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# Limits on carbon sequestration in arid blue carbon ecosystems

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**Abstract.** Coastal ecosystems produce and sequester significant amounts of carbon (“blue carbon”), which has been well documented in humid and semi-humid regions of temperate and tropical climates but less so in arid regions where mangroves, marshes, and seagrasses exist near the limit of their tolerance for extreme temperature and salinity. To better understand these unique systems, we measured whole-ecosystem carbon stocks in 58 sites across the United Arab Emirates (UAE) in natural and planted mangroves, salt marshes, seagrass beds, microbial mats, and coastal sabkha (inter- and supratidal unvegetated salt flats). Natural mangroves held significantly more carbon in above- and belowground biomass than other vegetated ecosystems. Planted mangrove carbon stocks increased with age, but there were large differences for sites of similar age. Soil carbon varied widely across sites (2–367 Mg C/ha), with ecosystem averages that ranged from 49 to 156 Mg C/ha. For the first time, microbial mats were documented to contain soil carbon pools comparable to vascular plant-dominated ecosystems, and could arguably be recognized as a unique blue carbon ecosystem. Total ecosystem carbon stocks ranged widely from 2 to 515 Mg C/ha (seagrass bed and mangrove, respectively). Seagrass beds had the lowest carbon stock per unit area, but the largest stock per total area due to their large spatial coverage. Compared to similar ecosystems globally, mangroves and marshes in the UAE have lower plant and soil carbon stocks; however, the difference in soil stocks is far larger than with plant stocks. This incongruent difference between stocks is likely due to poor carbon preservation under conditions of weakly reduced soils (200–350 mV), coarse-grained sediments, and active shoreline migration. This work represents the first attempt to produce a country-wide coastal ecosystem carbon accounting using a uniform sampling protocol, and was motivated by specific policy goals identified by the Abu Dhabi Global Environmental Data Initiative. These carbon stock data supported two objectives: to quantify carbon stocks and infer sequestration capacity in arid blue carbon ecosystems, and to explore the potential to incorporate blue carbon science into national reporting and planning documents.

**Key words:** Abu Dhabi; *Arthrocnemum macrostachyum*; *Avicennia marina*; blue carbon; carbon pools; carbon stocks; *Halodule uninervis*; *Halophila ovalis*; *Halophila stipulacea*; United Arab Emirates.

## INTRODUCTION

Vegetated coastal ecosystems produce and sequester significant amounts of organic carbon (Chmura et al. 2003, Duarte et al. 2005, Donato et al. 2011, McLeod et al. 2011, Fourqurean et al. 2012a), generating worldwide interest in the management, conservation, and restoration of mangroves, marshes, and seagrasses for the purpose of climate change mitigation (McLeod et al. 2011, Pendleton et al. 2012). The recent increase in attention to these “blue carbon” ecosystems has exposed considerable gaps in our understanding of carbon pools and sequestration rates in coastal environments, creating

challenges for the application of coastal ecosystem carbon research at local and regional scales. A major limitation is that field research has focused primarily on study sites located in humid regions at temperate and tropical latitudes (Chmura et al. 2003, Donato et al. 2011, Adame et al. 2013, Fourqurean et al. 2012a, Kauffman et al. 2014, Alongi et al. 2015), with relatively few studies in sub-humid or arid regions (Adame et al. 2013, Ezcurra et al. 2016) where differences in rainfall, evapotranspiration, and soil conditions could affect carbon storage. The limited range of climates examined makes it difficult to assess the potential for carbon-based ecosystem management across sites that vary tremendously across gradients of coastal climate, hydrology, geomorphology, and tide range (Sifleet et al. 2011), and limits our ability to generalize knowledge outside of warm humid regions. Perhaps the least-studied intertidal marine ecosystems

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occur in arid regions. Coastlines in the Arabian Gulf contain a mosaic of productive ecosystems, including coastal sabkha (broad, flat inter- and supratidal salt flats lacking vascular plants), mudflats, cyanobacterial mats (hereafter microbial mats), mangroves, seagrasses and coral reefs, among others, that provide food and habitat for diverse ecological communities and support over half a billion dollars in fisheries activities annually (Burt 2014). There is presently a dearth of research in arid tidal wetland and seagrass (herein blue carbon) ecosystems even though large investments have been made in creation, restoration and protection activities by nations of the Arabian Peninsula (Aoki and Kugaprasatham 2009).

Although plants in arid systems are adapted to survive under these conditions, they exist near the limit of their tolerance for extremes in temperature, rainfall, and salinity. Despite these potential limits (Noy-Meir 1973), low primary production does not necessarily prevent long-term accumulation of large soil carbon pools in blue carbon ecosystems, provided that soil carbon is preserved by development of anaerobic soil conditions. For example, mangrove forests that differ widely in plant biomass (e.g., 6.8–194.3 Mg/ha; Lovelock et al. 2005) nonetheless can form deep (7 m), organic (80% organic matter) soil profiles. Furthermore, low primary production in northern peatlands outweighs very slow decomposition rates over millennia, resulting in extremely carbon rich soils despite that fact that plant production ranks near the bottom of terrestrial ecosystems (Frolking et al. 2001). On the other hand, labile carbon inputs are required to develop highly reducing anaerobic soil conditions, so there is a conceptual minimum rate of primary production required to accumulate significant soil carbon pools and plants in some arid regions might possibly fall below that rate (Meron et al. 2004).

Our objective was to conduct the first comprehensive analysis of carbon stocks in coastal ecosystems of an arid region. We quantified carbon stocks in salt marshes, seagrass beds, and natural and planted mangroves along 600 km of coastline of the United Arab Emirates (UAE). The UAE seagrass portion of our project was previously analyzed in detail by Campbell et al. (2015), so we only include seagrass data in cross-ecosystem comparisons. We compared the stocks in these blue carbon ecosystems with other sites throughout the world. Further, we quantified carbon stocks in two coastal ecosystems, microbial mats and coastal, that are rarely studied in a carbon context. Based on our understanding of tidal inundation on carbon stocks in temperate and tropical wetland ecosystems, we hypothesized that carbon stocks in the intertidal ecosystems would decrease with decreasing flooding frequency, and be greater than carbon stocks of subtidal seagrass beds. Furthermore, we hypothesized that plant carbon pools in this arid environment would be lower than comparable ecosystems in humid tropical and subtropical systems due to lower primary production. We did not have a specific hypothesis for soil carbon pools because large pools occur in systems with both high and

low net primary production, and in regions of high and low temperature.

### Study sites

We studied coastal and near-shore ecosystems within the UAE (Fig. 1). Along the Arabian Gulf, air temperatures seasonally range from 12° to >50°C, and water temperatures at the coastal margins range seasonally from 10° to 36°C (EAD 2007, Piontkovski et al. 2012). Average annual rainfall is <100 mm and is much less than evaporation rates of 1000–2000 mm (Evans et al. 1973). Salinity in the Arabian Gulf is high due to restricted tidal exchange and high rates of evaporation, reaching values >70 PSU in lagoons and other shallow waters during summer (EAD 2007). Localized areas of lower salinity are created by urban water outflows, through drainage networks (i.e., wadis) from mountain areas to the north and east, and increased water circulation following channel construction and dredging (Embabi 1993). Along the Gulf of Oman, average air temperature is 28°C and rainfall amounts range from 12 to 331 mm, averaging 138 mm in Khalba (Böer 1997). Tides are complex, driven by interfering standing waves across the Arabian Gulf, resulting in a mix of diurnal and semi-diurnal tides, with a spring range of approximately 2.5 m (see Appendix S1 for further details).

Mangroves within the UAE currently consist solely of *Avicennia marina* and are particularly well developed on the inland side of barrier islands and within lagoons (Kenig et al. 1990, Embabi 1993). Large areas of mangroves and other coastal ecosystems have been lost to recent and current coastal development (Embabi 1993), but mangrove planting has occurred since the 1960s, including revegetation along channels and degraded sites formerly occupied by mangroves (Saenger et al. 2004, Sheppard et al. 2010).

