Key biogeochemical factors affecting soil carbon storage in *Posidonia* meadows

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Key points: Interactions of biogeochemical factors control organic carbon storage in seagrass soils / Higher organic carbon storage driven by higher plant inputs / Soil accumulation rates and sediment grain-size control organic carbon storage

Keywords: Carbon Sinks, Blue Carbon, Global Change, Marine Sediments, Coastal Ecosystems

Abstract

Biotic and abiotic factors influence the accumulation of organic carbon (C_{org}) in seagrass ecosystems. We surveyed *Posidonia sinuosa* meadows growing in different water depths to assess the variability in the sources, stocks and accumulation rates of C_{org}. We show that over the last 500 years, *P. sinuosa* meadows closer to the upper limit of distribution (at 2-4 m depth) accumulated 3 to 4-fold higher C_{org} stocks (averaging 6.3 kg C_{org} m^{-2}) at 3 to 4-fold higher rates (12.8 g C_{org} m^{-2} y^{-1}) compared to meadows closer to the deep limits of distribution (at 6-8 m depth; 1.8 kg C_{org} m^{-2} and 3.6 g C_{org} m^{-2} y^{-1}). In shallower meadows, C_{org} stocks were mostly derived from seagrass detritus (88% in average) compared to meadows closer to the deep limit of distribution (45% on average). Also, soil accumulation rates and fine-grained sediment content (<0.125 mm) in shallower meadows (2.0 mm y^{-1} and 9%, respectively) were approximately 2-fold higher than in deeper meadows (1.2 mm y^{-1} and 5%, respectively). The C_{org} stocks and accumulation rates accumulated over the last 500 years in bare sediments (0.6 kg C_{org} m^{-2} and 1.2 g C_{org} m^{-2} y^{-1}) were 3 to 11-fold lower than in *P. sinuosa* meadows, while fine-grained sediment content (1%) and seagrass detritus contribution to the C_{org} pool (20%) were 8 and 3-fold lower than in

Posidonia meadows, respectively. The patterns found support the hypotheses that C_{org} storage in seagrass soils is influenced by interactions of biological (e.g. meadow productivity, cover and density), chemical (e.g. recalcitrance of C_{org} stocks) and physical (e.g. hydrodynamic energy and soil accumulation rates) factors within the meadow. We conclude that there is a need to improve global estimates of seagrass carbon storage accounting for biogeochemical factors driving variability within habitats.

1. Introduction

The recent focus on carbon trading has intensified the interest in quantifying the capability of a variety of ecosystems to store carbon, since carbon storage provides one means of valuing these ecosystems. The role of seagrass meadows in absorbing and storing carbon dioxide over centennial to millennial scales is being evaluated in the context of climate change mitigation (Fourqurean et al. 2012; Duarte et al. 2013). Seagrasses occupy only 0.1% of the ocean surface but are considered one of the largest carbon sinks worldwide (Duarte et al. 2005, 2010; Mcleod et al. 2011). Unlike terrestrial ecosystems, which store organic carbon (C_{org}) mainly in the living biomass, C_{org} stocks in seagrass meadows are mainly found in their soils, where it can accumulate over millennia (Mateo et al. 1997). The substrate where seagrasses grow meet the requirements for sediment to be considered a soil (Serrano et al. 2012), despite marine ecologists broadly refer to seagrass substrates as sediments (Kristensen & Rabenhorst, 2015).

Seagrasses encompass a wide variety of species across a range of depositional environments and water depths (Carruthers et al. 2007), and the variability in the soil C_{org} stocks among seagrass habitats had been found to be high (up to eighteen-fold;

Lavery et al. 2013). However, there has been a tendency to simplify regional and global estimates of C_{org} stocks in seagrass ecosystems from a very limited data set, based on few species and habitats (Nelleman et al. 2009; Fourqurean et al. 2012). Geomorphological settings (i.e. topography and hydrology), soil characteristics (e.g. mineralogy and texture) and biological features (e.g. primary production and remineralization rates) control soil C_{org} storage in both terrestrial ecosystems (Amundson, 2001, De Deyn et al. 2008; Jonsson and Wardle, 2009) and in mangrove and tidal salt marshes (Donato et al. 2011; Adame et al. 2013; Ouyang and Lee, 2014). However, our understanding of the factors regulating this variability in seagrass meadows is limited (Nellemann et al. 2009; Duarte et al. 2010; Serrano et al. 2014).

Based on the terrestrial analogues and the limited research undertaken on seagrasses, it is likely that multiple factors may influence C_{org} storage within seagrass meadows, including biotic and abiotic factors acting in the water column, canopy and the soils. The seagrass itself may exert a primary control on C_{org} storage through its biomass, productivity and nutrient content (Lavery et al. 2013; Serrano et al. 2014; Miyajima et al. 2015), and all of which are highly variable depending upon seagrass species and habitat conditions (Alcoverro et al. 1995; Collier et al. 2007). Seagrass density, biomass and productivity are strongly related to the underwater light penetration (Dennison, 1987; Duarte, 1991). Therefore, it can be expected that different irradiance regimes (and therefore depth) would influence the C_{org} storage capacity of seagrasses (Serrano et al. 2014).

Once C_{org} is buried in the soil biotic and abiotic factors are likely to control the degree of C_{org} accumulation and preservation (Burdige, 2007). The rates of soil accumulation, the sediment structure and the biochemical composition of the organic matter buried may strongly influence C_{org} accumulation and preservation, and are highly variable among seagrass meadows (De Falco et al. 2000; Kennedy et al. 2010; Duarte et al. 2013). Soil accumulation may be a function of the seagrass canopy structure (De Falco et al. 2000; Gacia and Duarte, 2001; Peralta et al. 2008; Hendriks et al. 2010), the availability of suspended particles to settle out of the water column and the production of biogenic carbonates within the meadow (De Falco et al. 2000; Mazarrasa et al. 2015). If the accumulated sediments are fine, then they are likely to enhance the preservation of C_{org} since they tend to limit oxygen exchange and redox potentials, which reduce remineralization (e.g. Keil and Hedges, 1993). And finally, while both authoctonous (e.g. plant detritus and epiphytes) and allochthonous (e.g. seston and terrestrial matter) sources contribute to the C_{org} pool in seagrass soils (Kennedy et al. 2010) the proportion of seagrass-derived C_{org} may be an important factor controlling C_{org} storage capacity. Seagrass tissues contain relatively high amounts of degradation-resistant organic compounds (e.g. lignin and cellulose; Harrison, 1989; Klap et al. 2000; Torbatinejad et al. 2007; Burdige, 2007) compared to seston and algal detritus (Laursen et al. 1996), which are more prone to remineralization during early diagenesis (Henrichs, 1992).

From the above, it is clear that a large number of factors can potentially influence the stocks and accumulation rates of C_{org} in seagrass meadows. Here we studied *Posidonia sinuosa* meadows across a depth gradient, aiming to highlight key biogeochemical factors affecting C_{org} storage in seagrass soils that need to be accounted for when attempting to produce regional or global estimates of C_{org} storage in seagrass meadows. Previous research at this site (Collier et al. 2007, 2008) showed significant variation in plant biomass and productivity, water quality and sediment biogeochemistry parameters across this depth gradient. Bare sediments were also sampled and studied in order to determine the 'background' C_{org} stocks and fluxes in the absence of a seagrass meadow.

2. Material and methods

2.1. Study site and sampling

The study was conducted at Cockburn Sound in Western Australia (Figure 1), in dense and monospecific *P. sinuosa* meadows across a significant depth gradient. Cockburn Sound is a sheltered marine embayment consisting of a deep central basin surrounded by shallow sand banks and seagrass meadows (Kendrick et al. 2002). Four vertical cores were sampled at four water depths in vegetated areas (1.6 m, 4 m, 5.7 m and 8 m), while a single core at 4 m water depth was collected from a bare area located at about 2 km distance from the nearest seagrass meadow. It was difficult or impossible to find a 'pure control' (as per ecological definition) for this study. Shallow unconsolidated substrates in the study area should be occupied by seagrasses unless anthropogenic disturbances or hydrodynamic energy preclude so. In our case, the reference site was chosen based on the absence of seagrass at least since 1960s (Kendrick et al. 2002), similar water depth (4 m), and the low likelihood of seagrass detritus from surrounding meadows being exported and accumulated in the area (Skene et al. 2005).

