

# Contemporary Rates of Carbon Sequestration Through Vertical Accretion of Sediments in Mangrove Forests and Saltmarshes of South East Queensland, Australia

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5	forests and saltmarshes of South East Queensland, Australia
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## Abstract

Mangrove forests and saltmarshes are important habitats for carbon (C) sequestration in the coastal zone but variation in rates of C sequestration and the factors controlling sequestration are poorly understood. We assessed C sequestration in Moreton Bay, South East Queensland in mangrove forests and saltmarshes that span a range of environmental settings and plant communities, including mangrove forests and tidal marshes on the oligotrophic sand islands of the eastern side of Moreton Bay and on the nutrient enriched, western side of the bay adjacent to the city of Brisbane. We found that rates of C sequestration in sediments were similar among mangrove forests over the bay, despite large differences in the C density of sediments, because of different rates of vertical accretion of sediments. The C sequestration on the oligotrophic sand island tidal marshes, dominated by *Juncus kraussii*, had the highest rate of C sequestration in the bay while the western saltmarshes, which were dominated by *Sarcocornia quinqueflora*, had the lowest rate of C sequestration. Our data indicate C sequestration varies among different tidal wetland plant community types, due to variation in sediment characteristics and rates of sediment accretion over time.

# Key words

Avicennia marina; rod surface elevation tables; sediment nutrients; carbon:phosphorus ratio

#### Introduction

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Mangrove forests and saltmarshes have large amounts of carbon (C) stored within their sediments (Chmura et al. 2003; Mcleod et al. 2011). High levels of C accumulate in these tidal wetland habitats because sediments accrete over time (add volume) in response to rising sea levels due to inputs of sediments and detritus (e.g. McKee et al. 2007; McKee 2011). The detritus in mangrove forest and saltmarsh sediments can be autochthonous, comprised predominantly of roots (Middleton and McKee 2001) but also allochthanous, with contributions from seagrass, terrestrial soils and macroalgal sources (Middelburg et al 1997; Bouillon et al. 2003; Adame et al. 2012). Decomposition of material is impeded by flooded, anoxic sediment conditions thereby facilitating C sequestration (Mcleod et al. 2011). The large stocks of carbon within sediments and the potential for its emission once these habitats are disturbed (Lovelock et al. 2011) has resulted in proposals to introduce mangrove forests for their C values into conservation schemes such as Reducing Emissions from Deforestation and Degradation (REDD+) (Siikaamaki et al. 2012). Additionally, the accumulation of C within sediments of mangrove forests is a means of mitigating increasing C dioxide concentrations in the atmosphere, thereby providing an incentive for restoration and improved management of coastal wetlands in order to increase C sequestration. Most estimates of C stocks and rates of accumulation have come from work with sediment cores, where rates of accumulation are estimated based on dating of accumulated sediment C over long periods of time (e.g. Chmura et al. 2003). While knowledge of past rates are essential for establishing the potential of mangrove forests and salt marshes to sequester C they do not inform us of current rates of sequestration because over time, vegetation, hydrology and levels of nutrient availability may change, all of which will affect rates of C sequestration (Alongi 2012). Current rates of C sequestration in coastal habitats can be estimated from restoration or natural chronosequences (e.g. Alongi et al. 2008; Lovelock et al. 2010; Osland et al. 2012). Additionally, measures of sediment surface elevation change in conjunction with C density of sediments can be used to estimate rates of C sequestration (e.g. Howe et al. 2009; Rogers et al. 2013).

Some of the main factors that are likely to influence C sequestration in coastal wetland habitats are geomorphic setting, plant species composition and nutrient availability. Geomorphic settings influence mangrove forests and saltmarsh through their effects on a range of factors, including the type and abundance of sediments and nutrient availability. Estuarine systems often have a higher availability of fine sediments, nutrients and allochthonous materials that can be incorporated into tidal wetland sediments compared to other settings (e.g. oceanic) (Kristensen et al. 2008; Adame et al. 2010; Adame et al. 2012). In estuarine settings, fine sediments and nutrients lead to high rates of primary production of mangrove forests (Lovelock et al. 2007) which can lead to stimulation of root growth and increased rates of deposition of root detritus to sediments (McKee 2011), but sediments may also dilute autochthonous C additions (Mcleod et al. 2011). Additionally, high contributions of allochthonous organic matter may prime decomposition pathways (Bianchi 2011), which may increase microbial oxidation of organic matter and thus reduce C sequestration. High nutrient concentrations may also reduce allocation of C to roots and root detritus and stimulate decomposition (McKee et al. 2007).