Salt marshes of the UAE are dominated by the low succulent shrub *Arthrocnemum macrostachyum*, are limited in areal extent, and occur higher in elevation than mangroves or microbial mats but lower in elevation than sabkha (Zahran and Al-Ansari 1999, Gul and Khan 2001, Khan et al. 2005). *Arthrocnemum macrostachyum* is found in tidal wetlands of arid and semiarid climates in northeastern Africa, southeastern Asia, and the Mediterranean (Ghazanfar 1999, Serag 1999, Khan et al. 2005, Redondo-Gómez et al. 2010).

Microbial mats form along tidal margins where very high soil salinity levels (60–200 on the Practical Salinity scale) exclude vascular plants. Large expanses of mat are formed by stratified layers of cyanobacteria, colorless sulfur bacteria, purple sulfur bacteria, and sulfate-reducing bacteria (Kenig et al. 1990, Abed et al. 2007, Scherf and Rullkötter 2009). Globally, similar ecosystems are located near salt lakes and intertidal areas in Australia, the United States, and the Caribbean (Kendall and Skipwith 1968). These mats have different surface morphologies depending on species, location, salinity, and hydrology (Kendall and



FIG. 1. Site map of all intertidal sampling locations.

Skipwith 1968, Abed et al. 2007), forming moist “leather” mats 5–20 cm thick in sheltered, frequently flooded areas, or “blistered” mats 1–3 mm thick in areas of high evaporation or regular disturbance (Kendall and Skipwith 1968). Our study appears to be the first to quantify carbon stocks in microbial mat ecosystems.

Coastal sabkha ecosystems are found worldwide, but the largest expanses are in the UAE (Evans and Kirkham 2002). They are hypersaline, inter- or supratidal ecosystems largely devoid of vegetation (Kendall et al. 2002). Soils are unconsolidated carbonate sediments that are high in gypsum and anhydrite precipitates (Evans and Kirkham 2002). Coastal sabkha is typically flooded several times per year during spring tides and when strong northerly winds drive seawater inland (Embabi 1993).

A total of 58 sites were sampled across coastal UAE, with replication at each site: 18 natural mangroves, seven mangrove plantations, five salt marshes, five microbial mats, five coastal sabkha, and 18 seagrass beds (Appendix S2: Table S1; Campbell et al. 2015). Intertidal sites were selected to represent a range of environmental settings (sheltered vs. wave exposed), co-locating ecosystems when possible. Mangrove plantations were sampled to examine changes in carbon stock with age at Jubail (3-, 7-, and 10-yr old sites) and Abu al Abyad (3-, 5-, 10-, and

15-yr old sites) Islands. Samples were collected in January 2013 and November 2014.

## METHODS

### *Carbon stock measurements*

*Plant carbon pools.*—Plant carbon for mature mangrove trees were measured following methodology from Kauffman and Donato (2012). Due to their smaller structure, all trees with stems >3 cm diameter at breast height (dbh; 1.3 m in height) within the 7-m plot were measured instead of restricting measurement to trees with dbh > 10 cm (Appendix S2: Fig. S1a). Standing dead trees and downed woody debris were found at some Gulf of Oman sites and pools were quantified appropriately (Kauffman and Donato 2012). In the planted mangrove sites, five 2-m radius plots were established at 10-m intervals along a 40-m transect (Appendix S2: Fig. S1b). When stands contained individuals <1.3 m tall, we measured the crown diameter and main stem diameter at 30–50 cm in height. In the 3-, 5-, and 10-yr old planted mangrove sites in Abu al Abyad, trees were planted in an evenly spaced grid; therefore, the plant density was calculated by measuring the average plant spacing and main stem and crown diameter of 50–75 trees.

TABLE 1. Allometric equations used to calculate above- and belowground biomass for *Avicennia marina* and *Arthrocnemum macrostachyum*.

Species	Ecosystem	Equation	$R^2$	Source	Location developed
Aboveground					
<i>A. marina</i>	mature mangroves	$B = 0.17758 \times D^{2.2990}$		Clough et al. (1997)	Australia
<i>A. germinans</i> ( $<4$ cm dbh)	planted mangroves	$B = 200.4 \times D^{2.1} \times 0.001$		Fromard et al. (1998)	French Guinea
<i>A. macrostachyum</i>	salt marshes, $V < 0.16 \text{ m}^3$	$\ln B = 0.38 (\ln V) + 0.64$	0.62	This study	United Arab Emirates
	salt marshes, $V > 0.16 \text{ m}^3$	$\ln B = 0.56 (\ln V) - 0.40$	0.61	This study	United Arab Emirates
Belowground					
<i>A. marina</i>	mature mangroves	$B = 1.28 \times D^{1.17}$	0.98	Comley and McGuinness (2005)	Australia
<i>A. marina</i>	planted mangroves	$B = 0.923 \times \text{AGB}$		Comley and McGuinness (2005)	Australia
<i>A. macrostachyum</i>	salt marshes	$B = 0.9 \times \text{AGB}$		Neves et al. (2010)	Portugal

Note:  $B$ , biomass (kg);  $D$ , diameter at breast height (cm);  $V$ , canopy volume ( $\text{cm}^3$ ); AGB, aboveground biomass.

Salt marsh transect length and plot spacing were the same as with the mature mangroves, although the plot radius ranged from 1–4 m depending on plant density. The height and elliptical crown area (perpendicular crown widths centered on the canopy) were measured on every plant rooted in each plot.

Biomass for *A. marina* and *A. macrostachyum* were calculated using allometric equations (Table 1). Global tree carbon percentages of 48% and 39% for above- and belowground biomass, respectively, were applied (Kauffman and Donato 2012). To examine differences in average annual carbon sequestered in planted mangrove trees, we divided total biomass for each stand by the number of years since plantation establishment. We developed allometric equations for *A. macrostachyum* aboveground biomass, as none previously had been published. Twenty-four plants were collected from three sites and measured for crown dimensions and succulent and woody tissue fresh mass. A subsample of each tissue type from every plant was weighed fresh and dry (constant mass at  $50^\circ\text{C}$ ) to calculate a wet-to-dry mass conversion factor for the entire plant. Simple linear regression of natural log-transformed oven-dry biomass and plant volume (height  $\times$  elliptical crown area) were calculated, producing two different relationships depending on plant size (Table 1). Tissue samples were analyzed for percent carbon and nitrogen; carbon content of woody ( $n = 12$ ) and succulent ( $n = 10$ ) tissue averaged 45.5% and 34.0%, respectively (SE  $\pm 0.7\%$  for both). We used the proportion of 52% woody tissue reported in Neves et al. (2010) to calculate carbon content for aboveground biomass as  $40.3\% \pm 1.4\%$  C. The reported root to shoot ratio of *A. macrostachyum* measured in Portugal (Neves et al. 2010) is likely a conservative estimate of root biomass, as soil cores were taken to a depth of 15 cm instead of 20–30 cm as in other studies (reviewed in Curco et al. 2002).

*Soil carbon pools.*—At mangrove and salt marsh plots, undisturbed soil samples were collected following

methodology from Kauffman and Donato (2012) using a 1 m long gouge auger with an open-face, semi-cylindrical chamber of 5.1 cm radius. Soils were cored to 3 m or until coarse marine sands or coral rubble representing the parent material was encountered. The soil core was divided into depth intervals of 0–15, 15–30, 30–50, 50–100, and  $>100$  cm, or until refusal. Subsamples collected from the center of each interval were analyzed for bulk density (dry mass per unit volume) and carbon concentration (organic and inorganic). If encountered, unique soil layers were sampled separately. The same soil sampling methodology was used within microbial mats and coastal sabkha; the number of plots sampled per transect varied from three to six plots spaced at 20-m intervals along a transect. We determined soil carbon stocks following methods outlined in Fourqurean et al. (2012a), which are designed to account for soils containing carbonates.