The core barrels consisted of PVC pipes (65 mm inside diameter) with removable coring heads to cut fibrous material and minimize core shortening (compression) during coring (Serrano et al. 2012). The core barrels were driven into the soil by a hydraulic drill (LHD 23M, Atlas-Copco) that combined percussion and rotation. All cores were sealed at both ends, transported vertically to the laboratory and stored at 5°C before processing.

The lengths of soil recovered ranged from 57 to 123 cm. Compression of loose soils during coring is an inevitable phenomenon and is routinely corrected by distributing the spatial discordances proportionally between the expected and the observed soil column layers (e.g. Glew et al. 2001). The overall degree of core shortening was low (less than 12%) in all cases (corrected decompressed depths ranged from 65 to 134 cm). The results reported in this study (i.e. density, soil accumulation rates, and C_{org} stocks and accumulation rates) have been corrected for compression.

2.2. Laboratory procedures

The cores were cut longitudinally into two halves and sliced at regular intervals (i.e. 1 cm-thick slices). Each slice/sample was weighed before and after oven drying to constant weight at 70°C (DW), and subsequently sub-divided for analysis. The C_{org} elemental and isotopic composition of the organic matter was measured in milled subsamples from every second slice. These sub-samples were acidified with 1 M HCl, centrifuged (3500 RPM; 5 minutes) and the supernatant with acid residues was removed using a pipette, then washed in deionized water once, the residues were centrifuged again and the supernatant removed. The residual samples were re-dried (70°C) before carbon elemental and isotopic analyses. Samples were acid-rinsed to ensure complete removal of inorganic carbon (i.e. carbonates) before C_{org} analysis, despite this procedure may lead to an underestimation of soil C_{org} stocks (Phillips et al. 2011; Brodie et al. 2011). The C_{org} elemental and isotopic composition was also analyzed in *P. sinuosa* macro-detritus (i.e. sheaths, roots and rhizomes) collected at different depths along all seagrass cores for the carbon source study. The samples were washed in deionized water, dried at 70°C, encapsulated and the C_{org} elemental and isotopic composition was analyzed using a Micro Cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at University California Davis Facilities. The relative contents of C_{org} were calculated for the bulk (pre-acidified) samples. Carbon isotope ratios are expressed as δ values in parts per thousand (‰) relative to VPDB (Vienna Pee Dee Belemnite).

For sediment grain-size analysis, a Mastersizer 2000 laser-diffraction particle analyzer was used following digestion of bulk samples with 10% hydrogen peroxide. Sediments were classified as coarse sand (<1 mm and >0.5 mm) medium sand (<0.5 mm and >0.25 mm), fine sand (<0.25 mm and >0.125 mm), and very fine sand plus mud (<0.125 mm).

2.3. Age-depth chronology

The age of the soil along the cores was determined combining ^{210}Pb and AMS-^{14}C techniques for the recent (c.a. <100 y BP) and older (c.a. <500 cal y BP) material, respectively. Concentrations of ^{210}Pb were determined by alpha spectrometry through the measurement of its granddaughter ^{210}Po, assuming radioactive equilibrium between the two radionuclides (Sánchez-Cabeza et al. 1998). Between 150 and 300 mg aliquots of each sample were acid digested after addition of ^{209}Po as spike and polonium isotopes were plated onto pure silver disks, and their alpha emissions were measured by alpha spectrometry. The concentrations of ^{210}Pb at depths were found to be constant were used to determine the average supported ^{210}Pb concentrations, which were then used to obtain the concentrations of excess ^{210}Pb. A selection of samples of each core was measured for ^{226}Ra by gamma spectrometry to confirm the validity of the estimates of ^{210}Pb-supported values. Concentrations of ^{226}Ra were determined using a high-purity Ge well-type detector (CANBERRA, mod. GCW3523) through the 351 keV emission line of ^{210}Pb.

For radiocarbon analyses, four samples of shells and one sample of *P. sinuosa* sheath remains were radiocarbon dated at the National Ocean Sciences AMS Facility (Woods Hole Oceanographic Institution, Woods Hole, MA; Table A in supporting information) following standard procedures (Stuiver and Pollack, 1977). Sheaths and shells were washed in ultrapure MQ water in order to remove fine sediment particles, examined under a stereomicroscope for lack of attached reworked materials, and dried at 60 °C before radiocarbon dating. The conventional radiocarbon ages were converted into calendar dates in years BP (cal y BP) using the Calib 7.1 software (Marine13 curve) and the local marine reservoir effect due to the C dissolved in marine water was adjusted by deducting 71 years from the calibrated radiocarbon ages (Ulm, 2006). The calibrated ^{14}C ages corrected for the marine reservoir effect were used to produce an age-depth model (linear regression; present is 2012).

2.4. Numerical procedures

The C_{org} stocks per unit area (kg C_{org} m^{-2}) were estimated by computing the cumulative mass of C_{org} accumulated over the last ca. 100 years and 500 years (inventories in 13 to 30 cm and 40 to 75 cm thick deposits, respectively). The short- and long-term accumulation rates (g DW m^{-2} y^{-1}) of C_{org} were calculated by dividing the C_{org} inventories in the soil by the ages (for 100 and 500 years old deposits, respectively). The decay rates of soil C_{org} were calculated by fitting an exponential equation to the decreasing trends in C_{org} content (mg C_{org} cm^{-3}) with aging. The data reported for seagrass soil properties at different water depths and bare sediments

(Average ± SE) were normalized for ca. 100 and/or 500 years old deposits (specified in each case).

A one-way ANOVA was applied to test for any significant effect of water depth on the C_{org} elemental and isotopic composition, C_{org} stocks and accumulation rates, and fine sediment content (<0.125 mm). When significant effects were detected, pairwise *a posteriori* comparisons were performed using a Tukey's HSD test. Data were fourth root transformed to meet ANOVA assumptions. Pearson correlation analysis was used to test for significant relationships among the variables studied.

The Bayesian mixing model SIAR 4.2 (Parnell et al. 2010) was used to estimate the contribution of potential sources to the sedimentary C_{org}. The model was run with 3 sources (seagrass detritus, epiphytes/macroalgae, and seston). Separate mixing models were computed for each core, and for both 100 and 500 years of accumulation. The $\delta^{13}C$ values for all sources were assumed to be constant for each core, except the $\delta^{13}C$ signatures of seagrass detritus. Previous studies showed that the $\delta^{13}C$ values of *P. sinuosa* varied along this depth gradient (Collier et al. 2008). To account for this variability in seagrass tissue $\delta^{13}C$, the $\delta^{13}C$ signatures of seagrass detritus measured directly in the seagrass detritus present in each core were used in the corresponding mixing model. Concentration dependence was incorporated to the model because elemental concentrations were different between sources (Phillips and Koch 2002). We did not consider any fractionation with aging (0 ± 0‰) in the model because previous studies suggest small diagenetic shifts for $\delta^{13}C$ during decomposition (Zieman et al. 1984; Mateo et al. 2010).

3. Results

The soil characteristics of the *P. sinuosa* meadows in Cockburn Sound changed significantly with soil depth (and thus age), starting as low-density, highly organic soils that turned into inorganic-dominated material 20 cm below the soil surface (after c.a. 50 to 150 years of burial; Figure B in supporting information). Over 500 years of accumulation, soils in the *P. sinuosa* meadows closer to the upper limit of distribution (at 2 and 4 m depths) were significantly richer in C_{org} (mean ± standard error of the mean = 1.2 ± 0.2% C_{org}) than those from deeper areas (at 6 and 8 m depths; 0.5 ± 0.1% C_{org}; Table 1 and 2). The properties of the bare sediment core were homogeneous with depth/age (Figure B in supporting information) and, on average, the C_{org} content was lower (0.06%) and the density higher (1.2 g cm^{-3}) compared to the vegetated cores (Table 1 and 2). Medium and fine sands dominated in all seagrass cores (87% in average), while medium and coarse sands dominated in the bare sediment core (78% in total; Table 1 and Figure 2a). The proportion of fine grain-size material (<0.125 mm) increased from the bare core (averaging 1%) to *P. sinuosa* meadows closer to the deeper limit of distribution (4-5% at 6 and 8 m depth) and meadows closer to the upper limit of distribution (6 to 11% at 2 and 4 m depth; Table 1 and 2).