In non-estuarine systems, such as those in oceanic settings, associated with reefs or sand cays and islands, mineral sediments may also contribute to sediment volume (e.g. Lovelock et al. 2011; McKee et al. 2007). But organic matter composition of mangrove sediments in oceanic settings has been observed to be largely comprised of plant roots indicating that plant production, even if it is low compared to estuarine systems, can be the most important contributor to sediment C sequestration (McKee et al. 2007; McKee 2011; Adame et al. 2013). Extremely low nutrient availability in hydrologically isolated karstic settings, for example landward scrub forests, may result in such low levels of primary production that C sequestration may be low compared to areas with more regular tidal flushing (McKee et al. 2007; Adame et al. 2013).

The plant species composition may also strongly influence C sequestration in coastal vegetation. In
Caribbean peat sediments in mangrove forests are comprised of roots of <i>Rhizophora mangle</i> with
limited contributions from Avicennia germinans (McKee et al. 2007). The highly organic sediments in
the Indo-West Pacific are also associated with species within the family Rhizophoraceae (Donato et
al. 2011; Kauffman et al. 2011). Some saltmarsh species with highly developed rhizomes are
associated with highly organic sediments, for example Spartina alternifora in the USA (Chmura et al.
2003) and Juncus kraussii in Australia (Congdon and McComb 1980) while others, for example
communities of chenopods that occupy hypersaline sediments, may provide limited contributions to
sediment C. Additionally, different species of mangrove trees with their varying root morphologies
lead to different rates of increases in sediment volume, reflecting their belowground root growth
and also their capacity to trap and bind sediments (Krauss et al. 2003).
Here we used an array of surface elevation tables that measure increases in sediment volume over
time in conjunction with measurements of C density of surface sediments to estimate current rates
of C sequestration in a large subtropical embayment, Moreton Bay, South East Queensland. The Bay

 Rates of C sequestration differ among habitat types (mangrove vs saltmarsh) and with variation in plant communities (mangrove and saltmarsh species).

has both mangrove forests and saltmarsh communities over a gradient in nutrient availability. We

Rates of C sequestration are sensitive to nutrient supply, with declining rates of C sequestration at high levels of nutrient enrichment.

# **Materials and Methods**

test the following hypotheses:

Site description

Moreton Bay is a large semi-open embayment on the east coast of Australia. It is bound on the eastern side by sand islands that reach approximately 200 m in elevation and by a deltaic coast on the western side in which five rivers flow from their catchments to the bay. The city of Brisbane (population 3.5 million) resides on the western side of Moreton Bay. The climate is sub-tropical and thus the bay is fringed by mangrove forests low in the intertidal zone with saltmarsh and cyanobacterial mats in the high intertidal zone (Lovelock et al. 2011).

The mangrove forests of Moreton Bay are dominated by *Avicennia marina* on the western side of the Bay, but have a high abundance of *Rhizophora stylosa* in the eastern Bay (Dennison and Abal 1999). Saltmarsh communities are more variable in composition than mangrove forests. Where fresh water is abundant in the high intertidal, as it is in the eastern bay and in some locations in the west, the rush *Juncus kraussii* dominates while on the hypersaline high intertidal salt flats of the western bay communities are dominated by chenopod species from the genus *Sarcocornia* and *Suaeda*.

South East Queensland is subtropical and has annual variations in climate. Mean air temperature is highest from October to April (mean minimum temperature is 18 °C, mean maximum temperature 26 °C) and low in May-September (mean minimum temperature is 8 °C, mean maximum temperature 21 °C). Rainfall is highest in the warmer summer months from November to March (150 mm/month), with another smaller peak in rainfall in May (200 mm/month). Rainfall influences river flows, while wind speed affects resuspension of sediments in the bay through wave action (You 2005).

