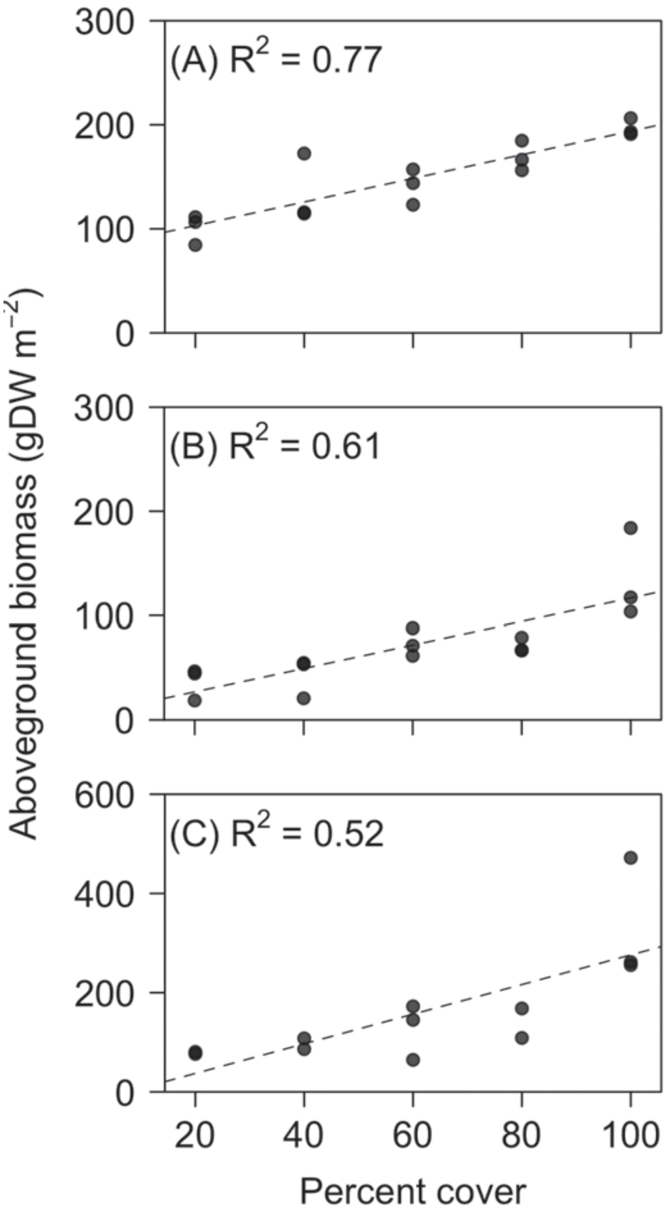

Figure 2A-C. Relationship between aboveground biomass and percent cover for (A) Thalassia testudinum*, (B)* Halodule wrightii *and (C)* Syringodium filiforme.