Concentration profiles of ^{210}Pb showed decreasing trends from the surface down to depths of 10 to 16 cm (decompressed depths). The concentrations of ^{226}Ra (average: 0.4 ± 2.1 Bq·kg^{-1}) were in agreement with those of ^{210}Pb in the deepest sections of the cores, indicating absence of excess ^{210}Pb ($^{210}Pb_{ex}$; Fig. 3). All cores had similar concentrations of supported ^{210}Pb (10.5 ± 0.9 Bq kg^{-1}), whereas the $^{210}Pb_{ex}$ inventories in the vegetated soils ranged from 427 ± 45 to 723 ± 48 Bq m^{-2}. Mixing of the upper soil layers was most severe in seagrass cores from the 2 and 6 m depth sites, where mixing was apparent in the top 3 and 7 cm, respectively. Average short-term soil accumulation rates (SAR; ca. last 100 years) for each core were determined by applying the CF:CS model below the base of the mixed layer (Krishnaswamy et al., 1971; Masqué et al. 2002; Figure 3), ranging from 1.3 ± 0.2 to 3.0 ± 1.1 mm y^{-1} (Table 3). Total ^{210}Pb concentrations measured in the reference core (i.e. bare sediment) were low (10.1 ± 1.2 Bq kg^{-1}) and not statistically different from the supported ^{210}Pb concentrations measured in the *P. sinuosa* cores (10.4 ± 1.2 Bq kg^{-1}). The absence of excess ^{210}Pb accumulation in bare sediment suggests negligible recent net accumulation of ^{210}Pb (and thus sediments) in the absence of vegetation (i.e. last ca. 100 years). According to the age-depth models based on ^{14}C ages, long-term SAR (ca. last 500 cal y BP) in *P. sinuosa* cores ranged from 0.8 to 1.3 mm y^{-1}, while long-term SAR in bare sediments averaged 1.5 mm y^{-1} (Table 3).

Over 100 and 500 years of accumulation, the shallow *P. sinuosa* meadows (at 2 and 4 m depths) stored more carbon (averaging 4.0 and 6.3 kg C_{org} m^{-2}, respectively) than the deeper counterparts at 6 and 8 m depths (1.2 and 1.8 kg C_{org} m^{-2}, respectively; Table 3 and Figure 4). The lowest C_{org} inventories (500 years of accumulation; 0.6 kg C_{org} m^{-2}) and accumulation rates (1.2 g C_{org} m^{-2} y^{-1} over 500 years) were found in the bare sediment core. The soil C_{org} content (mg C_{org} cm^{-3}) in the shallower meadows (at 2 and 4 m depth) decreased exponentially at rates of 0.0058 ± 0.0012 y^{-1} (R = 0.76) and 0.0043 ± 0.0005 y^{-1} (R = 0.86), respectively, while in meadows closer to the deeper limit of distribution (at 6 and 8 m depth) it decreased at 0.0037 ± 0.0014 y^{-1} (R = 0.65) and 0.0085 ± 0.0011 y^{-1} (R = 0.92), respectively.

The δ^{13}C values of sedimentary organic matter in soils from shallow meadows (at 2 and 4 m depths) were higher (-12‰) than those from the 6 and 8 m depths (-14‰ to -16‰; Fig. 2b; Tables 1 and 2). Organic carbon in bare sediments was the most depleted in ^{13}C (overall mean - 20‰). Carbon isotopic ratios in extant seagrass tissues also varied between cores (Table 4a). On average, $\delta^{13}C$ signatures of seagrass detritus preserved in the cores at 2, 4 and 6 m water depth were ^{13}C-enriched (-10 to -11‰) compared with those from 8 m depth (-13‰). The $\delta^{13}C$ signatures of living epiphytes and macroalgae at Cockburn Sound averaged -16 and -19‰, respectively (Table 4a).

The mixing models applied indicated that seagrass detritus was the most important source of soil C_{org} in all meadows studied (ranged from 43 to 94%; Table 4b) over 500 years of accumulation, but its contribution decreased with water depth. In meadows closer to the upper limit of distribution (at 2 and 4 m depth) seagrass-derived detritus contributed 80 to 94% of the sedimentary C_{org}, about 2-fold higher than in deeper meadows (at 6 and 8 m depth; ranging from 43 to 46%). The contribution of epiphytes/macroalgae was 3- to 10-fold higher in deeper meadows (ranging from 35 to 39%) compared to shallow meadows (4 to 11%; Table 4b). The contribution of seston increased with depth, but was always less than the contributions from *Posidonia* and epiphytes/macroalgae (Table 4b). Bare sediments had the lowest seagrass contribution to the C_{org} pool and the highest proportion from seston (20% and 58%, respectively; Table 4b).

Considering all soil layers from all cores, the C_{org} concentration increased with increasing fine sediment content ($r^2 = 0.52$), $\delta^{13}C$ values ($r^2 = 0.33$) and % contribution of seagrass detritus ($r^2 = 0.9$) (Fig 5). The $\delta^{13}C$ signatures and % particles <0.125 mm were positively correlated ($r^2 = 0.57$; Fig. 5).

4. Discussion

The results show a consistent decline in C_{org} stocks and accumulation rates with water depth in *P. sinuosa* meadows, where shallow meadows closer to the upper limit of distribution, accumulated 3 to 4-fold higher C_{org} stocks and at higher rates than those nearer the depth limits of distribution. We interpret the associated changes in biological (e.g. productivity, cover and density), chemical (e.g. recalcitrance of C_{org} stocks) and physical (e.g. hydrodynamic energy and SAR) factors within the meadows as evidence that the production, trapping and preservation of soil C_{org} in coastal areas is the result of complex interaction among all three sets of factors, as we represent in Figure 6, and discussed below.

The findings from this study are consistent and complement earlier findings by Serrano et al. (2014). The analyses of new variables in the same cores (i.e. ^{210}Pb dating, sediment grain-size, stable carbon isotopes in organic matter) provided new insights into the factors driving differences in C_{org} storage along a depth gradient. We also compare the biogeochemical characteristics of seagrass soils with adjacent bare sediments. Differences in C_{org} stocks and accumulation rates between this and the previous study (Serrano et al. 2014) are related to the new age-depth models obtained in the cores (i.e. based on ^{210}Pb dating). The results obtained lead us to conclude that in order to assess differences and compare C_{org} storage between seagrass habitats it is recommended to normalize C_{org} stocks by a period of accumulation (Rozaimi et al. 2016), rather than soil depth as commonly used (e.g. Serrano et al. 2014). Therefore, we present the results and develop the discussion according to the period of accumulation (^{210}Pb-derived, short-term, last 100 years; and ^{14}C-derived, long-term, last 500 years).

The results indicate that the *P. sinuosa* plants themselves play a key role in determining the amount of C_{org} available for burial along the depth gradient. It is well established that accumulation of C_{org} in sediments and soils is strongly affected by net primary production (Cao and Woodward, 1998; Serrano et al. 2014). The decline with depth of C_{org} stocks, C_{org} accumulation rates and seagrass-derived inputs into the sedimentary pool that we observed coincides with reduced seagrass abundance and production reported by Collier et al. (2007). These authors reported 18-24 fold reductions from shallow (2 m) to deep (8 m) *P. sinuosa* meadows in shoot density (from 1435 to 80 shoots m^{-2}), aboveground biomass (from 899 to 47 g DW m^{-2}) and belowground biomass (from 1028 to 43 g DW m^{-2}) on the same depth gradient. Similar trends in meadow structure and productivity with depth have been found in other *Posidonia* meadows, linked to reductions in irradiance (West, 1990; Duarte, 1991; Mateo and Romero, 1997; Alcoverro et al. 2001; Olesen et al. 2002).

Relationships between water column depth, seagrass canopy structure and C_{org} stocks have been reported for *Zostera muelleri* and *Halophila ovalis* meadows (e.g. Samper-Villarreal et. al. 2016). However, previous studies based their comparisons on soil thickness rather than C_{org} accumulation rates (e.g. period of accumulation) and rely on the assumption that environmental gradients linked to e.g. anthropogenic disturbances remained constant over the period reconstructed. Seagrass meadow structure (e.g. density, cover, biomass) and even presence/absence can vary over seasonal, annual and decadal time scales, in particular for short-lived and highly dynamic meadows such as those formed by genera *Zostera*, *Halophila* and *Halodule*. The presence of a clear and stable environmental gradient (i.e. depth) over the last millennia (Skene et al. 2005), together with the presence of seagrass remains along the cores studied, provide further strength on the relationships between biogeochemical factors and seagrass soil C_{org} storage reported in this study.