#### Experimental design

Three sites were chosen on both the eastern and western bay that comprised both mangrove and saltmarsh habitats (Figure 1). On the western bay, the three sites were located within the Tinchi Tamba Wetlands Reserve (Brisbane City Council), Nundah Creek (Boondall Wetlands Park) and in the

south at Halloran Reserve (Redlands Shire Council). At Tinchi Tamba and Nundah Creek the mangrove was comprised of *A. marina* of about 10 – 13 m in height. At Halloran Reserve *A.marina* was dominant but *Rhizophora stylosa* was also abundant. The saltmarsh in all sites was dominated by *Sarcocornia quinqueflora* with *Suaeda australis* also being present in most plots. In the eastern bay three sites were chosen along the western side of North Stradbroke Island. Two sites were north of the town of Dunwich, between Myora Light and Amity Point (Amity North and Amity South), while one was south of Dunwich, to the south of Adams Beach. The mangrove forests were approximately 10-15 m in height and were comprised of both *A. marina* and *R. stylosa*. The eastern saltmarsh was dominated by *Juncus kraussii*.

At each of the sites, three plots at least 30 m apart, were established and rod surface elevation tables and marker horizons (RSET-MH) were installed. Within the mangrove forests, plots were within 20 - 50 m of the creek bank or seaward edge. An additional three plots with RSET-MH were installed in the adjacent landward saltmarsh. In total, 36 RSET-MHs were installed throughout Moreton Bay. Detailed description of increment in surface elevation and local rate of sea level rise within Moreton Bay are available in Lovelock et al. (2011). The position of each RSET-MH in the mangrove forests were determined by measuring the depth of the water covering the site at high tide using dyed cotton strips (English et al. 2000). Sites on the eastern bay were lower in the intertidal than those on the western bay with a position of  $1.36 \pm 0.01$  m relative to the lowest astronomical tide (LAT) in the eastern bay compared to  $1.87 \pm 0.06$  m relative to LAT in the western bay. Saltmarsh sites are all infrequently inundated and are positioned more than 2.25 m above LAT.

Measurements of surface elevation increments

Changes in the surface elevation of wetlands were measured using the rod surface elevation table – marker horizon (RSET-MH) approach developed by Cahoon et al. (2002a and b). RSETs were installed between February and June of 2007. The depth of the benchmark varied between 4 – 17 m, with a mean of 12 m. A portable aluminum plank was used to access the benchmark rod, attach the RSET

and measure the surface elevation without disrupting surface sediments. Once the plank is in place and the RSET is attached to the base, the measuring arm is leveled horizontally. Nine fibre glass pins are then lowered to the surface. Elevation is measured as the amount of pin protruding above the measuring arm using a ruler with precision of 1 mm, where the change throughout the measurement interval is the change in pin length with reference to the base depth. The device has a range of fixed measurable positions around the rod. In this study, we used four measuring positions at 90° to each other to give 36 measurements for each plot. A mean of 36 measurements was calculated for each replicate RSET. For the first 18 months of the study, RSET-MHs were measured every 3-4 months, after which sampling intervals were lengthened to approximately 6 months to cover the winter dry (April – November) and summer wet seasons (November – April). Rates of surface elevation change (in mm y<sup>-1</sup>) are the slopes from the regression of surface elevation vs. time from June 2007 until November 2011.

### Sediment sampling

A known volume of surface sediments was sampled to 5 cm depth in July 2011 using a modified 50 ml plastic syringe. Three replicate sediment samples were collected from each experimental plot. To determine bulk density known volumes of sediment were dried at 60°C until samples reached a constant weight and then weighed. Dry bulk density was calculated as dry weight/volume. Samples were ground in a ball mill and then analysed for total C and nitrogen by combustion (LECO). Total sediment phosphorus was analysed using ICPMS. All analyses were performed at the Analytical Services Laboratory at the University of Queensland.

### Data analyses

The C sequestration (g C m<sup>-2</sup> y<sup>-1</sup>) was calculated as the rate of surface elevation change (mm y<sup>-1</sup>) multiplied by the C density of the sediment. Analysis of the variation in %C of sediments, bulk density, C sequestration and sediment nutrients was by generalized linear models where side of the

bay (east/west) and habitat (mangrove/saltmarsh) were fixed factors in the model and where site was nested (and random) in eastern/western side of the bay. The relationship between C sequestration and sediment nutrient concentrations and molar ratios was tested using regression analysis. Data was log transformed prior to analysis to normalize the variance of the data. Normality was assessed by inspecting residual plots. Analyses were performed using Data Desk (version 6.3, Data Descriptions Ithaca, NY, USA).