#### Pore water chemistry and soil respiration

A variety of soil biogeochemical measurements, soil respiration, elevation, and tidal data were collected in selected mangroves, salt marsh, microbial mats, and sabkha sampled in 2013; mangroves sampled in 2014 were not sampled. Redox potential ( $E_h$ ) was estimated from five replicate platinum-tipped electrodes inserted 10 cm into the soil for a period of 1–20 minutes and corrected for the potential of the calomel reference electrode by adding 244 mV (Magonigal and Rabenhorst 2013). At sites that had a shallow water table, soil pore water was collected from corer boreholes at 5–10 cm below the surface and analyzed by the standard methods described in Keller et al. (2009). Salinity was determined either by refractometer (values  $<160$ ) or calculated from  $[\text{Cl}^-]$  (values  $>160$ ); pH was measured in the field with a portable electrode. Pore water dissolved methane ( $\text{CH}_4$ ) was measured by headspace equilibration following Keller et al. (2009) and stored in evacuated Exetainer vials (Labco, High Wycombe United Kingdom) until analysis by Varian



450-GC gas chromatography (Varian Inc., Palo Alto, CA, USA). Pore water  $[\text{SO}_4^{2-}]$  and  $[\text{Cl}^-]$  were determined by Dionex ICS-2000 (Dionex Corporation, Sunnyvale, CA, USA) ion chromatography on filter-sterilized (0.22  $\mu\text{m}$ ), HCl-acidified samples, and the sulfate depletion ratio was calculated per Keller et al. (2009). Gas and filtered pore water samples were stored for four weeks before analysis, which is well within the capacity of the storage methods used. We quantified instantaneous  $\text{CO}_2$  gas exchange rates as a simple index of activity to assist with comparisons across the ecosystems in this study. Soil surface  $\text{CO}_2$  emissions were measured with a LICOR 6400 soil respiration analyzer (LI-COR Biosciences, Lincoln, NE, USA), with a range of 2–18 measurements per site, depending on time spent at each site and the rate of soil respiration; more measurements were possible at higher respiration rates.

### Statistical analysis

Analyses were run using SAS version 9.2 (SAS 2009). The data met the assumptions of normality and homogeneity of variance; soil depth and total organic carbon data were log- and square-root-transformed, respectively. Least square means (LSM) were used to assess differences across ecosystems. We considered comparisons of plant properties to be significant at  $P \leq 0.05$  and soil properties at  $P \leq 0.10$ . The different thresholds for statistical significance recognize that soil properties are inherently more variable than plant properties, and therefore soils carry a higher risk of type II error for a given sample size. Thus, the higher  $P$  value for soils is a compromise between type I and type II errors. Analysis of variance (ANOVA) was used to examine differences in total soil depth, bulk density with depth, and total carbon stock across ecosystems. Differences in average total mangrove biomass per site with longitude and salinity were tested for using a

simple linear regression. To further address potential variation with longitude and inherent site differences, mangrove sites also were grouped according to clearly defined regions: west ( $n = 3$ ), central ( $n = 5$ ), and north ( $n = 6$ ) UAE and the Gulf of Oman ( $n = 4$ ). Three ANOVAs were run to test for differences in total mangrove biomass, soil carbon, and total ecosystem carbon stocks by region.

To compare UAE plant and soil carbon stocks to blue carbon values globally, a database was created from published literature for mangrove, salt marsh, and seagrass stocks. Basic summary statistics (quantiles) were calculated for the comparisons. The global mangrove database was established with information on the region, country, site, and tree stature due to the consistent availability of detailed data. To account for variability within UAE mangrove plant and soil stocks, sites were grouped by region: west and central UAE regions and north UAE and Gulf of Oman regions. Due either to limited data or to the format in which the data were presented, salt marsh and seagrass data were grouped by country or region.

## RESULTS

### Plant biomass and carbon stocks

Biomass of natural mangroves varied widely across sites (Table 2; Appendix S2: Table S2). We found a significant but weak inverse relationship of mangrove biomass to salinity ( $F_{1,14} = 7.54$ ,  $P = 0.02$ ,  $R^2 = 0.30$ ). Spatially, this created a pattern of increasing mangrove biomass with longitude from west to east ( $F_{1,15} = 18.2$ ,  $P = 0.0007$ ,  $R^2 = 0.52$ ). Forests to the north and along the Gulf of Oman had greater biomass than those in the central and western regions (Fig. 2A;  $F_{3,14} = 15.47$ ,  $P = 0.0001$ ). Tree density varied widely across sites, with as few as 1887 trees/ha on Bu Tinah Island to as many as

TABLE 2. Biomass summary of mature *Avicennia marina* mangrove ecosystems per hectare; standard errors are in parentheses.

Site	Region	Salinity	Aboveground biomass (Mg/ha)	Belowground biomass (Mg/ha)	Total biomass (Mg/ha)
Bu Tinah Shamal	West UAE	55	38.3 (16.3)	28.4 (11.2)	66.7 (26.6)
Bu Tinah Janoub	West UAE	51 (2)	71.1 (41.4)	31.0 (17.1)	102.1 (57.2)
Marawah Is.	West UAE	65 (1)	23.1 (11.8)	26.3 (10.8)	49.5 (22.6)
Salaam	Central UAE	42 (1)	25.9 (11.7)	30.8 (11.9)	56.7 (22.8)
Eastern Mangrove	Central UAE	53 (1)	13.3 (5.9)	28.9 (23.6)	42.2 (29.4)
Jubail Island	Central UAE	57 (2)	15.1 (4.9)	53.9 (20.4)	68.9 (24.9)
Jubail Island East	Central UAE	49 (1)	7.3 (4.3)	9.9 (7.0)	17.1 (11.3)
Al Shalila	Central UAE	43 (1)	9.2 (2.4)	16.0 (4.3)	25.1 (6.2)
Al Khor	North UAE	67 (2)	140.0 (11.2)	90.3 (8.9)	230.6 (15.5)
Al Zorah	North UAE	44 (2)	92.1 (13.1)	128.7 (16.7)	220.9 (19.9)
Umm Al Quwain	North UAE	48 (1)	30.8 (5.4)	46.5 (8.1)	77.3 (13.1)
Sinnia	North UAE	46 (1)	72.6 (8.5)	131.1 (18.7)	203.7 (25.3)
Ras Al Kaimah	North UAE	45 (3)	134.4 (6.6)	125.8 (16.7)	260.2 (17.6)
Kor Al Rams	North UAE	40 (1)	56.8 (3.6)	77.1 (5.3)	133.9 (8.3)
Khalba North	Gulf of Oman	35 (1)	97.9 (20.2)	92.9 (17.9)	353.0 (37.8)
Khalba South	Gulf of Oman	41 (1)	243.6 (26.9)	78.4 (6.4)	190.7 (30.8)
Khalba East	Gulf of Oman	No data	144.8 (18.1)	86.1 (12.2)	230.8 (19.7)
Khalba West	Gulf of Oman	36 (0)	180.5 (34.8)	55.5 (6.8)	236.0 (40.6)
Average			77.6 (16.0)	63.2 (9.3)	140.8 (22.5)

Note: UAE, United Arab Emirates.

