CARBON STORAGE IN TIDAL WETLANDS OF SOUTHEAST AUSTRALIA

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CERTIFICATE OF ORIGINAL AUTHORSHIP

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree. I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

Signature of Student:

Date: 27th January 2017

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PREFACE

THESIS BY PUBLICATION

This is a thesis by publication. Consequently, there will be some repetition and redundancy of text particularly in the introductory, methods and reference sections of the various chapters. Chapters are formatted according the final publication format of the relevant journal for chapters which have already been accepted for publication (Chapters 2 and 5) or in the format required under submission for review for chapters yet to be published (Chapters 3 and 4). The introductory (Chapter 1) and conclusion (Chapter 6) chapters are not currently intended for separate publication and are therefore presented in a generic format.

PUBLICATIONS ARISING FROM THIS THESIS:

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Osland, M. J., Day, R. H., From, A. S., McCoy, M. L., McLeod, J. L., & Kelleway, J. J. (2015). Life stage influences the resistance and resilience of black mangrove forests to winter climate extremes. *Ecosphere*, 6(9), art160. doi:10.1890/ES15-00042.1

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ABSTRACT

Saltmarshes and mangroves are among the most productive and most at risk ecosystems to the impacts of human activity and climate change, globally. Along with seagrasses, these coastal vegetated ecosystems have been termed 'blue carbon' habitats due to their capacity to accumulate and store C. Consequently, there is interest in the processes which govern C accumulation and storage in these ecosystems and their potential to mitigate climatic change. While previous research has indicated high C stocks and accumulation in saltmarshes, there is substantial spatial variability in saltmarsh C. An understanding of the factors behind this variability is required to better inform regional and global C management. Within the study region of southeast (SE) Australia, this thesis therefore aims to: quantify and characterise saltmarsh C stocks; determine the role of geomorphic and vegetation factors in C accumulation and storage; assess variations in quantity and character of C with sediment depth and in relation to environmental change.

Analysis of sediment cores collected from 18 sites revealed mean (± SE) belowground C stocks of 164.45 ± 8.74 Mg C ha^{-1}, comparable to global values. Stocks were more than two times higher in fluvial (226.09 ± 12.37 Mg C ha^{-1}) relative to marine (104.54 ± 7.11) geomorphic sites, but did not vary between the saltmarsh vegetation structures tested. Vegetation type, however, was determined to play an important role in surface accumulation with mid- (19 month) and short-term (6 d) measures showing faster C accumulation in upper marsh rush saltmarsh relative to both succulent and grass lower marsh assemblages. Additionally, the encroachment of saltmarsh by high biomass mangrove trees and shrubs was shown to bring about substantial increases in C storage in both biomass and belowground C stocks. While there were general trends of decreasing C content with sediment profile depths, this was not always the case. The preservation of deep mangrove roots (in both contemporary saltmarsh areas as well as areas currently under mangrove encroachment) and/or remnant stable C sources (including char) were both responsible for peaks in C density down profile.

This thesis improves our understanding of the processes influencing coastal wetland C storage, with implications for the prioritisation of planning policies and on-ground activities which aim to maximise the benefits from wetland protection and restoration. Such initiatives have the potential to increase overall C storage, thereby presenting a negative feedback to global warming, while also presenting other ecosystem service benefits.

CHAPTER ONE

INTRODUCTION AND RESEARCH RATIONALE

1. Introduction

Coastal vegetated ecosystems – that is, saltmarshes, mangroves and seagrasses - contribute nearly 50% of the carbon (C) burial in marine sediments, despite occupying just 0.2% of the ocean surface (Chmura *et al.*, 2003, Duarte *et al.*, 2013, McLeod *et al.*, 2011). Together, these ecosystems have been termed ‘blue carbon’ habitats (Nellemann *et al.*, 2009) due to this exceptional capacity to accumulate and store C, potentially for centuries or millennia (Lo Iacono *et al.*, 2008, McKee *et al.*, 2007). Consequently, there has been growing interest in processes which govern C accumulation and storage in these ecosystems (Lavery *et al.*, 2013, McLeod *et al.*, 2011, Ouyang & Lee, 2014) and their potential to mitigate climatic change associated with anthropogenic inputs of C to the earth’s atmosphere (Duarte *et al.*, 2013, Murdiyarso *et al.*, 2015, Siikamäki *et al.*, 2013, Ullman *et al.*, 2013). This thesis focusses on the C dynamics of saltmarshes, but also considers saltmarsh-mangrove interactions.

2. Intertidal wetlands

2.1 Vegetation and distribution

Coastal saltmarshes are tidal wetlands vegetated by herbs, grasses, rushes and small shrubs which provide a permanent or temporary habitat for aquatic, intertidal and terrestrial fauna. They are dynamic ecosystems occurring in a range of sedimentary settings along low-energy coastlines and have a wide geographic distribution globally (Adam, 1993, Adam, 2002, Hoekstra & Molnar, 2010; Figure 1A), throughout Australia (Bucher & Saenger, 1991, Saintilan, 2009), and across the southeastern (SE) Australian state of New South Wales (NSW)(Creese *et al.*, 2009, West *et al.*, 1985) - the latter of which is the geographic focal point of this thesis.

The vegetation of SE Australian saltmarshes has been well studied. Comprehensive classifications have been made of plant community structure and composition of the central NSW coast in particular (Adam *et al.*, 1988, Zedler *et al.*, 1995). In the Sydney region, studies have focused on vegetation description and distribution (Clarke & Hannon, 1967, Hamilton, 1919), plant response to salinity and waterlogging (Clarke & Hannon, 1970), species interactions (Clarke & Hannon, 1971), relationships with mangroves (Mitchell & Adam, 1989, Pidgeon, 1940, Saintilan & Hashimoto, 1999), and restoration procedures (Laegdsgaard, 2002). These studies show the major controls on saltmarsh vegetation distribution to be elevation within the tidal frame, frequency of waterlogging, freshwater inputs and consequently, soil salinity.

Saltmarsh communities generally have low floral species richness compared to terrestrial communities, often being dominated by one or two species (Adam *et al.*, 1988). Along the NSW coast, for example, the majority of mid-intertidal marsh is considered a single community complex dominated by the low growing chenopod *Sarcocornia quinqueflora* and grass *Sporobolus virginicus* (Zedler *et al.*, 1995) and upper marsh communities by the rush *Juncus kraussii* (Adam *et al.*, 1988). Throughout SE Australia, saltmarshes are generally bordered by mangroves (intertidal trees and dwarf trees/shrubs) to the lower, estuarine side and terrestrial vegetation communities to the higher, landward side.

Globally, saltmarshes share a similar ecological niche in the intertidal zone with mangroves, though the two have different but overlapping latitudinal distributions. Mangrove range is limited chiefly by physiological intolerance to sub-freezing temperature, with most species confined to tropical or sub-tropical climes (Duke *et al.*, 1998, Giri *et al.*, 2011; Figure 1B). In contrast, saltmarshes appear to be less constrained by temperature, being found from tropical through to arctic zones, though extent and species diversity is greater in higher latitudes (Adam, 1993, Friess *et al.*, 2012), where mangrove distributions decline.

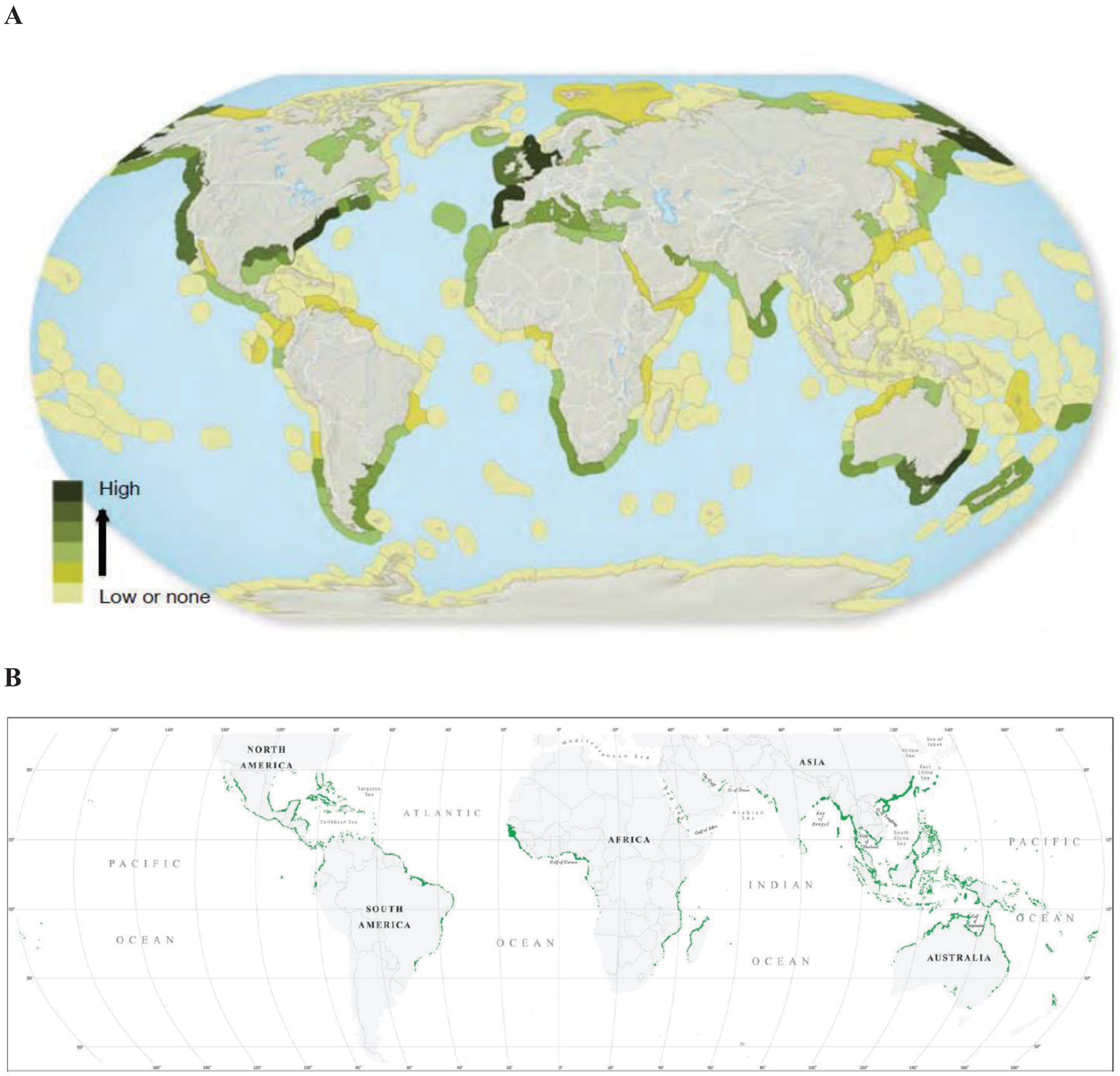

Figure 1. Global distribution of tidal salt marsh abundance by marine ecoregion (Hoekstra & Molnar, 2010) (A) and mangrove forest distribution (Giri *et al.*, 2011) (B).

2.2 Estuarine geomorphology

Within their physiological limits, saltmarshes are found in a variety of low wave energy settings, often associated with estuaries, but they may also grow along barrier islands, spits, embayments and low energy open shores (Adam, 2002, Allen, 2000). As NSW has a high energy open coastline, coastal wetlands, including saltmarshes and mangroves are limited to estuaries and marine embayments where hydrodynamic energy is sufficiently reduced to allow colonisation and survival of plants (Saintilan *et al.*, 2009, Saintilan & Williams, 1999, West *et al.*, 1985). Around the mainland coast of

Australia, saltmarsh is generally also restricted to the upper intertidal environment - i.e. approximately between the elevation of the mean high tide and the mean spring tide (Saintilan *et al.*, 2009).

The distribution of suitable intertidal habitat is partly a function of the historic development of an estuary in relation to sea level. Along the NSW coast, the most recent phase of estuarine sedimentation is thought to have initiated about 7000 – 8000 years ago near the end of the Post-glacial Marine Transgression (Roy, 1984, Roy & Thom, 1981). Since then, rates of infilling of individual estuaries have varied widely depending on the sediment load carried by rivers and the hydrodynamic conditions that transport sediment into the estuary (Roy *et al.*, 2001).

2.2.1 Types of estuaries in New South Wales

Barrier estuaries are the dominant geomorphic form of estuaries along the NSW coast (Roy *et al.*, 2001). These estuaries have tidal inlets that are constricted by wave-deposited sands, and consequently tidal ranges within estuary basins are usually considerably less (~ 5-10%) than the ocean (Roy *et al.*, 2001). Drowned valley estuaries typically occupy deeply incised bedrock valleys that open into semi-protected bays. Though less numerous, drowned valley estuaries contain larger spatial coverage of mangrove and saltmarsh on average per estuary (Roy *et al.*, 2001, West *et al.*, 1985), as most are associated with large coastal rivers and support wide, deltaic intertidal flats created during the infilling (i.e. geomorphic evolution) of these estuaries (Saintilan *et al.*, 2009). Saline coastal lagoons which have estuary mouths which are intermittently closed (due to small catchments/river discharges) represent the third broad geomorphic type of estuary to support significant saltmarsh extent in NSW.

2.2.2 Geomorphic zones

In each of the estuary types described above there are four distinct sedimentary environments which have characteristic water quality, nutrient cycling/primary productivity signatures and intertidal ecosystem coverage (Roy *et al.*, 2001). From the sea to upstream, these are the marine tidal delta, central mud basin, fluvial delta and riverine channel (Figure 2). Along the central coast of NSW, saltmarsh (and mangrove) may be found in any of these geomorphic zones, however coverage of saltmarsh is often greatest on deltas that develop where tributaries enter deeper waters (fluvial delta) and on back-barrier sands near the estuary mouth (marine tidal delta) (Kelleway *et al.*, 2007, Roy *et al.*, 2001, Saintilan & Rogers, 2013, West *et al.*, 1985).

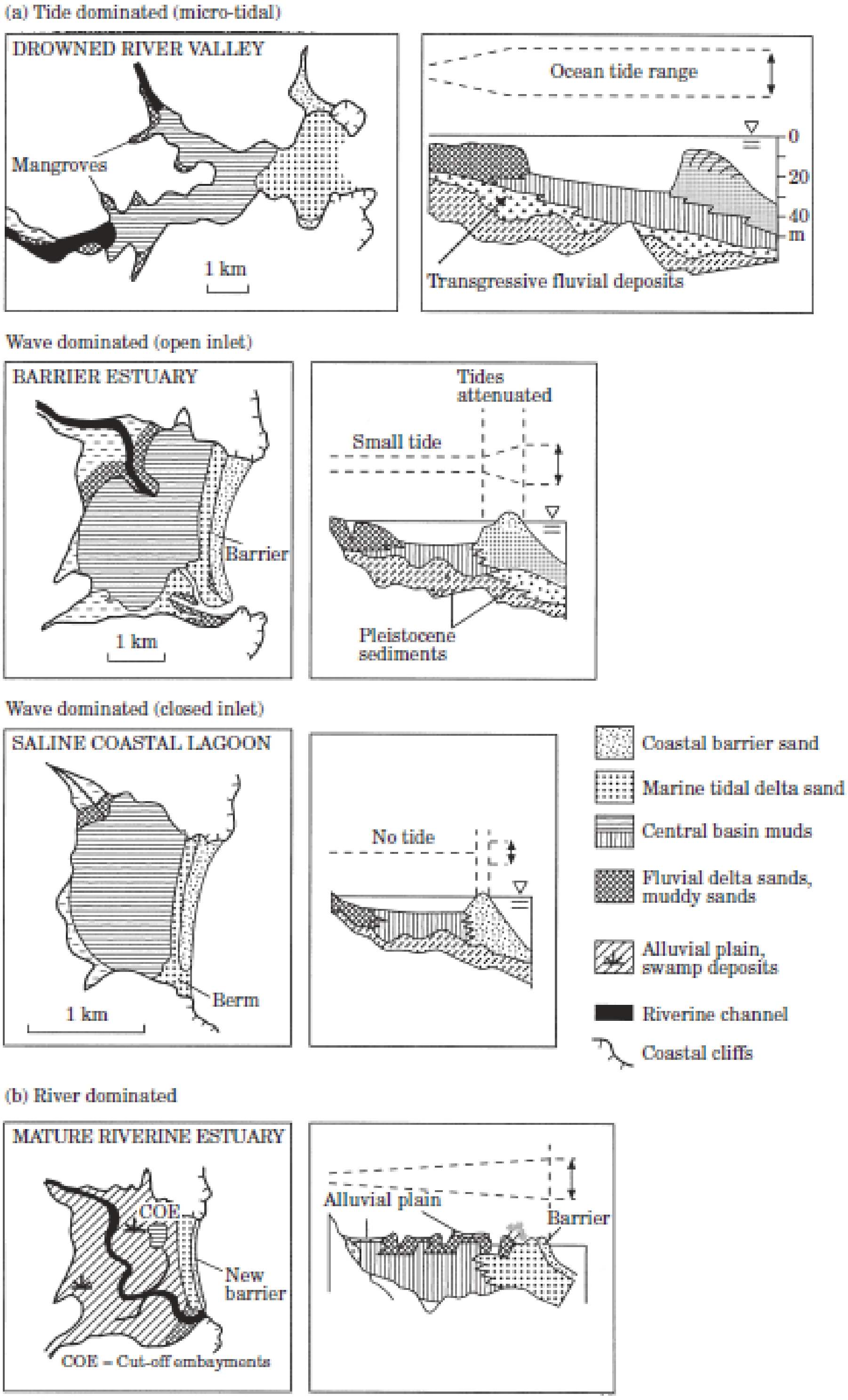

Figure 2. Idealised sediment distributions of the three main estuary types estuary in New South Wales (1. Drowned river valley; 2. Barrier estuary; 3. Saline coastal lagoon) (a). Within each estuary type, there are four broad geomorphic zones – the riverine channel, fluvial delta, central mud basin and marine tidal delta. Infilling of the estuary causes migration of the geomorphic zones until the system eventually becomes a mature riverine estuary (b) (Roy *et al.*, 2001).

2.3 Status and history

The most recent mapping of saltmarsh across NSW reports a state-wide aerial extent of 72.6 km^2, which is smaller than the extent of both mangroves and seagrasses (Table 1). The increase in saltmarsh extent relative to previous survey - i.e. 59.1 km^2 reported by (West *et al.*, 1985) –does not necessarily reflect an increase in distribution, but more likely improvements in the resolution of mapping effort and technology used (Kelleway *et al.*, 2009). In fact, a major factor in the modest contemporary coverage of saltmarsh is the scale of historic habitat loss. In SE Australia, it has been estimated that up to 70% of the aerial extent of coastal wetlands has been lost since European settlement, primarily due to agricultural drainage and structural flood mitigation works (Rogers *et al.*, 2015, Zann, 2000). The combination of such historic losses plus contemporary threats to remaining wetland extent is especially acute for saltmarshes, which are particularly subject to modification and destruction by human activity (Adam, 2002). In NSW this has led to the listing of coastal saltmarshes as an 'Endangered Ecological Community' under both the NSW *Threatened Species Conservation Act 1997* and the Commonwealth *Environmental Protection and Biodiversity Conservation Act 1999*. It has also sparked interest in management activities which might reverse the historic decline of saltmarsh extent and associated ecosystem services (Laegdsgaard *et al.*, 2009).

Table 1. Distribution of blue C habitats (saltmarsh, mangrove, seagrass) along the NSW coast of SE Australia. Data are derived from Creese *et al.* (2009) and are presented by former Catchment Management Authority (CMA) area.

		Area (km^2)	
CMA	**Seagrass**	**Mangrove**	**Saltmarsh**
Northern Rivers	15.9	36.3	22.4
Hunter - Central Rivers	92.1	54.9	32.8
Hawkesbury Nepean	2.8	10.0	2.9
Sydney Metro	7.8	8.4	1.9
Southern Rivers	42.0	16.3	12.6
NSW total	**160.6**	**125.9**	**72.6**

2.4 Saltmarsh and mangrove dynamics

Despite their somewhat opposing latitudinal distribution, saltmarsh and mangrove distributions often overlap along temperate and sub-tropical coastlines, forming adjacent and/or ecotonal communities in the intertidal zone (Osland *et al.*, 2013, Rogers *et al.*, 2006). In recent years, however, there has been growing awareness of changes in saltmarsh-mangrove dynamics along such coasts. Specifically, a poleward expansion of mangrove has been now been reported on each of the continents mangroves and saltmarshes co-inhabit - Asia, Africa, Australia/New Zealand, North America and South America (Saintilan *et al.*, 2014 and references therein). In south-eastern Australia, an upslope encroachment by mangroves (which generally occupy a lower position in the intertidal zone in this region) into saltmarsh communities is a near ubiquitous trend (Saintilan & Williams, 1999; Saintilan *et al.*, 2014). Mangrove expansion within areas previously dominated by saltmarsh species has also been reported in the Gulf of Mexico, with mangroves often growing at slightly higher elevations than the dominant saltmarsh species here, *Spartina alterniflora* (Bianchi *et al.*, 2013, Comeaux *et al.*, 2012). At a global scale, mangrove encroachment of saltmarsh may be driven by a suite of changing environmental factors favouring mangrove, including rising sea level, elevated atmospheric CO_2 and higher temperatures (McKee et al., 2012, Saintilan et al., 2014). In SE Australia, mangrove encroachment of saltmarsh was one of the principal factors behind reductions in the spatial extent of saltmarsh during the twentieth century (Saintilan & Williams, 2000).

3. An introduction to 'blue carbon'

There are three main reasons for the disproportionate contribution of 'blue C' habitats to global C pools. First, they are highly productive ecosystems converting CO_2 into plant biomass C, much of which is stored belowground (Alongi, 2002, Nixon, 1980). Second, they are depositional environments which trap particulate C from within the ecosystem (*autochthonous* C, including host plant litter or benthic algal biomass) and/or from external sources (*allochthonous* C, including particulate C derived from river catchment and/or marine sources) (Kennedy *et al.*, 2010, McLeod *et al.*, 2011, Saintilan *et al.*, 2013). Third, low oxygen conditions within sediments slow the decay of belowground organic matter (OM) and allow C to accumulate over centuries and millennia (Fourqurean *et al.*, 2012, Kristensen *et al.*, 2008, McLeod *et al.*, 2011). In essence therefore, the capacity of coastal wetlands to store C in the long-term is dependent upon the balance between OM inputs and their decay (Kirwan *et al.*, 2013). The factors which influence these inputs and decay will now be introduced in greater detail.

3.1 Productivity and biological factors

Saltmarshes and mangroves are among the most productive ecosystems in the world, with both considered net autotrophic ecosystems (Alongi, 2002, Gattuso *et al.*, 1998, Nixon, 1980). Generally, mangroves are more net autotrophic than saltmarshes (Gattuso *et al.*, 1998) with C storage potential associated with plant biomass much higher in mangroves (237-563 tonnes CO_2 equivalent ha^{-1}) than saltmarshes (12-60 tonnes CO_2 equivalent ha^{-1}) (Murray *et al.*, 2011). Currently very little biomass data is available from Australian temperate settings. Data that do exist suggest that aboveground biomass may be highly variable: (1) within a site; (2) between sites in the same estuary; and (3) between dominant plant species (Table 2). Importantly, these data support global observations of significantly higher standing biomass in mangrove over saltmarsh species, but also point to a differentiation between rush (*J. kraussii*) and grass/succulent (*S. virginicus/S. quinqueflora*) saltmarshes.