### Results

In the eastern bay % C per dry mass of sediment was highest in the *Juncus* saltmarsh habitat (mean  $15.1\pm se~3.0$  %) compared to mangrove sediments (mean  $1.3\pm se~0.3$  %) (Fig. 2). In contrast, in the western bay mangrove sediments had higher %C ( $8.4\pm se~0.5$  %) than the *Sarcocornia* dominated saltmarsh (mean  $2.2\pm 0.7$ %). These opposing patterns of %C in mangrove forest and saltmarsh sediments on either side of Moreton Bay gave rise to a highly significant bay x habitat interaction in the statistical model ( $F_{1,4}=96.2$ , P=0.0006).

Dry bulk density also varied between mangrove forests and saltmarsh, but in different ways depending on the location within the bay ( $F_{1,2}=76.12$ ,  $F_{1,4}=76.12$ ,  $F_{1$ 

side of the bay (Fig. 4). Mangrove forest sediments on the western side of the bay had a C density

that was approximately double that of mangrove forests in the eastern side of the bay.

Surface elevation change per year varied significantly among sites ( $F_{4,21} = 5.72$ , P = 0.003) (Table 1). Surface elevation gains tended to be higher on the eastern side of the bay than the western side of the bay ( $F_{1,4} = 7.42$ , P = 0.053) and higher in the mangrove forests compared to the saltmarsh ( $F_{1,4} = 7.42$ ). 6.91, P = 0.058). The difference between mangrove and saltmarsh surface elevation varied over sites (site x habitat interaction  $F_{1,21}$  = 5.59, P = 0.0029). Surface elevation gains in saltmarsh on the eastern side of the bay were higher at Adams Beach than at Amity North and South, and in the western bay were higher at Nundah Creek than in saltmarsh at Tinchi Tamba or Halloran Reserve. The C sequestration rates, calculated from changes in surface elevation over time (Table 1) and C density (Fig. 4) was significantly different among sites ( $F_{4,23} = 5.98$ , P = 0.0019) with C sequestration particularly high in Juncus saltmarsh at Amity North and Adams Beach in the eastern side of the bay (Fig. 5). In contrast C sequestration was very low in the Sarcocornia dominated marshes of the western bay (Fig. 5). Rates of C sequestration in mangrove forest sediments were fairly homogenous over all sites (grand mean  $76 \pm 16$  g C m<sup>-2</sup> y<sup>-1</sup>), although rates were low at Tinchi Tamba. There was no significant relationship between rates of C sequestration and P (g per sediment volume), N:P molar ratio or C:N molar ratio. Carbon sequestration varied significantly with N and C:P of sediments, but the relationships were highly variable (data not shown). Carbon sequestration was low with low C:P molar ratio and increased as C:P increased before declining at very high C:P ratios  $(F_{2,33} = 3.59, P = 0.039, R^2 = 0.179)$ . Rates of C sequestration increased with N of sediments, although the relationship was also variable ( $F_{1,33} = 6.66$ , P = 0.014,  $R^2 = 0.143$ ). However, assessment of the mean sediment nutrient characteristics over the different vegetation communities indicated that while P and N were particularly low in the eastern mangrove forest sediments, C:P and N:P ratios were highest in the eastern saltmarsh where C sequestration was also high (Table 2). N:P ratios were lower than or similar to the Redfield ratio (<16:1) in mangrove forests and western saltmarsh indicating N limitation to growth, but were significantly higher (40) in eastern saltmarsh. C:P ratios

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were between 170-576 in the mangrove forests and western saltmarsh but were over 1500 in the eastern saltmarsh (Table 2).

Rates of C sequestration in mangrove forests were within the range of those estimated from

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#### Discussion

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sediment cores, although on the low end of the range (global range of 20-949 g C m<sup>-2</sup> y<sup>-1</sup>, mean of 163 g C m<sup>-2</sup> y<sup>-1</sup>; Breithaupt et al. 2012; Chmura et al. 2003; Mcleod et al. 2011; Ruiz-Fernández et al. 2011). The rates of C sequestration were similar to those observed in riverine, mineral sediment-rich settings in tropical Australia (mean 180 g C m<sup>-2</sup> y<sup>-1</sup>, Brunskill et al. 2002) and in southern Australia (105 g C m<sup>-2</sup> y<sup>-1</sup>, Howe et al. 2009; 256 g C m<sup>-2</sup> y<sup>-1</sup>, Saintilan et al. 2013). The rates are low compared to those from the Caribbean region (Mexico and Florida) where sediments are highly organic (Chmura et al. 2003). Our estimates of C sequestration in mangrove sediments may be low due a range of physical and ecological processes, including lower primary productivity in subtropical forests, low inputs of allochthanous carbon sources and high rates of export (Twilley et al. 1992), but may also be due to limitations to our approach for estimating C sequestration based on C concentrations in surface sediments. Using C in the surface sediments may underestimate C sequestration because root detritus contributes to sediment C throughout the sediment profile. For example, mangrove roots tend to grow within older decomposing root structures (McKee 2001). Assessment of the amount of contemporary C sequestration throughout the sediment profile will require the development of new tools that can differentiate accumulation of contemporary C from prior forest (or saltmarsh) contributions. More likely our approach may give rise to overestimates because C concentrations in the top sediment surface layer may be higher than that incorporated into the sediment profile