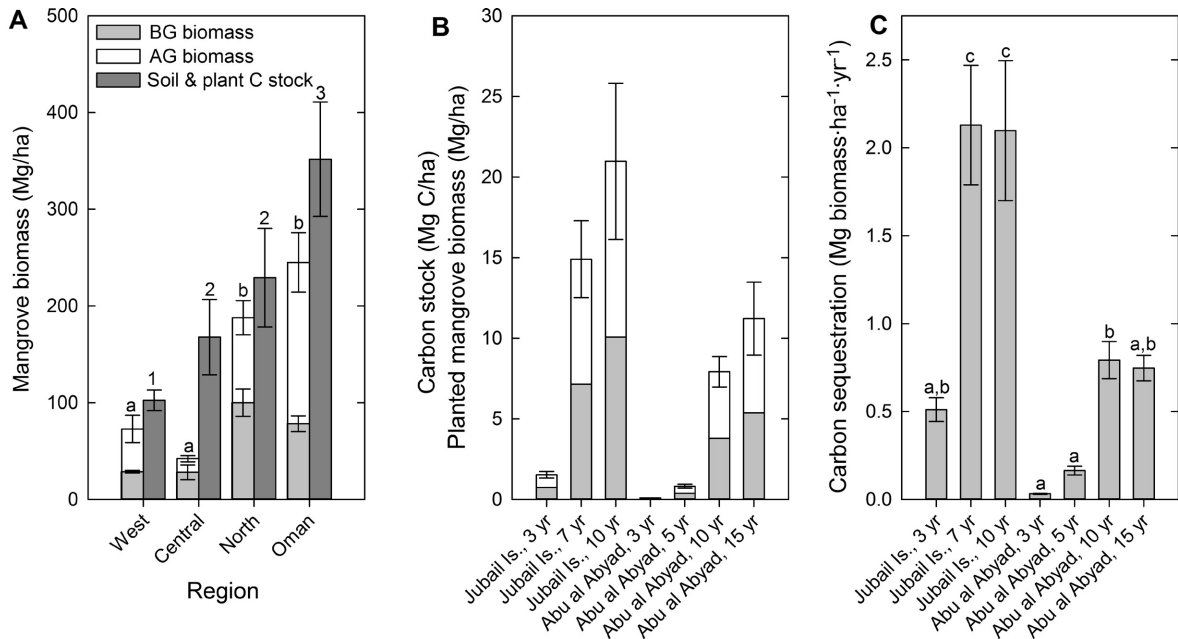


FIG. 2. (A) Above- and belowground (AG and BG, respectively) biomass and total ecosystem carbon stocks of mature mangroves by region (mean  $\pm$  SE). Different letters and numbers denote significant differences at  $P < 0.006$  and  $P < 0.05$  for total biomass and total C stock, respectively. (B) Planted mangrove stand biomass increases with age and at a faster rate at Jubail than at Abu al Abyad Islands (Abu al Abyad  $F_{1,2} = 65.1$ ,  $P = 0.02$ ,  $R^2 = 0.97$ ; Jubail Island  $F_{1,1} = 57.4$ ,  $P = 0.08$ ,  $R^2 = 0.98$ ). (C) Yearly biomass sequestration at Jubail and Abu al Abyad Islands (different letters denote significant differences at  $P < 0.02$ ).

41039 trees/ha at Sinnia in northern UAE (Appendix S2: Table S2).

Biomass of planted mangroves increased linearly with stand age within the two regions, yet at a faster rate on Jubail Island (Fig. 2B). Stands on Jubail Island had greater biomass than those on Abu Al Abyad across all ages; the 3-yr-old plantation biomass was 16 times as large and 10-yr-old plantation biomass was twice as large. Yearly sequestration in total plant biomass was four times greater in the oldest than in the youngest stands, but did not differ between the 7- and 10-yr stands at Jubail Island or the 10- and 15-yr stands at Abu al Abyad (Fig. 2C). The 15-yr-old plantation at Abu al Abyad had a surprising number of volunteer seedlings ( $42017 \pm 12223$  seedlings/ha), similar to the highest density measured in mature mangroves (Appendix S2: Table S2).

Salt marsh above- and belowground biomass varied little across sites, ranging from 2 to 4 Mg/ha (Table 3;  $F_{4,22} = 7.75$ ,  $P = 0.0005$ ); however, the site closest to the city of Abu Dhabi (Eastern Mangrove), amassed more than double the biomass of any other marsh site (Table 3;  $P < 0.005$ ). There was no vascular plant biomass measured at any of the sabkha or microbial mat sites.

As expected, the greatest average plant carbon pool, 62.1 Mg C/ha, occurred in a mature mangrove ecosystem ( $F_{3,34} = 19.0$ ,  $P < 0.0001$ ; Table 4, Fig. 3), yet mangrove carbon pools varied greatly across sites, ranging from 7 Mg C/ha in low density and stature mangroves to 147.5 Mg C/ha in the taller, denser mangroves of the Gulf of

Oman (Table 4). No significant differences in plant carbon pools were found across the other ecosystems ( $P > 0.99$ ).

Plant carbon stocks from UAE ecosystems were modest to low compared to the global blue carbon data set (Figs. 4 and 5). Total mangrove tree carbon stocks from sites along the western and central regions were within the 25% quantile (32.9 Mg C/ha) of those in our global data set (Appendix S2: Table S3; Fig. 4). Total tree carbon stocks from sites in the northern emirates and the Gulf of Oman were mostly within the 50% quantile (108.3 Mg C/ha), with two, Khor Khalba South and Ras Al Kaimah, falling within the 75% quantile (188.8 Mg C/ha). Aboveground carbon stocks for saltmarshes and total plant carbon stocks for seagrasses ranked at the 1% quantile across all studies examined (Fig. 5).

TABLE 3. *Arthrocnemum macrostachyum* biomass.

Site	Biomass (Mg/ha)		
	Aboveground	Belowground	Total
Al Aryam	4.2 (1.0)	3.7 (0.9)	7.9 (1.9)
Eastern Mangrove	9.5 (1.2)	8.5 (1.1)	18.0 (2.2)
Jubail Island East	3.2 (0.5)	2.9 (0.4)	6.1 (0.9)
Jubail Island	2.5 (1.4)	2.2 (1.3)	4.7 (2.7)
Marawah Island	4.2 (0.8)	3.8 (0.7)	8.0 (1.4)

Note: Numbers are means with SE in parentheses.



TABLE 4. Summary of soil depth and organic carbon stocks in blue carbon ecosystems of the United Arab Emirates.

Variable	Seagrass	Microbial mat	Mature mangrove	Planted mangrove	Salt marsh	Coastal sabkha
<b>Soil depth (cm)</b>						
Range	8.5–100	13–200	8–300	12–100	10–200	27–65
Mean	57.7	73.2	103.2	60.1	78.4	42.8
Median	60.2	43	70	62	54.5	40
<b>Soil (Mg C/ha)</b>						
Range	1.9–109.0†	18.6–242.4	36.7–367.0	50.9–175.8	29.5–163.7	51.0–120.5
Mean	49.1 <sup>a,†</sup>	133.5 <sup>b</sup>	156.3 <sup>b</sup>	102.3	80.4 <sup>a,b</sup>	82.4 <sup>a,b</sup>
Median	51.2†	153.6	124.8	87.8	71.1	90.4
<b>Aboveground biomass (Mg C/ha)</b>						
Range	no data	N/A	3.5–116.9	0.02–5.2	1.0–3.8	N/A
Mean	no data	N/A	37.3 <sup>a</sup>	2.0 <sup>b</sup>	1.9 <sup>b</sup>	N/A
Median	no data	N/A	30.7	1.9	1.7	N/A
<b>Belowground biomass (Mg C/ha)</b>						
Range	no data	N/A	3.8–51.1	0.02–3.9	0.9–3.4	N/A
Mean	no data	N/A	24.6 <sup>a</sup>	1.5 <sup>b</sup>	1.7 <sup>b</sup>	N/A
Median	no data	N/A	21.3	1.5	1.5	N/A
<b>Total biomass (Mg C/ha)</b>						
Range	0.3–1.1	N/A	7.3–147.5	0.04–9.2	1.9–7.2	N/A
Mean	0.4 <sup>a</sup>	N/A	62.1 <sup>b</sup>	3.6 <sup>c</sup>	3.6 <sup>c</sup>	N/A
Median	0.4	N/A	51.8	3.5	3.2	N/A
<b>Total carbon stock (Mg C/ha)</b>						
Range	2.2–109.3	18.6–242.4	77.4–514.5	51.3–182.3	31.4–205.0	51.0–120.5
Mean	49.6 <sup>a</sup>	133.5 <sup>a,b</sup>	218.4 <sup>b</sup>	105.7 <sup>a</sup>	97.1 <sup>a</sup>	82.4 <sup>a</sup>
Median	51.6	153.6	189.4	88.2	73.6	90.4

Notes: Different superscript letters denote differences at  $P \leq 0.10$  within a given carbon stock. N/A, not applicable.  
 †Data restricted to top 100 cm of soil.

*Soil carbon stocks*

Bulk density increased strongly with depth (from  $<1.0$  to  $>1.2$  g/cm<sup>3</sup>) in mangrove and microbial mat sites (Fig. 6). By comparison, bulk density was  $>1.2$  g/cm<sup>3</sup> and relatively constant at all depths in planted mangroves, salt marshes, seagrass beds, and coastal sabkha (Fig. 6). Microbial mat and

mangrove bulk density within the top 15 cm was significantly lower than all other ecosystems, but no differences in bulk density between ecosystem types were found at any other depth (Appendix S3: Table S1; Fig. 6). Across all samples, there was a negative exponential relationship between bulk density and soil organic carbon content (Appendix S2: Fig. S2;  $F_{8,1189} = 145.5, P < 0.0001; R^2 = 0.49$ ).