Saltmarsh C sequestration capacity may also be influenced by other biological processes. For instance, Australian saltmarsh invertebrates perform a range of ecosystem functions including the decomposition of OM (Roach & Lim, 2000) and the aeration and chemical alteration of sediments (Clarke & Hannon, 1967). Variations in plant species composition, primary productivity (including aboveground versus belowground allocation of biomass), decomposition and biological processes such as herbivory and bioturbation are likely to operate across spatial and temporal scales, potentially with implications for saltmarsh C dynamics. Trophic imports and exports may also represent C movement between saltmarshes and adjacent systems (e.g. Guest & Connolly, 2006, Mazumder *et al.*, 2009), however, these are considered outside of the scope of this thesis.

Table 2 - Published biomass estimates for temperate Australian saltmarsh and mangrove species. Mean (and range) data are presented in kg dry weight m^{-2}

Ecosystem	Species	Location	Total Biomass	Aboveground	Belowground	Reference
Mangrove	*Avicennia marina*	Hawkesbury River	36.94	26.19 (0.89 - 65.03)	10.75 (4.80 – 16.52)	Saintilan (1997)
Mangrove	*Aegiceras corniculatum*	Hawkesbury River	20.68	13.04 (1.89 – 35.87)	7.64 (4.03 – 18.12)	Saintilan (1997)
Mangrove	*Avicennia marina* (dwarf)	Hawkesbury River				Saintilan (1997)
		- Hypersaline point bars:	5.21			
		- Hypersaline marine:	6.01			
Mangrove	*Aegiceras corniculatum* (dwarf)	Hawkesbury River				Saintilan (1997)
		- Hypersaline point bars:	5.49			
		- Hypersaline marine:	5.25			
Saltmarsh	*Sarcocornia quinqueflora*	Jervis Bay (Currambene Creek and Carama Inlet)		0.32 (0.05 – 1.18)		Clarke and Jacoby (1994)
Saltmarsh	*Sporobolus virginicus*	Jervis Bay (Currambene Creek and Carama Inlet)		0.35 (0.15 – 0.85)		Clarke and Jacoby (1994)
Saltmarsh	*Juncus kraussii*	AGB: Port Hacking, Jervis Bay, Batemans Bay; BGB:		1.12 (0.10-4.40)		Clarke and Jacoby (1994)
Saltmarsh	*Juncus kraussii*	Jervis Bay (Carama Inlet & Moona Moona Ck)				Clarke and Jacoby (1994)
		- Surface:			0.54 (0.15 – 1.64); 0.19 (0.05 – 0.48)	
		- 10-20 cm depth:				
Saltmarsh	*Juncus kraussii*	Blackwood River Estuary, Western Australia		1.43 (1.08-2.07)	0.98 (0.52-1.65)	Congdon and McComb (1980)

3.2 Surface accumulation

Saltmarsh sediments may be minerogenic (dominated by mineral inputs) or organogenic (dominated by biomass, litter production and/or allochthonous OM inputs), although most sediments comprise both mineral and organic fractions (Adam, 2002, Baustian *et al.*, 2012). Saltmarshes (as well as mangroves and seagrasses) are highly efficient in trapping sediment and associated organic C – whether it originates from autochthonous or allochthonous sources (McLeod *et al.*, 2011). Consequently, the rate of surface C accumulation is extremely high in saltmarshes relative to terrestrial and most coastal ecosystems, globally (Ouyang & Lee, 2014). While much of this C is produced belowground by roots and rhizomes (Bull *et al.*, 1999, Howes *et al.*, 1985), contributions from aboveground sources may be significant (Boschker *et al.*, 1999, Zhou *et al.*, 2006).

Surface elevation and sedimentation dynamics are central to both coastal wetland survival under rising sea level (Baustian *et al.*, 2012, Kirwan & Megonigal, 2013) as well as the delivery and storage of OM (Duarte *et al.*, 2013, Lovelock *et al.*, 2013). There is now growing evidence of the capacity of coastal wetlands to keep pace with sea level rise in certain situations by increasing surface elevation through belowground production, enhanced trapping of sediments, or a combination of the two (Baustian *et al.*, 2012, Krauss *et al.*, 2014, McKee *et al.*, 2007). Where wetland assemblages are unable to maintain a suitable elevation relative to inundating water levels then vegetation shifts may occur, including the loss of marsh vegetation (Day Jr *et al.*, 1999, Day *et al.*, 2011, Rogers *et al.*, 2006). While wetland surface elevation is a function of multiple factors, including belowground production and decomposition, groundwater dynamics and sedimentary and regional subsidence (Cahoon *et al.*, 1999, Rogers & Saintilan, 2008), the retention of aboveground inputs plays a critical role in wetland survival under changing hydrological conditions (Day *et al.*, 2011).

3.3 Preservation conditions

Sediments in blue C ecosystems are frequently waterlogged due to their position within subtidal (seagrasses) or intertidal (seagrasses, mangroves, saltmarshes) elevations. Due to low oxygen diffusion in water-saturated sediments, microbial decomposition of OM in blue C sediments occurs mainly through anaerobic metabolic pathways (Howes *et al.*, 1984, King, 1983, Lord Iii & Church, 1983), whereby alternative electron acceptors (i.e. NO_3^-; Mn^{4+} Fe^{3+}, SO_4^{2-}) substitute O_2 (Ponnamperuma, 1972). As anaerobic metabolism of OM is a much less efficient process than aerobic metabolism, anaerobic conditions are more conducive to the preservation and therefore accumulation of C in coastal sediments (Burdige, 2007, Chmura, 2013, Kristensen *et al.*, 2008). The abundance of sulphate in marine sediments, including saltmarshes, allows sulphate-reducing bacteria to outcompete methanogens for energy sources, thereby limiting methane production (Bartlett *et al.*, 1987, Kristensen *et al.*, 2008). This may be of significance to the net capacity of a site to act as a C sink or source once the radiative forcing of atmospheric methane emissions is taken into account. Importantly, the decomposition of OM (whether through aerobic or anaerobic pathways) also increases the diversity of biomolecules in soils and sediments as microbes transform source materials, synthesise additional biochemicals for their own growth and excrete products of metabolic activity (Baldock *et al.*, 2013, Grandy & Neff, 2008).

Finally, because of the effective preservation of C within sediments, belowground C stocks (inclusive of belowground biomass) are the most significant C pool in coastal wetlands (Pendleton *et al.*, 2012). This potential for long-term storage of C – and conversely, the possibility of substantial C emissions if sediments are disturbed – also makes belowground C stocks the primary interest in coastal C initiatives (Sutton-Grier *et al.*, 2014). As sediment physical and chemical properties including bulk density, grain size distribution, moisture content, redox potential and soil salinity may all vary among saltmarsh communities (Adam, 1993, Clarke & Hannon, 1967, Crooks *et al.*, 2002, Vernberg, 1993) it is expected that the capacity of sediments to preserve inputs of C will be subject to significant spatial variability, both within and between saltmarsh sites.

4. Measuring Blue C

There are multiple ways in which the C sequestration and related bulk sediment dynamics are quantified and reported. The three measures most applicable to this thesis are illustrated in Figure 3 and detailed below.

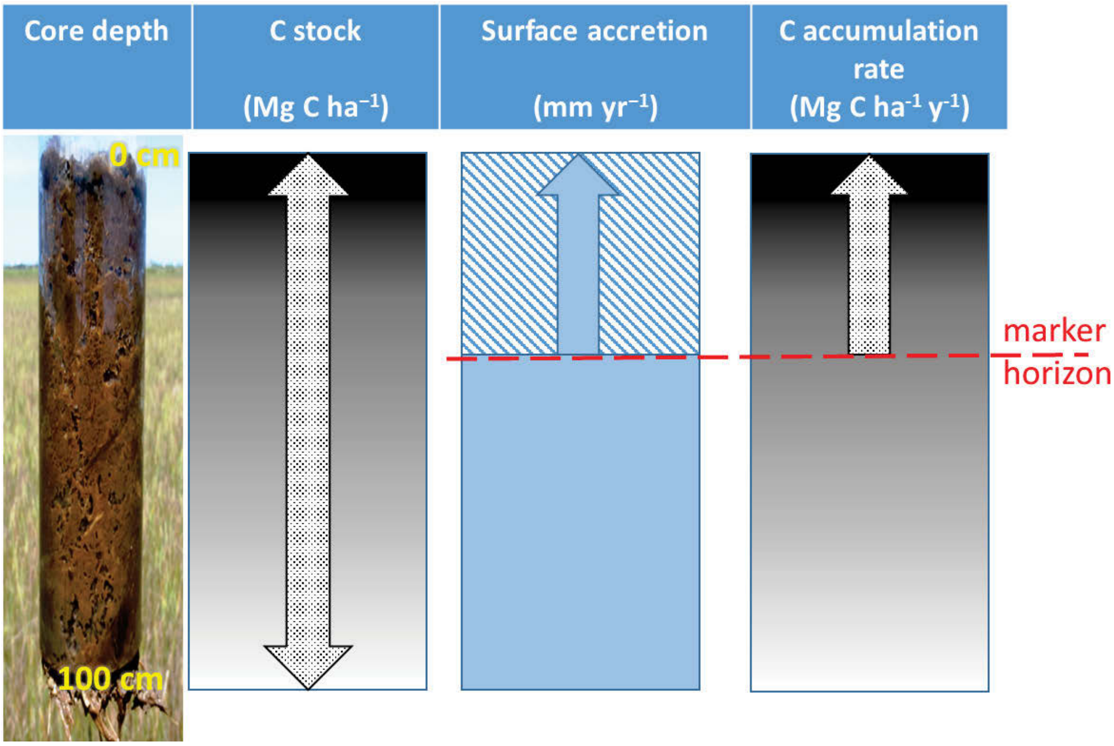

Figure 3. Schematic diagram of common C and surface accumulation parameters. C stock is generally reported as the density of C integrated over a 100 cm depth range of soil coring. Surface accretion and C accumulation rates are normally measured as an annual rate of addition above a physical or radiometric dating marker horizon. Surface accretion is a measure of bulk sediment (i.e. it is not directly related to C), while C accumulation rates are specific to the amount of C accumulating above the marker horizon.

4.1 Belowground C stocks

Belowground C stocks comprise both living belowground biomass and the non-living sediment C pool. As these two pools are often difficult to separate, most studies quantify them as a single ‘belowground C’ pool (Chmura *et al.*, 2003). Belowground C stocks in terrestrial and agricultural soils are typically characterised over the surface 30 cm, corresponding to depth to which activities such as tilling may affect the soil pool. In blue C habitats, however, it is standard practice to quantify C over the surface 100 cm (Howard *et al.*, 2014), because: 1) blue C habitats generally have organic rich deposits ranging up to much greater depths than terrestrial soils; and 2) disturbance to blue C habitats will likely affect stocks within the surface metre (Pendleton *et al.*, 2012).

4.2 Surface accretion

Surface accretion generally refers to the bulk vertical accumulation of material upon the surface (benthos) of a wetland (Cahoon & Turner, 1989). It is inclusive of both mineral and organic materials and consequently is not itself a quantification of C. Surface accretion measures are not only indicative of the capacity of an ecosystem to capture and accumulate materials, but are also of particular relevance (along with belowground processes) to the fate of tidal wetlands in response to changes in sea-level (Lovelock *et al.*, 2015, Rogers *et al.*, 2014, Rogers *et al.*, 2006).

4.3 C accumulation rates

Surface accumulation measures may be combined with C concentration data to determine surface C accumulation rates. C accumulation rates may be calculated on the basis of short to medium term (days to years) measures of surface accumulation (such as marker horizons) or longer term (decades to centuries) radiometric dating methods.

5. Estimates and variability of Blue C

Although coastal vegetated ecosystems are widely recognised as important sites of long-term C storage, substantial spatial variability exists in quantifications of these ‘blue C’ stocks at a global scale (Table 3). Globally, the mean rate of surface C accumulation is very high in saltmarshes (2.45 Mg C ha^{-1}), relative to terrestrial and most coastal ecosystems, however, there is also substantial variability associated with this measure (Ouyang & Lee, 2014).

Until recently, quantifications of coastal C in Australia were largely limited to mangrove ecosystems with a geographical bias toward the tropics (e.g. Alongi *et al.*, 1998, Brunskill *et al.*, 2002, Clough, 1998, Lovelock, 2008). In more recent years advances have been made in understanding Australia’s blue C and surface dynamics in sub-tropical latitudes for mangroves and saltmarshes (Adame *et al.*, 2010, Howe *et al.*, 2009, Livesley & Andrusiak, 2012, Lovelock *et al.*, 2013, Lovelock *et al.*, 2011, Rogers *et al.*, 2005, Rogers *et al.*, 2013, Rogers *et al.*, 2006, Saintilan *et al.*, 2013). Despite the obvious increase in the number of studies undertaken, however, most of the C quantifications associated with these studies are taken from a small number of sites and/or within single estuarine systems. To date, only the studies of Lovelock *et al.* (2013) and Saintilan *et al.* (2013) have compared C measurement across multiple estuaries, with only the latter covering a broad latitudinal range. In contrast, a network of surface elevation and accretion monitoring sites in the region (Lovelock *et al.*, 2015, Rogers *et al.*, 2006) provide valuable insight regarding intertidal surface dynamics across a broad geographical range and multiple geomorphic settings.

Notwithstanding spatial limitations, quantifications of blue C in Australia's sub-tropical saltmarshes and mangroves have – like global compilations – exhibited a high degree of variability. For example, comparisons of C stocks in both Westernport Bay, Victoria (Livesley & Andrusiak, 2012), and disturbed and undisturbed wetlands of the Hunter estuary, New South Wales, (Howe *et al.*, 2009) have found higher C stocks in saltmarsh relative to mangrove. Both of these localised studies, however, are at odds with broader comparison of saltmarsh and mangrove stocks in the region, which has shown the opposite to be true – i.e. C stocks are significantly higher in mangroves relative to saltmarshes (Saintilan *et al.*, 2013; Table 3). The regional comparison of Saintilan *et al.* (2013) also displayed differences among saltmarshes with those vegetated by *Juncus* containing greater C stocks than *Sarcocornia/Sporobolus* saltmarshes. Among mangrove and saltmarsh measurements, belowground C store also varied with geomorphic setting (fluvial > marine) though the relationship was weak ($P = 0.0699$). Across all sites the authors concluded C storage is high in temperate settings, particularly in mesotidal and fluvial geomorphic settings.

Similarly, sampling across multiple sites in Moreton Bay, Queensland, highlighted spatial differences in saltmarsh belowground C density with *Juncus* saltmarshes containing higher sediment C densities than *Sarcocornia* marshes (Lovelock *et al.*, 2013). However, attempts to ascertain C stock differences according to environmental setting (i.e. marine-influence oligotrophic island versus estuarine-influenced eutrophic sites) may have been confounded by differences in the vegetation composition of sites in each setting.

Together, these initial studies suggest Australian temperate saltmarshes contain a significant density of belowground C, within the range of values reported globally (Chmura *et al.*, 2003, Ouyang & Lee, 2014). Whilst comparative data from mangroves and saltmarshes in SE Australia broadly suggest that C stocks should increase with mangrove encroachment of saltmarsh, such findings are not universal (Howe *et al.*, 2009, Livesley & Andrusiak, 2012) and no specific measurements across encroachment fronts have been made to date.

Table 3. Literature values of belowground C stock, bulk surface accretion rates and C accumulation rates reported for saltmarsh and mangrove ecosystems globally and within SE Australia. For SE Australian saltmarsh, differences among *Juncus kraussii* (*Juncus*) and *Sarcocornia quinqueflora / Sporobolus virginicus* (*Sarc/Spor*) association saltmarshes are also provided. Values in parentheses indicate 1 standard deviation except where stated otherwise.

Ecosystem - Region	**Belowground C stock (Mg C ha^{-1})**	**Accretion rate (mm yr^{-1})**	**C accumulation rate (Mg C ha^{-1})**	**Reference**
Saltmarsh - Global	162 (max = 259)[a]	6.73 (0.7)[b]	2.45(3.12)[c]	[a] Pendleton *et al.* (2012) [b] Gattuso *et al.* (1998) [c] Ouyang and Lee (2014)
Saltmarsh - SE Australia	191 (range = 61-343)[d] *Juncus* > *Sarc/Spor*[d,f]	2.23 (range = 0.50 – 5.93)[e] *Juncus* = 1.76 (1.00)[d] *Sarc/Spor* = 1.11 (0.08)[d]	2.75[c] *Juncus* = 2.07 (1.32)[d] *Sarc/Spor* = 0.46 (0.37)[d]	[c] Ouyang and Lee (2014) [d] Saintilan *et al.* (2013) [e] Rogers *et al.* (2006) [f] Lovelock *et al.* (2013)
Mangrove - Global	255[g] (max = 684)[h]	5.47 (0.38)[b]	1.63 (95% CI = 1.32-2.03)[i]	[b] Gattuso *et al.* (1998) [g] Siikamäki *et al.* (2012) [h] Donato *et al.* (2011) [i] Breithaupt *et al.* (2012)
Mangrove - SE Australia	231 (range= 25-343)[d]	5.04 (range= 0.65 – 9.49)[e]	2.56 (2.24)[d]	[d] Saintilan *et al.* (2013) [e] Rogers *et al.* (2006)

6. Research Rationale and Aims

The following section summarises the state of science for four topics central to the C dynamics of saltmarshes in SE Australia. Gaps in knowledge are identified and research strategies which address these gaps and further our understanding are proposed. This section closes with an outline of the three broad research aims of this thesis.

6.1 Quantification of blue C stocks and accumulation in NSW saltmarshes

The saltmarshes and mangroves of SE Australia have been the subject of a broad array of studies which have greatly contributed to global understanding of tidal wetland geomorphology, vegetation distribution and biogeography, trophic energetics, and wetland responses to anthropogenic, climatic and sea level changes. Despite this rich research environment, comparatively little is known about the blue C of the region's saltmarshes and mangroves. While there has been an increase in blue C studies over recent years, for the most part these are limited to a small number of sites in few estuaries. In NSW, blue C data for saltmarshes is limited to just eight out of the >130 estuaries which are known to support saltmarsh (Creese *et al.*, 2009) and are biased toward the central section of the coast (i.e. the ~230 km section from the Hunter River to Jervis Bay).

Broad-scale survey of state's coastline, across a diversity of estuary types and previously unquantified locations is required to complement the limited datasets currently available. Such research effort may also provide insights into the processes which are most important to blue C storage as well as drivers of spatial variability.

6.2 Drivers of blue C variability

Whilst regional datasets from SE Australia indicate high C stocks and accumulation rates comparable to saltmarshes globally (Table 3), they also highlight the massive variability in saltmarsh C from local through to global scales (Duarte *et al.*, 2013). An understanding of the factors behind this variability, as well as improved knowledge of the key processes mediating C sequestration in these habitats is therefore required to better inform regional and global C management.

To date, comparative studies across multiple estuaries have suggested an overarching role of vegetation structure (mangrove versus *Sarcocornia/Sporobolus* saltmarsh versus *Juncus* saltmarsh) in defining spatial variability of blue C stocks and accumulation rates (Lovelock *et al.*, 2013, Saintilan *et al.*, 2013). It remains largely unknown however, whether differences among vegetation structural types are related to vegetative factors, physical factors influencing the distribution of the different vegetation types, or interactions among the two.

Outcomes of sedimentation dynamics research across a range of geomorphic settings (Oliver *et al.*, 2012, Rogers *et al.*, 2005, Rogers *et al.*, 2006) as well as relationships between geomorphology and ecosystem form and function (Roy *et al.*, 2001, Saintilan, 2004, Saintilan & Hashimoto, 1999, Saintilan & Wilton, 2001) provide a strong theoretical basis for improved testing of the role of geomorphic parameters on blue C dynamics (Figure 4). While the two comparative studies discussed above did report C variability among geomorphic factors, relationships were generally weaker than those observed for vegetation structure (Lovelock *et al.*, 2013, Saintilan *et al.*, 2013). The findings from these studies, however, may be confounded by unbalanced experimental designs, whereby different vegetation structures were not necessarily assessed within the same geomorphic settings. It therefore remains unclear to what extent vegetation and geomorphic parameters dictate blue C variability in SE Australia, and what interactions between the two might be important. This highlights the need for a robust experimental design to differentiate the relative roles of both geomorphic setting and vegetation types, and their interactions.

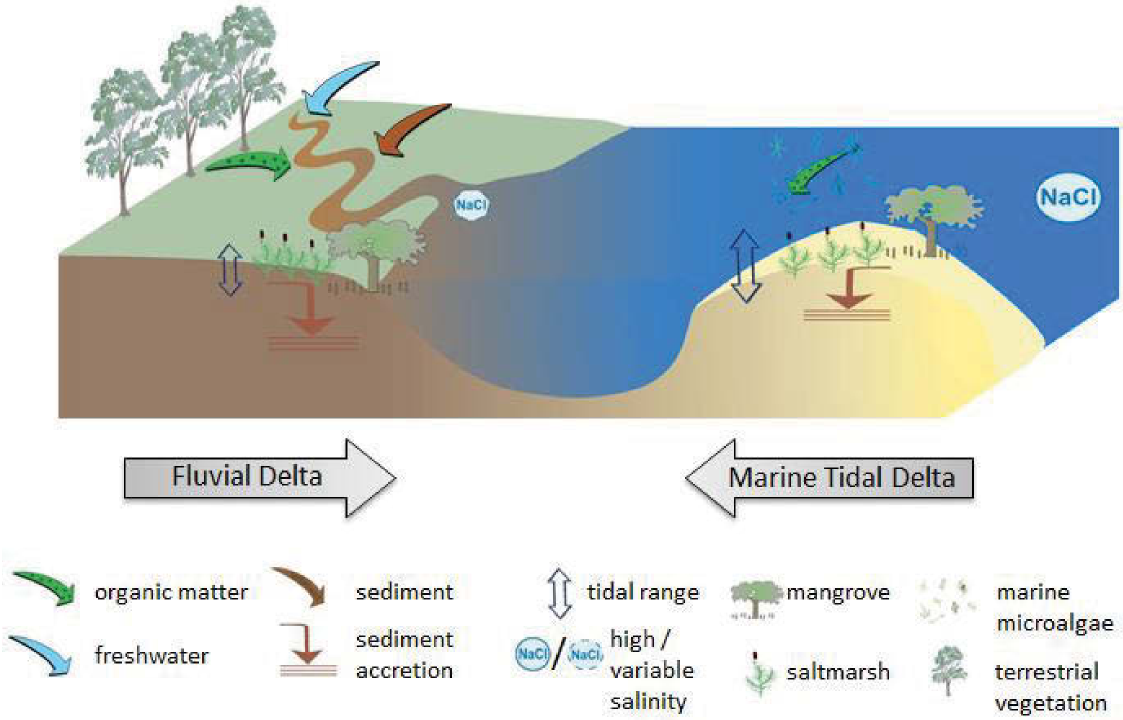

Figure 4. Conceptual diagram of potential influences on saltmarsh C dynamics in fluvial delta and marine tidal delta geomorphic zones. Differences in geomorphic setting are likely to influence a range of geochemical conditions (e.g. concentration and variability of salinity) and hydrological conditions (e.g. tidal range and suspended sediment loads) relevant to growth of vegetation as well as sediment C accumulation. Fluvial delta wetlands have greater proximity to terrestrial sources of C which enter the estuary through catchment runoff, while marine tidal delta wetlands may be subject to more marine sources of C.