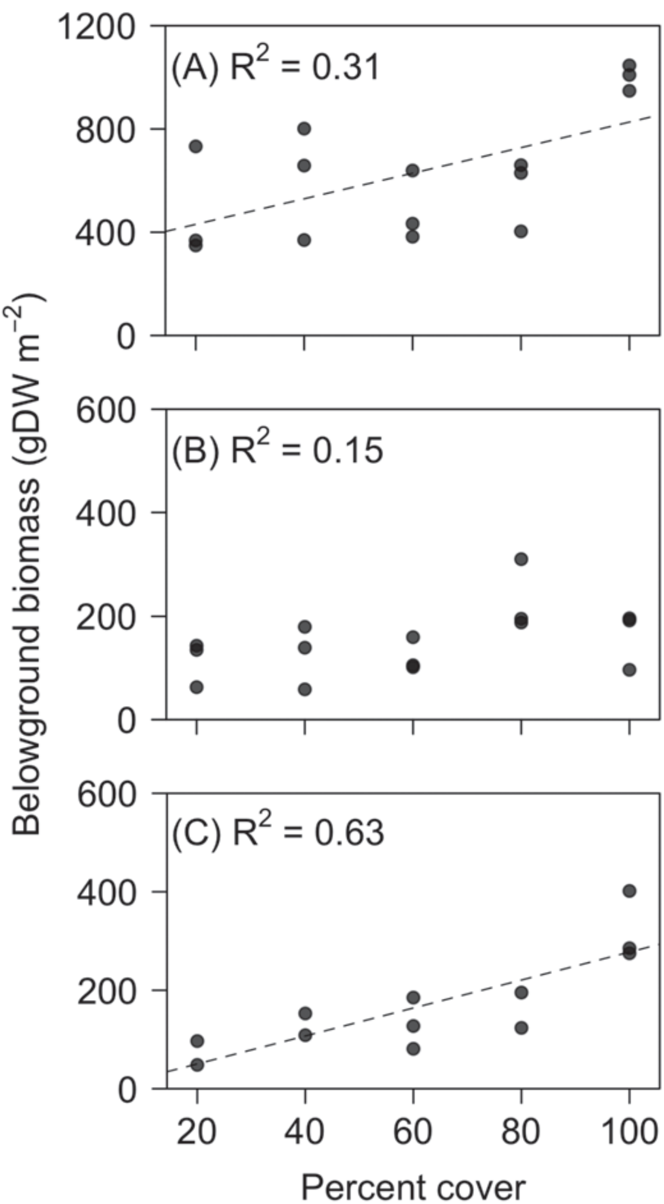

Figure 3A-C. Relationship between belowground biomass and percent cover for (A) Thalassia testudinum*, (B)* Halodule wrightii *and (C)* Syringodium filiforme.

Figure 3A,C). Belowground biomass did increase with cover but exhibited greater variability at intermediate levels of cover (Figure 3A-C). The average aboveground biomass was between 100.8 and 196.9 g DW m^{-2} (*T. testudinum*), 36.7 and 134.9 g DW m^{-2} (*H. wrightii*), and 78.6 and 329.7 g DW m^{-2} (*S. filiforme*). Belowground biomass ranged from 483.1–1001.1 g DW m^{-2} for *T. testudinum*, 113.7–231.0 g DW m^{-2} (*H. wrightii*), and 72.6–320.7 g DW m^{-2} (*S. filiforme*). Root:shoot ratio values were greatest for *T. testudinum* (4.2), followed by *H. wrightii* (2.5) and *S. filiforme* (1.1).

Carbon content and storage

Aboveground tissue carbon content (mean ± SE) for *T. testudinum*, *H. wrightii* and *S. filiforme* was 39.6 ± 0.53, 39.1 ± 0.66 and 35.4 ± 0.39 percent, respectively. Mean belowground tissue percent carbon was lower than aboveground carbon content values for all three species. Belowground carbon percentages were 33.5 ± 0.49 (*T. testudinum*), 35.7 ± 0.64 (*H. wrightii*) and 35.0 ± 0.63 (*S. filiforme*). Highest carbon stocks (up to 367 g C m^{-2}) were found in areas with greater percent cover and biomass (Figure 4). Mean total carbon stores (above- and belowground) for the regions in Texas were greatest in the Coastal Bend (176.0 ± 9.4 g C m^{-2}) and Lower Laguna Madre (152.7 ± 6.4 g C m^{-2}), followed by Upper Laguna Madre (90.6 ± 3.5 g C m^{-2}) and San Antonio Bay (55.5 ± 5.0 g C m^{-2}).

DISCUSSION

Biomass and cover measurements

Recent work by Carstensen and others (2016) point out that percent cover, depth and light attenuation only explained 56 percent of the variation in *Zostera marina* biomass. Since seagrass abundance (e.g., biomass) is a product of the combined interaction between a suite of environmental and anthropogenic drivers and stressors, and studies have shown that light (Dennison and Alberte 1985; Abal et al. 1994; Dunton 1994) and depth (Dennison and Alberte 1985; Dennison et al. 1993; Lee and Dunton 1996; Dawes 1998; Olesen et al. 2002) control seagrass abundance, it is reasonable that the inclusion of light attenuation and depth would bolster the performance of the relationship between cover and biomass. However, there are other abiotic factors that exert control on seagrass distribution and abundance such as salinity and nutrient availability, which could further complicate regression analyses and lead to over-fitting the model. This study shows that simple linear regressions significantly predict aboveground biomass for *T. testudinum*, *H. wrightii* and *S. filiforme* (Table 1).