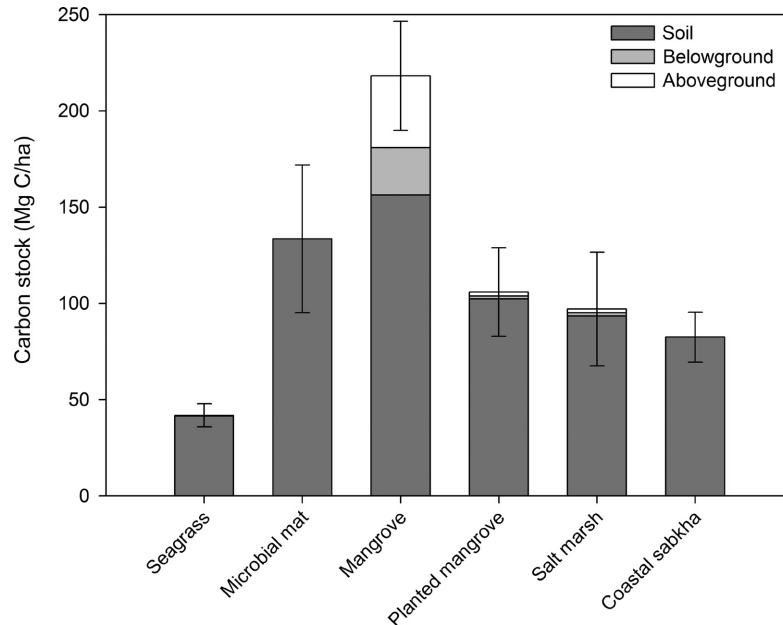


FIG. 3. Total carbon stock of each blue carbon ecosystem (mean ± SE).

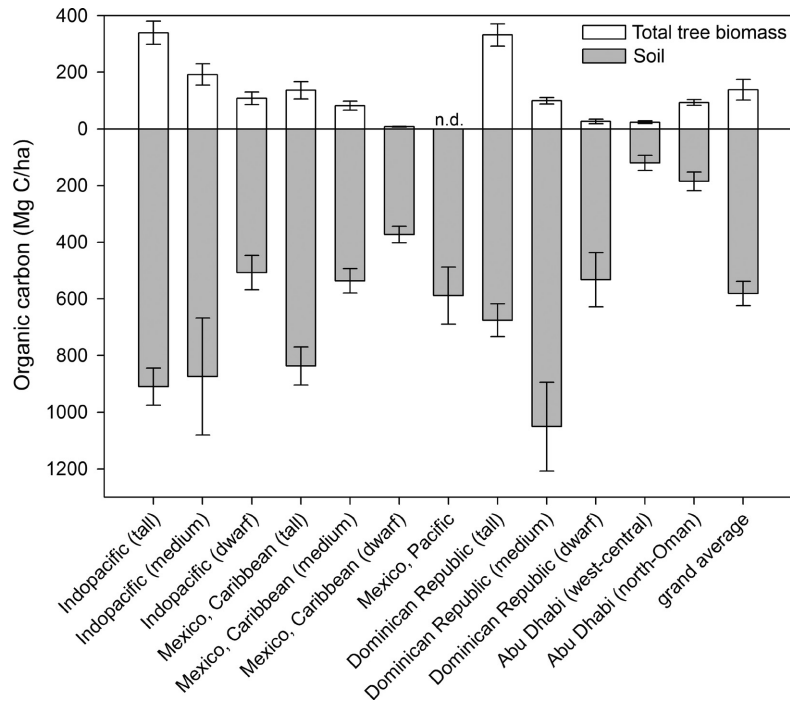


FIG. 4. Global carbon stock comparison for mangroves (source data: Indopacific [Donato et al. 2011, Murdiyarto et al. 2015], Mexico, Caribbean [Adame et al. 2013], Mexico, Pacific [Ezcurra et al. 2016], Dominican Republic [Kauffman et al. 2014]; Appendix S2: Table S3) Values are mean  $\pm$  SE, n.d. = no data.

Soil organic carbon followed a depth trend similar but inverse to bulk density, with microbial mat and mangrove soils containing more organic carbon, 3.6% and 2.2% carbon, respectively, in the top 15 cm than other ecosystems (Appendix S3: Table S1; Fig. 6). Below 15 cm, all soils contained approximately 1% organic carbon except for seagrass soils, which were consistently around 0.6% (Appendix S3: Table S1; Fig. 6). Mature mangroves were the only sites where soil organic carbon was >10%, yet this occurred rarely (Appendix S2: Fig. S2). A 5 cm wide buried organic horizon was encountered within the Al Aryam salt marsh that contained 9% organic carbon.

Soil organic carbon pools tended to be highest in mature mangroves (156.3 Mg C/ha) followed by microbial mat ecosystems (133.5 Mg C/ha), and both were greater than in seagrass beds (49.1 Mg C/ha; Appendix S3: Table S1; Fig. 3). No other significant differences were detected across other ecosystems, which cannot be explained by the fact that the number of replicate plots within each transect varied across ecosystems since they all had similar coefficients of variation (Appendix S3: Fig. S1). Across regions, no significant differences were detected within mature mangrove soil carbon stocks ( $F_{3,14} = 2.32$ ,  $P = 0.12$ ), despite the differences detected with total tree biomass.

Although UAE plant biomass was moderate to low compared to other climatic regions, soil carbon stocks fell predominantly within the 25% quantile (245.3 Mg C/ha) of other sites globally (Appendix S2: Table S3;

Fig. 4). Two sites, Ras Al Kaimah and Khor Khalba South, however, fell within the lower end of the 50% quantile (560.7 Mg C/ha). Soil bulk density below the peat layers averaged 1.0 g/m<sup>3</sup>, which is significantly larger than averages reported for semi-humid stands in Mexico ( $0.50 \pm 0.06$  g/m<sup>3</sup>; Adame et al. 2013) and the Dominican Republic ( $0.39 \pm 0.04$  g/m<sup>3</sup>; Kauffman et al. 2014). The deepest mangrove peat layers (if present) were approximately 15 cm thick, pools that are very small compared to mangroves in humid, tropical climates (Donato et al. 2011). Both salt marsh and seagrass soil carbon stocks were at the 1% quantile (Fig. 5).

#### Total carbon stocks

Total ecosystem (plant + soil) carbon stocks varied across ecosystems ( $F_{5,51} = 8.51$ ,  $P < 0.0001$ ; Table 4, Fig. 3) with natural mangroves possessing the largest carbon stock followed by microbial mats, which had 61% of the mangrove mean stock (Table 4, Fig. 3). About 5% of salt marsh carbon was in plant biomass, compared to almost 30% in mangroves. Planted mangroves, salt marshes, and coastal sabkha were comparable in their stocks (Table 4, Fig. 3). Seagrasses had the lowest total carbon stocks, but stocks did not differ with other ecosystems except for mature mangroves (Table 4, Fig. 3). Across regions, mangroves in the Gulf of Oman had the highest average total carbon stocks (Fig. 2;  $F_{3,14} = 3.91$ ,  $P = 0.03$ ).