6.3 Understanding relationships between surface accretion, C accumulation and sea level rise

Globally, there is a growing awareness and understanding of the biological, physical and interactive processes which influence tidal wetland surface elevation dynamics and response to changes in sea level. Studies investigating these processes, however, are largely focussed on northern hemisphere saltmarshes of the genus *Spartina* (e.g. Baustian *et al.*, 2012, Mudd *et al.*, 2010, Mudd *et al.*, 2009, Nyman *et al.*, 2006), which does not occur in SE Australia. While research conducted in SE Australian saltmarshes and mangroves has been integral to understanding bulk sediment dynamics (Lovelock *et al.*, 2015, Rogers *et al.*, 2012, e.g. Rogers *et al.*, 2006), data are limited within the region regarding the contribution of autochthonous versus allochthonous materials to bulk sediment accretion and C accumulation. For example, the only research to investigate the sources of C sequestered in temperate Australian saltmarshes is that of Saintilan *et al.* (2013). Their results suggest an important contribution of autochthonous plant material to the sub-surface

C store, while surface C accumulation appears to be dominated by allochthonous sources. Other than the proposed role of tidal transport for allochthonous C delivery (Saintilan *et al.*, 2013), little is currently known about what above- and below-ground processes may be contributing to this phenomenon. It is also unknown whether C contributions from autochthonous and allochthonous sources differ according to vegetation structure or among geomorphic settings.

Broad-scale characterisations among tidal wetlands are needed to determine variability in C sources and accumulation rates at the estuary level (i.e. among geomorphic settings). In contrast, site-specific process studies will likely be better suited for determining variability in surface dynamics and C accumulation among vegetation types and for determining any biophysical interactions.

6.4 Environmental change and the preservation of blue C

The dynamic nature of environmental conditions and ecosystem structure within the intertidal zone has long been acknowledged (Allen, 2000, Ball, 1980, Pidgeon, 1940). Despite this, relatively few studies have investigated the impacts of ecosystem scale changes on blue C stocks. For example, in terrestrial systems, it has been well acknowledged that shrub encroachment into terrestrial grasslands may incur significant increases in aboveground and belowground C pools (Eldridge *et al.*, 2011 and references therein). In analogous estuarine settings – i.e. mangrove encroachment of saltmarsh – however, attempts to quantify changes in C have been relatively few, geographically restricted to the southern United States, and for the most part have been inconclusive (e.g. Comeaux *et al.*, 2012, Perry & Mendelssohn, 2009), perhaps due to the sporadic nature of encroachment and retreat in relation to freeze events. The more continuous record of mangrove encroachment in Australia presents an opportunity in which to assess the response of ecosystem change on C pools over a longer timeframe.

The dynamic nature of environmental conditions within blue C habitats is seemingly at odds with the long-term stability which their C storage capacity implies. At present there is very little information on the effect of environmental change (whether anthropogenic, climatic, or sea-level related) on the preservation capacity of blue C stocks in SE Australia. Investigations of C stocks and their molecular composition among 1) potential C sources; and 2) various sediment depths may provide insights into the fate of blue C over time as well as the influence of different environmental conditions on C inputs and decay. This thesis will use both historic aerial photograph records and the environmental reconstruction through the analysis of sediment cores to provide new insights into the relationships between ecosystem change and C storage.

6.5 Aims of this thesis

The objectives of this thesis are to address gaps in scientific knowledge identified through analysis of the literature and to lay a platform for the effective management of coastal wetlands in NSW and their associated C sequestration capacity. To achieve these objectives, three broad aims have been defined. This thesis aims to:

- **1.** Quantify and characterise saltmarsh C stocks, including in relation to the phenomenon of mangrove encroachment;
- **2.** Determine the role of geomorphic and vegetation factors in C accumulation and storage;
- **3.** Assess variations in quantity and character of C with sediment depth.

While these three aims operate across the entire thesis, more specific research objectives and hypotheses are presented in each of the four experimental chapters which follow.

7. Thesis structure

Chapter 1 – Introduction and research rationale

(This chapter)

Chapter 2 – Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes

Broad scale survey of saltmarsh belowground C stores along the New South Wales (NSW) coast to determine spatial variability between geomorphic settings and vegetation assemblages.

Chapter 2 has been published in *Ecosystems*:

Kelleway J.J., Saintilan N, Macreadie P.I., Ralph P.J. (2016) Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes. *Ecosystems*. DOI: 10.1007/s10021-016-9972-3

Chapter 3 – Sediment and carbon accumulation vary among vegetation assemblages in a coastal saltmarsh

Marker horizon study comparing rates of accretion, C content, source and stability between different vegetation assemblages.

Chapter 3 has been formatted for submission to *Biogeosciences*.

Chapter 4 – Geochemical analyses reveal the importance of environmental history for blue carbon sequestration

Environmental reconstruction and detailed analysis of sediment cores collected from four different sites to determine the importance of environmental history and C preservation to contemporary measures of C stocks and accumulation rates.

Chapter 4 has been formatted for submission to *Journal of Geophysical Research - Biogeosciences.*

Chapter 5 – Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes

A spatial and temporal quantification of biomass and belowground C in two wetlands of different geomorphic setting which have experienced mangrove expansion over a > 70 year period.

Chapter 5 has been published in *Global Change Biology*:

Kelleway JJ, Saintilan N, Macreadie PI, Skilbeck CG, Zawadzki A, Ralph PJ (2016) Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. *Global Change Biology*, 22: 1097-1109. DOI: 10.1111/gcb.13158

Chapter 6 – Conclusions and recommendations

An integration of the findings from the experimental chapters and discussion of the 'new knowledge' obtained from this thesis, as well as its implications for coastal wetland management and future research.

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CHAPTER TWO

SEDIMENTARY FACTORS ARE KEY PREDICTORS OF CARBON STORAGE IN SE AUSTRALIAN SALTMARSHES

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ECOSYSTEMS

Sedimentary Factors are Key Predictors of Carbon Storage in SE Australian Saltmarshes

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ABSTRACT

Although coastal vegetated ecosystems are widely recognised as important sites of long-term carbon (C) storage, substantial spatial variability exists in quantifications of these 'blue C' stocks. To better understand the factors behind this variability we investigate the relative importance of geomorphic and vegetation attributes to variability in the belowground C stocks of saltmarshes in New South Wales (NSW), southeast Australia. Based on the analysis of over 140 sediment cores, we report mean C stocks in the surface metre of sediments (mean ± SE = 164.45 ± 8.74 Mg C ha^{-1}) comparable to global datasets. Depth-integrated stocks (0–100 cm) were more than two times higher in fluvial (226.09 ± 12.37 Mg C ha^{-1}) relative to marine (104.54 ± 7.11) geomorphic sites, but did not vary overall between rush and non-rush vegetation structures. More specifically, sediment grain size was a key predictor of C density, which we attribute to the enhanced C preservation capacity of fine sediments and/or the input of stable allochthonous C to predominantly fine-grained, fluvial sites. Although C density decreased significantly with sediment depth in both geomorphic settings, the importance of deep C varied substantially between study sites. Despite modest spatial coverage, NSW saltmarshes currently hold approximately 1.2 million tonnes of C in the surface metre of sediment, although more C may have been returned to the atmosphere through habitat loss over the past approximately 200 years. Our findings highlight the suitability of using sedimentary classification to predict blue C hotspots for targeted conservation and management activities to reverse this trend.

Key words: carbon sequestration; blue carbon; saltmarsh; salt marsh; spatial variability; geomorphic setting; ecosystem services; tidal marshes.

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CHAPTER THREE

SEDIMENT AND CARBON ACCUMULATION VARY AMONG VEGETATION ASSEMBLAGES IN A COASTAL SALTMARSH

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Sediment and carbon accumulation vary among vegetation assemblages in a coastal saltmarsh

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Abstract. Coastal saltmarshes are dynamic, intertidal ecosystems which are increasingly being recognised for their contributions to ecosystem services, including carbon (C) accumulation and storage. The survival of saltmarshes and their capacity to store C under rising sea levels, however, is partially reliant upon surface sedimentation rates and influenced by a combination of physical and biological factors. In this study, we use several complementary methods to assess short-term (days) deposition and medium-term (months) accretion dynamics within three saltmarsh vegetation types common throughout southeast (SE) Australia.

We found that surface accretion varies among vegetation assemblages, with medium-term (19 month) bulk accretion rates in the upper marsh rush (*Juncus*) assemblage (1.74 ± 0.13 mm y^{-1}) consistently in excess of estimated local sea level rise (1.15 mm y^{-1}). Accretion was lower and less consistent in both the succulent (*Sarcocornia*) (0.78 ± 0.18 mm y^{-1}) and grass (*Sporobolus*) (0.88 ± 0.22 mm y^{-1}) assemblages located lower in the tidal frame. Short-term (6 d) experiments showed deposition within *Juncus* plots to be dominated by autochthonous organic inputs with C deposition rates ranging from 0.41 ± 0.15 g C cm^{-2} y^{-1} (neap tidal period) to 0.87 ± 0.16 g C cm^{-2} y^{-1} (spring tidal period), while minerogenic inputs and lower C deposition dominated *Sarcocornia* (0.03 ± 0.01 to 0.23 ± 0.03 g C cm^{-2} y^{-1}) and *Sporobolus* (0.06 ± 0.01 to 0.15 ± 0.03 g C cm^{-2} y^{-1}) assemblages.

Elemental (C:N), isotopic ($\delta^{13}C$), mid infrared (MIR) and ^{13}C NMR analyses revealed little difference in either the source or character of materials being deposited among neap versus spring tidal periods. Instead, these analyses point to substantial redistribution of materials within the *Sarcocornia* and *Sporobolus* assemblages, compared to high retention and preservation of organic inputs in the *Juncus* assemblage. By combining medium-term accretion quantification with short-term deposition measurements and chemical analyses we have gained novel insights into biophysical processes responsible for regional differences in surface dynamics among key saltmarsh vegetation assemblages. Our results suggest that unless belowground processes (e.g. root production) make substantial contributions to surface elevation gain, then *Sarcocornia* and *Sporobolus* assemblages may be particularly susceptible to changes in sea level, with implications for the future structure and function of these saltmarsh areas.

1 Introduction

1.1 Coastal wetlands

Coastal saltmarshes are dynamic ecosystems, vegetated by herbs, grasses and rushes that are found in a range of sedimentary settings along low-energy coastlines. Globally, vegetation type and floristic assemblage have been used to classify broad types of saltmarsh (Adam, 1990; Adam, 2002). At the local scale, vegetation zonation is one of the most striking ecological features of many saltmarshes, reflecting the elevation requirements of a small number of dominant species, although mosaics of species within a zone are also common (Adam, 2002; Hickey and Bruce, 2010). Whilst the biodiversity values and exceptional productivity of coastal wetlands have been long recognised, increasing attention is now being focused upon ecosystem services such as carbon (C) accumulation and storage (Chmura et al., 2003; Duarte et al., 2013), and the response of these coastal ecosystems to changes in climate (Kirwan and Mudd, 2012) and sea level (Rogers et al., 2013).

Surface elevation and sedimentation dynamics are central to both coastal wetland survival under rising sea level (Baustian et al., 2012; Kirwan and Megonigal, 2013; Kirwin et al., 2016) and to the delivery and storage of organic matter (OM) (Duarte et al., 2013; Lovelock et al., 2013). Saltmarsh sediments may be minerogenic (dominated by mineral inputs) or organogenic (dominated by biomass and litter production and/or allochthonous OM inputs), although most sediments comprise both mineral and organic fractions (Adam, 2002; Baustian et al., 2012). Consequently, sediment properties and surface dynamics may be influenced by both physicochemical and biological factors. Physical drivers of accretion (the vertical accumulation of sediment) in intertidal wetlands include the suspended sediment supply of inundating waters (Zhou et al., 2007); as well as the tidal range of a site and position within the tidal range (Ouyang and Lee, 2014; Saintilan et al., 2013; van Proosdij et al., 2006). High tides may play an important role in importing sediment into saltmarshes (Rosencranz et al., 2015), while low-tide rainfall may act to redistribute or export materials, including particulate organic carbon (Chen et al., 2015).

Numerous studies have investigated the interactions between vegetation and marsh surface dynamics, although the majority of these studies have focussed on the genus *Spartina* (e.g. Baustian et al., 2012; Mudd et al., 2010; Mudd et al., 2009; Nyman et al., 2006). Broadly, these studies have shown that the presence of vegetation may have a significant positive influence on surface accretion through: 1) accumulating organic matter; and 2) helping to trap mineral sediments (Morris et al., 2002; Mudd et al., 2010; Nyman et al., 2006). Comparative studies of the effect of vegetation composition in the intertidal zone, however, vary from no difference in accretion among different vegetation species in the wetland (e.g. Culberson et al., 2004) to sizeable differences among mangroves and different saltmarsh species (e.g. Saintilan et al., 2013).

1.2 C storage

Globally, the rate of sediment carbon accumulation is extremely high in saltmarshes, relative to terrestrial and most coastal ecosystems, with a mean ± SE accumulation rate of 0.024 ± 0.003 g C cm^{-2} y^{-1} (Ouyang and Lee, 2014). While much of this C is produced belowground by roots and rhizomes, contributions from aboveground sources may be significant (Boschker et al., 1999; Zhou et al., 2006). Sources of aboveground C may include both autochthonous (produced within the community) and allochthonous (deposited from outside the community) OM, although their relative contributions may vary within and among saltmarsh settings (Kelleway et al., 2016a).

Regardless of OM source, the capacity of coastal wetlands to store carbon in the long-term remains dependent upon the balance between OM inputs and their decay (Kirwan et al., 2013). While there is considerable debate as to which factors most influence the long-term retention of C in soil pools, litter quality has long been identified as a key driver of decay rates (Cleveland et al., 2014; Enríquez et al., 1993; Josselyn and Mathieson, 1980; Kristensen, 1994) and is of particular relevance to C stock accumulation on the sediment surface.

1.3 Measuring surface deposition and accretion

A variety of methods have been developed for measuring and monitoring surface dynamics in tidal wetlands (for reviews see Nolte et al., 2013; Thomas and Ridd, 2004). These include techniques relevant to short-term *deposition* events (of sediments and plant litter) through to medium- and long-term measures of *accretion* or *accumulation* (the net effect of multiple deposition and removal events) as well as *surface-elevation change*. Methods also vary in their effectiveness of trapping and retaining different materials, meaning a combination of techniques may be required to identify the different physical and biotic influences on deposition and accretion (Nolte et al., 2013). In this study, we use several methods to assess short-term (days) deposition and medium-term (months) accretion dynamics within three saltmarsh vegetation assemblages common throughout southeast (SE) Australia. We hypothesise that: 1) deposition and accretion will vary among assemblages, in accordance with differences in vegetation structure and location within the saltmarsh; and 2) the source and character of material deposited will vary temporally according to tidal inundation patterns. This study also presented an opportunity to compare wetland sedimentation methods. Together, we expect this information will improve our understanding of how materials (including C) accumulate in coastal wetlands and how these ecosystems might respond under rising sea level.

2 Methods

2.1 Study setting

Towra Point Nature Reserve is located within the oceanic embayment Botany Bay, approximately 16 km south of central Sydney, Australia's largest city. The intertidal estuarine wetland complex at this site is the largest remaining within the Sydney region and is listed as a Ramsar Wetland of International Importance. Within the site, a large saltmarsh area adjacent to Weeney Bay was chosen as a study site (Fig. 1) as this area exhibits vegetation zonation typical of SE Australian saltmarshes. The lower saltmarsh is bordered by the mangrove *Avicennia marina*, beyond which seagrass meadows (including *Posidonia australis*) occur within the subtidal zone. In some areas the upslope limit of saltmarsh extends into small patches of the supratidal trees *Casuarina glauca* and *Melaleuca ericifolia,* but for the most part is bordered by a levee which was constructed between 1947 and 1951. Previous investigation has revealed vegetation zonation across the site coinciding with elevation measurements and tidal extent modelling (Hickey and Bruce, 2010).

Saltmarsh within this site comprises two broad vegetation communities – an association of the perennial succulent *Sarcocornia quinqueflora* (C3 photosynthetic pathway) and the perennial grass *Sporobolus virginicus* (C4 photosynthetic pathway), mostly intermixed across the lower and middle marsh. The upper marsh assemblage is dominated by the rush *Juncus kraussii* (C3), with *S. virginicus* (C4) ubiquitous as a sub-dominant lower stratum across this assemblage.

Fifteen plots were selected for study on the basis of saltmarsh vegetation zonation – five plots randomly chosen within the *Juncus*-dominated assemblage, and 10 plots strategically selected within the *Sarcocornia-Sporobolus* association (five plots vegetated exclusively by *Sarcocornia,* and five vegetated exclusively by *Sporobolus*). Hereafter, these three assemblages are referred to by genus (*Sarcocornia; Sporobolus; Juncus*), while reference to the plant species themselves involves the species name (*S. quinqueflora; S. virginicus; J. kraussii*).

Data previously collected within the study region showed a substantial difference in aboveground biomass of the rush assemblage (Juncus mean = 1116 g m^{-2}), compared to that of the non-rush assemblages (*Sarcocornia* mean = 320 g m^{-2}; *Sporobolus* mean = 350 g m^{-2}) - importantly, there do not appear to be distinct seasonal patterns of biomass stock for any of these species (Clarke and Jacoby, 1994). Both *Sarcocornia* and *Sporobolus* are perennial species, while *J. kraussii* culms undergo initiation and senescence throughout the year, but with peak culm initiation before and after summer flowering and fruiting (Clarke and Jacoby, 1994). Belowground biomass data are rare, though on the basis of data presented by Clarke and Jacoby (1994) we have calculated a mean aboveground : belowground biomass ratio of 1.5 for *Juncus*. No belowground data have been reported for either *Sarcocornia* and *Sporobolus*. More broadly, the saltmarshes of southeast (SE) Australia have been classified within the temperate group of saltmarshes which also includes those of Europe, the Pacific coast of North America, Japan and South Africa (Adam, 1990). These are distinct from the well-studied *Spartina*-dominated marshes of North America's Atlantic coast.

Tides along the New South Wales coast are semidiurnal (two flood and two ebb periods each lunar day) with a maximum spring tidal range of 2.0 m (Roy et al., 2001). Astronomical (i.e. predicted) maxima occur during the new moon in summer and during the full moon in winter (spring tides). Tidal inundation to and recession from the study area occurs via Weeney Bay, with the causeway acting as a barrier to surface water exchange with the western section of the Nature Reserve and Woolooware Bay. The linear rate of sea level rise in Botany Bay since local records commenced in 1981 is 1.15 mm y^{-1} (Kelleway et al., 2016b).

2.2 Elevation measurement

Within each plot, elevation was measured using a modified version of the tidal inundation method described by English et al. (1994), whereby three vertical rods marked with water-soluble dye were inserted into the ground immediately prior to a summer spring tide (23/01/2015; measured tidal height of 1.897 m above lowest astronomical tide (LAT) datum at nearest tidal gauge). Depth of inundation above the saltmarsh surface was measured immediately after the tide receded and subtracted from the predicted tide height to obtain an estimate of surface elevation. Care was taken during the measurement procedure and in the selection of a calm day (to minimise wind and waves effects) to minimise discrepancies between measurements at different plots. Comparison of three replicate rods revealed a standard error of the mean < 1.3 cm for each plot.

2.3 Feldspar marker horizons

The feldspar marker horizon (MH) technique (Cahoon and Turner, 1989) has been proposed as a suitable method to investigate the effects of aboveground vegetation structure on the accretion (vertical accumulation) of material on the marsh surface over the medium-term (Nolte et al., 2013). A total of 45 feldspar MHs were installed across the study site on 23 January 2014, comprising three replicates in each of the 15 study plots. Accretion was determined at later dates as the height difference between the marsh surface and the feldspar (i.e., the material accumulated above the MH), and was recorded as the mean of three replicate measurements from within the marker horizon at each sampling event. Measurements were taken 11, 13, 15, 17 and 19 months after installation.

During the later sampling events many MHs in *Sarcocornia* and *Sporobolus* plots became increasingly difficult to discern within the sediment, probably due to bioturbation and mixing of sediments (Cahoon and Turner, 1989; Krauss et al., 2003). Consequently, monitoring of all plots was terminated after 19 months.

2.4 Sedimentation traps

Two complementary types of sedimentation trap were installed concurrently for the purpose of quantifying short-term deposition of materials among the three vegetation assemblages. First, pre-weighed, 50 mL centrifuge vials (30 mm mouth diameter; 115 mm depth) were placed into the ground, so that the 'lip' of each tube was 10 mm above the ground surface. This vial method has a bias towards the collection of non-buoyant materials washing over the mouth of the tube (i.e. mineral matter) and a bias against collection of coarse and/or buoyant materials, including large fragments of plant litter. Second, a modified version of the filter paper method described by Reed (1989) and Adame et al. (2010) was used to quantify 'passive' sedimentation and litter accretion on the saltmarsh surface. Pre-weighed 90 mm hydrophilic nylon filters (pore size 0.45µm) were placed over 90 mm upturned plastic Petri dishes, and attached to the sediment by two small staples, so that the nylon filter lay level with the sediment surface. The resolution of this method, using a 90 mm filter has been calculated as 0.0015 mg cm^{-2} (Thomas and Ridd, 2004).

Three replicates of each short-term trap were installed at the centre of each of the study areas described above during the summer of 2014/15. Traps were deployed for 6 d (12 high tides) periods on four instances, on the basis of tide chart predictions. Two neap ('December neap' and 'January neap') periods were selected to reflect periods when high tides were at their lowest. While these neap periods were intended to measure periods without any inundation, higher than predicted tides occurred in both neap periods. Although unconfirmed, inundation of some plots within lower elevation zones of the study area were expected to have occurred at least once during the December neap (up to 80% of *Sarcocornia* plots and 100% of *Sporobolus* plots) and/or the January neap (up to 60% of *Sarcocornia* plots only) (Table S1). Two other periods ('December spring' and 'January spring') were selected as maximum saltmarsh inundation events with between five and ten high tides inundating each plot in each period (Table S1). Although unintended, the fact that a small number of inundations were likely captured during neap tides more accurately reflects the differences in tidal behaviour that naturally occurs among the three vegetation assemblages (i.e. lower elevation assemblages are subject to a greater number of high tides throughout the year than higher elevation assemblages). Consequently, all results from short-term measures were considered in the context of these varied inundation patterns.

Great care was taken not to disturb sediments or litter collected on, or surrounding the removable traps during their installation and collection. Filters with visible crab-excavated sediment (n = 23/180) or physically upturned during inundation (n = 3 January spring inundation only) were excluded from analysis, although all plant (autochthonous and allochthonous) materials were retained for analysis as we considered these to be largely unaffected by crab excavation.

In the laboratory, vials were centrifuged, the supernatant decanted and vial placed in an oven for drying. All samples and vessels (filters and centrifuge vials) were dried at 60ºC until constant weight was achieved (≤ 72 h) and subtracted from initial vessel mass to obtain the dry weight of material collected. In addition, all identifiable litter was removed from each filter, identified to the species level and weighed. Litter samples of the main saltmarsh species encountered (*S. quinqueflora, S. virginicus* and *J. kraussii*), wrack of the seagrass *Posidonia* *australis* and macroalga *Hormosira banksii*, fresh leaves of the mangrove *Avicennia marina,* as well as composite samples of all residual sediment (mineral component and unidentified organic matter; referred hereafter as 'residue') from filters were also prepared for chemical analyses.

2.5 Elemental and isotopic analysis

Dried aboveground plant biomass, litter and residues were homogenised and ground into a fine powder using a ball mill. The 'Champagne test' (Jaschinski et al., 2008) was used to determine that no residue samples contained inorganic C. Consequently, acidification of samples was deemed unnecessary. Organic %C, %N, and δ^{13}C were measured for all samples using an Isotope Ratio Mass Spectrometry – Elemental Analyzer (Thermo DeltaV) at University of Hawaii (HILO).

