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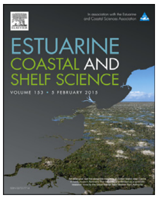

Sea level and turbidity controls on mangrove soil surface elevation change

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ABSTRACT

Increases in sea level are a threat to seaward fringing mangrove forests if levels of inundation exceed the physiological tolerance of the trees; however, tidal wetlands can keep pace with sea level rise if soil surface elevations can increase at the same pace as sea level rise. Sediment accretion on the soil surface and belowground production of roots are proposed to increase with increasing sea level, enabling intertidal habitats to maintain their position relative to mean sea level, but there are few tests of these predictions in mangrove forests. Here we used variation in sea level and the availability of sediments caused by seasonal and inter-annual variation in the intensity of La Nina-El Nino to assess the effects of increasing sea level on surface elevation gains and contributing processes (accretion on the surface, subsidence and root growth) in mangrove forests. We found that soil surface elevation increased with mean sea level (which varied over 250 mm during the study) and with turbidity at sites where fine sediment in the water column is abundant. In contrast, where sediments were sandy, rates of surface elevation gain were high, but not significantly related to variation in turbidity, and were likely to be influenced by other factors that deliver sand to the mangrove forest. Root growth was not linked to soil surface elevation gains, although it was associated with reduced shallow subsidence, and therefore may contribute to the capacity of mangroves to keep pace with sea level rise. Our results indicate both surface (sedimentation) and subsurface (root growth) processes can influence mangrove capacity to keep pace with sea level rise within the same geographic location, and that current models of tidal marsh responses to sea level rise capture the major feature of the response of mangroves where fine, but not coarse, sediments are abundant.

1. Introduction

Increases in sea level have strongly influenced mangroves in the past (Woodroffe, 1995) and are a threat to current mangrove distributions if mangrove soil elevation cannot keep pace with sea level rise (Lovelock et al., 2007; Gilman et al., 2008; Day et al., 2008). Although losses of tidal wetlands are widely anticipated with sea level rise (Nicholls et al., 1999), over a range of plausible sea level rise scenarios coastal wetlands are proposed to adjust towards an equilibrium position, keeping pace with sea level due to a number of feedbacks that allow them to maintain their soil elevation relative to the height of mean tide (Allen, 2000; Morris et al., 2002; Kirwan and Murray, 2007; D'Alpaos et al., 2007). Accretion of material on the soil surface, often through sedimentation, leads to increases in soil surface elevation that can result in the wetland maintaining its relative position in the intertidal with sea-level rise (Allen, 2000). Sedimentation increases with the availability of suspended sediments in tidal waters. A wide range of factors determine the level of suspended sediments in the water column, these include runoff from the land associated with rainfall and river flows, and resuspension of sediments by turbulence caused by wind and waves and tidal currents (see Figure S1 for the conceptual framework modified from Allen, 2000). Additionally, sedimentation increases with the duration and depth of tidal inundation due to increases in the amount of material delivered (e.g. French and Stoddard, 1992; Furukawa and Wolanski, 1996;

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Cahoon et al., 2006; Adame et al., 2010). Sediment and organic matter are trapped due to the aboveground structures of mangrove forests (e.g. stems, aboveground roots) which reduce the velocity of tidal flows thereby enhancing retention of sediment and organic material within the wetland (Furukawa and Wolanski, 1996; Allen, 2000). The depth and duration of tidal flooding of mangrove forests is determined by the position of the forest in the intertidal zone, but is also influenced by variations in sea level (Rogers et al., 2014). Thus, both variation in sediment availability and sea level can influence gains in soil surface elevation in mangrove forests.

Accumulation of plant biomass can also contribute to increases in soil surface elevation through accumulation of surface organic matter and roots that increase soil volume (McKee, 2011). Increases in soil surface elevation of mangrove forests have been observed with increases in root growth due to fertilization (McKee et al., 2007) and during forest regeneration (Rogers et al., 2005). Conversely, losses in surface elevation have been observed with death of trees (Krauss et al., 2014). Numerical models have explored the potential role of plant production and sediment inputs in maintaining soil elevation with sea level rise. In tidal marshes where plant production is important for soil elevation gains, Morris et al. (2002) predicted that there is an optimal rate of sea level rise at which the equilibrium elevation and depth of tidal flooding is optimal for plant growth and soil elevation gain. However, the optimum was observed to be at the upper limit of the tidal range, such that with high rates of sea level rise the plant community could not sustain an elevation that was within the range of the physiological tolerance of the plants (Morris et al., 2002). In contrast, in marshes where sediments are abundant marsh surface elevation was predicted to be maintained at equilibrium elevation at approximately mean sea level as long as the amount of sediments delivered in tidal flows were sufficiently high (Temmerman and Govers, 2004). Kirwan and Murray (2007), in their three dimensional model that included tidal creeks as well as the marsh platform, predicted that an increase in the rate of sea-level rise would increase rates of sediment deposition and biomass productivity that would lead to a metastable state, but if marshes were disturbed or the vegetation died marshes would rapidly degrade, widening creeks and channels. In addition to marshes, mangrove forests are highly vulnerable to sea level rise, yet there are few tests of the roles of plant production and sediment availability on the maintenance of soil surface elevation with sea level rise in these widespread and important tropical and subtropical ecosystems.