Visualization techniques have proven insufficient in providing reliable belowground biomass estimates (Mellors 1991). We found that percent cover was a moderate predictor of belowground biomass, however, low coefficients of determination, particularly for *H. wrightii*, suggest that additional factors are influencing belowground biomass (Table 1; Figure 3B). For example, biomass harvested at 40 and 80 percent cover was often greater than that at higher levels of percent cover (Figure 3B); these cores also consisted predominantly of sandy sediments (pers. obs). Onuf (1996) found that *H. wrightii* belowground biomass corresponded with sediment grain size, indicating that variation in belowground biomass allocation is

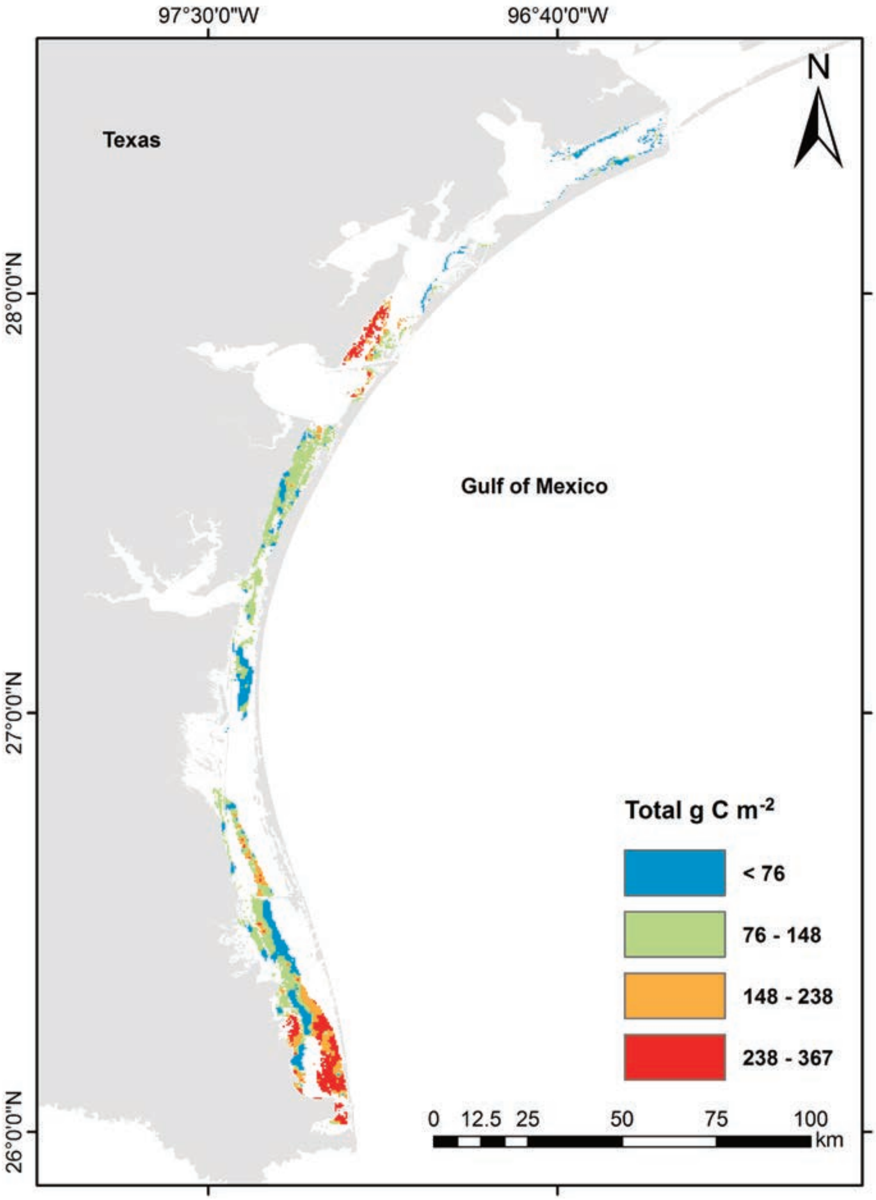

Figure 4. Distribution of total seagrass carbon inventories for the Texas coast based on percent cover observations obtained from the Texas Statewide Seagrass Monitoring Program (www. texasseagrass.org) for 634 stations in 2015. Greater carbon storage capacity is associated with Thalassia testudinum *distribution and abundance, which is greatest in south Lower Laguna Madre and west Redfish Bay.*

strongly influenced by differences in sediment composition. In our study, increased quantities of *H. wrightii* belowground tissues seemed associated with larger sediment grain sizes and reduced biomass in silts and clays. Despite these effects, percent cover can provide a quick and coarse estimate of belowground biomass, particularly for more robust species such as *T. testudinum* and *S. filiforme*.