2.6 MIR

Diffuse reflectance mid-infrared (MIR) spectroscopy was used to assess the composition of biomass, litter and residue samples. MIR spectroscopy characterises the bulk composition and is therefore inclusive of both mineral and organic components. Spectra were acquired using a Nicolet 6700 FTIR spectrometer (Thermo Fisher Scientific Inc., Waltham, MA, USA) following the specifications and procedures outlined by Baldock et al. (2013a). Spectra were acquired over 8000–400 cm^{-1} with a resolution of 8 cm^{-1}, but were truncated to 6000–600 cm^{-1}. Spectra were baseline-corrected using a baseline-offset transformation and then mean-centred using the Unscrambler 10.2 software (CAMO Software AS, Oslo, Norway) before conducting principal component analysis (PCA).

2.7 ^{13}C NMR

Solid-state ^{13}C nuclear magnetic resonance (NMR) spectroscopy was used to quantify the contribution of C functional groups to live plant biomass, litter and residue samples. Residue samples were treated with 2% hydrofluoric acid (HF) according to the method of Skjemstad et al. (1994) to remove paramagnetic materials and concentrate organic C for ^{13}C NMR analyses. Cross-polarization ^{13}C NMR spectra were acquired using a 200 MHz Avance spectrometer (Bruker Corporation, Billerica, MA, USA) following the instrument specifications, experimental procedures and spectral processing outlined by Baldock et al. (2013b). ^{13}C NMR data are presented as the proportion of integral area under each of eight chemical shift regions corresponding to main types of organic functional groupings found in natural organic materials: Alkyl C (0-45 ppm), *N*-Alkyl/Methoxyl (45-60 ppm), *O*-Alkyl (60-95 ppm), Di-*O*-Alkyl (95-110 ppm), Aryl (110-145 ppm), *O*-Aryl (145-165 ppm), Amide/Carboxyl (165-190 ppm) and Ketone (190-215 ppm) (Baldock and Smernik, 2002).

2.8 Statistical analyses

Separate simple linear regression analyses were conducted using all feldspar MH measurements for each of the three vegetation assemblages for the purpose of obtaining accumulation rates over 19 months and to assess the strength of linear fits for these data. Bulk short-term deposition variables (bulk material collected in vials; bulk material collected on filters) were log-transformed to achieve normality and analysed with separate linear mixed models, to test main and interactive effects of vegetation assemblage (*Sarcocornia*, *Sporobolus*, *Juncus*) and tidal event (repeated measures: December neap, December spring, January neap, January spring). Elevation was included as a covariate for each of these analyses. Covariance structure was selected for each model through comparison of Akaike's Information Criterion (AIC) of four covariance structures (unstructured, compound symmetry, diagonal, scaled identity). Where main effects presented significance differences ($P < 0.05$), post hoc tests (with conservative Bonferroni adjustment) were used to determine difference among levels of vegetation and tidal event factors. Statistical analyses were performed using SPSS v19 (IBM, USA), Origin Pro 2015 (OriginLab, USA) and PRIMER v6 (PRIMER-E, UK).

2.8.1 Isotope mixing model

A two-source, single isotope mixing model (Phillips, 2012) was used to estimate the proportion of C3 (f_1 in equation (1)) and C4 (f_2 in equation (2)) plants to the unidentified organic residue:

$$f_1 = \frac{\delta^{13}C_{residue} - \delta^{13}C_{C4}}{\delta^{13}C_{C3} - \delta^{13}C_{C4}} \quad (1)$$

$$f_2 = 1 - f_1 \quad (2)$$

where $C_{residue}$ denotes the residue organic C, C_{C3} denotes the $\delta^{13}C$ of the relevant C3 plants (*S. quinqueflora* litter for *Sarcocornia*-*Sporobolus* association residues or *J. kraussii* litter for *Juncus* assemblage residues) and C_{C4} denotes $\delta^{13}C$ of litter of the C4 species (*S. virginicus*).

2.8.2 MIR analysis

Principal components analysis (PCA) was performed using the transformed MIR spectra to: 1) identify differences in composition among samples due to sample type and vegetation assemblage; and 2) define the MIR spectral components most important to differentiating the samples. Loadings were plotted for the first two principal components to assist in the latter and to guide interpretation of differences in composition among samples.

3 Results

3.1 Feldspar MHs

Positive and consistent accretion was measured among *Juncus* plots throughout the entire 19 months, reflected in the moderate-strong linear fit ($R^2 = 0.68$; $P < 0.001$) and a mean accumulation rate with relatively low variance (1.74 ± 0.13 mm y^{-1}). In contrast, accumulation above the feldspar MHs was more varied and slower overall in the *Sarcocornia* ($R^2 = 0.16$; $P < 0.001$; 0.76 ± 0.18 mm y^{-1}) and *Sporobolus* plots ($R^2 = 0.14$; $P < 0.001$; 0.88 ± 0.22 mm y^{-1}) (Figure 2). Accretion varied both spatially and temporally within the *Sarcocornia* and *Sporobolus* assemblages. Across *Sporobolus* plots, there was relatively high accretion recorded at the 11-month interval, followed by multiple peaks and troughs in the amount of height of material measured above MHs, with some similarity among replicate plots in the timing of these (Fig 2b). After modest gains at the 11-month interval, *Sarcocornia* accretion diverged among plots with two plots (*Sarcocornia* 2 and 5) experiencing continued accretion, whilst *Sarcocornia* 3 and 4 appeared to lose surface material through the remainder of the study. The pattern of accumulation and loss observed between 13-19 months at *Sarcocornia* 1 was mirrored in the nearby *Sporobolus* 1 plot.

3.2 Short-term deposition

3.2.1 Vials

Mean bulk material deposition rates as determined by vials were higher than filter bulk deposition rates across all sampling events and vegetation assemblages (Table 1). Observations of materials retained within vials suggested a dominance of mineral matter and unidentified detritus, except in *Juncus* plots where *Juncus kraussii* fragments were the dominant material.

Deposition varied significantly among tidal events ($F_{6, 42} = 10.01$; $P < 0.001$), with post-hoc tests revealing each event as significantly different to the others. Despite large differences in mean deposition among the three vegetation assemblages during December spring, January neap and January spring events (Table 1), vegetation assemblage was not a significant factor when elevation was included as a covariate ($F_{2, 45.8} = 1.06$; $P = 0.36$). There was, however, a significant event × assemblage interaction ($F_{6, 42} = 10.01$; $P < 0.001$), with deposition in *Sarcocornia* vials higher during January neap relative to December spring for *Sarcocornia* plots, but not so for *Sporobolus* and *Juncus* vials (Table 1). Deposition into vials was lowest for all three assemblages during December neap (Table 1) and was highest overall in *Sarcocornia* vials during January spring (100.78 ± 32.73).

Regression of the log (mass of material retained within vials) versus plot surface elevation revealed no clear relationship between the two variables during the December neap period (Fig. S1a), but significant negative relationships ($P<0.001$, $R^2>0.35$) existed for all other time periods (Fig. S1b-d). That is, there were broad trends of higher sedimentation at lower elevation plots than higher elevation plots during these periods.

3.2.2 Filters

Retention of bulk materials on filters also varied among all four tidal periods ($F_{3, 109.3} = 48.82$; $P < 0.001$), with overall deposition highest in January spring, followed by December spring (Table 1, Fig. 3). Bulk deposition on filters varied among vegetation assemblages ($F_{2, 30.85} = 48.82$; $P = 0.004$), with lower deposition in *Sporobolus* plots relative to both *Sarcocornia* and *Juncus* plots across all tidal events (Fig. 3; Table 1). In contrast to the vials, there was no clear relationship between bulk material retained on filter papers and plot surface elevation during either of the neap or spring tidal events (Fig. S2).

Although the mass of bulk material retained on filters was similar across *Sarcocornia* and *Juncus* plots, Fig. 3 demonstrates that different materials were contributing to surface accumulation among the two vegetation assemblages. In *Juncus* plots, autochthonous plant litter (that is, from the dominant species *Juncus* kraussii and the sub-dominant species *Sporobolus* virginicus) contributed between 66% (December neap) and 78% (both December spring and January neap) of all deposited material. In contrast, litter contributions were low (≤ 12% of all deposited material) in both *Sarcocornia* and *Sporobolus* assemblages, regardless of tidal period. Contributions from identifiable allochthonous materials were low in all cases, with negligible quantities of *Posidonia australis* litter (recorded in five out of all 60 *Sporobolus* filters) and a single large piece of *Hormosira banksii* deposited on a *Sporobolus* filter during December spring – the latter was considered an outlier and was therefore excluded from Fig 3.

Chemical analysis of the unidentified portion of material deposited on filters also highlights differences between the vegetation assemblages. The organic content (%C, %N) of unidentified material pooled across *Juncus* plots was much higher than for the other assemblages (Table S2), with this difference also apparent in the disparity between C accumulation rates in *Juncus* versus *Sarcocornia* and *Sporobolus* assemblages (Table 1).

3.3 Elemental and isotopic ratios

Elemental C:N ratios and δ^{13}C values of plant biomass, litter and unidentified residues are presented in Table 2. The biomass and litter samples of the C4 grass *Sporobolus* were more enriched in ^{13}C relative to those of the C3 species *Sarcocornia* and *Juncus* (Table 2). This distinction, however, was not as great for the unidentified residue samples, with δ^{13}C values from all assemblages sitting between the δ^{13}C values of the C3 and C4 saltmarsh plants. Outputs from the isotope mixing model (Table 1) highlighted differences in source contribution among the vegetation assemblages. *Sarcocornia* residues showed a higher contribution of C3 plant material during spring tides relative to the neap tides. Further, similar contribution from the host plant (i.e. C3 in *Sarcocornia* and C4 in *Sporobolus*) to residues was apparent for all tidal periods except January neap, when the C4 contribution to *Sporobolus* residue was higher. Overall, contributions of the host plant ranged from 59.6 – 77.5 % in *Sarcocornia* plots and 61.7 - 80.1% in *Sporobolus* plots.

Source contributions across the four tidal periods were most consistent in the *Juncus* assemblage, where estimates ranged between 78.8% and 84.6% for C3 plant material and 15.4 - 21.2% for C4 plant material. These contributions aligned well with visual observations of plant cover across plots (where the C3 plant *J. kraussii* is dominant over the C4 plant *S. virginicus* in approximately an 80:20% biomass mix). Quantification of litter fall onto filters, however, highlighted a skew towards *J. kraussii* litter (85.9 – 97.0%) over *S. virginicus* litter (3.0 – 14.1%) across the *Juncus* assemblage. Residue C:N ratios were also highest for *Juncus*, followed by *Sporobolus* then *Sarcocornia*. While *Juncus* litter samples had a higher C:N, relative to all other *Juncus* biomass (Table 2), this difference was not noted for *Sarcocornia* nor *Sporobolus*.

3.4 MIR and ^{13}C NMR

Together, the first two principal components explained 96.4% of the variation in MIR spectra of all samples assessed. A clear separation of residue samples from litter and biomass is apparent along PC1 (Fig 4A) with inspection of the loadings plot (Fig 4B) highlighting variation in the range 600-2000 cm^{-1} (quartz), and distinct troughs at 3400 cm^{-1} (water) and 2900 cm^{-1} (OM-alkyl). Residue samples are separated along PC2, with differentiation among vegetation assemblages, regardless of tidal event. The loadings plot for PC2 (Fig 4C) also exhibits variation in the range 600-2000 cm^{-1} (quartz), a peak at 2900 cm^{-1} (OM-alkyl) and also 3600-3700 cm^{-1} (kaolinite).

The proportions of C within each of eight organic functional groupings for each sample analysed with ^{13}C NMR are presented in Table 2. For all samples O-Alkyl C was the most abundant. O-Alkyl C content was higher in live plant biomass than litter for both *Sarcocornia*, but less so for *Sporobolus* and essentially unchanged for *Juncus*. Generally, residues were higher in Alkyl C, and Amide/Carboxyl C, and lower in O-Alkyl, Di-O-Alkyl and aromatics relative to litter and biomass samples. There were differences in residue C composition according to which vegetation assemblage they were collected from –aromatics (higher in *Juncus* and *Sporobolus*), Alkyl C and Amide/Carboxyl (higher in *Sarcocornia*). There was high similarity between residues collected under the two different tides, however, for both the *Sarcocornia* and *Sporobolus* assemblages. These similarities among tides are mirrored in the similarity of the residue C:N values. There was insufficient residue material available for analysis from *Juncus* neap tide, even though samples were pooled across a large number of filters, further highlighting the small contribution of unidentifiable sedimentary components within this assemblage.

4 Discussion

In this study we have compared sediment and C accretion dynamics among three vegetation assemblages within an intertidal wetland complex. Our findings, across a range of methods, showed that there were substantial differences among assemblages in: 1) the types of materials deposited on the marsh surface; and 2) the quantities of material accumulated over 19 months. Here, we first consider the accumulation differences among assemblages over the medium-term, and then discuss the interactions among vegetation, physical and degradation processes which are likely driving these differences. We conclude with an assessment of the implications for C accumulation and storage, and response to relative sea level rise (RSLR).

4.1 Accretion varies among vegetation assemblages

Surface accretion above feldspar MHs over a period of 19 months and deposition within short-term sedimentation traps provide evidence of the multiple ways in which accretion dynamics differ between saltmarsh vegetation assemblages. First, feldspar MHs highlight a record of continued and consistent accretion across the upper marsh *Juncus* assemblage, amounting to a reliable ($R^2 = 0.68$) accretion rate of 1.74 ± 0.13 mm y^{-1} (Fig. 2). This value is remarkably similar to the mean accretion rate measured over 10 years above feldspar MHs of 1.76 mm y^{-1} by Saintilan et al. (2013) for *Juncus* saltmarshes across a range of sites in SE Australia. In contrast, accretion above MHs in *Sarcocornia* and *Sporobolus* assemblages varied substantially– both spatially and temporally – in our study (Fig. 2), possibly due in part to the influence of bioturbation and sediment mixing above MHs (Cahoon and Turner, 1989; Krauss et al., 2003). While our mean accretion estimates for both *Sarcocornia* and *Sporobolus* are lower than the regional estimate for *Sarcocornia*/*Sporobolus* associations (1.11 ± 0.08 mm y^{-1}) (Saintilan et al., 2013), this regional mean is within the 95% confidence interval for both species at Towra Point (Table 1). Critically, accretion rates in the *Juncus* assemblage consistently exceed contemporary rates of sea level rise within Botany Bay (1.15 mm y^{-1}), while mean accretion rates for both *Sarcocornia* and *Sporobolus* (and even the upper 95% confidence interval of *Sarcocornia)* are below the contemporary rate of sea level rise.

4.2 Processes driving spatial variability in deposition and accretion

One of the key strengths of using short-term accumulation methods is the ability to identify and quantify the composition of inputs which may be contributing to differences observed over the medium-term. In this study, a distinction was observed between the organogenic deposition which dominated the *Juncus* assemblage (where medium-term accretion rates were consistently high) and the minerogenic deposition of the *Sarcocornia* and *Sporobolus* assemblages (where medium-term accretion rates were lower and more varied). This distinction was best exemplified by the results of the filter method (Fig 3.), where differences in the contributions of autochthonous litter and the residual sediment (comprising mineral and organic residue components) were stark.

There was further evidence of this in the vial results, where mineral-biased deposition was high in the lower elevation, non-rush assemblages, and low in the higher elevation *Juncus* assemblage during multiple experimental periods (Table 1; Fig. S1). Although higher than predicted tides likely influenced some short-term traps during neap experimental periods (Table S1), the fact that deposition into vials was lower during December neap (when up to 80% of *Sarcocornia* plots and 100% of *Sporobolus* plots would have been subjected to at least one tidal inundation) relative to January neap (up to 60% of *Sarcocornia* plots; no inundation of *Sporobolus* plots), suggests that this had a small impact relative to other influences.

Together, the vegetation assemblage scale differences in short-term deposition and longer-term accumulation patterns observed in this study suggest further consideration of the biological, physical and interactive processes which are most responsible for the dynamics of saltmarsh surface materials is warranted.

4.2.1 The role of vegetation

There are fundamental differences in vegetation structure and function which can at least partly account for the variations in the quantity and type of materials being retained in rush (*Juncus*) versus non-rush (*Sarcocornia* and *Sporobolus*) assemblages. First, *Juncus* assemblages have massive potential for direct organic sedimentation through the annual replacement of their significant aboveground biomass (1116 g m^{-2}) (Clarke and Jacoby, 1994). No clear patterns of annual turnover have been observed in *Sarcocornia* and *Sporobolus* assemblages, where standing biomass is only about one-third that of the *Juncus* assemblage (Clarke and Jacoby, 1994).

There may also be indirect vegetation effects on the deposition and accumulation of surface materials. For instance, the tall (~1 m), dense structure of the *Juncus* assemblage is likely to enhance: 1) the retention of autochthonous litter which may have otherwise been exported during tidal recession, and 2) the capture of mineral particles on plant stems (Morris et al., 2002; Mudd et al., 2004). Dense saltmarsh vegetation also has the capacity to enhance sedimentation by reducing the turbulent energy of inundating waters, with Mudd et al. (2010) demonstrating that this phenomenon was responsible for virtually all of the sedimentation increase observed when standing plant biomass of *Spartina alterniflora* was artificially increased. The high litter deposition rates we observed during neap tides (Fig. 3a,c) and the increased contribution of both mineral and litter components during spring tides (Fig 3b,d) suggested that each of these direct and indirect plant-mechanisms may be operating and contributing to the relatively high medium-term accretion rates within *Juncus* assemblages. This supported the first element of our first hypothesis - that assemblage differences can be (at least partly) explained by differences in vegetation structure.

4.2.2 The role of physical factors

Differences in suspended sediment supply and tidal flooding characteristics (tidal range, position within the tidal prism) have been identified as key physical drivers of saltmarsh accretion (Chmura and Hung, 2004; Rogers et al., 2014). Generally, lower elevation within the tidal frame and closer proximity to the source of tidal inundation result in higher sedimentation rates. This is because: (1) greater flooding depth allows for greater sediment volume and higher sedimentation, and (2) the increase in flooding duration increases the time for sediment deposition to occur (Baustian et al., 2012; Harter and Mitsch, 2003; Morris, 2007; Oenema and DeLaune, 1988). If these processes were operating in our site, we would have expected to observe higher sedimentation rates in the *Sarcocornia* and *Sporobolus* assemblages, which were generally both lower in the tidal frame (Table S1) and nearer to tidal sources (Fig. 1). Indeed, when measurements relevant to the mineral component were considered, our results appeared to be consistent with this. First, overall mineral retention on filters (Fig. 3) was highest in the *Sarcocornia* and *Sporobolus* assemblages. Second, mineral-biased deposition into vials was shown to have a significant log-linear relationship with elevation during the periods of greatest tidal inundation (December spring, January spring), and during January neap when significant rainfall (Fig. S3) as well as some inundation of low elevation sites likely occurred (Table S2). These mineral deposition results were therefore supportive of the role of physical position within the saltmarsh towards differences among assemblages (i.e. part two of our first hypothesis).

Importantly, however, the deposition-elevation relationship expressed by the mineral component, did not apply when bulk results of the passive filter method were considered. With the mineral bias effectively removed, no clear relationship between elevation and bulk deposition was observed across any of the tidal periods (see Fig. S2). Instead, total deposition was similar between the minerogenic, lower elevation *Sarcocornia/Sporobolus* plots, and the organogenic, higher elevation *Juncus* plots.

The lack of an elevation relationship in terms of bulk material deposition is somewhat contrary to spatial patterns expected on the basis of physical sedimentary processes in the tidal zone. This disparity extended to medium-term accretion results, where lower marsh (*Sarcocornia* and *Sporobolus*) assemblages accrete at a slower rate than upper marsh (*Juncus*), both in our study, and regionally (Saintilan et al., 2013). This relationship doesn't necessarily downplay the importance of tidal influence on surface dynamics in SE Australian saltmarshes. An alternative explanation is that these physical processes, in interaction with biological factors, are instead remobilising and redistributing materials across the lower marsh assemblages, rather than depositing significant amounts of 'new' allochthonous material.

4.2.3 Redistribution of surface materials

The second hypothesis of our study was that the source and character of materials deposited would vary temporally with tidal inundation patterns. For the most part, however, this was not observed, with high degrees of within-assemblage similarity for neap and spring tide samples across the various analyses undertaken (Table 2; Fig. 4). Instead, our results provide multiple lines of evidence that point to the redistribution of surface materials across the saltmarsh, mediated by a range of biological, physical and interactive processes.

The first indication of redistribution of surface materials was the mismatch between rates of short-term bulk deposition and patterns of medium-term accretion among vegetation assemblages. This was best exhibited in the *Sarcocornia* plots, where short-term measures showed deposition to be as high or higher in *Sarcocornia* plots relative to the other assemblages (Table 1; Fig. 3), while medium-term accretion was actually lowest here (Fig. 2). This suggests that short-term measures in this assemblage were capturing materials which were being moved or redistributed across the saltmarsh, but not necessarily retained in a given location over longer time periods (i.e. months). While the short- versus medium-term discrepancy was not as large for the *Sporobolus* assemblage, the temporal variability in feldspar MH measurements (i.e. multiple peaks and troughs across the 19 month period for most plots) also suggested significant redistribution of materials over time in this assemblage. Such movement of materials within the *Sarcocornia* and *Sporobolus* assemblages also fits with the expectation that hydrodynamic energy, and therefore potential for sediment redistribution, would be highest in the saltmarsh zones lower in the tidal frame and located closer to tidal sources (Fig. 1, Table S1). We also attribute the fading of feldspar horizons in many *Sarcocornia* and *Sporobolus* plots over time to mixing of sediments (Cahoon and Turner, 1989) in this active zone, with assistance from bioturbation (Cahoon and Turner, 1989; Krauss et al., 2003). In contrast, these temporal discrepancies and variations (including fading of MHs) were not observed in the *Juncus* assemblage, where hydrodynamic energy is expected to be greatly reduced as a result of both its position within the marsh and the influences of plant biomass (see discussion above).

Next, it was not expected that tidal inundation would substantially increase saltmarsh plant litter production. We therefore interpret the increased concentration of autochthonous litter in *Juncus* plots during spring tides relative to neap tides (Fig. 3) as evidence of the redistribution and trapping of autochthonous material within this assemblage. That is, the 'extra' spring tide litter was material that had been remobilised by inundating water and redistributed within the same community, resulting in a larger amount of material being caught on the *Juncus* filters. The fact that no identifiable *Juncus* litter was collected on any of the *Sporobolus* filters, despite their position being within the expected path of receding tides (Fig. 1), further highlights the retaining capacity within the *Juncus* assemblage. While it is not known over what scale the litter redistribution is occurring in the *Juncus* assemblage, we expect it to be highly localised, given the dense structure of standing vegetation here and its capacity to impede movement of coarse litter particles.

Finally, by placing our *Sarcocornia* and *Sporobolus* plots within small patches vegetated exclusively by either the C3 species (*S. quinqueflora*) or the C4 species (*S. virginicus*), we are able to estimate the contribution of each resident plant to the residue collected from within its assemblage. While the dominance of resident plant signatures suggested a strong autochthonous contribution in all instances (see mixing model results in Table 1), residue signatures across all tidal periods reveal a mixture of sources both present (i.e. the resident plant) or neighbouring (i.e. the other co-dominant plant in the association) to the plots. The fact that contributions of sources other than the resident plant were in the order of 20 – 40% (Table 1) during the neap tides suggest significant mixing across scales greater than the monospecific patches (i.e. several metres or more). While some of this movement of materials may have been due to the creep of the highest neap period tides into the lower elevation plots (though this appears small - see section 4.2), non-tidal agents such as redistribution by rainfall (Chen et al., 2015) and faunal activity (Guest et al., 2004) may have also contributed.