The higher SAR, fine-grained sediment contents and plant detritus inputs in meadows closer to the upper limit of distribution would contribute to higher accumulation and preservation of C_{org} after burial. The SAR in seagrass meadows is mainly controlled by the canopy structure, which affects the trapping and retention of sediment particles (Gacia and Duarte, 2001; Peralta et al. 2008; Hendriks et al. 2010), the hydrodynamic energy, the availability of fine-grained suspended particles in the water column, and the production of biogenic carbonates within the meadow (De Falco et al. 2000, 2010; Mazarrasa et al. 2015). High plant biomass and density is associated with greater retention of particles (in particular, fine-grained sediments), lower hydrodynamic energy, and higher production of biogenic carbonates within the meadow (De Falco et al. 2000), ultimately enhancing soil accumulation. The presence of a dense rhizome mat underlying shallow meadows may provide a positive feedback mechanism for enhanced SAR (i.e. presence of cavities reducing erosion and increasing soil accumulation; De Falco et al. 2000; Le Hir et al. 2007). The higher content of fine sediments we observed in shallow meadows would contribute to the higher C_{org} accumulation, since fine sediments generally retain more C_{org} compared to medium and coarse sands (Keil and Hedges, 1993; Burdige, 2007), and because remineralization rates tend to be reduced in fine sediments due to lower oxygen exchange and redox potentials (Hedges and Keil, 1995; Dauwe et al. 2001; Burdige, 2007; Pedersen et al. 2011).

The differences in decay rates highlight different levels of C_{org} preservation in the different meadows. This is likely a result of both the sources of C_{org} being buried and the biogeochemical conditions within the soils. Previous studies demonstrated that both autochthonous (e.g. seagrass and epiphyte detritus) and allochthonous (seston and terrestrial matter) sources contribute to the C_{org} pool in seagrass soils (50% each on average; Kennedy et al. 2010). Here, we observed larger amounts of seagrass-derived C_{org} in shallow meadows (85% in average), pointing to an important factor driving their higher C_{org} storage capacities compared to that of deeper meadows, namely the carbon preservation potential. *Posidonia* tissues contain relatively high amounts of degradation-resistant organic compounds in their tissues (e.g. lignin and cellulose; Harrison. 1989; Klap et al. 2000; Torbatinejad et al. 2007) and high C/N ratios (Duarte, 1990; Pedersen et al. 2011; Kaal et al. 2016). In contrast, seston and algal detritus, which contributed as much as 64-75% of the C_{org} in the deeper sites, have a higher labile C_{org} content (Laursen et al. 1996) more likely to be remineralized during early diagenesis (Henrichs, 1992), potentially explaining the higher soil C_{org} decay rates in the deep (at 8 m) *P. sinuosa* meadows. However, the soil C_{org} decay rates in *P. sinuosa* meadows at 6 m depth were in the range of those found at 2 and 4 m depths. This may be due to the limitations of the approach used here. For example, we assumed that C_{org} inputs (i.e. quantity and quality) and decomposition have been constant during the period of accumulation under study, but this may not have been the case. Further, obtaining reliable estimates of C_{org} decay rates is also complicated by the presence of living biomass in the upper part of the soils, which is the case for the seagrass core sampled at 6 m depth, where fluctuations in the concentration of C_{org} are evident.

The C_{org} decay rates of *P. sinuosa* meadows (0.0056 y^{-1} in average) are much higher than those reported for the similarly sized species *P. oceanica* (ranging from 0.00008 to 0.0005 y^{-1}; Mateo et al. 1997; Serrano et al. 2012). This may contribute to the up to 16-fold lower C_{org} stocks and accumulation rates in the soil beneath *P. sinuosa* compared to *P. oceanica* (Serrano et al. 2014).

Despite the limitations involved in using bare sediments as reference sites (e.g. inherent biogeochemical differences that preclude the settlement of seagrasses in bare sediments), the results suggest that C_{org} stocks and accumulation rates are much higher in seagrass meadows than in adjacent bare sediments. The 3 to 11-fold lower

C_{org} storage capacity of bare sediments compared to *P. sinuosa* meadows at comparable depths is due mainly to the absence of seagrass inputs. However, it may also result from the absence of a canopy that would otherwise enhance the trapping and retention of organic-rich, fine sediment particles (Hendriks et al. 2008), as reflected in the low content of fine-grained sediments. Since all continental margins store $C_{org,}$ there is a need to account for the net C_{org} storage capacity due to the presence of seagrasses when evaluating their role as carbon sinks.

The processes described in this study highlight the importance of meadow structure and productivity for C_{org} accumulation, supporting the hypothesis that the higher production of shallow meadows lead to higher accumulation rates of soil, fine-grained particles and seagrass detritus, which ultimately lead to the higher preservation and accumulation of C_{org}. The relative importance of the biogeochemical factors identified in this study (e.g. hydrodynamic energy, sediment accumulation rates, fine sediment content, water depth, seagrass net primary production and density) in driving C_{org} storage was not addressed, but rather we discussed the reasons why they can play a role in driving organic carbon storage and highlight potential synergistic and/or antagonistic interactions among them. Understanding the factors controlling C_{org} storage in seagrasses is at its onset, and a much better understanding is required before being able to disentangle the relative role/importance of each factor.

Acknowledgements

This work was supported by the ECU Faculty Research Grant Scheme, the ECU Early Career Research Grant Scheme, and the CSIRO Flagship Marine & Coastal Carbon Biogeochemical Cluster (Coastal Carbon Cluster) with funding from the CSIRO Flagship Collaboration Fund and the Generalitat de Catalunya (MERS, 2014 SGR–

1356). PM was supported in part by a Gledden Visiting Fellowship awarded by the Institute of Advanced Studies at The University of Western Australia and AAO by a PhD grant of Obra Social "la Caixa”. The authors are grateful to A. Gera, P. Bouvais and A. Esteban for their help in field and/or laboratory tasks.

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Table 1. Average ± SE density (in g cm^{-3}), C_{org} content (in %), $\delta^{13}C$ signatures and sediment grain-size content at Cockburn Sound (normalized for ca. 500 years old deposits).

Habitat	Water depth (m)	Thick (cm)	Age (cal yr BP)		Density (g cm^{-3})		C_{org} (%)		$\delta^{13}C$ (‰)		% Sediment grain size (mm)			
											<0.125	>0.125<0.25	>0.25<0.5	>0.5<1
				N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
P. sinuosa	2	66	498	61	0.86 ± 0.03	31	1.28 ± 0.22	28	-11.6 ± 0.2	28	11 ± 0.8	43 ± 1.0	36 ± 0.8	9 ± 0.9
	4	75	485	67	0.96 ± 0.02	34	1.06 ± 0.16	31	-12.2 ± 0.3	34	6 ± 0.3	47 ± 1.0	43 ± 0.4	5 ± 0.6
	6	40	490	35	0.90 ± 0.04	18	0.59 ± 0.15	18	-13.9 ± 0.4	18	5 ± 0.4	44 ± 0.9	46 ± 0.4	5 ± 0.5
	8	53	497	47	1.04 ± 0.02	24	0.38 ± 0.10	24	-16.2 ± 0.4	23	4 ± 0.7	43 ± 0.7	47 ± 0.7	6 ± 0.5
bare	4	75	490	70	1.22 ± 0.02	36	0.06 ± 0.00	36	-20.3 ± 0.1	36	1 ± 0.2	21 ± 0.7	51 ± 0.2	27 ± 0.8

Table 2. a) Results of one-way ANOVA on soil properties (normalized for ca. 500 years old deposits). P-values correspond with those provided by F-test. **b)** Results of statistical testing (Tukey's HSD) for significant effects of water depth on the physicochemical parameters in the cores. Levels of significance are as follows: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; NS, $P \geq 0.05$

a)

	df	SS	F	P
C_{org} (%)	4	5.16	36.28	<0.001
Error	138	4.91		
$\delta^{13}C$ (‰)	4	1610	210.90	<0.001
Error	1320	252		
C_{org} stock (g cm^{-3})	4	39.98	40.16	<0.001
Error	138	33.48		
<0.125 mm (%)	4	25.49	60.99	<0.001
Error	131	13.69		

b)

	C_{org} (%)				
$\delta^{13}C$ (‰)	2 m	4 m	6 m	8 m	Bare
2 m		NS	*	***	***
4 m	NS		*	***	***
6 m	***	**		NS	***
8 m	***	***	***		***
Bare	***	***	***	***	

	<0.125 mm (%)				
C_{org} stock (g cm^{-3})	2 m	4 m	6 m	8 m	Bare
2 m		NS	*	***	***
4 m	NS		NS	NS	***
6 m	**	**		NS	***
8 m	***	***	NS		***
Bare	***	***	***	***	

Table 3. Soil accumulation rates (SAR), C_{org} accumulation rates and C_{org} inventories in the seagrass cores studied (average ± SD). Estimates over short-term (derived from ^{210}Pb dating, last 100 years) and long-term (derived from ^{14}C dating, last 500) periods are provided. The thicknesses of seagrass soils corresponding to 100 and 500 years are provided.