(Breithaupt et al. 2012) as a large proportion of organic matter may be lost through diagenesis within the first year of deposition (Duarte and Cebrián 1996). We sampled sediments that represent more than one year of sediment deposition (top 5 cm, or 5-50 years of accumulation) to account for this potential problem, but overestimation may still occur if C mineralization rates are high. Additionally, C can be lost from deep in the sediment profile in porous, sandy sediments which could also lead to overestimates of long term C storage (Rogers et al. 2013). Rates of C sequestration in saltmarsh sediments were highly variable. Marshes dominated by Juncus had higher rates of sequestration than the hypersaline saltmarshes dominated by Sarcocornia (Fig. 5). The rates of C sequestration in the Juncus marshes in our study were similar to those reported for more southern *Juncus* marshes in Australia (207 g C m<sup>-2</sup> y<sup>-1</sup>, Saintilan et al. in review) and higher than rates observed in other salt marshes in North America and Europe (mean 105  $\pm$  55 g C m<sup>-2</sup> y<sup>-1</sup>; Chmura et al. 2003). The high rates of C sequestration in *Juncus* marshes may reflect the important role of plants with perennial rhizomes in promoting C sequestration in coastal marshes. In contrast, C sequestration in Sarcocornia marshes was very low (mean 8.6 ± 4.0 g C m<sup>-2</sup> y<sup>-1</sup>). Values for C sequestration in Sarcocornia marshes in Moreton Bay were much lower than those reported for similar vegetation at a more southern site (137 g C m<sup>-2</sup> y<sup>-1</sup>, Howe et al. 2009), but within the range of that reported for a number of south eastern Australian sites (mean of 46 g C m<sup>-2</sup> y<sup>-1</sup>, Saintilan et al. 2013). In the study of Howe et al. (2009) vertical accretion rates of sediments were ten-fold higher in the saltmarsh in the Hunter River than they are in Moreton Bay. High vertical accretion in the Hunter River may be because of high sediment availability and also that the saltmarsh is lower in the tidal frame at this site than it occurs in Moreton Bay thereby favoring high sedimentation rates. In Moreton Bay mangrove forests sediment accretion is higher lower in the intertidal zone (Lovelock et al. 2011). Additionally, in the study of Howe et al. (2009) root contributions of rhizomes of the grass Sporobolus virginicus may have also contributed to high rates of C sequestration. Although S. virginicus is an important component of saltmarsh in South East Queensland (Traill et al. 2011), it did

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not occur in our plots.

Across the bay, opposing patterns of variation in %C and bulk density of sediments gave rise to a high level of homogeneity in rates of C sequestration in mangrove forests despite vastly different sediment characteristics (Fig. 3 and 4). While mangrove sediments in the east had low %C and high dry bulk density due to high contributions of sand, those in the west had higher %C but lower dry bulk density. Additionally, surface elevation changes were lower in the west compared to the east (Table 1) largely because of subsidence or compaction of the sediments in the western bay (Lovelock et al. 2011), which may be related to differences in the species composition of the forests and their differences in root production and root structural traits (Krauss et al. 2003), as well as due to differences in sediment characteristics. In the west there are few *R. stylosa* and *A. marina* is dominant, while the eastern bay has a higher abundance of *R.stylosa*.