Carbon content and storage

Biomass carbon inventories derived from the application of percent cover observations and the linear regressions produced from this study show that highest carbon stores (up to 367 g C m^{-2}) corresponded with greater percent cover and biomass (Figure 4). These values are higher than the global mean of carbon inventories in living seagrass biomass reported by Fourqurean et al. (2012), which reflect the favorable environmental conditions for seagrasses in the coastal waters of Texas. Previous studies (Dawes and Lawrence 1979; Zieman et al. 1984) have shown that younger blades possess higher nitrogen content but have lower lignin and cellulose content. Therefore, our biomass and cover relationships could underestimate carbon stores because we processed young leaf tissue for carbon content.

The distribution of carbon is driven by the most robust species, *T. testudinum*, which dominates south Lower Laguna Madre and west Redfish Bay (see www.texasseagrass.org). Additionally, the Coastal Bend and Lower Laguna Madre boast the highest carbon stores in comparison with Upper Laguna Madre and San Antonio Bay that are dominated by *H. wrightii*. Belowground tissues comprise a large proportion of the estimated carbon stores in living biomass, and root and rhizome tissues are approximately four times that of aboveground biomass for *T. testudinum* and up to three times for *H. wrightii* (Dunton 1996). Since aboveground tissue can fluctuate seasonally (Dunton 1994), it is important to identify changes in the distribution of belowground biomass because it comprises such a substantial portion of total carbon stores in living biomass. Our biomass relationships are limited to the summer and reflect peak leaf-on conditions, and thus are not applicable to other periods when seagrass biomass is naturally lower in response to seasonally lower temperatures and irradiance.

Applicability across large spatial scales

These relationships allow for the scaling-up of biomass estimates for *T. testudinum*, *H. wrightii* and *S. filiforme* over a large geographic extent by using percent cover observational data commonly used for seagrass habitat assessment by numerous monitoring programs throughout the Gulf of Mexico. Percent cover observations provide a rapid and less invasive approach to assess seagrass condition and allows for the conversion of this parameter into a relevant currency, carbon, using biomass measurements.

Locations with increased canopy complexity and greater biomass could facilitate particle trapping and enhance sediment accretion (Gacia et al. 1999). The carbon buried within the sediments of seagrass meadows are derived from a variety of sources, and composed of both autochthonous and allochthonous carbon (Kennedy et al. 2010; Marbà et al. 2015).

The capacity for seagrass meadows to efficiently remove and store vast amounts of carbon are a few of the reasons they are considered important components of global carbon budgets; however, living biomass composes a minor fraction of the total carbon storage potential, which is buried in soils up to a meter deep (Fourqurean et al. 2012).

Studies suggest that increasing seagrass abundance yields greater long-term carbon storage capacity (Duarte et al. 2010; Duarte et al. 2013a), and based on the direct relationship between belowground plant biomass and soil carbon content (Luo et al. 2004; Armitage and Fourqurean 2015), percent cover and biomass relationships could provide coarse estimates for total carbon storage across large spatial scales. However, it is important to acknowledge the limitations of this study in providing total carbon storage estimates for seagrass meadows. Specifically, even if we could accurately estimate the carbon stores in living biomass, the relative contribution of organic carbon is minor in comparison to the organic carbon that is buried deep within the sediments (Fourqurean et al. 2012). Additionally, the coefficients of determination of our regressions, specifically belowground biomass, allude to a complex relationship between environment and seagrass abundance. The synergistic relationship between seagrass species (Lavery et al. 2013; Lyons et al. 2015), changes in community composition (Howard et al. 2016), and hydrologic (Lavery et al. 2013) and nutrient regimes (Armitage and Fourqurean 2015) are important considerations to improve our estimates of carbon inventories across spatial and temporal scales.

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