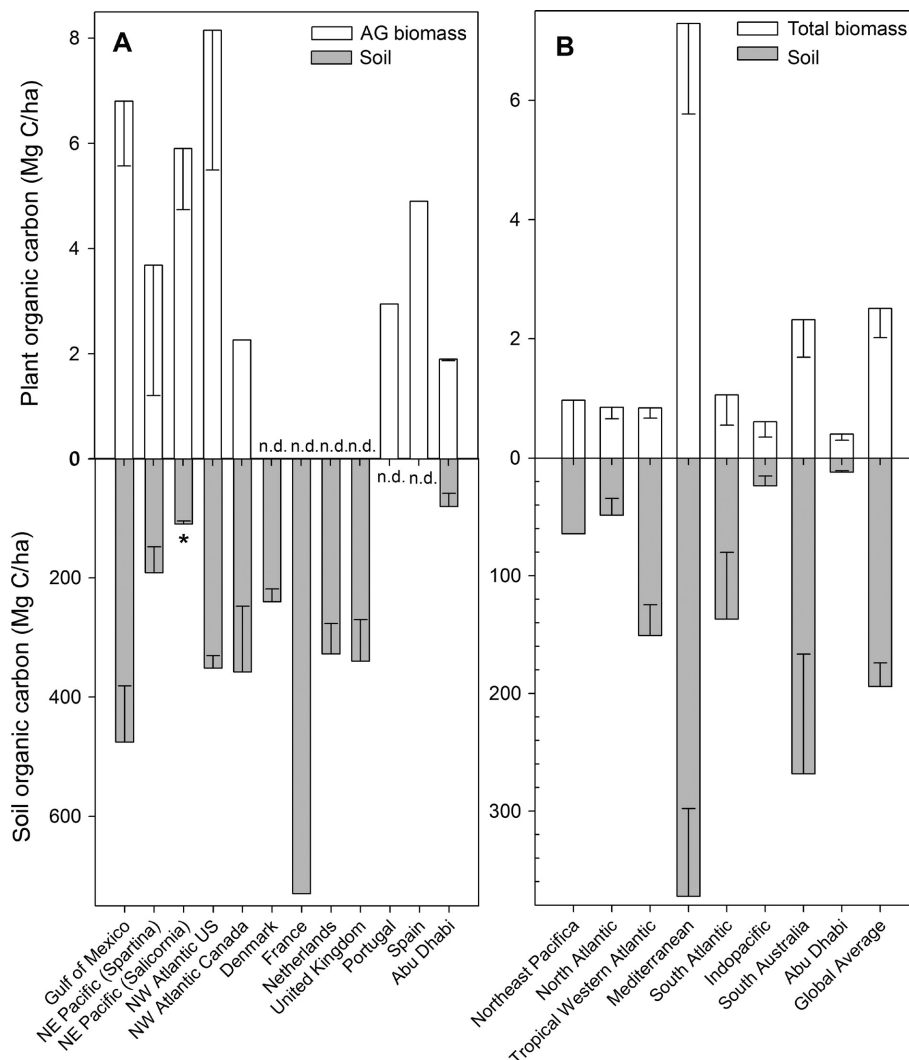


FIG. 5. Global carbon stock comparisons for (A) salt marshes and (B) seagrasses (\* soil carbon data collected to 50 cm depth, not to refusal). All data for salt marsh comparisons are from Sifleet et al. (2011) except for the northeast Pacific (*Salicornia*) data, which are from Callaway et al. (2012). All global data for seagrass carbon stocks are from Fourqurean et al. (2012a) and Campbell et al. (2015). Values are mean  $\pm$  SE, n.d. = no data. Abbreviations are NE, northeast; NW, northwest.

*Pore water chemistry and soil respiration*

Ecosystems supporting vascular plants had pore water salinities of  $\sim 50$ , comparable to local seawater salinity, while unvegetated ecosystems (coastal sabkha and microbial mats) were hypersaline at mean salinities of  $\sim 150$ – $250$  PSU (Fig. 7). A variety of biogeochemical data suggest that intertidal soils in mangroves, salt marshes, and microbial mats were hypoxic and weakly reducing, not anaerobic. Mean  $E_h$  at 10 cm depth was  $>200$  mV at all sites other than the planted mangroves where  $E_h$  was 84 mV (Fig. 7). Pore water  $[CH_4]$  was elevated slightly above ambient atmospheric levels of  $\sim 2$  ppm on most sites (Fig. 7). The sulfate depletion ratio in mangroves, salt marshes, and planted mangroves were comparable to a temperate salt marsh (Keller et al. 2009; Fig. 7). Sabkha and microbial mats had values that were nearly 10 times

that of the other systems, likely reflecting the higher seawater sulfate pool in these hypersaline environments (Fig. 7). Compared to the other intertidal sites, planted mangrove had the lowest  $E_h$ , highest  $[CH_4]$ , and lowest soil  $CO_2$  efflux rates.

DISCUSSION

*Carbon pools in United Arab Emirate blue carbon ecosystems*

Blue carbon ecosystems of a large arid region in which the dominant autotrophic inputs ranged from trees to mat-forming microbial assemblages exhibited a wide range in carbon stocks that are generally consistent with patterns expected from our understanding of humid and

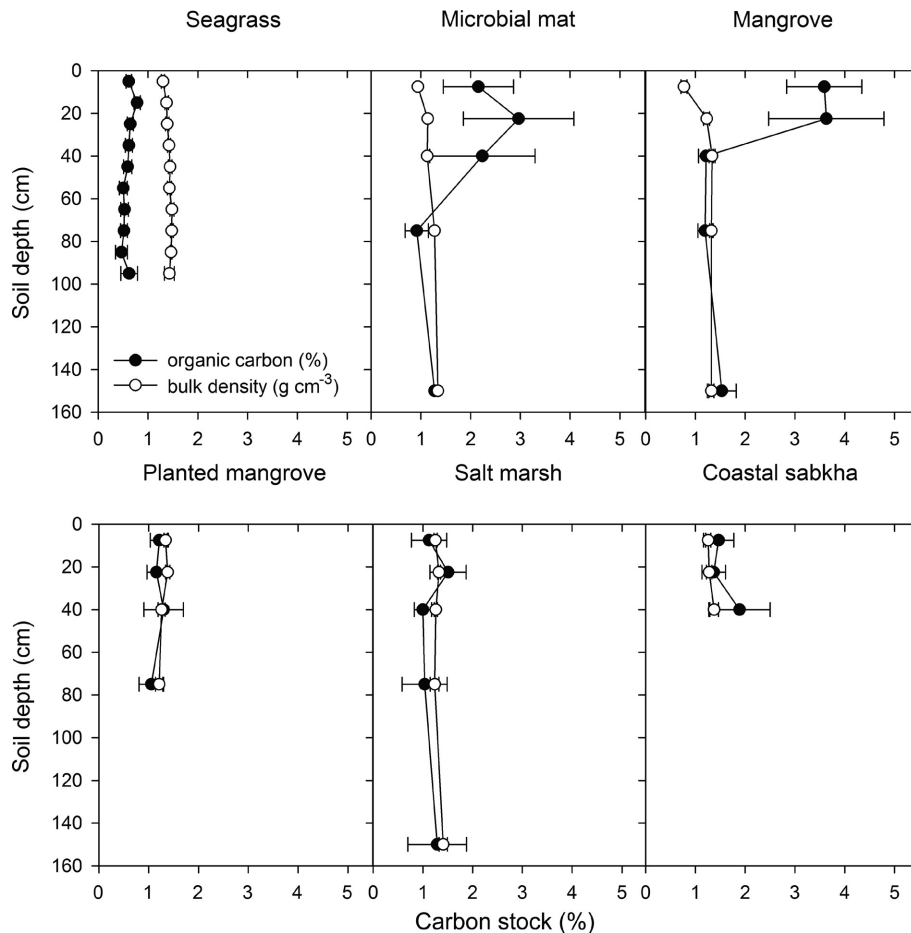


FIG. 6. Percent organic carbon and bulk density with depth for each coastal ecosystem (mean  $\pm$  SE). Depths represent the midpoint of each depth class.

semi-humid systems. Natural mangroves had the largest plant and largest soil carbon pools, while seagrass beds had the lowest (Fig. 3). Carbon sequestration in wood biomass accounted for 1–55% of total mangrove ecosystem carbon pools, compared to 2–51% in non-arid mangrove ecosystems (Donato et al. 2011) and 1–6% in UAE salt marshes. Thus, trees are particularly important for carbon sequestration in this arid region. Despite highly diverse carbon inputs in terms of both carbon quantity and quality, average soil carbon pools across intertidal ecosystems varied over a relatively narrow range of 80–156 Mg C/ha, and all were significantly larger than seagrass soil pools of 49 Mg C/ha. The largest soil carbon pools were ~50% higher in mature mangroves than coastal sabkha, which completely lacked plants (Table 4, Fig. 3). Despite having an autotrophic source of carbon input, seagrass bed soils contained one-third of the carbon found in mangroves.

Mangroves were the only ecosystem type to develop an organic-rich surface horizon, but this horizon was poorly developed compared to non-arid systems, ranging in thickness from <1 cm to 20 cm and containing 2–29%

organic carbon in soil surface horizons. Factors that could favor higher soil carbon accumulation rates in some mangrove stands include (1) longer periods of soil saturation due to lower elevations (Appendix S1: Fig. S2); (2) higher vascular plant production rates, which increase carbon inputs and decrease decomposition by favoring microbial  $O_2$  consumption and reduced soil conditions; and (3) producing more recalcitrant plant litter that is more resistant to decay than seagrass plant litter. Understanding the relative contributions of these factors to regulating soil carbon sequestration rates is important because mangroves are regional hotspots of soil carbon, and have the most potential for significant carbon management.