Carbon sequestration was not strongly correlated with nutrient concentrations of sediments or molar ratios of elements, although there was weak evidence for increasing C sequestration with increasing %N and non-linear trends with C:P ratios of sediments. These highly variable trends likely reflect the multiple factors that influence root production, trapping of allochthanous C and decomposition of organic matter in tidal wetlands. Low rates of plant production and root contributions to sediments may limit C sequestration in low nutrient habitats (McKee et al. 2007; Castaneda-Moya et al. 2011; Adame et al. 2013). But low levels of nutrient availability may also favour plant species that allocate a high proportion of fixed carbon to roots and that have tissues that decompose slowly (Chapin 1980). Although high nutrient environments increase plant production, decomposition of organic matter can also be enhanced (Quall and Richardson 2000) which may lead to reductions in C sequestration. Across our study sites in Moreton Bay the lowest rates of C sequestration occurred at Tinchi Tamba where C:P and C:N ratios were very low, indicating nutrient enrichment. Extremely high sediment P concentrations that are caused by pollution from agriculture and urban development are likely to be detrimental to C sequestration in tidal wetland ecosystems.

The highest rates of C sequestration of sediments in Moreton Bay occurred where plants have rhizomes, sediments are highly organic with relatively low bulk density, where rates of elevation change are moderate and where sediment C:P ratio and C:N ratios are high. Our study indicated factors that reduce surface elevation gains or C inputs, e.g. reduced sediment availability and nutrient pollution are likely to reduce rates of C sequestration within Moreton Bay, while moderate rates of sea level rise and reductions in nutrient pollution in Moreton Bay are likely to increase C sequestration.

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Research Initiative, the National Centre of Excellence for Groundwater Research and Training and
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# 422 **Figure Captions** 423 Figure 1. Location of study sites within Moreton Bay, Queensland, Australia (A). An example of the 424 location of the mangrove forest and saltmarsh plots within a study site, in this case Nundah Creek 425 (B). M1, M2 and M3 are within the mangrove forest (stippled), while SM1, SM2 and SM3 are located 426 within the saltmarsh (open). 427 Figure 2. Carbon concentration in sediments (% per dry mass) in mangrove forests (black) and 428 saltmarshes (grey) at six sites in Eastern and Western Moreton Bay. Values are means and standard 429 errors of 3 plots per site. 430 Figure 3. Dry bulk density of surface sediments in mangrove forests (black) and saltmarshes (grey) at 431 six sites in Eastern and Western Moreton Bay. Values are means and standard errors of 3 plots per 432 site.

Figure 4. Volume-specific sediment carbon content in mangrove forests (black bars) and saltmarshes (grey bars) in Moreton Bay. Values are means and standard errors of 3 plots per site.

Figure 5. Carbon sequestration in g C  $m^{-2}$   $y^{-1}$  in surface sediments in mangrove forests (black) and saltmarshes (grey) at six sites in Eastern and Western Moreton Bay. Values are means and standard errors of 3 plots per site.

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	Surface elevation change mm year <sup>-1</sup>		
	Mangrove	Saltmarsh	
Eastern Moreton Bay			
Amity North	5.89 ± 0.95	-0.08 ± 0.18	
Amity South	$7.05 \pm 0.82$	0.18 ± 0.61	
Adams Beach	6.23 ± 1.11	5.92 ± 0.35	
Western Moreton Bay			
Tinchi Tamba Reserve	$0.41 \pm 0.57$	0.45 ± 0.32	
Nundah Creek	$2.34 \pm 0.56$	1.22 ± 0.92	
Halloran Reserve	2.42 ± 1.21	0.11 ± 0.09	

Table 2. The dominant plant species and growth form and the mean sediment nutrient characteristics (± standard error, N= 9) for mangrove forests and saltmarshes on the eastern and western side of Moreton Bay, Queensland, Australia. Carbon:phosphorus (C:P), nitrogen:phosphorus (N:P) and carbon:nitrogen (C:N) ratios are expressed as molar ratios. Different letters after the means indicate significant differences at P<0.05.

	Eastern Bay		Western Bay	
	Mangrove	Saltmarsh	Mangrove	Saltmarsh
Dominant species	Avicennia marina, Rhizophora stylosa	Juncus krausii	Avicennia marina	Sarcocornia quinqueflora
Plant form	tree	rush	tree	herb
Total phosphorus (mg cm <sup>-3</sup> )	63 ± 7 a	222 ± 74 a	356 ± 51 b	363 ± 49 b
Total nitrogen (g cm <sup>-3</sup> )	0.0157 ± 0.0032 a	0.272 ± 0.139 b	0.204 ± 0.027 b	0.196 ± 0.057 b
C:P	576 ± 45 a	1898 ± 512 b	392 ± 60 a	170 ± 35 c
N:P	6.35 ± 1.0 a	40.4 ± 6.7 b	15.5 ± 1.7 c	12.1 ± 2.5 c
C:N	120 ± 28 a	65 ± 21 b	25 ± 3 c	16 ± 3 c