A two source (C3 plant v C4 plant) mixing model probably presents an overly simplified estimate of source matter contributions. This is because it does not account for other potential sources which have δ^{13}C values within or near the range of saltmarsh plant sources prescribed in the mixing model. These include mangroves (-28.7 ± 0.3 ‰), seagrass (-12.3 ‰), macroalgae (-17.7 ‰) and benthic algae (-15.0 ± 0.4 ‰). Of these, benthic algae would have the greatest potential to contribute to *Sarcocornia* residue, as vegetation is sparsest here (and therefore light penetration to benthos the greatest), while the MIR PC plot (Fig. 4) also points to a similarity in chemical composition between the two. However, the fact that *Sporobolus* residues are consistently depleted in ^{13}C, relative to both the resident plant (*S. virginicus*) and benthic algae, show that our interpretation of mixing between both C3 and C4 sources is warranted at least in that assemblage. In contrast, the constancy of isotope signatures and their overall similarity with the mix of C3- and C4-derived biomass in the *Juncus* plots provide further evidence of the autochthonous nature and trapping capacity of this assemblage.

Together, these findings allow several conclusions to be made about redistribution of surface materials. First, short-term deposition measures may capture a significant proportion of within-marsh redistribution and therefore may not necessarily equate with longer term accretion. Second, the capacity of vegetation to retain autochthonous sedimentation appears to vary substantially among species assemblages. Third, redistribution is likely to be greatest in more exposed, lower-biomass assemblages. These findings also highlight the importance of considering redistributed materials in quantifications of wetland surface dynamics, and likely shortcomings for studies which attempt to assess surface dynamics using only short-term methods.

4.3 Implications for wetland function

Understanding the biological and physical feedbacks which affect surface dynamics is critical to the survival of intertidal wetlands and their associated ecosystem services, under changing environmental conditions (Kirwan and Megonigal, 2013). To this end, the data collected as part of this study reveal patterns of how C sequestration capacity, organic matter decomposition and vulnerability to sea level rise vary among saltmarsh assemblages.

4.3.1 C deposition and sequestration rates

The distinction between organogenic and minerogenic assemblages, and their respective locations within the tidal frame, has important implications for surface C sequestration rates. Here we estimate mean C deposition rates ranging from 0.03 to 0.23 g C cm^{-2} y^{-1} across the four tidal periods for the minerogenic *Sarcocornia* and *Sporobolus* assemblages and 0.41 to 0.87 g C cm^{-2} y^{-1} for the organogenic *Juncus* assemblage (Table 1). It should be noted that such short-term C deposition rates inclusive of plant litter will likely represent a massive overestimation of C that is retained and sequestered over longer timescales, due to diagenesis of deposited OM (Duarte and Cebrian, 1996), and the potential for materials to be redistributed or even exported by tidal and non-tidal processes (see section 4.2.3). Therefore, these deposition rates are not directly comparable to C accumulation rates determined by medium-term (e.g. feldspar MH) or longer term (e.g. radiometric dating) techniques. Notwithstanding this, the magnitude of the differences we report among assemblages above fit broadly with differences in regional estimates of C accumulation over the medium-term (10 y MH experiments) which have been estimated as 4.5 times higher in *Juncus* relative to *Sarcocornia*-*Sporobolus* saltmarsh (Saintilan et al., 2013). Similarly, our results are also in agreement with findings further north in Moreton Bay, where Lovelock et al. (2013) reported much higher C sequestration rates on oligotrophic sand island marshes dominated by *J. kraussii*, than *S. quinqueflora* dominated marshes on the western side of that bay.

4.3.2 Decomposition of organic matter varies among assemblages

We have assessed the chemistry of aboveground biomass, litter and unidentified residues through elemental (C:N) and spectrometric (MIR, ^{13}C NMR) methods. Together, these analyses have revealed insights into the fate of aboveground organic matter and the likelihood of their contribution to longer-term sedimentary carbon stocks. Most importantly, our results highlight among assemblage differences in the transformation of OM along the biomass-litter-sediment decay continuum.

Shifts in the bulk composition of materials was best seen in the principal components plots of MIR spectra, where biomass, litter and sediment residue samples varied across PC1 (Fig. 4a). Broadly, the separation of residues from litter and biomass was primarily due to the addition of mineral components in the residues, however, there was also evidence of a shift in alkyl OM. Specifically, the presence of a single peak at ~2900 cm^{-1} in the loadings plot (Fig. 4b) was indicative of a declining cellulose content across PC1, that is, in the general order live biomass – litter – residue. Importantly, cellulose also appears to be a factor in the separation of residues from the three different saltmarsh assemblages along PC2 (Fig. 4c), suggesting higher content in the two *Juncus* samples, followed by *Sporobolus* and then *Sarcocornia* samples. This finding was confirmed by ^{13}C NMR data, which showed greater proportions of plant compounds (carbohydrates more broadly, as well as lignin) were retained within the *Juncus* litter and residue relative to the other species (Table 2). In contrast, the higher proportions of alkyl–C and amide/carboxyl–C within *Sarcocornia* and *Sporobolus* residues were indicative of higher protein and lipid contents, consistent with bacterial biomass and marine algae signatures (Dickens et al., 2006). However, they may also be partly explained by the selective retention of resistant plant waxes, such as suberin and cutan.

There are multiple mechanisms which may explain the greater retention of plant-derived C along the biomass-litter-residue pathway for *Juncus*, relative to the other assemblages. The simplest explanation is that a high turnover of *Juncus* biomass (and its exclusion of other sources through shading and/or structural impedance) ensures ample supply of plant-derived C to the benthos. Our data, however, reveal an important biomass-to-litter transformation in *Juncus* that was not observed in either the *Sarcocornia* or *Sporobolus* assemblage. That is, the C:N of *Juncus* litter increased substantially relative to live biomass. Such an increase is commonly observed in terrestrial (McGroddy et al., 2004) and marine (Stapel and Hemminga, 1997) plants and may be explained by the selective resorption of nutrients (but not carbon) by the plant prior to, or during, senescence (McGroddy et al., 2004; Stapel and Hemminga, 1997). Such a mechanism was supported by the constancy of molecular C composition between *Juncus* biomass and litter (Table 2). The selective resorption of N by a plant has important implications for the fate and processing of the resulting litter and residue, as tissue C:N is considered a primary determinant on saltmarsh organic matter decomposition (Minden and Kleyer, 2015). By retaining nutrients within the living tissues, the plant effectively decreases the lability of resulting litter and residual sediments and makes them less attractive to the microbial decomposer community (Reddy and DeLaune, 2008). This will have the effect of lowering OM remineralisation rates in *Juncus* relative to other assemblages, a result which also coincides with the bacterial biomass increases suggested for *Sarcocornia* and *Sporobolus*, but not apparent within the more recalcitrant *Juncus* residues (Table 2). Finally, there may also be an element of physical protection, with the closed structure of the *Juncus* assemblage potentially offering increased protection against decomposition with lower, more stable temperatures expected at ground level, relative to the more exposed *Sarcocornia* and *Sporobolus* assemblages.

Together, these data from SE Australia contribute to a broader pattern of plant assemblage differences in saltmarsh surface dynamics and C sequestration potential (Minden and Kleyer, 2015; Saintilan et al., 2013; Wang et al., 2003). They also highlight the likely processes behind the high capacity of *Juncus* saltmarshes to accumulate significant C stocks globally (0.034 g C cm^{-2} y^{-1}), relative to most other saltmarsh genera (mean C accumulation rate = 0.024 g C cm^{-2} y^{-1}) (Ouyang and Lee, 2013).

4.3.3 Vulnerability to sea level rise

There is growing evidence of the capacity of coastal wetlands to maintain surface elevation with relative sea level rise (RSLR), in certain situations, by increasing surface elevation through belowground production, enhanced trapping of sediments, or a combination of the two (Baustian et al., 2012; Kelleway et al., 2016b; McKee et al., 2007). Where wetland assemblages are unable to maintain a suitable elevation relative to inundating water levels then vegetation shifts may occur, including the loss of marsh vegetation (Day Jr et al., 1999; Day Jr et al., 2011; Rogers et al., 2006). While wetland surface elevation is a function of multiple factors, including belowground production and decomposition, groundwater dynamics and sedimentary and regional subsidence (Cahoon et al., 1999; Rogers and Saintilan, 2008), the retention of aboveground inputs play a critical role in wetland survival under changing hydrological conditions (Day et al., 2011).

With this in mind, our medium-term accretion data suggest that *Sporobolus* and *Sarcocornia* assemblages may be particularly vulnerable to current RSLR, with mean surface accretion rates either lower (*Sarcocornia* = 0.92 mm y^{-1}) or only marginally higher (*Sporobolus* = 1.30 mm y^{-1}) than contemporary rates of local sea level rise within Botany Bay (1.15 mm y^{-1}). In fact, there is already evidence of this across much of the Towra Point Nature Reserve, as well as elsewhere in the region, where upslope encroachment of mangrove shrubs into *Sarcocornia*-*Sporobolus* association is occurring (Kelleway et al., 2016b). In contrast, vegetation change (either in the form of mangrove encroachment or dieback) has not been widely reported for *Juncus* assemblages across SE Australia over recent decades, suggesting relative stability during a time of changing sea levels. While belowground biomass production likely plays a role, average *Juncus* surface accretion rates (1.70 mm y^{-1} in this study; 1.76 mm y^{-1} regionally) in excess of local RSLR suggest a potential role of aboveground inputs towards maintaining surface elevation. Dependence upon organogenic inputs for accretion, however, also means the response of *Juncus* assemblages to RSLR may vary with shifts in productivity or decomposition dynamics (e.g. changes in climate and/or nutrient status). Under present conditions, at least, our analyses have shown these organic inputs to be relatively resistant to early decomposition. In all, our findings are also supportive of recent research which suggests organic sediment accretion may be of critical importance in marsh survival under RSLR, particularly in areas most removed from inorganic sediment delivery (D'Alpaos and Marani, 2015). Whether belowground organic matter production makes substantial contributions to Australian saltmarsh surface elevation dynamics and vulnerability to sea level rise remains unknown, and represent an important area for further research. Better understanding of the temporal dynamics of organic and mineral contributions to elevation maintenance is also required, including in relation to expected non-linear increases in sea level.

By combining medium-term accretion quantification with short-term deposition measurements and chemical analyses we have gained insights into the various processes behind observed differences in accretion among saltmarsh vegetation assemblages. While our study highlights assemblage scale differences in potential response to RSLR, it represents only a small part of the information needed to accurately predict the future of SE Australian saltmarsh assemblages. Further measures of short-term deposition and medium-term accretion across a broader range of geographical settings, longer-term studies of soil elevation change among assemblages and modelling of vegetation response thresholds are all required.

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Table 1. Summary of sediment measure techniques; mean and standard error values for feldspar marker horizon (MH), vial and filter bulk sediment measures; mean and standard error of C deposition rates; and contributions of C3 and C4 vegetation to deposition among vegetation assemblages. Accretion rates slower than local sea level rise (1.15 mm y^{-1}) are in red. DN = December neap; DS = December spring; JN = January neap; JS = January spring.

Technique	**Parameter** *Measure* Temporal scale Biases/issues	**Period**	 ***SARCOCORNIA***		 ***SPOROBOLUS***		 ***JUNCUS***	
Feldspar MH								
	**Bulk measure**				**accretion rate (mm y^{-1})**			
	sediment accumulation		**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
	mid-term (days to years)	0-19 mo.	0.78	0.18	0.88	0.22	1.74	0.13
	MH may be lost through erosion or bioturbation	95% CI lower	0.42		0.44		1.48	
		95% CI upper	1.14		1.32		2.00	
					see also Figure 2			
Vial								
	**Bulk measure**				**bulk deposition rate (g cm^{-2} y^{-1})**			
	sediment deposition		**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
	short-term (hours to days)	DN	3.41	1.14	2.74	0.90	3.79	1.25
	Biased towards materials entrained by water. Biased against coarse litter larger than vial mouth	DS	25.19	3.88	66.52	10.47	18.13	3.26
		JN	38.67	9.20	18.84	5.49	4.99	1.33
		JS	100.78	32.73	80.94	8.92	14.92	2.14
Filter					**bulk deposition rate (g cm^{-2} y^{-1})**			
	**Bulk measure**		**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
	sediment deposition	DN	1.47	0.19	1.09	0.26	1.24	9.7E-04
	short-term (hours to days)	DS	2.18	0.35	1.31	0.10	2.37	2.5E-03
		JN	0.79	0.20	0.43	0.05	1.02	2.0E-03
		JS	3.04	0.79	2.50	0.46	2.55	2.8E-03
	Filter + material identification							
	composition of material deposited				*see Figure 3*			
	Filter + elemental analysis				**C deposition rate (g C cm^{-2} y^{-1}) [a]**			
	C deposition rate		**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
		DN	0.10	0.02	0.08	0.02	0.44	0.06
		DS	0.09	0.02	0.12	0.02	0.87	0.16
		JN	0.03	0.01	0.06	0.01	0.41	0.15
		JS	0.23	0.03	0.15	0.03	0.73	0.17
	Filter + isotopic analysis				**isotope mixing model - plant contribution (%)**			
	sources contributing to sediment residue		**C3**	**C4**	**C3**	**C4**	**C3**	**C4**
		DN	59.61	40.39	38.3	61.7	80.2	19.79
		DS	77.50	22.50	25.0	75.0	84.6	15.38
		JN	67.94	32.06	19.9	80.1	81.0	18.98
		JS	72.39	27.61	26.0	74.0	78.8	21.21
					see also Table 2			
	Filter + MIR & ^{13}C NMR							
	character of deposited materials				*see Figure 4 & Table 2*			

[a] Calculated by multiplying bulk accumulation for individual plots by %C values obtained for pooled litter and residue samples

Table 2. Results of ^{13}C NMR, δ^{13}C and elemental (C:N) analyses for each component of three saltmarsh plant assemblage, plus other potential sources. ^{13}C NMR outputs are the average of two samples for each of biomass and litter components (except *Sporobolus* litter, for which only one reliable spectrum was obtained). δ^{13}C and C:N values are the mean (±SE) of biomass (n=3) and litter (n=4) samples. Residue samples were pooled from 15 filters in each vegetation assemblage.

Community	Component	Tide	^{13}C NMR chemical assignment and region (ppm)								δ^{13}C	C:N
			Alkyl (0 - 45)	N-Alkyl/Methoxyl (45 - 60)	O-Alkyl (60 - 95)	Di-O-Alkyl (95 - 110)	Aryl (110 - 145)	O-Aryl (145 - 165)	Amide/Carboxyl (165 - 190)	Ketone (190 - 215)		
Sarcocornia	biomass	n/a	14.4	6.6	45.0	10.6	10.5	4.4	7.1	1.4	-26.5 ± 0.5	38.0 ± 4.2
	litter	combined	10.2	5.1	34.0	9.0	16.3	8.6	13.2	3.6	-25.7 ± 0.1	33.0 ± 1.2
	residue	neap	23.1	8.2	33.7	7.3	11.3	4.3	11.0	1.1	-22.1 ± 0.3	14.2 ± 0.4
		spring	25.1	8.1	32.8	7.1	10.5	4.0	11.3	1.1	-23.3 ± 0.2	14.2 ± 0.7
Sporobolus	biomass	n/a	8.6	4.6	51.0	12.0	11.5	4.6	6.5	1.3	-14.9 ± 0.1	59.8 ± 6.3
	litter	spring	5.2	4.5	47.1	12.0	14.6	6.6	8.0	2.0	-15.8 ± 0.2	59.4 ± 5.2
	residue	neap	19.2	7.9	36.5	8.3	12.6	5.0	9.4	1.2	-18.7 ± 0.6	15.5 ± 0.5
		spring	18.5	7.3	36.6	8.4	13.0	5.2	9.5	1.4	-18.4 ± 0.0	16.3 ± 1.1
Juncus	biomass	n/a	8.6	5.4	51.8	12.2	11.2	4.6	5.2	1.1	-24.8 ± 0.3	61.3 ± 5.6
	litter	combined	5.6	5.4	52.2	12.8	11.9	5.4	5.4	1.3	-25.6 ± 0.1	89.9 ± 4.5
	residue	neap	*insufficient material available for ^{13}C NMR analysis*								-23.7 ± 0.0	19.6 ± 0.0
		spring	15.4	7.2	35.7	8.8	15.4	6.6	9.2	1.7	-23.8 ± 0.2	18.2 ± 0.4
Other sources	algal mat	n/a	14.3	5.6	37.5	8.7	11.5	4.9	14.8	2.6	-15.0 ± 0.4	13.2 ± 0.1
	mangrove leaf	n/a	16.4	6.4	40.6	9.1	12.8	4.8	8.7	1.1	-28.7 ± 0.3	24.8 ± 1.7
	seagrass wrack	spring	11.6	3.9	33.3	8.0	14.4	7.7	16.4	4.6	-12.3	29.2
	macroalga wrack	spring	6.0	2.6	52.5	14.0	5.5	6.6	11.5	1.3	-17.7	57.8

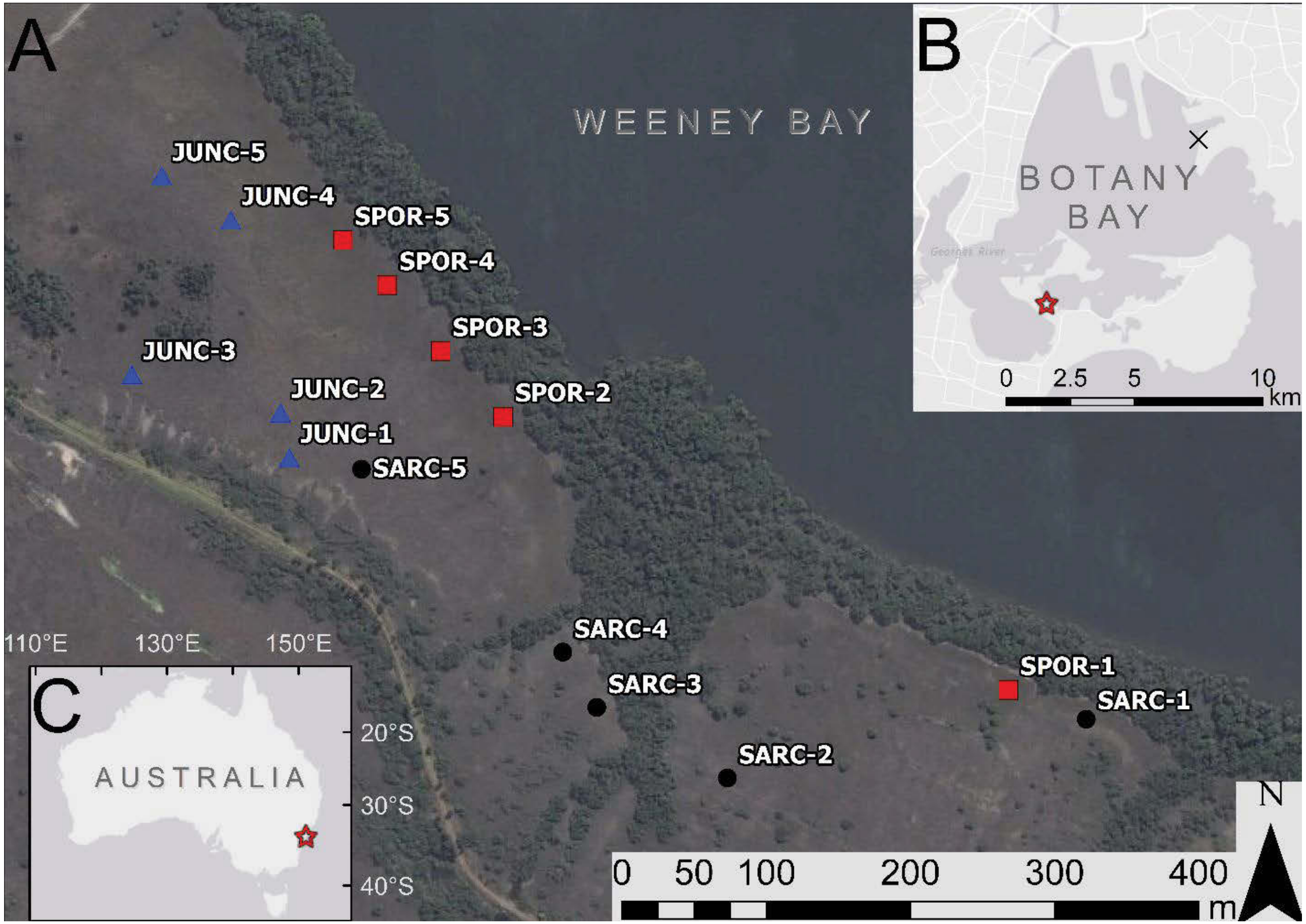

Fig 1. Location of experimental plots within Weeney Bay saltmarsh of Towra Point Nature Reserve (A), located along the southern shoreline of Botany Bay (B) in southeast Australia (C). Location of nearest tidal gauge is marked by an X in inset B. SARC = *Sarcocornia quinqueflora* assemblage; SPOR = *Sporobolus virginicus* assemblage; JUNC = *Juncus kraussii* assemblage.

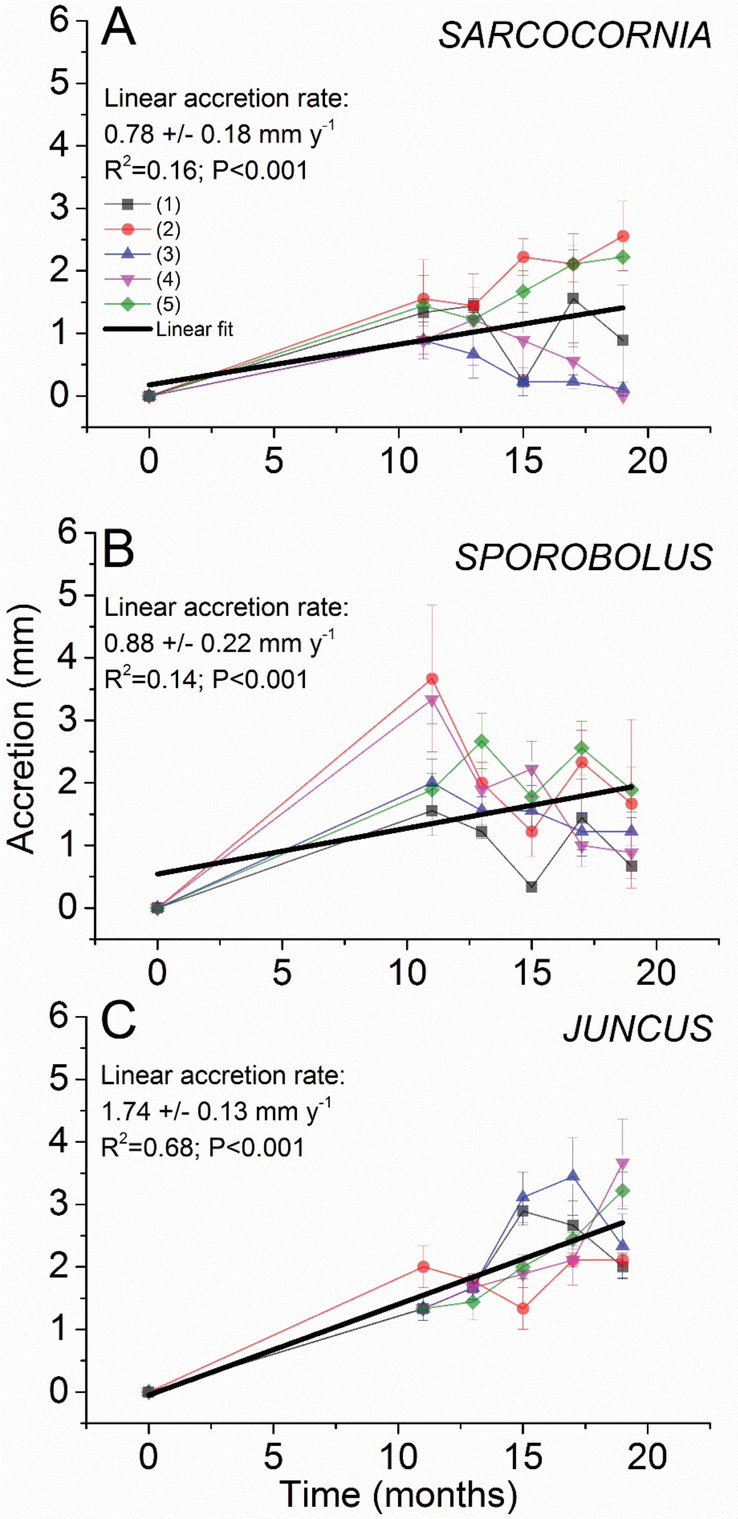

Fig 2. Surface accretion above feldspar marker horizons. Data are presented as the mean ± SE of three replicate plots in each of five locations for each vegetation assemblage. A linear fit was applied on the basis of all data points (n=90) for each vegetation assemblage.