Spatial variation in UAE mangrove carbon pools was large, varying 10- and 20-fold in soil and tree carbon pools, respectively. Mangrove stands along the northern Arabian Gulf and the Gulf of Oman had the lowest salinity (Table 2) and supported larger trees, denser forests, deeper soils, and larger carbon pools than stands on the Arabian Gulf (Appendix S2: Tables S1 and S2). Additional factors such as landscape context (lagoon

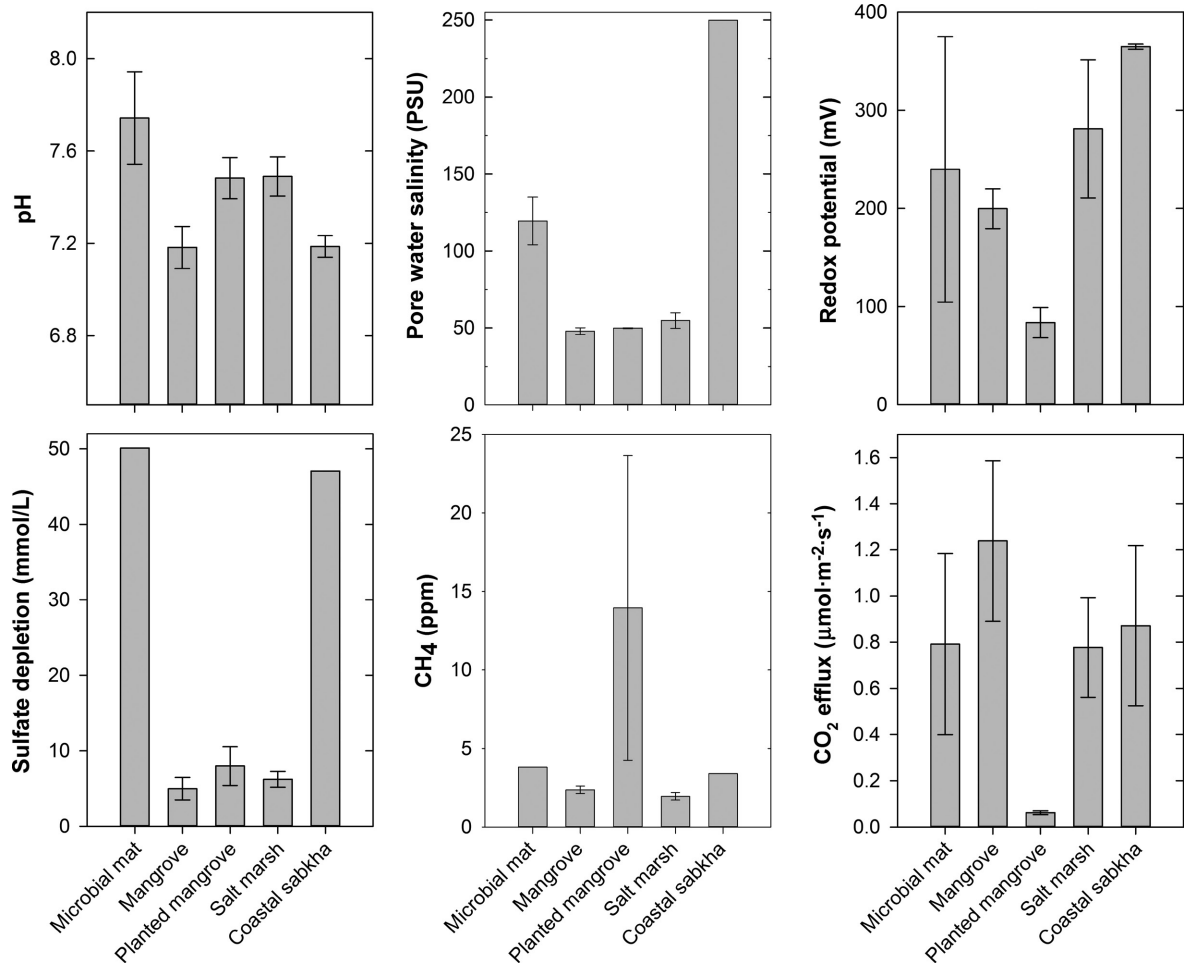


FIG. 7. Pore water chemistry, CO<sub>2</sub> flux, and redox potential data for intertidal ecosystems. Values are mean ± SE.

vs. wind/wave exposed), intertidal slope, tidal flushing, freshwater input, and nutrient availability all could affect plant production, resiliency, and carbon pools within this patchy coastal ecosystem.

Salt marshes dominated by *A. macrostachyum* had the second highest plant carbon pools, but they were nonetheless 20-fold lower than in mature mangroves (Fig. 3) and similar in size to planted mangroves (Table 4). Salt marsh soil carbon pools were comparable to sabkha ecosystems, despite the absence of vascular plants. Both systems are relatively high in tidal elevations (Appendix S1: Fig. S2), which do not favor the low redox, anaerobic soil condition required to preserve carbon (Fig. 7).

An intriguing and somewhat unexpected aspect of this project was the high soil carbon storage potential of microbial mats, with organic carbon values ranging from 0.2% to 7.8%. Microbial mats and biofilms are composed of bacteria, archaea and other microorganisms embedded in a matrix of extracellular polymeric substances (EPS). EPS are composed mostly of polysaccharides that constitute 50–90% of mat carbon (Vu et al. 2009), and are

transformed by heterotrophic bacteria from labile to refractory forms that accumulate as sediment organic matter (Braissant et al. 2009). Biofilms enhance organic matter preservation by increasing water-holding capacity (Bhaskar and Bhosle 2005) and decreasing water infiltration rates (Vandevivere and Baveye 1992). Evidence that these features preserve sediment organic matter are reports that such ancient microbial mats contributed to the substantial production of fossil fuels in the region (Cardoso et al. 1978). We demonstrate that microbial mats store carbon at rates comparable to vegetated intertidal ecosystems, and argue that they meet the criteria of a blue carbon ecosystem. To our knowledge there are no formal policies that recognize ecosystem services that these systems may provide.

Carbon stocks in sabkha were entirely in soil pools and fell within the range of most mangrove and salt marsh sites (Table 4, Fig. 3). The fact that soil organic carbon was at approximately 1% of total soil mass suggests that allocthonous deposition of carbon is the source of recalcitrant soil carbon in these hyper-arid blue carbon ecosystems. Recalcitrant forms of plant tissue or deposition of black

carbon (particulate matter caused by the incomplete combustion of fossil fuels or biomass) are potential sources (Schmidt and Noack 2000). We also observed buried organic-rich soil surfaces up to 10 cm thick, indicating that rapid transitions to less-frequently inundated ecosystem types has occurred and remained in the soil (Evans et al. 1973, Kendall et al. 2002).

#### *Global comparisons*

Plant carbon stocks in mangrove, marsh, and seagrass ecosystems of this arid region were low, but not markedly so, compared to similar ecosystems in other climatic regions of the world. By contrast, soil carbon stocks were consistently within the lower 25% quantile (Figs. 4 and 5). If blue carbon ecosystem soils preserve a constant fraction of the net primary production, as some carbon accretion models assume (Morris et al. 2002), then UAE soil carbon pools may have been expected to be higher than observed, falling within the 25–50% quantile of global comparisons. These observations suggest that preservation of wetland plant biomass is generally lower in the UAE than in similar ecosystems elsewhere.