		Short-term (100 years)				Long-term (500 years)			
Habitat	Water depth (m)	Thick (cm)	Stock (kg C_{org} m^{-2})	SAR (mm yr^{-1})	C_{org} acc. rates (g C_{org} m^{-2} y^{-1})	Thick (cm)	Stock (kg C_{org} m^{-2})	SAR (mm yr^{-1})	C_{org} acc. Rates (g C_{org} m^{-2} y^{-1})
P. sinuosa	2	30	4.5	3.0 ± 1.1	44.9 ± 6.5	66	6.0	1.3 ± 0.1	12.1 ± 0.6
	4	20	3.4	2.0 ± 0.7	34.3 ± 7.1	75	6.5	1.5 ± 0.1	13.5 ± 0.7
	6	16	1.2	1.6 ± 0.7	11.8 ± 3.5	40	1.7	0.8 ± 0.03	3.5 ± 0.1
	8	13	1.1	1.3 ± 0.2	11.4 ± 1.0	53	1.8	1.1 ± 0.04	3.7 ± 0.1
bare	4	16	0.1	1.6 ± 1.8	1.1 ± 0.3	75	0.6	1.5 ± 0.1	1.2 ± 0.1

Table 4. a) Stable carbon isotopic composition values ($\delta^{13}C$) of potential organic matter sources used for the different sources in the Bayesian mixing models. Data for *P. sinuosa* detritus (sheaths, roots and rhizomes) along the cores at 2, 4, 6 and 8 m water depth is presented. **b)** Relative contributions of potential sources of organic carbon to soils of *P. sinuosa* meadows in different depths and bare sediment (over 500 years of accumulation) as modeled by SIAR. Mean and lower and upper 95% credible interval (CI95) for all the range of feasible solutions in each bayesian mixing model.

a)

Source		$\delta^{13}C$ (‰)		References
	N	Mean	SD	
P. sinuosa 2m	8	-11.5	1.4	this study
P. sinuousa 4m	6	-10.6	1.9	this study
P. sinuosa 6m	6	-10.3	1.7	this study
P. sinuosa 8m	7	-13.3	1.2	this study
Epiphytes	6	-15.9	0.4	this study
Macroalgae	6	-18.6	1.8	this study
Seston	40	-24.2	0.6	Waite et al. 2007

b)

Habitat	*Posidonia sinuosa*		Macroalgae + Epiphytes		Seston	
	mean	CI95	mean	CI95	mean	CI95
2m	0.94	0.88-0.99	0.04	0.00-0.09	0.02	0.00-0.05
4m	0.83	0.70-0.90	0.11	0.00-0.23	0.06	0.00-0.12
6m	0.46	0.29-0.63	0.35	0.01-0.64	0.20	0.01-0.38
8m	0.43	0.20-0.65	0.39	0.01-0.75	0.18	0.01-0.34
Bare	0.20	0.11-0.31	0.22	0.01-0.40	0.58	0.48-0.69

Figure 1. Location of the study sites, Cockburn Sound, Western Australia (Australia). White dot points represent the coring sites in seagrass *P. sinuosa* meadows at 2, 4, 6 and 8 m depth (from West to East). Bare sediment core is indicated by a black dot point.

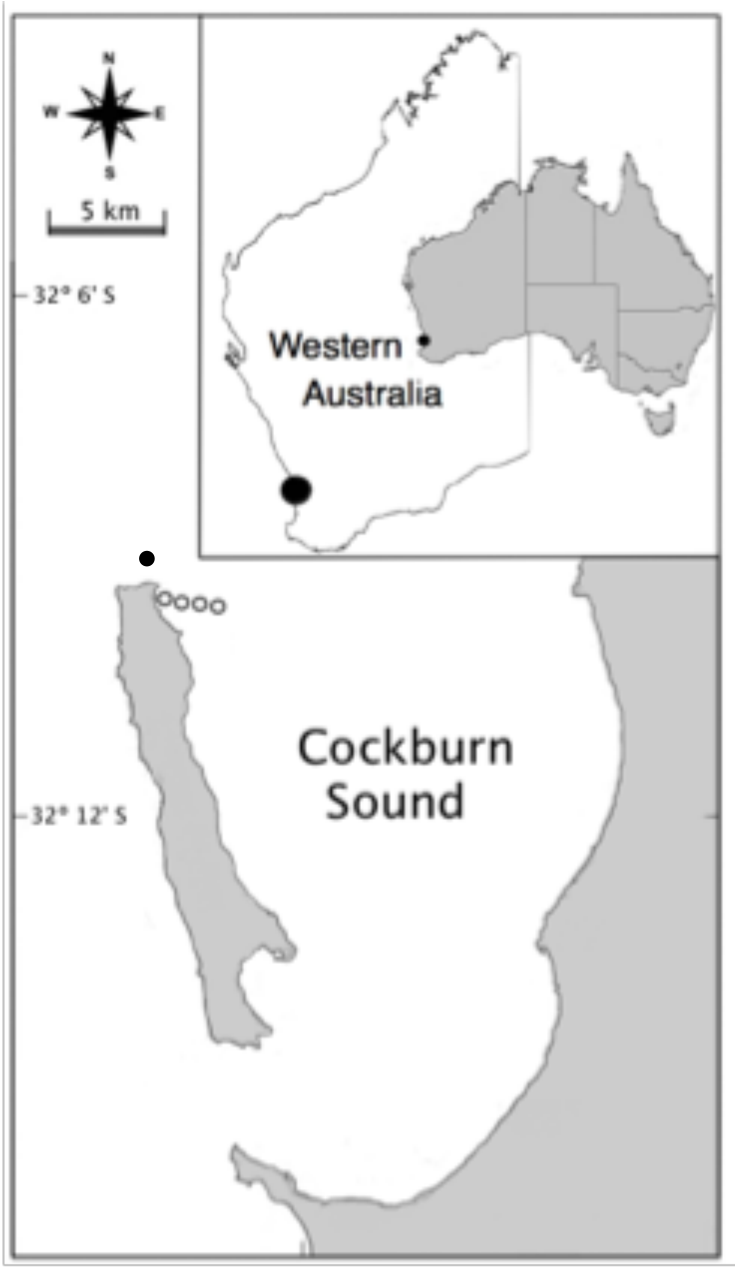
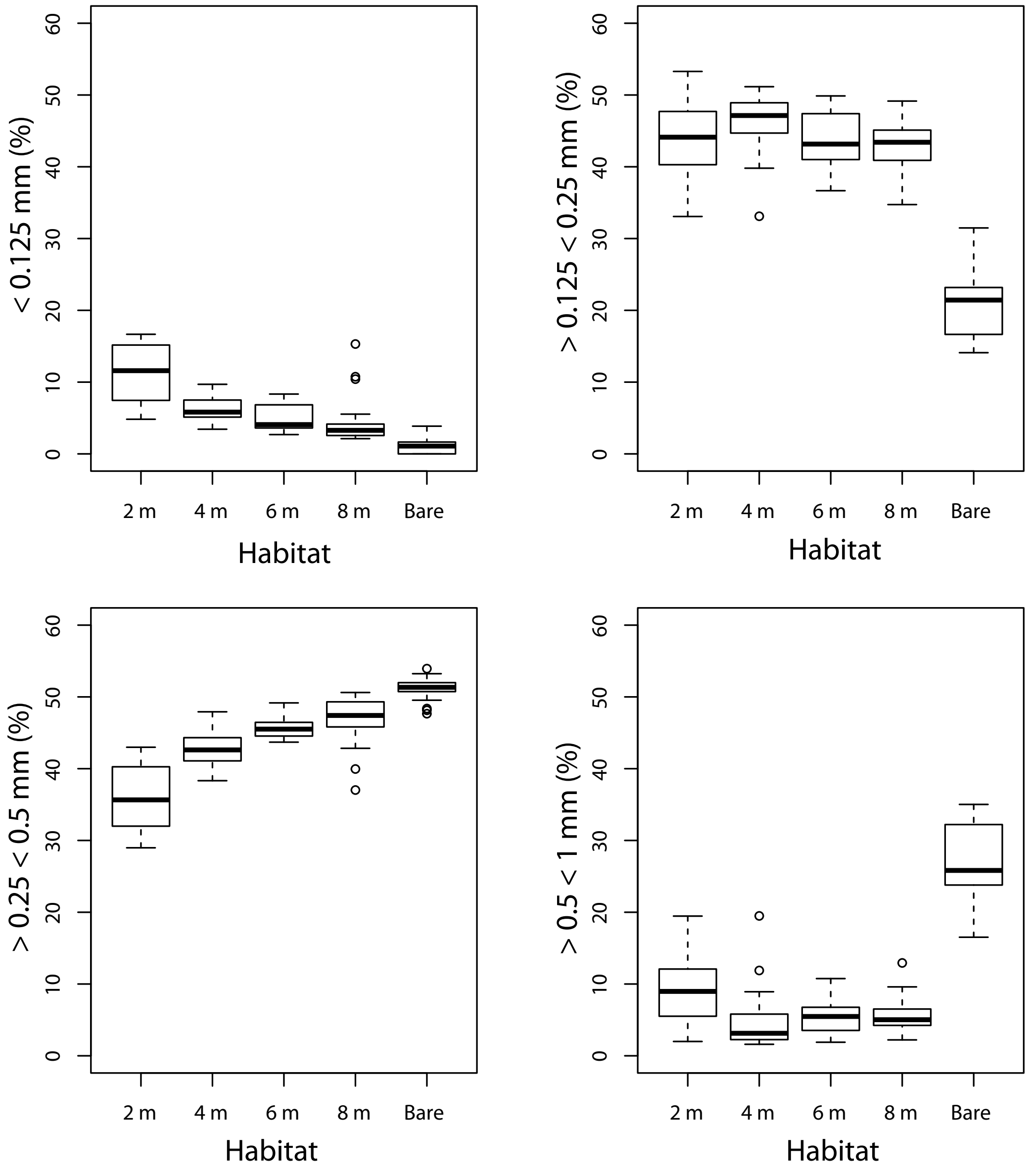