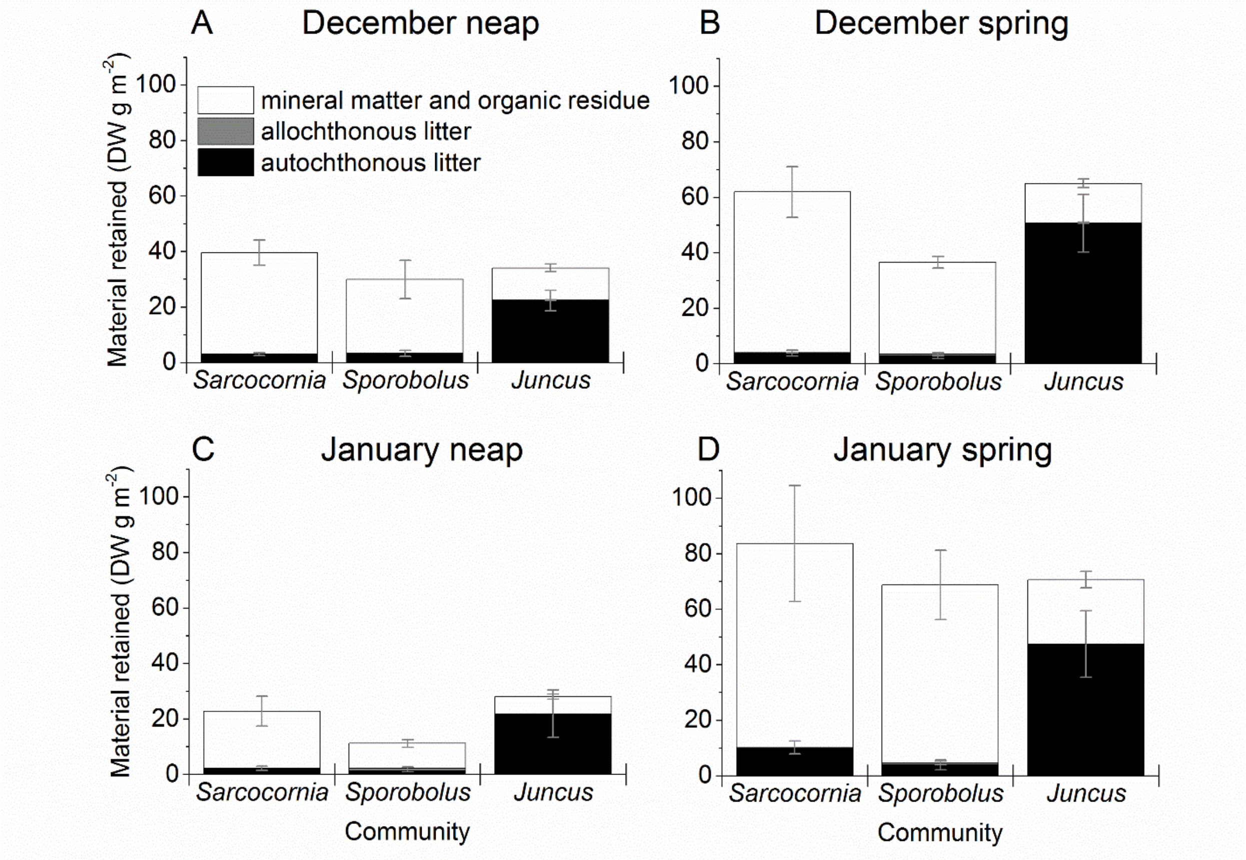

Fig 3. Mean mass of autochthonous litter, allochthonous litter and mineral matter / organic residue retained on filters at end of 6d deployment during December neap (A), December spring (B), January neap (C) and January spring (D) tidal periods. Error bars are presented for each component and represent 1 standard error each side of the mean.

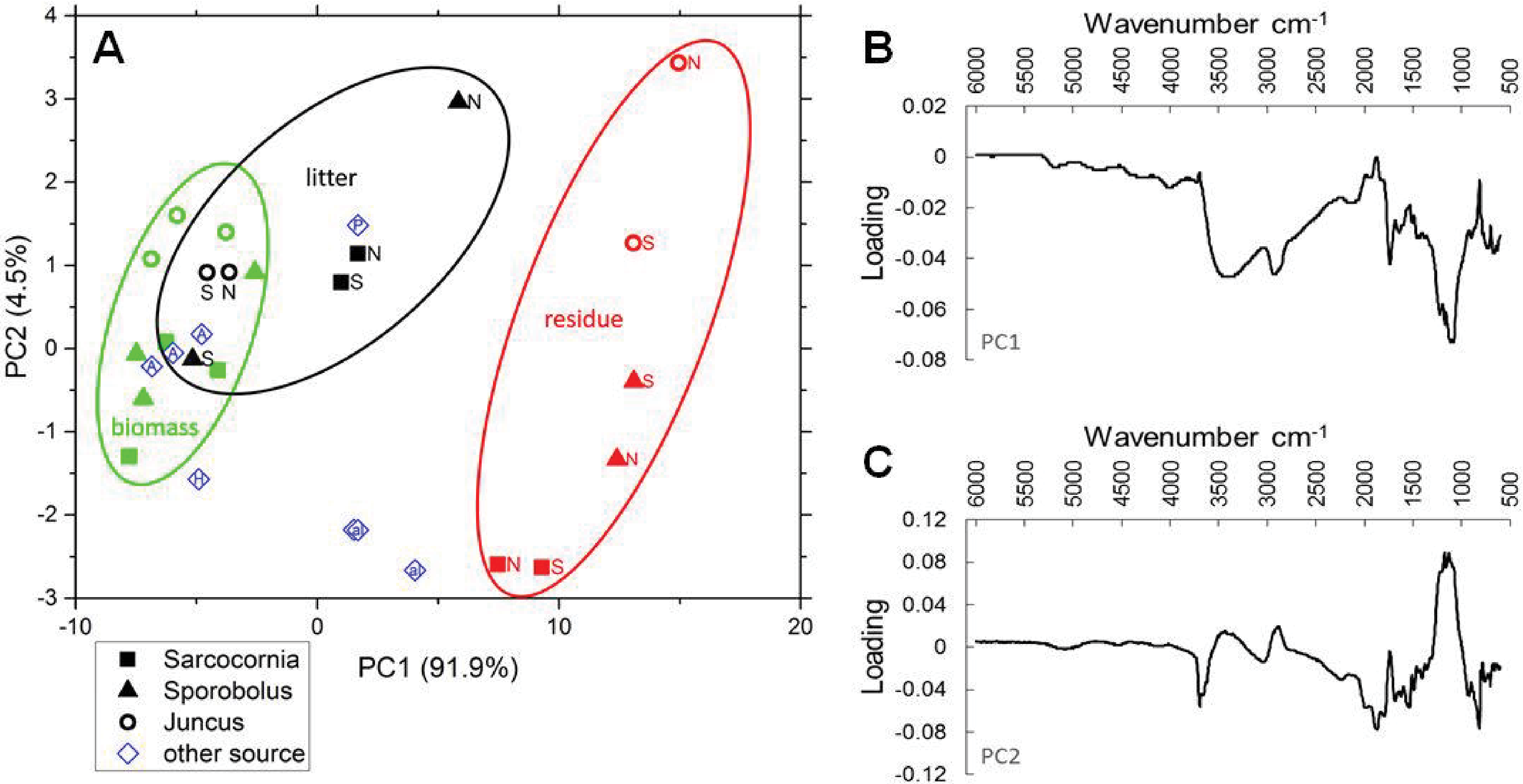

Fig 4. Principal component analysis of MIR spectra with the proportion of variance explained by each component is given in parentheses (A); spectral loading plots for PC1 (B) and PC2 (C). S = spring tide samples; N = neap tide samples; H = *Hormosira banksii* (macroalga) wrack; P = *Posidonia australis* (seagrass) wrack; A = *Avicennia marina* (mangrove) leaf; al = benthic algae mat.

SUPPLEMENTARY INFORMATION

Table S1. Elevation data (mean ± standard error) for each of five replicate plots in each vegetation assemblage. The number of tides exceeding each mean plot elevation at a nearby tidal gauge are provided as an indicator of likely inundation patterns for the four deployment periods

Vegetation assemblage	Plot #	Elevation (mean ± SE)	December neap	December spring	January neap	January spring
		cm above LAT	Number of tides exceeding mean plot elevation			
Sarcocornia	1	151.20 ± 0.58	3	7	1	6
	2	155.20 ± 0.57	1	7	0	6
	3	151.40 ± 1.22	3	7	1	6
	4	148.30 ± 0.59	3	8	2	10
	5	178.37 ± 0.33	0	6	0	5
Sporobolus	1	155.17 ± 0.91	1	7	0	6
	2	156.63 ± 0.35	1	7	0	6
	3	156.90 ± 0.50	1	7	0	6
	4	158.27 ± 1.29	1	6	0	6
	5	162.80 ± 0.44	1	6	0	6
Juncus	1	181.33 ± 0.45	0	6	0	5
	2	185.70 ± 0.17	0	6	0	5
	3	187.10 ± 0.29	0	6	0	5
	4	179.70 ± 0.45	0	6	0	5
	5	183.37 ± 0.44	0	6	0	5

Table S2. Elemental composition and C:N ratio for organic component of unidentified residues collected on filter papers.

Community	Tide	%C	%N	C:N
Sarcocornia	December neap	4.18	0.31	13.59
	December spring	3.37	0.25	13.69
	January neap	3.07	0.21	14.72
	January spring	3.56	0.24	14.65
Sporobolus	December neap	4.50	0.31	14.72
	December spring	6.56	0.37	17.81
	January neap	3.88	0.24	16.26
	January spring	4.04	0.27	14.80
Juncus	December neap	16.66	0.85	19.57
	December spring	14.36	0.81	17.62
	January neap	16.81	0.85	19.70
	January spring	9.05	0.48	18.72

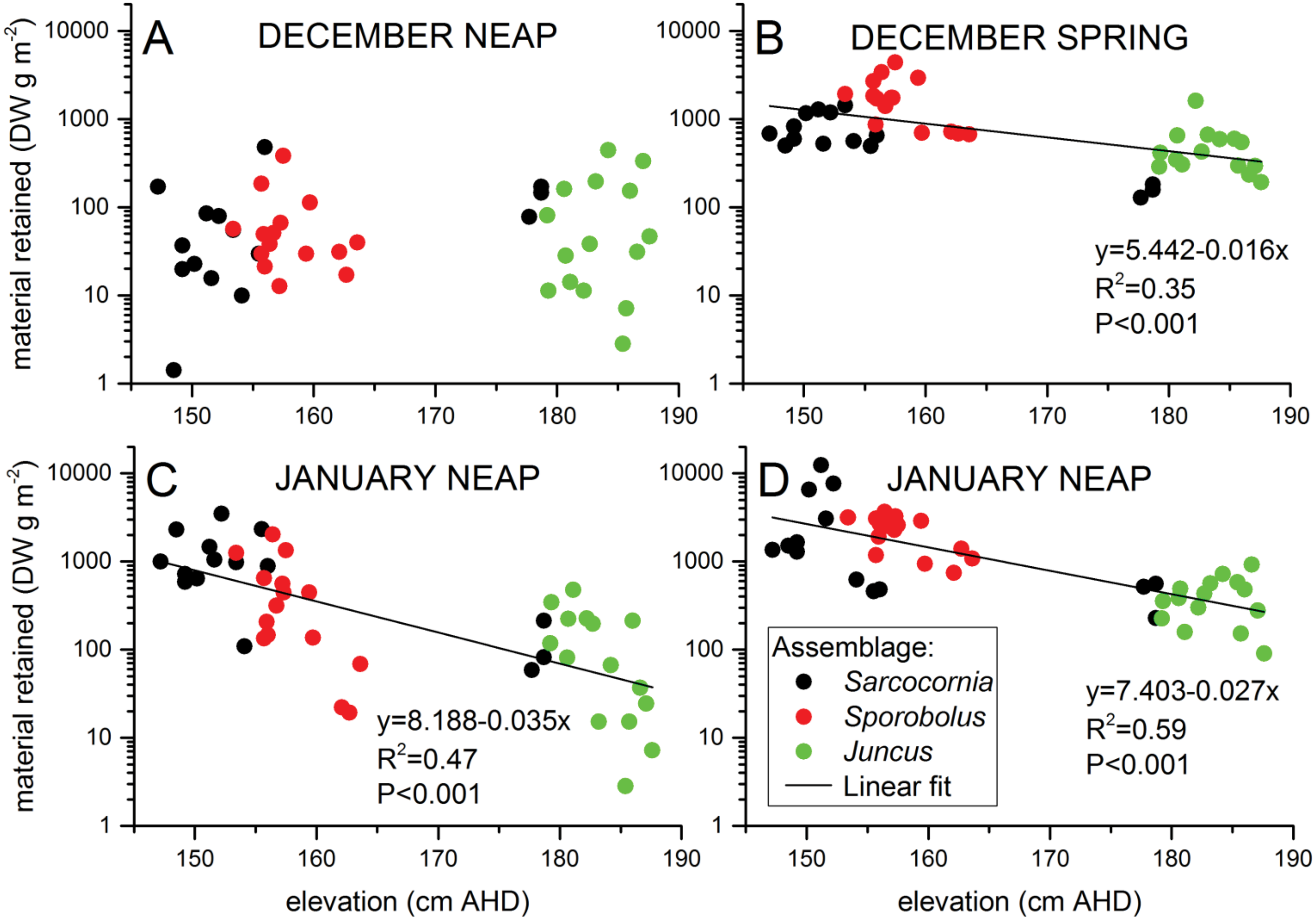

Fig S1. Scatterplots of bulk material retained within vials against the surface elevation of the study plot each vial was located within. Regression line and statistics are included where there was a significant ($P<0.05$) linear fit. Note the log scale on the Y axes.

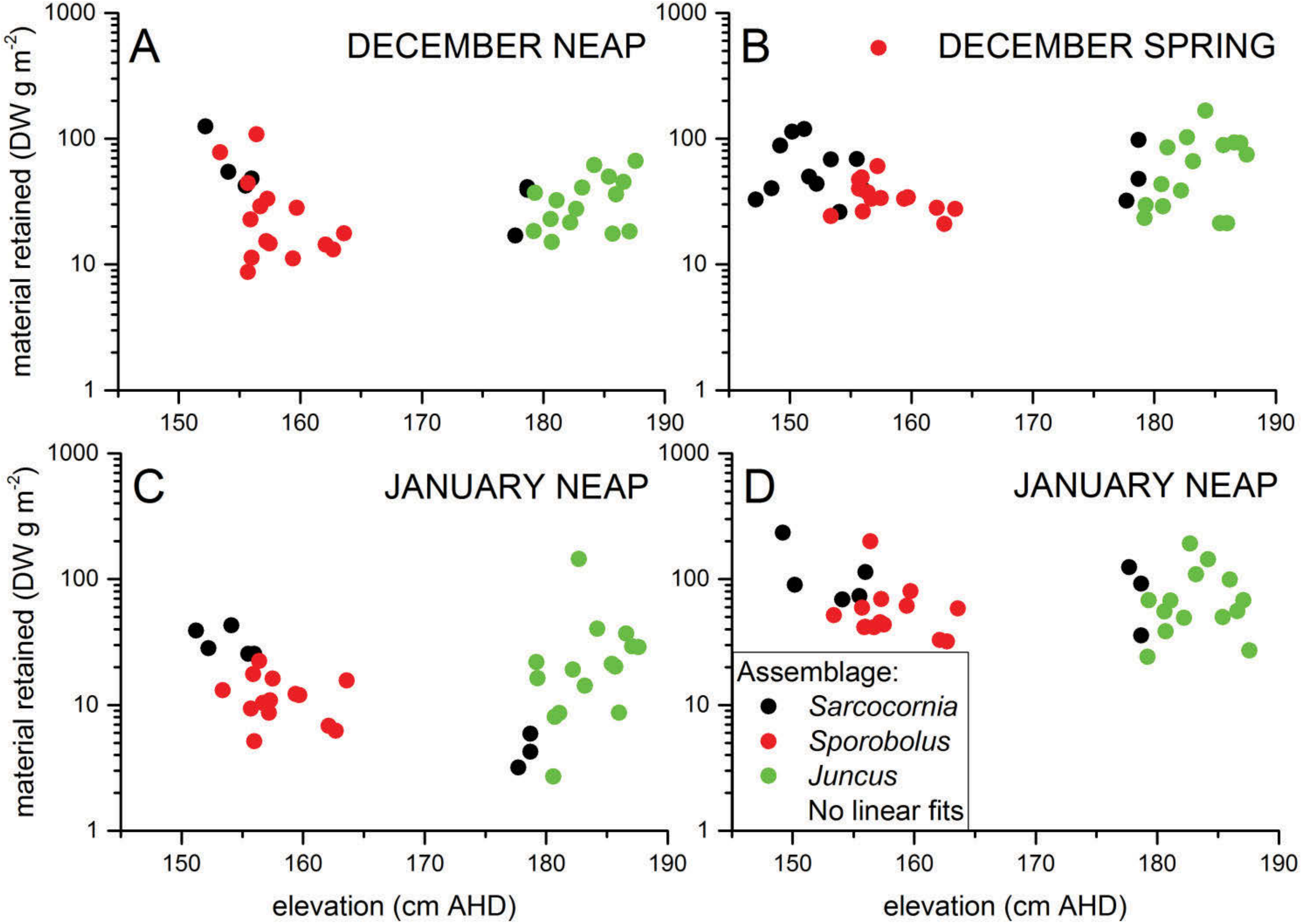

Fig S2. Scatterplots of bulk material retained on filters against the surface elevation of the study plot each filter was located within. There were no significant ($P<0.05$) linear fits. Note the log scale on the Y axes.

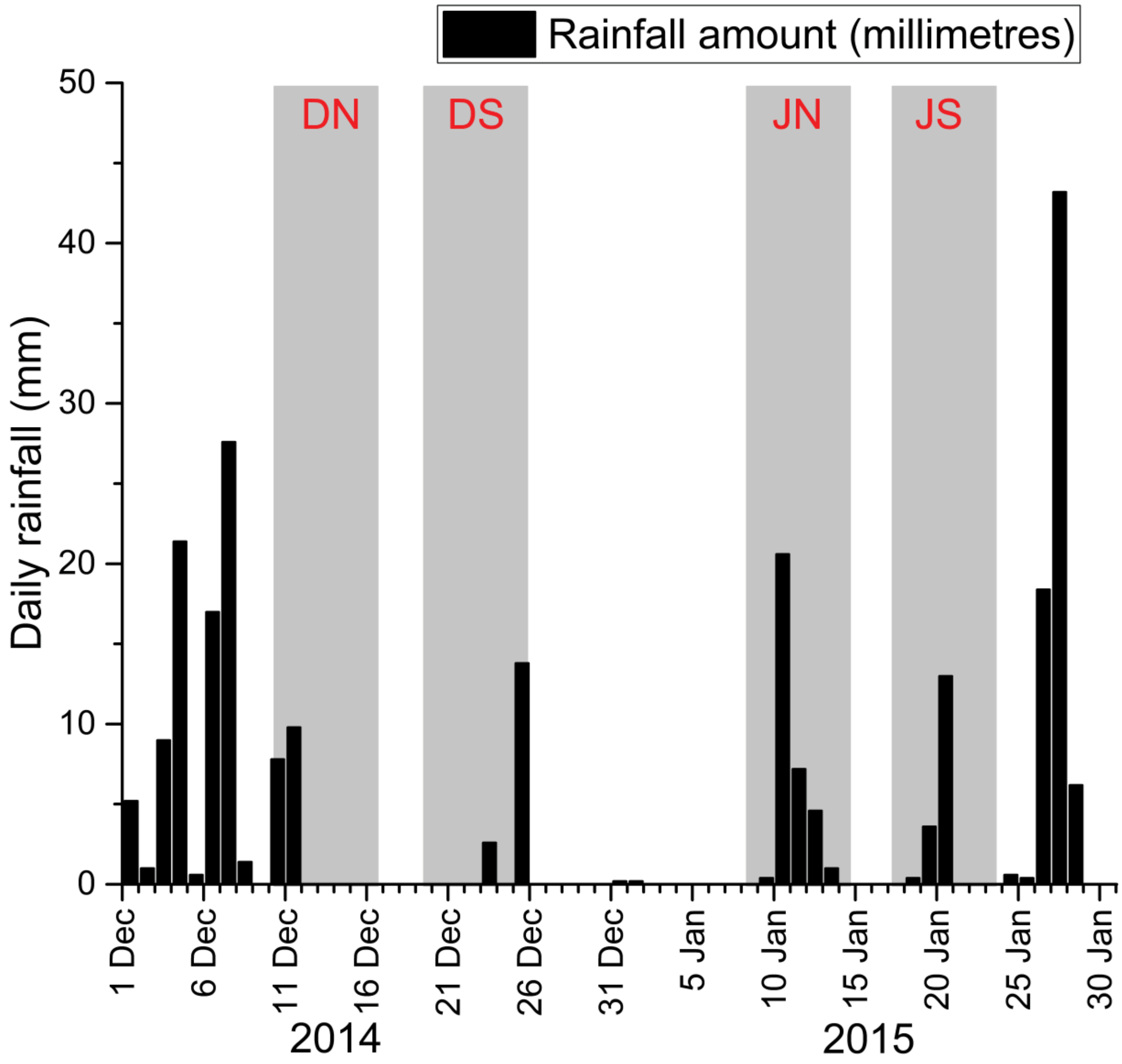

Fig S3. Daily rainfall (mm) records before, during and after filter and vial installation periods. Installation periods are shaded in grey. DN = December neap; DS = December spring; JN = January neap; JS = January spring.