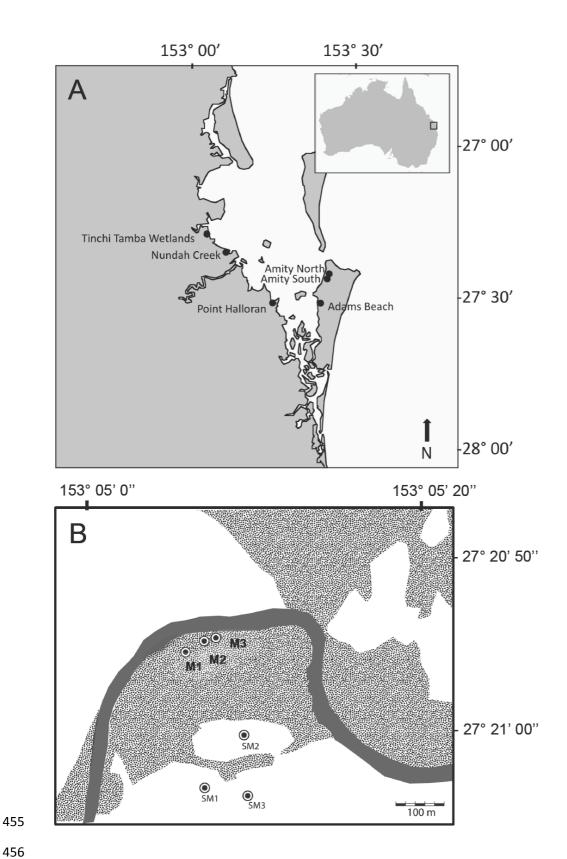
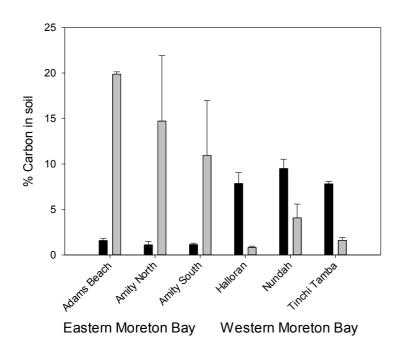


Figure 1. Location of study sites within Moreton Bay, Queensland, Australia (A). An example of the location of the mangrove forest and saltmarsh plots within a study site, in this case Nundah Creek (B). M1, M2 and M3 are within the mangrove forest (stippled), while SM1, SM2 and SM3 are located within the saltmarsh (open).



464 Figure 2

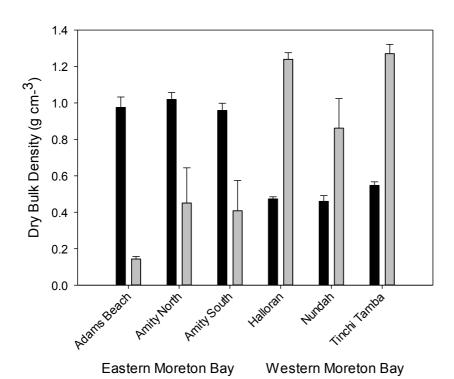
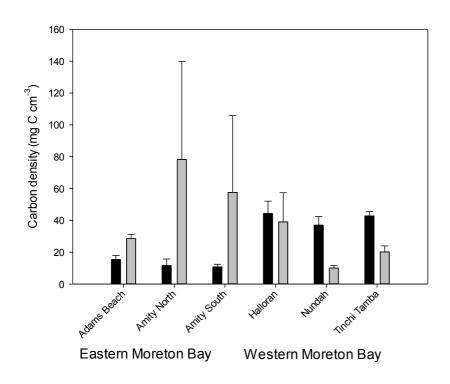
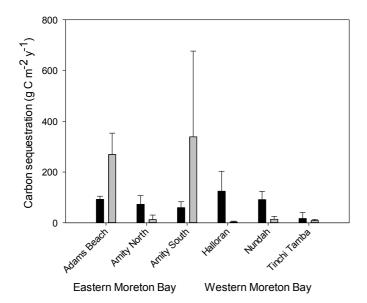


Figure 3.



477 Figure 4.



481 Figure 5.