Figure 2. a) Sediment grain-size contents in *P. sinuosa* meadows (at 2, 4, 6 and 8 m depth) and bare sediment cores (normalized for 500 years old deposits) at Cockburn Sound; **b)** $\delta^{13}C$ signatures of the sedimentary organic carbon in *P. sinuosa* meadows (at 2, 4, 6 and 8 m depth) and bare sediment cores from Cockburn Sound (normalized for 500 years old deposits). Boxplot from top to bottom: largest observation, upper interquartile, median, lower interquartile and lowest observation.

a)



b)

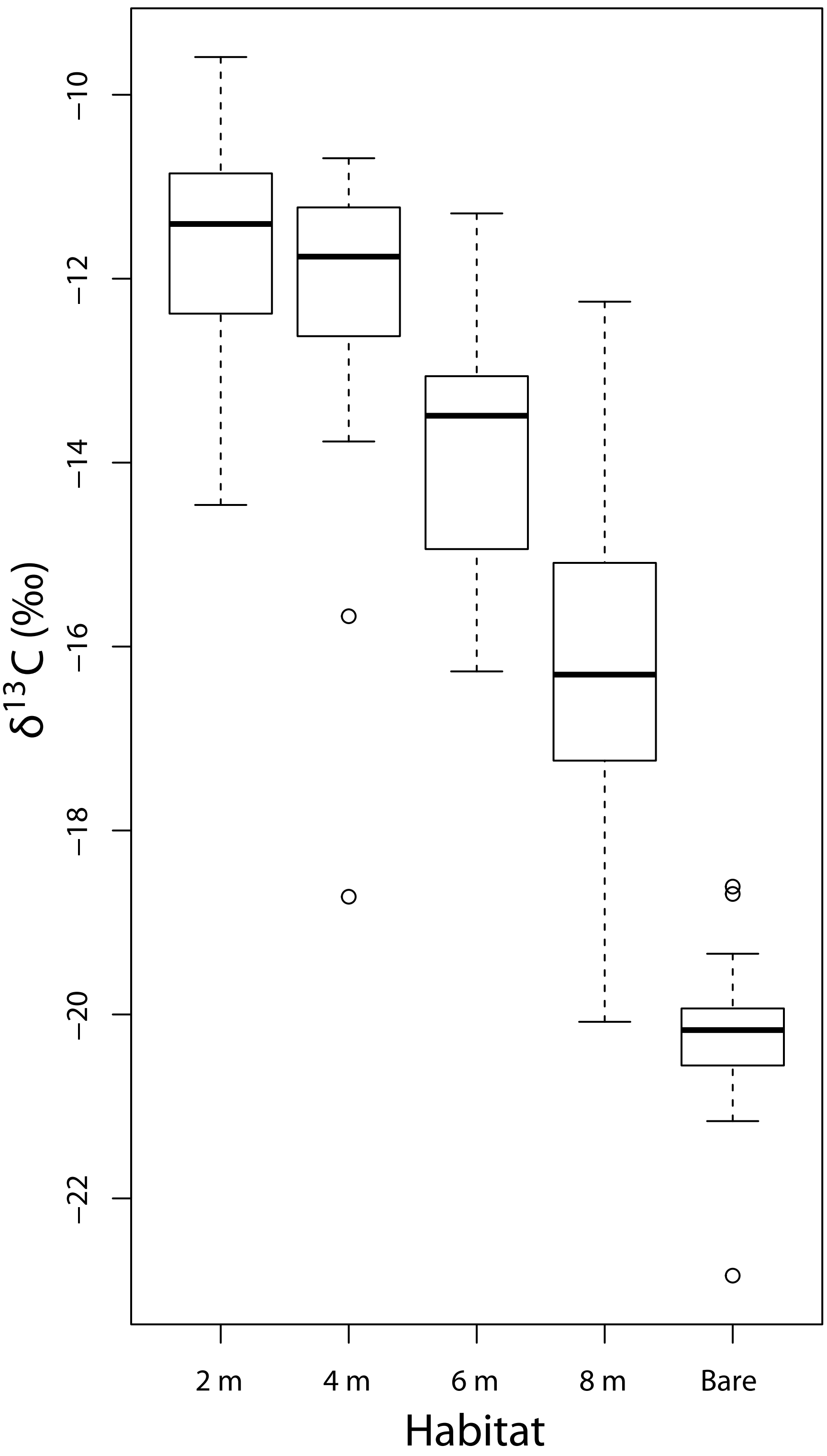


Figure 3. Concentration profiles of total and excess ^{210}Pb in seagrass and bare sediment cores from Cockburn Sound. Grey shaded area indicates the concentration of supported ^{210}Pb ($^{210}Pb_{sup}$).