The majority of natural mangrove plant carbon stocks in the UAE were comparable to short stature mangroves from the Caribbean and Indopacific, with the exception of the two northern/Gulf of Oman sites that were more similar to medium stature stands in the Caribbean and Indopacific (Appendix S2: Table S3). Compared to mangrove soil carbon stocks in arid Baja California, Mexico, UAE mangrove carbon stocks were approximately half (Appendix S2: Table S3; Ezcurra et al. 2016). Salt marsh aboveground organic carbon was lower than *A. macrostachyum* (i.e., shrub-dominated) salt marshes in the Ebro delta, Spain (Curcó et al. 2002) and in Portugal (Neves et al. 2010), and also lower than herbaceous marshes in the northwest Atlantic coast of Canada, where cold temperatures limit growth (Frolking et al. 2001). Salt marsh soil carbon stocks in the UAE were the lowest out of all the global data compiled (Curcó et al. 2002, Neves et al. 2010, Sifleet et al. 2011). Carbon stock data, particularly soil stocks, are sparse for salt marshes generally, and even more so for marshes dominated by woody species such as those in the UAE. This highlights a surprising need for more deep (1 m minimum) soil carbon data in tidal marshes. Compared to other seagrass systems for which C stocks have been estimated worldwide, lower carbon storage in Arabian Gulf beds was not unexpected considering the relatively small biomass of these particular seagrass species, which all share a small stature and short life span (Fig. 5B; Fourqurean et al. 2012b). However, the low biomass and small size of the UAE seagrasses cannot be explained completely as a function of the arid nature of the region, as dense beds of relatively large-bodied seagrasses are found along the shore of deserts in North Africa (Sghaier et al. 2013) and Australia (Fourqurean et al. 2012b).

#### *Potential factors limiting carbon storage*

Managing coastal ecosystems for carbon sequestration services in arid environments requires identifying the factors that account for their relatively small soil carbon pools. Coastal wetlands in the UAE could have been expected to support larger soil carbon stocks based on climatic factors alone; indeed, large soil carbon pools occur in comparable ecosystems elsewhere under conditions that suppress plant production (e.g., nutrient limitation) or enhance decomposition (e.g., tropical climates; McKee et al. 2007). The interactions that control organic matter preservation are complex and may operate relatively inefficiently in these systems due to several factors. The soils in coastal UAE were often coarse textured, carbon poor, and weakly reducing (Fig. 7). Coarse-textured soils generally have high water infiltration rates that allow hypoxic pore water (if present) to be rapidly replaced by O<sub>2</sub>-rich tidal water or air. Given the circum-neutral soil pH,  $E_h$  values >200 on many of the sites suggest that microbial activity is dominated by aerobic respiration (Meronigal and Rabenhorst 2013), with anaerobic respiration restricted to microsites. The O<sub>2</sub> consumption rate in these soils may also be limited by the low supply of labile organic carbon required for microbial respiration. Collectively, these traits are expected to inhibit development of the highly reducing, anoxic conditions found in sites with large soil carbon pools, and to favor nearly complete oxidation of organic carbon to CO<sub>2</sub> (Kenig et al. 1990). Indeed, soil organic matter concentrations in some study sites averaged 1% across all soil depths (Fig. 6), which is comparable to upland forests and deserts below the A horizon. The relatively high soil carbon content of some microbial mats (up to 7.8% organic carbon) is evidence that that microbial biofilms can alter the redox environment of these coarse-textured soils, presumably by increasing the length of time a soil remains saturated (Vandevivere and Baveye 1992).

The highly dynamic and low-gradient UAE coastline is very sensitive to small changes in relative sea level (Kendall et al. 2002) that may prevent plant carbon inputs from persisting in one location long enough to accumulate large soil carbon pools (Craft et al. 2003). We observed buried organic-rich soil surfaces up to 10 cm thick, indicating rapid transitions to less-frequently inundated ecosystem types (Evans et al. 1973, Kendall et al. 2002). The ecosystems with the largest soil carbon pools, mangroves and microbial mats, had enriched soil carbon profiles less than 30 cm deep (Fig. 6), which contrasts with many comparable ecosystems in humid and semi-humid climates where soil profiles develop in the same location over thousands of years (Drexler et al. 2009).

#### *Potential management applications and policy implications*

Interest in mangrove, marsh, and seagrass carbon stocks and sequestration rates has grown rapidly since the publication of *Blue Carbon. A Rapid Response Assessment*



(Nelleman et al. 2009), which highlighted the fact that these ecosystems are hot spots for carbon storage when compared to other terrestrial, aquatic, and marine ecosystems. This is the first study to recognize that other coastal ecosystems, sabkha and microbial mats, also support carbon stocks, and may therefore be important features in arid coastal landscapes. These data enabled identification of Ecologically or Biologically Significant Marine Areas (EBSA) under criteria developed by the Convention on Biological Diversity (CBD), and contributed toward RAMSAR designation for coastal sabkha as a distinct intertidal ecosystem because of its carbon storage, with potential application to other coastal blue carbon ecosystems.

Mangrove ecosystem creation and restoration are growing practices in Abu Dhabi. We found that UAE mangrove ecosystems are critical for carbon sequestration compared to other blue carbon ecosystems, and report evidence that mangrove creation project designs may not consistently promote the successful establishment of mature mangrove forests. We found striking differences between two created mangrove chronosequences that are consistent with the tenet that flooding stress limits tree growth (Megonigal et al. 1997). Stands at Abu al Abyad were planted ~50 cm lower in the tidal frame than on Jubail Island, resulting in significantly longer hydroperiods and reduced growth up to 15-fold (Fig. 2B; Appendix S1: Fig. S2). Indeed, many of the seedlings at Abu al Abyad were covered in barnacles. Future planting and restoration efforts will require research to establish the optimum tidal elevations required to minimize inundation stress and maximize growth and carbon storage in this arid environment (UNEP and CIFOR 2014).

Despite containing the lowest plant and soil carbon pools (Fig. 3), seagrass beds are the most widely distributed blue carbon ecosystem in the UAE, cumulatively contain the largest carbon pool within the UAE (Erftemeijer and Shuail 2012, Campbell et al. 2015), and provide critical habitat for the second largest dugong (*Dugong dugon*) population (Preen 2004). Thus, critical attention should be placed on preserving this important blue carbon ecosystem and preventing the negative impacts of development and oil exploration (Campbell et al. 2015).

The carbon values determined by this study form the basis of country-specific carbon stock values to aid the UAE inventory compilers in their calculations of carbon stock changes with management activities. The UAE is also one of the first countries to test and release the application of the 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories for Wetlands for its GHG Inventory at the Abu Dhabi level (IPCC 2014), providing feedback to the United Nations Framework Convention on Climate Change on the inclusion of wetlands within the national greenhouse gas inventories of other countries.

### Summary

We measured plant and soil carbon pools in mangroves, salt marshes, seagrass beds, microbial mats, coastal sabkha, and planted mangroves at 58 sites across the United Arab Emirates for the first comprehensive investigation of carbon stocks in an arid climate. Mangroves contained the highest plant and soil carbon pools, while microbial mats, which have no emergent vegetation, had the second largest soil carbon pools. Average seagrass carbon stock was three to four times lower than the other intertidal ecosystems examined, yet contained more carbon than any other coastal ecosystem due to its expansive coverage. This study is the first to identify microbial mats as a potentially new blue carbon ecosystem that can store soil carbon at rates commensurate to vegetated ecosystems. Coastal sabkha have been identified as an associated blue carbon ecosystem, as it can overtop former vegetated or microbial mat systems. Plant and soil carbon stocks in these arid blue carbon habitats are smaller compared with many regions of the world, but perhaps for different reasons. While relatively low rates of NPP are likely due to low nutrient availability and plant stress, we hypothesize that small soil carbon pools reflect low carbon preservation due to weakly reducing soil conditions, which in turn reflect coarse soil texture, high hydraulic conductivity, and low moisture-holding capacity. The time period over which carbon has been accumulating may also explain the relatively small carbon pools. Currently, we do not have sufficient data to disentangle these factors. As in other regions of the world, blue carbon ecosystems of the UAE are the most carbon dense features of the landscape, providing ecosystem services other functions such as supporting fish, sea turtle, and dugong populations, biodiversity, and cultural values.

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J. Glavan, S. Crooks, J. W. Fourqurean, J. B. Kauffman, and J. P. Megonigal conceived of the study; S. Crooks, J. W. Fourqurean, J. B. Kauffman, J. P. Megonigal, L. M. Schile, and J. Glavan performed the research; L. M. Schile and J. P. Megonigal wrote the manuscript; S. Crooks, J. W. Fourqurean, J. B. Kauffman, and J. Glavan contributed to the manuscript; and L. M. Schile, J. P. Megonigal, and J. B. Kauffman analyzed the data.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1489/full>

## DATA AVAILABILITY

Data associated with this paper have been deposited in DataONE digital repository <https://doi.org/10.15146/R3K59Z>