CHAPTER FOUR

GEOCHEMICAL ANALYSES REVEAL THE IMPORTANCE OF ENVIRONMENTAL HISTORY FOR BLUE CARBON SEQUESTRATION

This chapter has been formatted for submission to the *Journal of Geophysical Research - Biogeosciences*:

Kelleway J.J., Saintilan N, Macreadie P.I., Baldock, J.A., Heijnis, H., Zawadzki, A., Gadd, P., Jacobsen, G. & Ralph P.J. Geochemical analyses reveal the importance of environmental history for blue carbon sequestration.

Geochemical analyses reveal the importance of environmental history for blue carbon sequestration

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Key Points:

- Multiple ecosystem shifts were observed within the surface 1 m of blue carbon sediments
- Preservation of inputs from prior ecosystem formation can make large contributions to contemporary carbon stocks
- Heterogeneity of historical influence needs to be accounted for in regional assessments of carbon storage

Abstract

Coastal habitats including saltmarshes and mangroves are able to accumulate and store significant blue carbon stocks, which may persist for millennia. Despite this implied ecosystem stability, the distribution and structure of intertidal-supratidal wetlands is known to respond to changes imposed by geomorphic evolution, climatic, sea-level and anthropogenic influences. In this study we reconstruct environmental histories and biogeochemical conditions in four wetlands of similar contemporary vegetation in SE Australia, with the broad objective of assessing the importance of historic factors to contemporary organic carbon (C) stocks and accumulation rates. Results from the four contemporary saltmarsh cores – two collected from marine influenced saltmarshes (WAP-M and POR-M) and two from fluvial influenced saltmarshes (WAP-F and POR-F) – highlight different environmental histories and preservation conditions among the four sites. High C stocks were associated with the presence of a mangrove phase below the contemporary saltmarsh sediments in the POR-M and POR-F cores. ^{13}C NMR analyses showed this historic mangrove root C to be remarkably stable in its molecular composition despite its age, consistent with its position in deeper sediments where reducing conditions prevail. WAP-M and WAP-F cores did not contain mangrove root C, however, significant preservation of char C (up to 46% of C in some depths) in WAP-F reveals the importance of historic catchment processes to this site. Together, these results highlight the importance of integrating historic ecosystem and catchment factors into attempts to upscale C accounting to broader spatial scales.

CHAPTER FIVE

SEVENTY YEARS OF CONTINUOUS ENCROACHMENT SUBSTANTIALLY INCREASES 'BLUE CARBON' CAPACITY AS MANGROVES REPLACE INTERTIDAL SALT MARSHES

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Kelleway J.J., Saintilan N., Macreadie P.I., Skilbeck C.G., Zawadzki A., Ralph P.J. (2016) Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. *Global Change Biology*, 22: 1097-1109. DOI: 10.1111/gcb.13158

Global Change Biology

Global Change Biology (2016) **22**, 1097–1109, doi: 10.1111/gcb.13158

Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes

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Abstract

Shifts in ecosystem structure have been observed over recent decades as woody plants encroach upon grasslands and wetlands globally. The migration of mangrove forests into salt marsh ecosystems is one such shift which could have important implications for global 'blue carbon' stocks. To date, attempts to quantify changes in ecosystem function are essentially constrained to climate-mediated pulses (30 years or less) of encroachment occurring at the thermal limits of mangroves. In this study, we track the continuous, lateral encroachment of mangroves into two south-eastern Australian salt marshes over a period of 70 years and quantify corresponding changes in biomass and belowground C stores. Substantial increases in biomass and belowground C stores have resulted as mangroves replaced salt marsh at both marine and estuarine sites. After 30 years, aboveground biomass was significantly higher than salt marsh, with biomass continuing to increase with mangrove age. Biomass increased at the mesohaline river site by 130 ± 18 Mg biomass km^{-2} yr^{-1} (mean ± SE), a 2.5 times higher rate than the marine embayment site (52 ± 10 Mg biomass km^{-2} yr^{-1}), suggesting local constraints on biomass production. At both sites, and across all vegetation categories, belowground C considerably outweighed aboveground biomass stocks, with belowground C stocks increasing at up to 230 ± 62 Mg C km^{-2} yr^{-1} (± SE) as mangrove forests developed. Over the past 70 years, we estimate mangrove encroachment may have already enhanced intertidal biomass by up to 283 097 Mg and belowground C stocks by over 500 000 Mg in the state of New South Wales alone. Under changing climatic conditions and rising sea levels, global blue carbon storage may be enhanced as mangrove encroachment becomes more widespread, thereby countering global warming.

Keywords: biomass, blue carbon, carbon sequestration, climate change, ecosystem services, mangrove, mangrove encroachment, salt marsh, saltmarsh, sea level rise

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CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

1. Thesis aims

Three broad aims were determined for this thesis. These were to:

1. Quantify and characterise saltmarsh carbon stocks, including in relation to the phenomenon of mangrove encroachment;
2. Determine the role of geomorphic and vegetation factors in carbon accumulation and storage;
3. Assess variations in quantity and character of carbon with sediment depth.

Important insights were gained in relation to each of these aims over the four experimental Chapters. The purpose of this concluding Chapter is to integrate these findings and assess the new knowledge gained in relation to the above aims. This discussion is undertaken in two broad contexts – i) geomorphic and sedimentary settings; and, ii) vegetation processes and ecosystem change. This Chapter also identifies remaining knowledge gaps and presents recommendations for how these might be overcome. It concludes with a summation of management implications and opportunities for coastal wetlands and their associated blue carbon (C) in a time of substantial change.

2. Geomorphic and sedimentary settings

2.1 Quantifying C stocks

The findings of this thesis present a paradigm shift in the understanding of C stock variability in SE Australian saltmarshes. That is, geomorphic and sedimentary factors, rather than vegetation structure, are the primary drivers of variability of C stocks in this ecosystem. The importance of geomorphic and sedimentary factors in comparison to vegetation is most clearly displayed in Chapter 2, where a factorial design involving the analysis of >140 sediment cores was used to specifically test the importance of geomorphic setting and vegetation structure to C stocks. Although there were good theoretical reasons to suspect higher C stocks in fluvial sites relative to marine sites, the magnitude of the difference (i.e. mean fluvial C stocks were more than two times higher than marine C stocks) was surprising, considering that previous studies had been unable to find clear geomorphic trends, albeit without using the same sampling effort or design. While common in ecological studies, the use of robust experimental designs and appropriate replication is often lacking in the geosciences due to logistical and time constraints. The outcomes of Chapter 2 highlight the importance of such a comprehensive approach in circumstances where understanding spatial variability is important, and where multiple, potentially confounding factors may exist.

Although limited to just one and two estuaries, respectively, saltmarsh C stocks reported in Chapters 4 and 5 were consistent with the findings of Chapter 2, in that stocks derived from fluvial sites were higher than those from marine sites in the same estuary. However, for cores collected from mangroves (Chapter 5), or where mangrove roots were found below the contemporary saltmarsh surface (Port Stephens sites, Chapters 2 & 4), these geomorphic differences were either not as distinct, or were mostly absent. For example, while there was a 2.4-fold difference between fluvial (mean ± SE = 173.2 ± 17.1 Mg C ha^{-1}) and marine (72.0 ± 8.1 Mg C ha^{-1}) saltmarsh stocks reported in Chapter 5, C stocks of mature mangrove stands within the same sites were not significantly different (324.7 ± 40.0 versus 267.4 ± 40.6 Mg C ha^{-1}). Among the transitional mangrove stands, only 57/58-70 y old mangroves differed substantially between the two geomorphic zones (see Figure 3 in Chapter 5), with this likely related to a restrained biomass response in the marine site for this age class (Figure 2B in Chapter 5). Similarly, the influence of well-preserved mangrove roots under saltmarshes in both Port Stephens sites (Chapter 4) appears to have diminished any difference in C stocks between the two geomorphic zones (see Table 1 in Chapter 4). Together these results strongly suggest that although geomorphic differences exist more broadly for saltmarsh C stocks, such a distinction may not necessarily be true for mangrove ecosystems where belowground root C stocks are more substantial. Such a disparity between ecosystems may also have implications for the practice of combining datasets from different blue C ecosystems (saltmarsh, mangrove, seagrass) to assess drivers of spatial variability (e.g. Chmura *et al.*, 2003, Lovelock *et al.*, 2013, Saintilan *et al.*, 2013).

In Chapter 2 it was also revealed that C densities were related to broad classifications of sediment grain character in both geomorphic settings and across the three depth intervals studied (Chapter 2 Figure 4). In fact, the CART model developed in that study (Chapter 2: Figure 3) identified sediment grain type (fine, mixed, sand) as the primary variable to predict saltmarsh C density of all variables measured (including the broader classification of geomorphic setting). While there are multiple mechanisms discussed in Chapter 2 which may explain this strong relationship between C density and sediment grain class (including mineral protection and oxygen exposure time), these were not specifically tested in the study, so further investigation is warranted. Also, as grain size was only broadly characterised and not explicitly quantified, it is not clear if there are more specific relationships between C density and specific grain size distributions.

Quantification of grain size distribution across the four cores studied in detail in Chapter 4 reveal some important insights regarding C density prediction. First, results are consistent with the broad classification undertaken in Chapter 2 – C stocks are higher in sites with fine-grained, fluvial sediments relative to sandy, marine sites. Second, grain size distribution may vary down-profile in accordance with the environmental history of a site. This is seen most clearly by the increase in the <60 μm fraction during the development of the wetland phase above marine sands (dominated by fractions > 250 μm) in the POR-M core (Chapter 4: Figure 3A). The same trend is repeated, albeit in a coarser fraction (i.e. increases in the <250 μm fraction) and to a lesser extent in the WAP-M core (Chapter 4: Figure 2A).

The deep penetration of roots can limit the applicability of only using grain size distribution to predict belowground C density. In the case of the POR-M, the deep penetration of mangrove roots into previously low-C sub-surface sediments has enriched the C content of sandy sediments well above the values predicted by the CART model (Chapter 2: Figure 3). A similar scenario was also observed at Towra Point (Chapter 5), where sub-surface depths of recent (<70 y) saltmarsh-mangrove transition areas are experiencing a proliferation of deep mangrove roots (and associated increase in C) into sandy (and previously low C) sub-surface sediments. Therefore, the applicability of using grain size as a predictor of saltmarsh C variability, once again, may not extend to mangrove (or saltmarsh that was previously mangrove) environments where substantial root biomass inputs appear to (at least partly) override sedimentary and geomorphic factors.

2.2 Surface accumulation

Importantly, geomorphic factors also influence C dynamics at the within-site scale. In Chapter 3 the elevation of sampling points within the tidal frame was found to play an important role (in interaction with vegetation structure) in whether surface materials were redistributed (lower marsh assemblages) or retained (higher marsh assemblage) under tidal inundation and rainfall events. The implications of this are lower, more varied surface accretion (bulk material) and lower C deposition rates in the lower marsh assemblages compared to the upper marsh assemblage (Chapter 3: Table 1). These findings are largely incongruous with models of tidal wetland accumulation derived from North American *Spartina alterniflora* studies (e.g. Mudd *et al.*, 2004) which predict increased sedimentation with proximity to tidal sources and lower elevation within the tidal frame. Our study, however, was restricted to a single marine embayment site, where suspended sediment supply is likely very low compared to other estuarine settings. On the basis of previous literature, it is expected that sites subject to inundation by waters with higher suspended sediment loads (for example, fluvial delta and riverine saltmarshes) would have higher bulk sediment accretion rates, as well as higher surface C accumulation rates relative to our study site (Chmura *et al.*, 2003, Ouyang & Lee, 2014, Rogers *et al.*, 2006). Comparison of surface accumulation results from Wapengo Lagoon and Port Stephens, however, suggest that may not always be the case, with WAP-M bulk accumulation rates substantially higher than those calculated for WAP-F (Chapter 4: Table 1). Despite this, surface C accumulation rates were higher in both the Wapengo and Port Stephens fluvial sites relative to marine sites, suggesting a preferential settling of allochthonous C in fluvial sites. Replication of the methods used in Chapter 3 (i.e. a combination of mid-term and short-term accretion/deposition measurements and compositional analyses) in a broader range of sites, including those subject to fluvial influence is therefore recommended.

2.3 C character and preservation

One of the major reasons why the relationship between carbon stocks and geomorphic setting was first explored in this thesis was the expectation of contributions from different types of allochthonous materials into fluvial versus marine influenced saltmarshes (e.g. Chapter 1: Figure 4). Comparisons of isotopic and molecular compositions across multiple studies in this thesis reveal that there are important distinctions in the sources of C, and in the ultimate stability of different types of C in the longer-term. This applies to both estuary-scale geomorphic zones and within-site geomorphic gradients.

At the estuary scale, substantial differences in C stocks among geomorphic zone appear to be partly due to differences in materials accumulating in fluvial versus marine saltmarshes (Chapter 2). Higher C:N (Chapter 2: Table 2) and more depleted $\delta^{13}C$ (Chapter 2: Figure 5) fluvial saltmarsh sediments, relative to marine saltmarsh sediments indicated greater contributions originating from C3 vascular plants to fluvial sediments. While it is difficult to distinguish between terrestrial (catchment) sources and local (C3 saltmarsh) or nearby (C3 mangroves) plant sources on the basis of bulk isotopic values, other results suggest terrestrial contributions may be large. For instance, ^{13}C NMR analyses of fluvial saltmarsh sediments from Wapengo Lagoon reveal contributions of catchment-derived char ranging from 8-46% of all organic C (Chapter 4: Figure 4). While high contributions in deep sediments may indicate the selective preservation of this terrestrial C (which is itself important), the 22% contribution observed in near-surface sediments (ROI-2) where fresh inputs from live root are also expected, reveal it is not merely a case of selective preservation. Further, as char C represents just one form of refractory terrestrial C, char values may will almost certainly represent underestimates of the total contribution of terrestrial C to fluvial saltmarsh sediments.

The state-wide assessment of saltmarsh C also revealed within-site distinctions in C sources. Again, C:N and $\delta^{13}C$ values were used to determine the greater importance of allochthonous inputs to C stocks in areas generally lower in the tidal frame and nearer tidal sources (i.e. succulent/grass saltmarshes) relative to upper marsh, more landward zones (i.e. rush saltmarshes) (Chapter 2: Table 2; Chapter 2: Figure 5). This finding was confirmed in the surface dynamics study (Chapter 3) where a combination of manual material separation and quantification, C:N, $\delta^{13}C$ and molecular (^{13}C NMR) analyses quantified these differences in contributions. Together, these revealed a redistribution rather than accumulation of C in lower marsh plots where hydrodynamic forces are greatest, and more effective retention and accumulation of C at higher elevations. It remains unclear, however, to what extent these differences are due specifically to geomorphic processes versus key vegetation factors (such as plant productivity, biomass and structure), or their interaction. Lessons from the assessment of saltmarsh C stocks (Chapter 2 and preceding studies) suggest that rigorous experimental approaches will be required to determine respective influences here.

2.4 Summary

In summary, it has been comprehensively demonstrated that geomorphic and sedimentary factors are of primary importance in understanding variability of saltmarsh C stocks. These physical factors also play a role in surface accumulation dynamics, though their importance relative to vegetation factors remains less clear on the basis of current information. Furthermore, the suggestion that geomorphic/sedimentary distinctions are subdued or absent where there is influence from mangroves, highlights the need to further consider vegetation factors and their interaction with wetland geomorphology.

3. Vegetation processes and ecosystem change

3.1 The role of vegetation

The finding that geomorphic and sedimentary factors are of primary importance in explaining C stock variability in saltmarshes, may upon first consideration, suggest that vegetation factors are of limited interest. After all, analysis across all the cores collected in the state-wide survey (Chapter 2), revealed a remarkable similarity in mean C stocks among rush (mean±SE = 167±11 Mg C ha^{-1}) and grass/succulent (162 ± 13 Mg C ha^{-1}) saltmarsh assemblages. This overall similarity, however, belies the importance of vegetation processes in determining saltmarsh C sequestration capacity.

First, despite C stock similarities in the overall dataset, CART analysis (Chapter 2: Figure 3) revealed important interactions between sediment type (i.e. the primary predictor of C density) and vegetation factors (vegetation structure and vegetation cover) which were secondary predictors of C density. That is, even though sandy sites contained the lowest C densities overall, there was a significant (albeit small) difference between sandy rush saltmarshes relative succulent/grass saltmarshes. This probably points to differences in belowground biomass between the two vegetation types, which although not quantified, is expected to be higher in rush communities. Similarly, the higher C density in mixed sediment plots which had extremely high vegetation cover (>95% coverage) points to a biomass effect; however, it is unknown to what extent aboveground (e.g. litterfall and/or particle retention) versus belowground (root production and/or preservation) processes contribute in this regard.

3.2 Aboveground processes

When considering the potential role of vegetation structure and composition on C sequestration capacity, it is important to note the distinction between approaches which quantify C stocks versus those which quantify C accumulation rate. Whilst vegetation structure does not have a primary influence on saltmarsh C stocks (Chapter 2), it has been shown in Chapter 3 and by other studies in the region (Lovelock *et al.*, 2013, Saintilan *et al.*, 2013) as well as globally (Ouyang & Lee, 2014) that C accumulation rates can vary substantially according to saltmarsh vegetation assemblage.

Previous research has estimated C accumulation rates in *Juncus* to be more than 4.5 times higher than in *Sarcocornia/Sporobous* saltmarshes (Lovelock *et al.*, 2013, Saintilan *et al.*, 2013). This high surface C accumulation capacity appears to be partially a function of their capacity to accumulate bulk materials at a faster rate than *Sarcocornia/Sporobolus* saltmarshes (Chapter 3; Saintilan *et al.* (2013)). This is not the whole explanation, however, as the relationship between bulk material and C accumulation rates may vary among sites (Chapter 4) and among assemblages (Chapter 3). For example, although two of the *Sarcocornia/Sporobolus* cores (WAP-M and POR-F) analysed in Chapter 4 displayed bulk surface accretion rates higher than the regional average of *Juncus* (1.70 mm y^{-1} (Saintilan *et al.*, 2013)), both these cores were well below the regional average of *Juncus* in terms of C accumulation. This therefore points to a particular and consistently high organic content of the materials accumulating on the surface of *Juncus* assemblages. Identification of materials accumulating within this assemblage under both tidal inundation and outside of tidal inundation showed this C rich material to be overwhelmingly derived from *Juncus* litterfall (Chapter 3: Figure 3). The consistent similarity of *Juncus* sediments isotopic values to C3 tidal wetland plants in both fluvial and marine settings (with only occasional enrichments of $\delta^{13}C$ in marine sites, compared to substantial enrichment in non-rush sediments) (Chapter 2: Figure 5) provides further evidence for the particular role of autochthonous plant material to the exceptional C accumulation capacity of *Juncus* saltmarshes.

The reduced capacity of *Sarcocornia* and *Sporobolus* assemblages to accumulate surface C is likely due to several factors, which are discussed in Chapter 3. Briefly, these include the low (and expected slow turnover of) aboveground biomass of these species, as well as a lower capacity to retain surface materials while being situated in more hydrologically active areas than *Juncus* assemblages. *Sarcocornia* and *Sporobolus* litter may also be more easily decomposed relative to *Juncus* litter (Chapter 3: Table 2), with a similar finding expressed in Chapter 4, where *Sarcocornia/Sporobolus* roots were considered broadly less stable than mangrove roots.

It is expected that aboveground processes will play an increasingly important role in the C sequestration capacity of tidal wetlands as mangroves encroach into saltmarshes in SE Australia and elsewhere. Over the past 70 y substantial increases in aboveground biomass have occurred as part of this vegetation shift (Chapter 5: Figure 2), with increases generally more rapid than those observed in belowground C pools (Chapter 5: Figures 3; Doughty *et al.*, 2015). At present, it remains unquantified what changes in other aboveground processes associated with C storage - including plant litter production/turnover and allochthonous C accumulation – result from mangrove encroachment.

3.3 Belowground processes

In contrast to the limited information regarding aboveground vegetation processes, a clearer understanding is emerging of the belowground and surface building processes under shifting saltmarsh-mangrove dynamics. First, the preservation of former mangrove root networks in two of the four saltmarsh cores analysed in Chapter 4 adds to the previously reports of historic mangrove distributions below contemporary saltmarsh in the region (Saintilan & Hashimoto, 1999, Saintilan & Wilton, 2001). In Chapter 5 it had been proposed that deep penetration by encroaching mangrove roots into (former) saltmarsh sediments may: 1) increase C preservation through storage deep in the profile; or alternately 2) alter redox potential down-profile by introducing oxygen to previously anoxic depths. The findings in Chapter 4 support the former more than the latter, as in both cores there was effective preservation of mangrove roots (and consequently C density) deep in the profile, coinciding with predominantly reducing conditions. There was, however, evidence of very localised redox transitions throughout these depths which were probably associated with the roots, although the effect of this on root remineralisation appeared to be small. If such remarkable preservation of mangrove root C (i.e. after ~1,800 y or more) is achieved by mangrove roots under contemporary encroachment, then the substantial increases in belowground C reported here (Chapter 5: Table 1; this Chapter: Figure 1) will prove to be effective in the long-term sequestration of atmospheric C.

It has also been shown that belowground production by mangroves can be of significance to saltmarsh C accumulation and storage, even in locations where mangrove encroachment is not obviously occurring. The lateral expansion of mangrove roots below the *Sporobolus* POR-F saltmarsh surface highlights the capacity of nearby mangroves to contribute to both near-surface and deep 'saltmarsh' C stocks (Chapter 4: Figure 3B). Such an occurrence of live mangrove pneumatophores within the saltmarsh zone is far from rare in SE Australia, as highlighted by previous saltmarsh botanical surveys (Adam *et al.*, 1988 and references therein). Although Adam *et al.* (1988) report pneumatophores occurring up to 5 m away from the nearest mangrove canopy, field observations undertaken for this thesis suggest distances of 20 m or more from the nearest canopy edge are not uncommon. Given the contiguous and often ecotonal nature of mangrove and saltmarsh distributions in SE Australia, as well as the narrow width of many saltmarshes in the region, pneumatophore contributions to overall saltmarsh C may be substantial. Further, as mangroves continue to expand their distribution and as environmental constraints to mangrove productivity ease – for example, under warming climate and increasing atmospheric CO_2 concentration (Saintilan & Rogers, 2014) – the lateral belowground input of mangrove biomass into saltmarshes is likely to become even more common. The evidence from the POR-F core suggests that while the pneumatophore had a strong influence on localised redox conditions, its presence represented an important addition to belowground C stocks

3.4 Summary

It is clear that both above and belowground vegetation processes contribute to C accumulation in saltmarshes and their encroachment by mangroves. This fact, coupled with the role of vegetation parameters in predicting C stock in certain sedimentary settings highlights the importance of plant processes to the overall C sequestration capacity of tidal wetlands. The dynamic nature of tidal wetlands and their capacity to respond to environmental changes has significant implications for blue

C, as it has been demonstrated that shifts in vegetation structure can alter C stocks and C accumulation/sequestration rates.