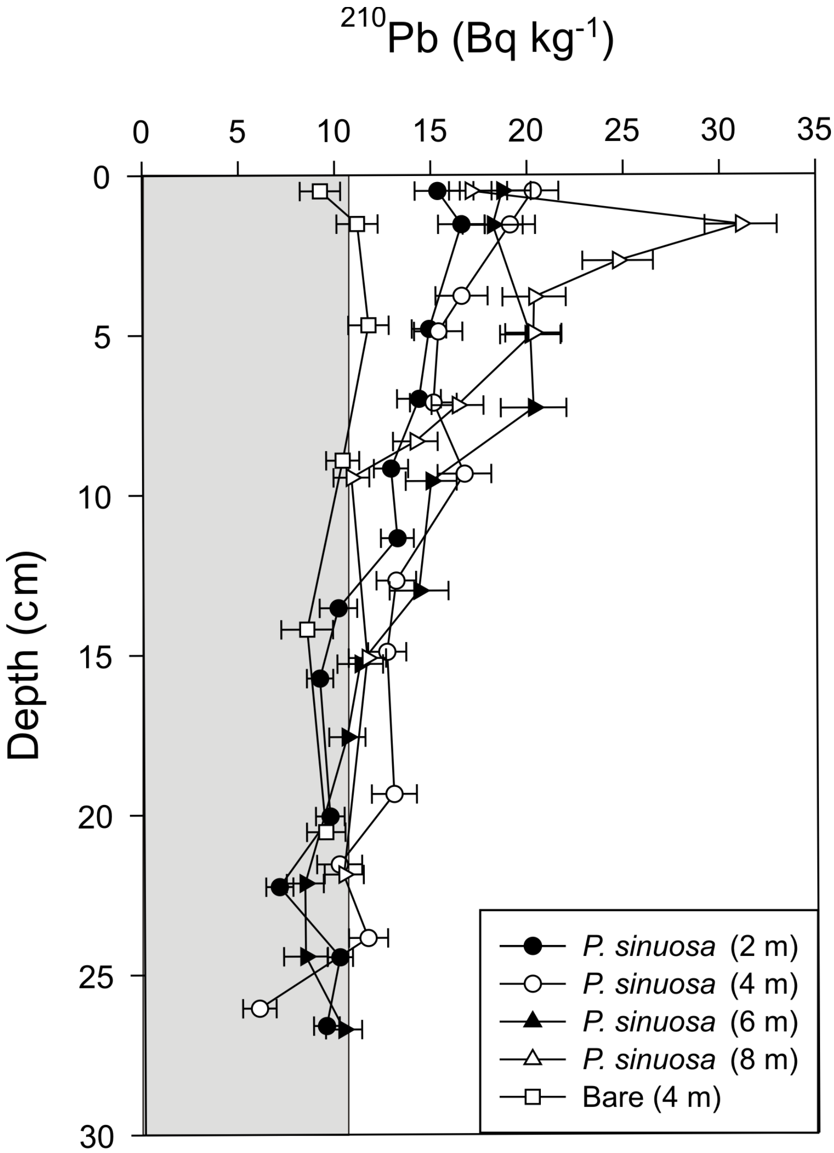


Figure 4. Inventories of C_{org} (kg C_{org} m^{-2}) in *P. sinuosa* meadows (at 2, 4, 6 and 8 m depth) and bare sediments at Cockburn Sound ((normalized for ca. 500 years old deposits).

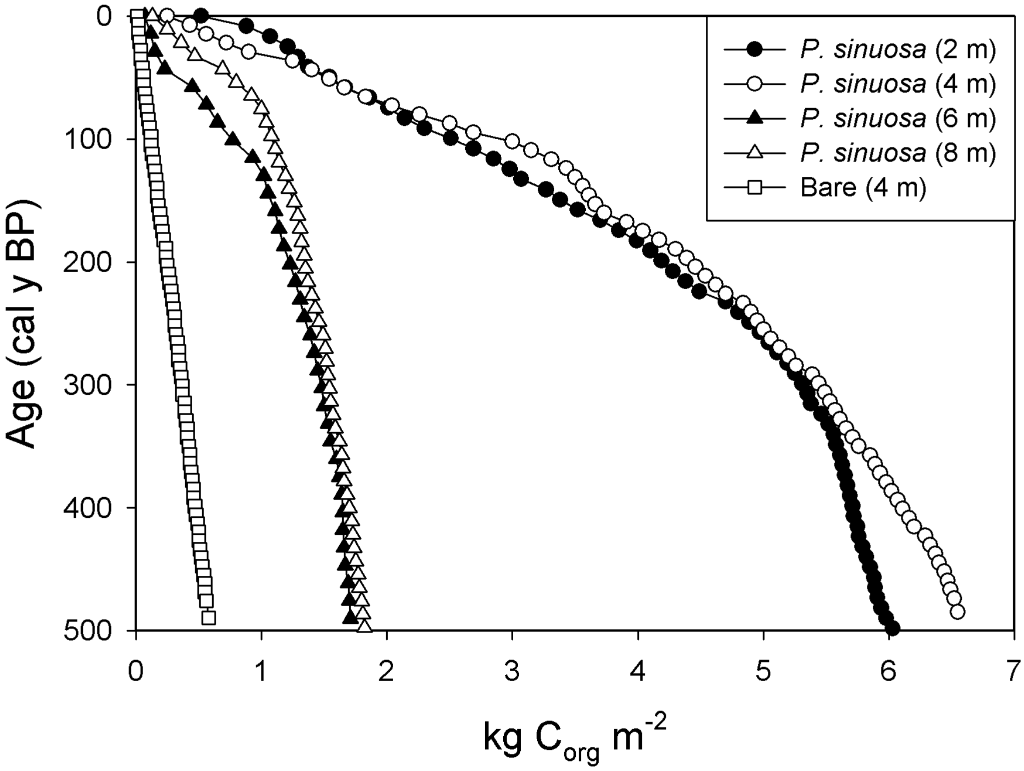


Figure 5. Biplots showing the relationships among the variables studied in the seagrass and bare sediment cores from Cockburn Sound (normalized for 500 years old deposits). **a)** $\delta^{13}C$ signatures (‰) plotted against C_{org} stocks (mg C_{org} cm^{-3}); **b)** Sediment grain size <0.125 mm (%) plotted against C_{org} stocks (mg C_{org} cm^{-3}); **c)** $\delta^{13}C$ signatures (‰) plotted against sediment grain size <0.125 mm (%); and d) Contribution of seagrass detritus (%) plotted against soil C_{org} stocks (kg C_{org} m^{-2}, over 100 years – small symbols – and 500 years – big symbols – of accumulation).

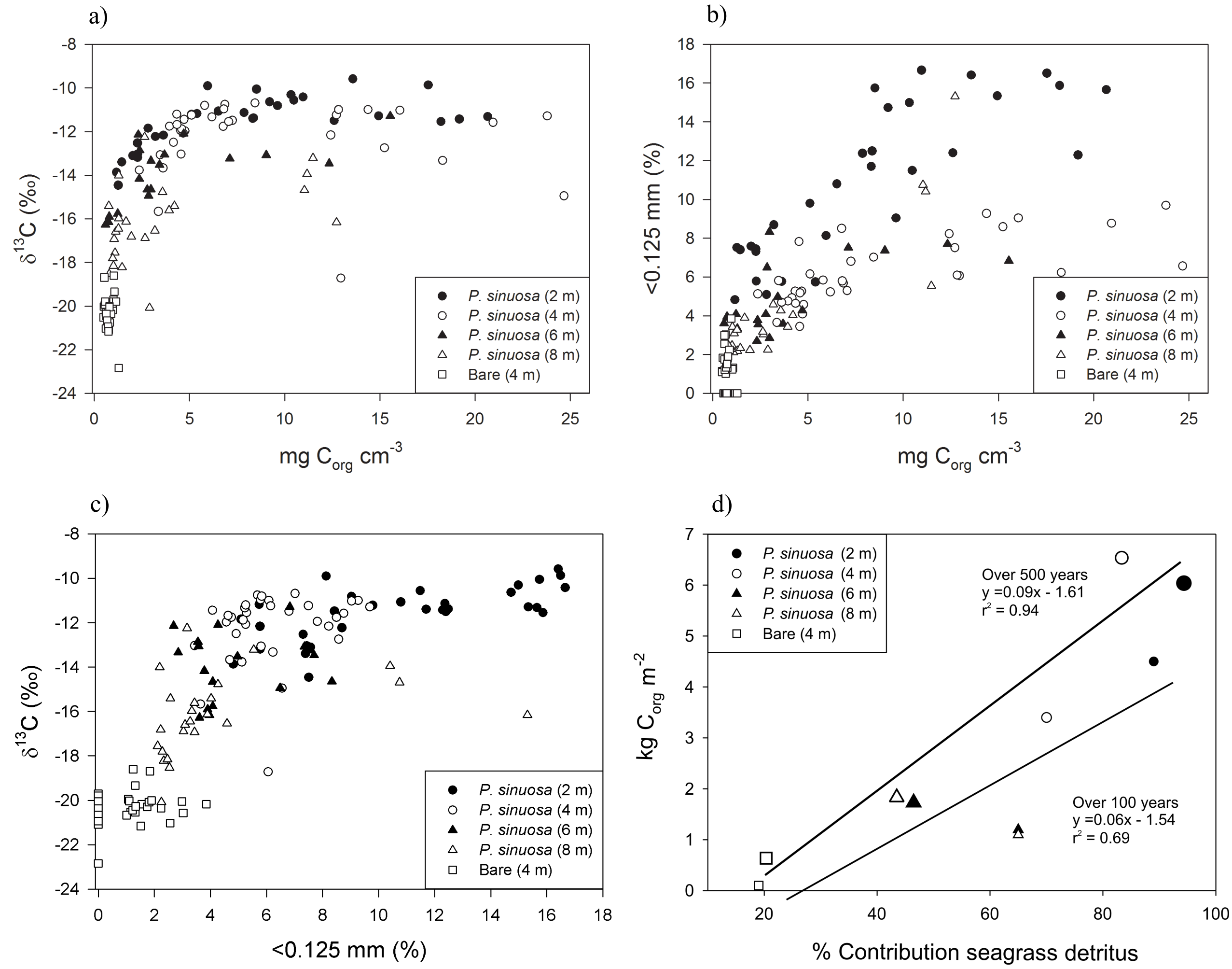
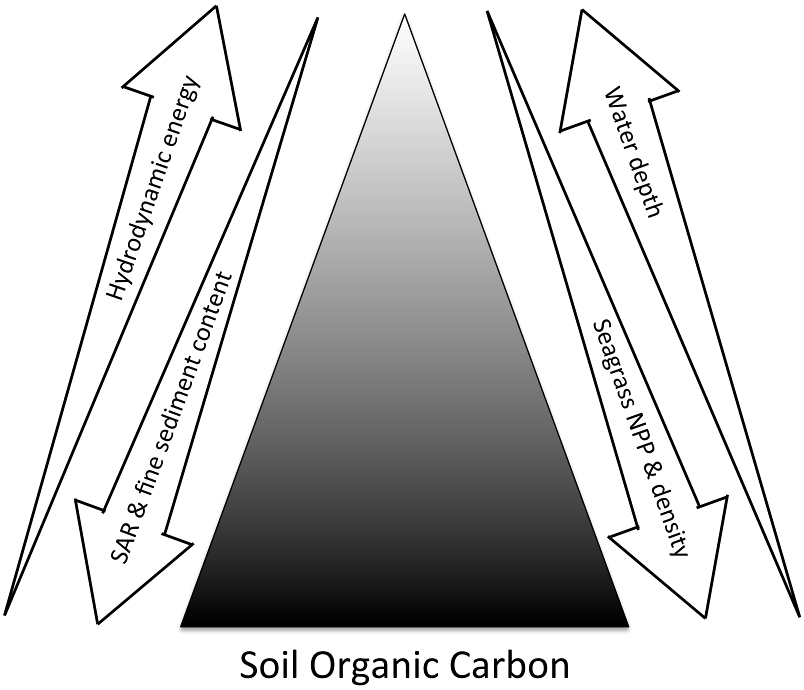


Figure 6. Influence of biogeochemical factors on the organic carbon storage capacity of seagrass ecosystems. Organic carbon in seagrass soil increases with high SAR, fine sediment content, seagrass NPP and density; and decreases with high hydrodynamic energy and water depth. SAR, soil accumulation rates; NPP, net primary production.

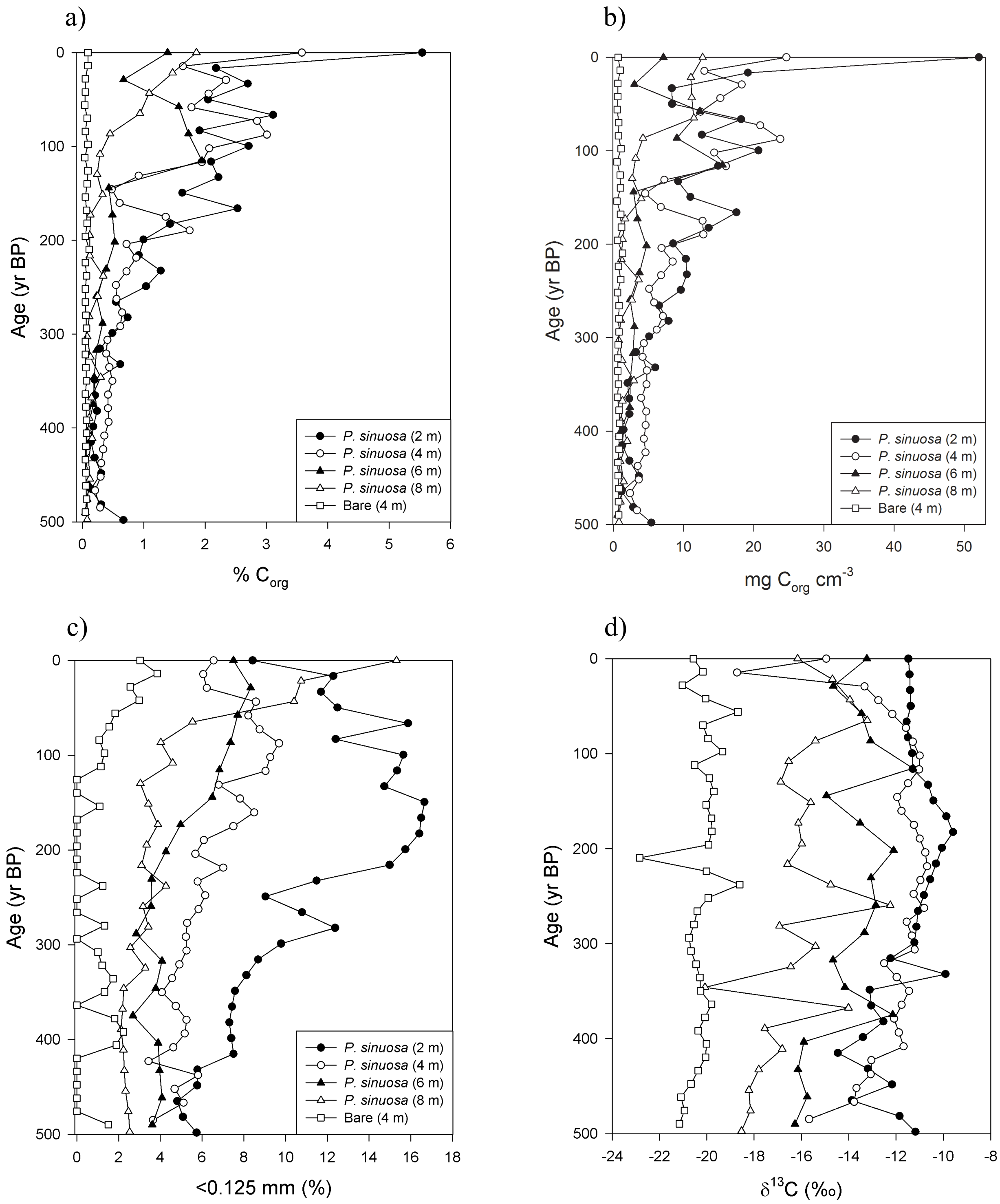


Supporting information

Table A. Details of radiocarbon dating of the *P. sinuosa* sheaths and shells from the cores. The accession laboratory sample assigned by NOSAMS is indicated.

Habitat	Water depth (m)	Soil depth (cm)	NOSAMS #	Raw age (year BP)	Age error (+/-)	Material
P. sinuosa	2	87	109170	803	25	shell
	4	79	109174	600	25	sheath
	6	64	109171	1020	20	shell
	8	97	109173	1120	20	shell
bare	4	75	109172	530	30	shell

Figure B. Substrate properties plotted against age at Cockburn Sound (*P. sinuosa* cores at 2, 4, 6 and 8 m depth and bare sediment core at 4 m depth). **a)** Organic carbon content (%); **b)** Organic carbon stocks (mg C_{org} cm^{-3}); **c)** Sediment grain size <0.125 mm; **d)** $\delta^{13}C$ signatures (‰) of organic carbon.


a)
b)
c)
d)
Age (yr BP)
0
100
200
300
400
500
% C$_{org}$
0 1 2 3 4 5 6
mg C$_{org}$ cm^{-3}
0 10 20 30 40 50
<0.125 mm (%)
0 2 4 6 8 10 12 14 16 18
δ^{13}C (‰)
-24 -22 -20 -18 -16 -14 -12 -10 -8
● *P. sinuosa* (2 m)
○ *P. sinuosa* (4 m)
▲ *P. sinuosa* (6 m)
△ *P. sinuosa* (8 m)
□ Bare (4 m)