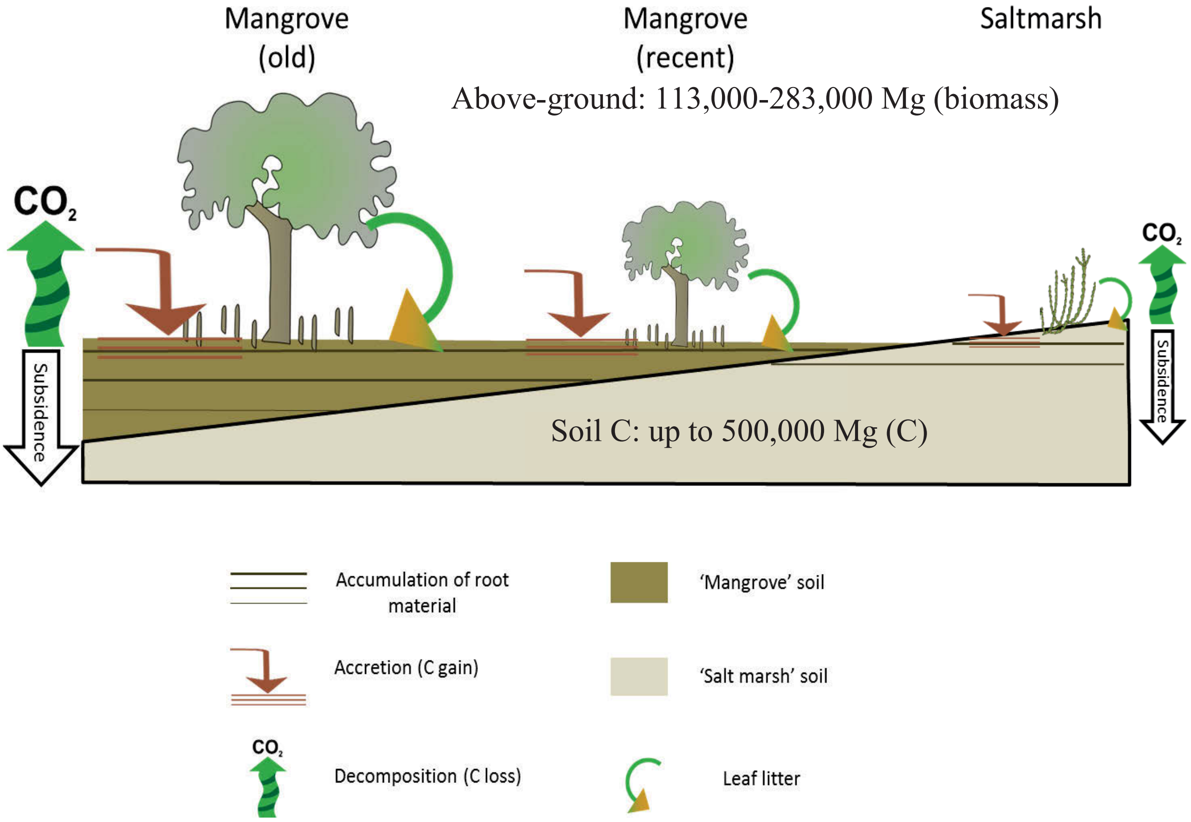

Figure 1 - Conceptual diagram of carbon dynamics of mangrove encroachment into saltmarsh. As mangroves mature, belowground production not only increases carbon storage, but may also build surface elevation, which may allow mangroves to keep pace with rising sea level.

4. Knowledge gaps and research needs

While the outcomes of this thesis and other studies undertaken across a range of habitats in recent years has greatly improved understandings of the key processes related to blue C, there remains a range of knowledge gaps to be addressed. Here, some of the research needs most relevant to saltmarsh C storage and issues associated with mangrove encroachment of saltmarsh are discussed.

4.1 Accurate upscaling of C

Most continental or global estimates of blue C stock and C accumulation capacity have been derived by multiplying global mean value (and error estimate) per unit area by the extent of ecosystem area (Duarte *et al.*, 2005, McLeod *et al.*, 2011, Murray *et al.*, 2011, Ouyang & Lee, 2014, Siikamäki *et al.*, 2013). This same approach was taken in Chapter 2 where mean saltmarsh C stocks were multiplied by the total area of saltmarsh in NSW to generate a state-wide estimate of C. Alternate methods which incorporate known landscape heterogeneities which influence C stock (such as geomorphic setting or sediment grain size) will provide more accurate estimates of saltmarsh C stocks at broader scales.

Adequate mapping of the distribution and character (type) of an ecosystem is an important pre-requisite for the accurate upscaling of C stock and accumulation estimates. In NSW, reliable estimates of the distribution of saltmarsh and mangrove (as separate ecosystems, but with neither differentiated by sedimentary or species composition) are available thanks to state-wide mapping which is comprehensive, of adequate resolution (digitised at 1:1,500) and relatively recent (2006 onward) (Creese *et al.*, 2009). More explicit mapping of ecosystem type, for example separating *Sarcocornia/Sporobolus* saltmarsh from *Juncus* saltmarsh, as well as mapping of geomorphic and sedimentary types will be required to allow more accurate, spatially explicit upscaling of saltmarsh C at this regional scale.

Although there are (now) comprehensive datasets of saltmarsh C collected from SE Australia, little to no data is available from the tropical north of the Australia (where the collective area of saltflats and saltmarsh is extensive), and very limited information available from other sub-tropical coasts (i.e. Western Australia, South Australia, Tasmania). Previous upscaling of Australian saltmarsh C accumulation rates (Ouyang & Lee, 2014) on the basis of a small number of data from SE Australia has led to an unreliable continental estimate of saltmarsh sequestration capacity. At the global scale, estimates of C stock and accumulation are far more numerous; however, the inadequacy of global mapping efforts – which suffer from 20-fold uncertainties (Duarte *et al.*, 2013) – also make current global extrapolations largely unreliable. There is an obvious need to collate more reliable distribution data for saltmarshes, with accurate mapping of global saltmarsh extent a clear priority. Furthermore, regular monitoring of changes in ecosystem extent (including mangrove encroachment of saltmarsh) will be needed if accurate estimates of changing C dynamics are to be understood at broad spatial scales.

4.2 Quantifying sequestration processes

On the basis of data collected throughout this thesis it has been speculated, and in some cases specifically demonstrated, that both the character of C inputs and the biogeochemical conditions within which they are found contribute to long-term C sequestration in saltmarshes and mangroves. For the most part, however, it remains difficult to isolate the relative importance of each of these two broad factors, let alone quantify them. To do so, a number of knowledge gaps must first be addressed. These include:

- Quantification of C sequestration rates across a broader range of sites, including multiple sedimentary and vegetation settings
- Quantification of aboveground versus belowground partitioning of biomass for key saltmarsh species as well as encroaching mangroves;
- Characterisation of belowground preservation/decay processes, particularly within *Juncus* saltmarshes (for example, a similar investigation to that undertaken for *Sarcocornia*/*Sporobolus* saltmarshes in Chapter 4);
- Quantification of C preservation due to mineral interactions in tidal wetland sediments;
- Improved understanding of the drivers of peat formation (and therefore high C preservation) in both saltmarshes (e.g. WAP-F in Chapter 4) and mangroves (e.g. Georges River mangroves in Chapter 5);

- Characterisation of the molecular composition and isotopic signatures of a broader range of autochthonous and allochthonous sources, with particular emphasis on aboveground versus belowground plant tissues, and terrestrial and marine source endmembers (e.g. terrestrial vegetation and soils; marine phytoplankton and macroalgae/seagrass wrack);
- Identification of the regional distribution of mangrove deposits under contemporary saltmarshes, in order to identify the importance of this phenomenon at the regional scale;
- Identification and quantification of autochthonous versus allochthonous contributions to C accumulation under mangrove encroachment (Figure 1). Do mangroves promote more effective trapping of allochthonous inputs or are C increases primarily due to root proliferation?

4.3 Understanding the fate of wetland C

Within the broader C cycle, this thesis focused largely on the amount and character of C accumulating within saltmarshes (and encroaching mangroves) and C ultimately preserved belowground over annual through millennial timescales. That is, C inputs and C stocks. There were multiple lines of evidence, however, which point to remineralisation of C with the system, including mismatches between short-term and medium-term accumulations of C (Chapter 3), broad declines in C density with sediment depth (i.e. time) (Chapter 2) and changes in the molecular composition of C consistent with microbial processing (Chapter 3 and 4). For SE Australian saltmarshes, this flux of C remains largely unquantified and uncharacterised. It also remains unknown what influence mangrove encroachment of saltmarshes will have on overall C flux into the atmosphere (Figure 1). At present, the only published values for the region come from Westernport Bay in Victoria, where CO_2 emissions varied seasonally, but was generally higher in shrub/succulent saltmarshes relative to mangroves and supratidal *Melaleuca* wetlands (Livesley & Andrusiak, 2012). Interestingly, that study also showed saltmarshes to be a weak CH_4 source (<5 mg C m^{-2} h^{-1}), with CH_4 flux increasing down the tidal wetland transect to releases of up to 375 mg C m^{-2} h^{-1} in the mangrove zone during Summer. As CH_4 flux has a higher radiative forcing capacity than CO_2, this finding may raise issues regarding the broader potential of mangrove encroachment to mitigate atmospheric C. Worse still, no data appears to be currently available on the role of aquatic (tidal or groundwater) or trophic export of C in the region, including whether the former can include significant concentrations of CH_4. Clearly, much broader investigation of the greenhouse gas fluxes from SE Australian tidal wetlands is needed, with seasonal, spatial and ecosystem scale variabilities all requiring attention.

5. Implications for management in a time of change

There is growing awareness among governments, coastal resource managers, industries concerned with C management and the broader community regarding the capacity of coastal wetlands to sequester C (Sutton-Grier & Moore, 2016, Sutton-Grier *et al.*, 2014). At the international level, the United Nations Framework Convention on Climate Change (UNFCCC) and the Kyoto Protocol require signatory nations to report on their greenhouse gas emissions, with targets set for reductions over a fixed time period. In Australia, tidal wetlands are not currently included in the National Greenhouse Accounts, however, the publication of the Wetlands Supplement (Hiraishi *et al.*, 2014) by the International Panel on Climate Change provides the framework for Australia and other nations to quantify tidal wetland C emissions. Similarly, the Australian Government's primary policy relevant to carbon management – the Emission Reduction Fund (ERF) – does not currently cover emissions reduction or emission avoidance related to tidal wetlands. Outside of government, recent publication of the Verified Carbon Standard (VCS) Methodology for Tidal Wetland and Seagrass Restoration (Restore America's Estuaries & Silvestrum, 2015) could attract carbon credits for saltmarsh restoration, although to date it does not appear that any such project has been undertaken in Australia.

As the above government and non-government schemes mature and expand to include Australian tidal wetlands, they will require knowledge of C dynamics in these systems, how they might be best protected to manage existing C stocks and how they might be harnessed to store more C. It is hoped that the findings of this thesis shed light upon these questions. In this final section, therefore, the legacy of past management failures and ongoing threats are discussed alongside new opportunities to manage these important ecosystems and the C they sequester.

5.1 Coastal wetlands can be important C sinks.

This thesis shows that on a per hectare basis, NSW saltmarshes contain similar carbon stocks to saltmarshes globally. The aerial extent of saltmarshes in NSW, however, is modest (7,259 ha; Creese *et al.*, 2009) when compared to many other temperate coastlines. This is due in part to the broader geomorphologic setting of NSW (with its relatively narrow coastal zone and the absence of broad intertidal zones in larger drowned valley estuaries) as well as significant reclamation. Simple projection by multiplying mean carbon stock in our study (164.45 Mg C ha^{-1}) by state-wide habitat extent presents a first estimate of 1.2 million tonnes (Mg) or more of carbon stored in NSW saltmarshes (Chapter 2). Importantly, our understanding of the spatial variability of these C stocks has greatly improved, with geomorphic and sedimentary factors identified as being key predictors of C stocks. Consequently, there is now an opportunity for resource managers and/or spatial scientists to develop more accurate, spatially-explicit estimates of C stocks for NSW. Outputs from this thesis - for example, the predictive model of C density (Chapter 2: Figure 3) and values discriminating C stocks among geomorphic zones – provide appropriate resources upon which revised upscaling can be undertaken.

Substantial losses of coastal wetlands are known to have occurred historically throughout the SE Australia. In Chapter 2 it was identified that upward of 70% of the pre-European extent of saltmarsh in the region may have been lost, mainly during draining of coastal floodplains for agricultural production and by infilling for coastal development purposes. It was also estimated that 1.4 million tonnes of C, or more, may have been returned to the atmosphere as a results of these habitat losses. Together, these estimates of current C stocks (~1.2 million tonnes) and historic losses (>1.4 million tonnes), suggest significant net emission of C to the atmosphere as a result of poor land management practices.

Changes to the planning status of saltmarshes in NSW over recent decades, such as the designation of *SEPP 14 Coastal Wetlands* and listing of Coastal Saltmarsh as an Endangered Ecological Community under the NSW *Threatened Species Conservation Act (1997),* has substantially slowed rates of anthropogenic ecosystem loss. These development controls, however, do not guarantee future protection of wetland extent or function, nor do they currently provide resources for the management, restoration or creation of habitat. It is hoped that growing knowledge of the capacity of coastal wetlands to deliver ecosystem services, including long-term C storage, may provide incentive for governments, non-government organisations and landholders to undertake effective and restorative management into the future.

5.2 Prioritising for C management

The broad outcomes of this thesis suggest that planning policies and on-ground activities which protect remaining wetland areas and reverse historic declines of coastal saltmarsh will increase overall C storage, thereby presenting a negative feedback to global warming. More specifically, however, it showed that not all wetlands are equal. Instead, there may be substantial variability in C accumulation or storage due to a range of geomorphic/sedimentary, biogeochemical and ecological factors. If management efforts are to be prioritised in order to maximise gains in C sequestration, it is therefore important to understand what this variability means for management aims.

5.2.1 Managing existing C stocks

Where the key interest is identifying sites which, if disturbed or inadequately managed, may result in the release of significant amounts of stored C, then consideration of C stocks is paramount. For this scenario, results from this thesis have comprehensively shown that geomorphic and sedimentary factors are the primary predictors of C stocks. Therefore, sites subject to greater fluvial influence and/or those displaying fine sediment distributions would rank of highest priority when conserving current C stocks. More broadly, it appears most appropriate to use sedimentary and geomorphic classification systems to identify blue C hotspots for targeted conservation and management activities at the regional scale. Examples include the predictive CART model developed in Chapter 2 and broad geomorphic classifications such as that developed in Roy *et al.* (2001).

5.2.2 Capturing C faster

Where the key interest is the capacity of saltmarshes to sequester ‘new’ C from the contemporary atmosphere, then the balance between C accumulation rates and C loss (through remineralisation, trophic or tidal export) will be most important. The findings from this thesis, and other studies in the region (Lovelock *et al.*, 2013, Saintilan *et al.*, 2013) suggest *Juncus* saltmarshes substantially outperform *Sarcocornia/Sporobolus* saltmarshes in terms of their C accumulation rates. C accumulation rates also appear to be higher in fluvial influenced saltmarshes where there is greater access to more stable, terrestrial C inputs, while results in Chapter 5 demonstrated the exceptional capacity of mangrove encroachment to increase biomass and belowground C pools.

Importantly, however, our knowledge of the processes of C export from these systems is limited. Information regarding the magnitude and type (e.g. CO_2 versus CH_4) of atmospheric and aquatic (tidal or groundwater) C flux is required across a range of spatial and temporal scales before reliable management prioritisations can be made.

Finally, regardless of what prioritisation approach might be taken, it needs to be acknowledged that coastal wetlands are dynamic ecosystems. This means they are likely to continue to undergo change in terms of their structure and function in response to anthropogenic, climatic and sea-level drivers.

5.3 Threats and opportunities in a time of change

It is broadly acknowledged that coastal wetlands are among the most at risk global ecosystems to the impacts of human activity and climate change (Kirwan & Megonigal, 2013). As saltmarshes and mangroves exist within intertidal through supratidal elevations, they are particularly sensitive to predicted rises in mean global sea level, which have been predicted to be as great as 0.82 m over the course of the 21st century (Pachauri *et al.*, 2014). While this will represent a significant threat to current distributions of saltmarshes and mangroves, it also presents unique opportunities for coastal resource managers to adapt to and partially mitigate these forces of change.

There are two main mechanisms by which tidal wetlands may persist under rising sea level. Most obviously, where the wetland is bordered to the landward side by suitable topography (i.e. higher elevation land, ideally with a low gradient) the ecosystem may undergo lateral migration. Second, in some circumstances tidal wetlands may be able to maintain their current location by building their vertical position during times of sea level rise, normally through a combination of sediment accretion and/or belowground biomass production (Krauss *et al.*, 2014).

One of the key findings of this thesis was the increase in C sequestration that occurs as mangroves encroach into saltmarshes (Chapter 5). Concomitant with this C sequestration is the observation that mangroves are not only spreading upslope (i.e. into saltmarsh) but may also rapidly build their surface elevation (Chapter 5: Figure 5) during a time of known sea level. While this is good news for mangroves and their C sequestration, in many cases there is little capacity for saltmarshes to migrate upslope due either to natural (topographic) or anthropogenic barriers (artificial levees, floodgates, roads, etc.) (Figure 2A). As sea levels continue to rise and mangroves migrate further upslope, these same barriers will eventually limit mangrove expansion and their future C sequestration potential (Figure 2B). In Figure 2C the C benefits of removing barriers preventing upslope migration are presented. Here it can be seen that there are two areas of 'new' C sequestration – the C-rich surface building of the mangroves (discussed above), and the new blue C sequestered by the upslope range expansion of saltmarsh.

Recent modelling of a similar scenario in the Hunter River estuary (NSW) proposed removal of such barriers (in this case the opening of floodgates and breaching of levees) would allow for effective retreat of saltmarsh and mangrove wetlands, with potential carbon burial gains of up to 280,000 tonnes by 2100 (Rogers *et al.*, 2013). In their survey of NSW estuaries and coastal rivers, Williams and Watford (1997) identified 4,300 barriers to tidal flow, of which a significant number (1,388) were identified as being easily removable or modifiable to allow the re-establishment of tidal exchange. While not all of these instances will be amenable to mangrove and/or saltmarsh colonisation or migration, these two studies highlight the enormous potential in terms of C sequestration and the extensive range over which such a management strategy could be applied. In addition to the C sequestration benefits demonstrated, increasing the available accommodation space for saltmarsh and mangrove adaptation under rising sea level will likely have substantial co-benefits in terms of other ecosystem services (e.g. fisheries productivity and threatened species habitat) and biodiversity conservation.

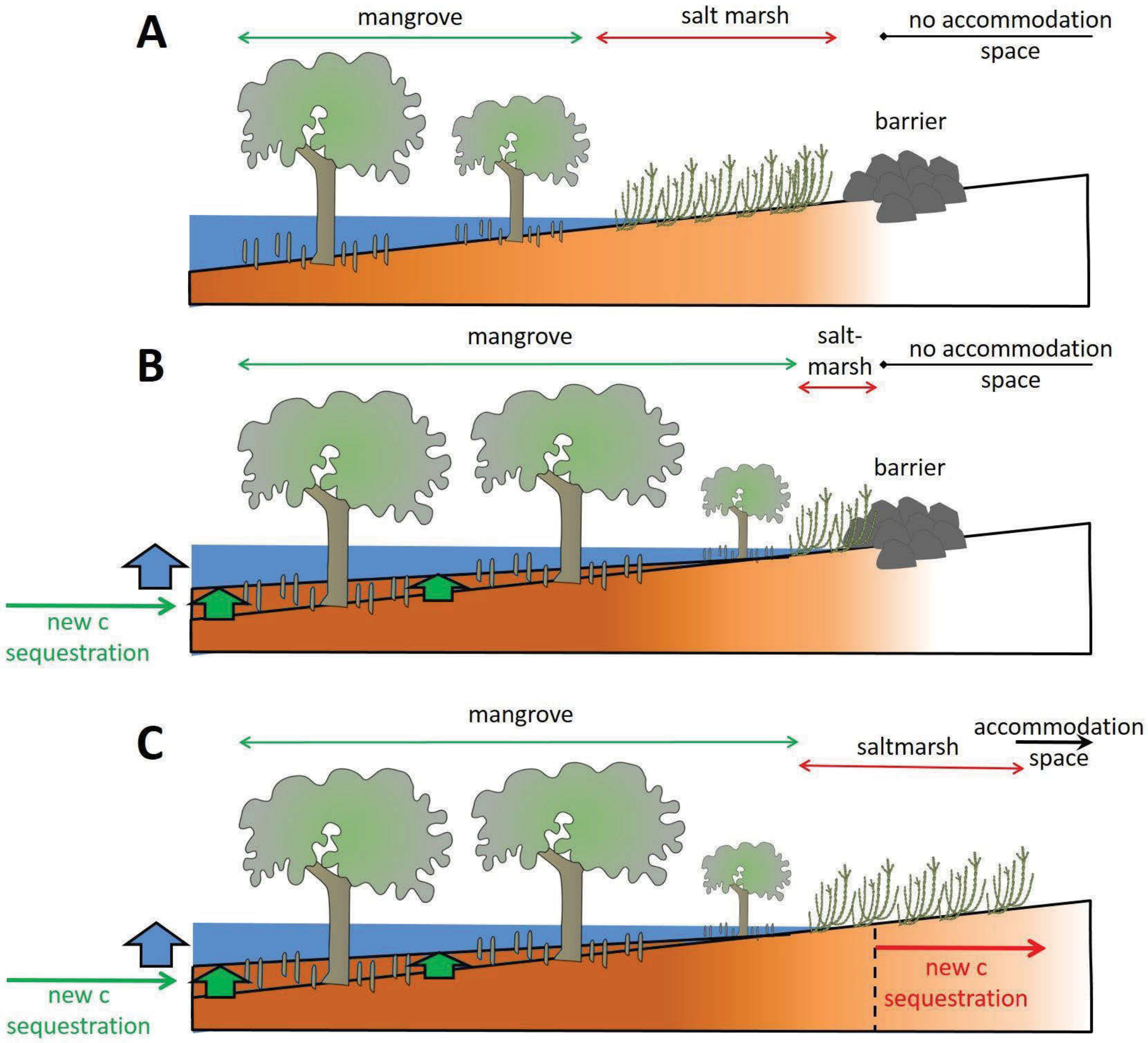

Figure 2 – Accommodating for more C sequestration under rising sea levels. The distribution of mangrove and saltmarsh and their associated C stocks prior to current phase of sea-level rise (A). As sea-level rises (blue arrow), mangroves migrate upslope and replace saltmarsh (B). Where anthropogenic or natural barriers exist upslope of saltmarsh 'coastal squeeze' causes the loss of saltmarsh area. The capacity of mangroves to build their elevation relative to rising sea-level with C rich materials (green arrows) prevents the mangroves at the seaward edge from drowning. When barriers to upslope migration are removed or modified (C) saltmarsh and eventually mangrove will be able to migrate, accumulating and storing new 'blue carbon' in the now tidal sediments.

6. Concluding remarks

During the course of this PhD (2013-2016) the concentration of CO_2 in the Earth's atmosphere surpassed 400 ppm. As this concentration continues to rise, so too will the magnitude of current and future changes in climate and sea level affecting natural and human (socioeconomic and geopolitical) systems. For the most severe of these changes to be mitigated, we will need to make substantial changes in the way we humans utilise and interact with natural ecosystems. A greater understanding of the complexity of natural systems and the way in which they adapt to environmental change will be central to this.

This thesis has investigated the interactions between geomorphology, biology and chemistry, (among other scientific spheres) which operate in coastal, tidal wetlands. It builds upon the important advances that were made in the fields of coastal geomorphology, biology and biogeochemistry well before the term 'blue C' was even coined. Although the present body of research relates to just one of the many ecosystem services provided by coastal wetlands, it is hoped that it will play a role in enhancing the broader perception of these historically underappreciated ecosystems. Equally, this research is intended to provide a platform upon which natural resource managers and wetland scientists can develop strategies to effectively mitigate the impacts of human-induced climate change and enable these important natural systems to migrate and adapt during times of substantial change.

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