In mangrove forests in Belize that grow in sediments comprised of peat, observations from deep cores have found that soil surface elevation kept up with high rates of sea level rise in the early Holocene, but have slowed in concert with slowing sea level rise later in the Holocene (McKee et al., 2007). Additionally, mangrove forests occurring at sea level are currently accreting at a similar rate as sea level rise, while those lower in the intertidal, where growth rates are very low, are not keeping pace (McKee et al., 2007), conforming to many of the predictions of the Morris et al. (2002) and Kirwan and Murray (2007) models. In mangrove forests in settings with high sediment supply, the equilibrium models suggest that increasing sea level will enhance rates of sediment deposition, which would lead to soil surface elevation gains as observed by Temmerman and Govers (2004) in tidal marshes. But productivity of the plant community may also be important in these settings (Rogers et al., 2005; Kirwan and Murray, 2007; Kirwan and Guntenspergen, 2012). An improved understanding of the importance of sediment availability and mangrove plant production in maintaining soil surface elevation with sea level rise is needed in order to guide management of the coastal zone, particularly management of sediments and nutrients, and for planning coastal landscapes for accommodation of mangrove forests with accelerating sea level rise (Runting et al., 2013).

In Moreton Bay, Queensland, Australia, sea level and suspended sediments in coastal waters varies due to seasonal influences of tides, rainfall and river flows and with variation in the strength of El Nino Southern Oscillation (ENSO) cycles. On the east coast of Australia, El Nino events, where atmospheric pressure differentials across the Pacific Ocean cause an accumulation of water mass in the eastern Pacific (Aubrey and Emery, 1986; Feng et al., 2008), result in lower than normal sea levels, as well as reduced rainfall and other climatic changes. In Europe the North Atlantic Oscillation (NAO) has been shown to have a strong influence on salt marshes through its effects on water levels and waves (Kim et al., 2013). In this study we investigate the influence of sea level and turbidity, which correlates strongly with suspended sediments within Moreton Bay (Hossain et al., 2004), on surface elevation change. In the subtropics growth of mangrove trees is highly seasonal (Mackay et al., 1993; Rogers et al., 2005, 2014), thus we used seasonal variation in plant growth to assess the role of root production in maintaining soil elevation. We tested three hypotheses:

1. Soil surface elevation gains of mangroves in Moreton Bay will increase during periods of higher sea-level and high turbidity and decrease in periods with lower sea level and low turbidity.
2. Soil surface elevation gains during periods of higher sea level and turbidity are correlated with increases in accretion of sediments on the soil surface.
3. Soil surface elevation gains are positively influenced by increases in root growth.

2. Methods

2.1. Site description

Our experimental sites lie within Moreton Bay, Queensland, which is a large semi-open embayment on the east coast of Australia (Fig. 1). It is bound on the eastern side by sand islands that reach approximately 200 m in elevation and by a deltaic coast on the western side in which five rivers flow from their catchments to the bay. The city of Brisbane which is one of the fastest growing cities in Australia, with a population of 2.15 million people (Australian Bureau of Statistics, 2011) resides on the western side of Moreton Bay. The bay is fringed by mangroves positioned lower in the intertidal zone with salt marsh and cyanobacterial mats adjacent in the high intertidal zone. The mangroves and salt marsh provide a range of ecosystem services in the region, from amenity for recreation to the support of species important for commercial fisheries of the Bay (Meynecke et al., 2008). The mangrove forests of Moreton Bay are dominated by *Avicennia marina* on the western side of the Bay, but have a high abundance of *Rhizophora stylosa* in the eastern Bay (Dennison and Abal, 1999).

Within Moreton Bay, the long term rate of sea-level rise is 1.982 mm/year (tide gauge on Bishop Island at the mouth of the Brisbane River from 1984 to 2011, GLOSS number 58, Lovelock et al., 2011), which is similar to the global average sea-level rise of 1.7 mm/year (Church and White, 2006). Estimated long-term (5×10^7 years) changes in the elevation of the Australian coast is very small (Aubrey and Emery, 1986) and was therefore not considered in our analyses. Moreton Bay is subtropical with semi-diurnals tides (mean range of 2 m, Dennison and Abal, 1999). Mean annual minimum air temperature is 15.5 °C and mean maximum is 25.3 °C. Wind speed varies over the year with maximums from September to January and lower values from April to

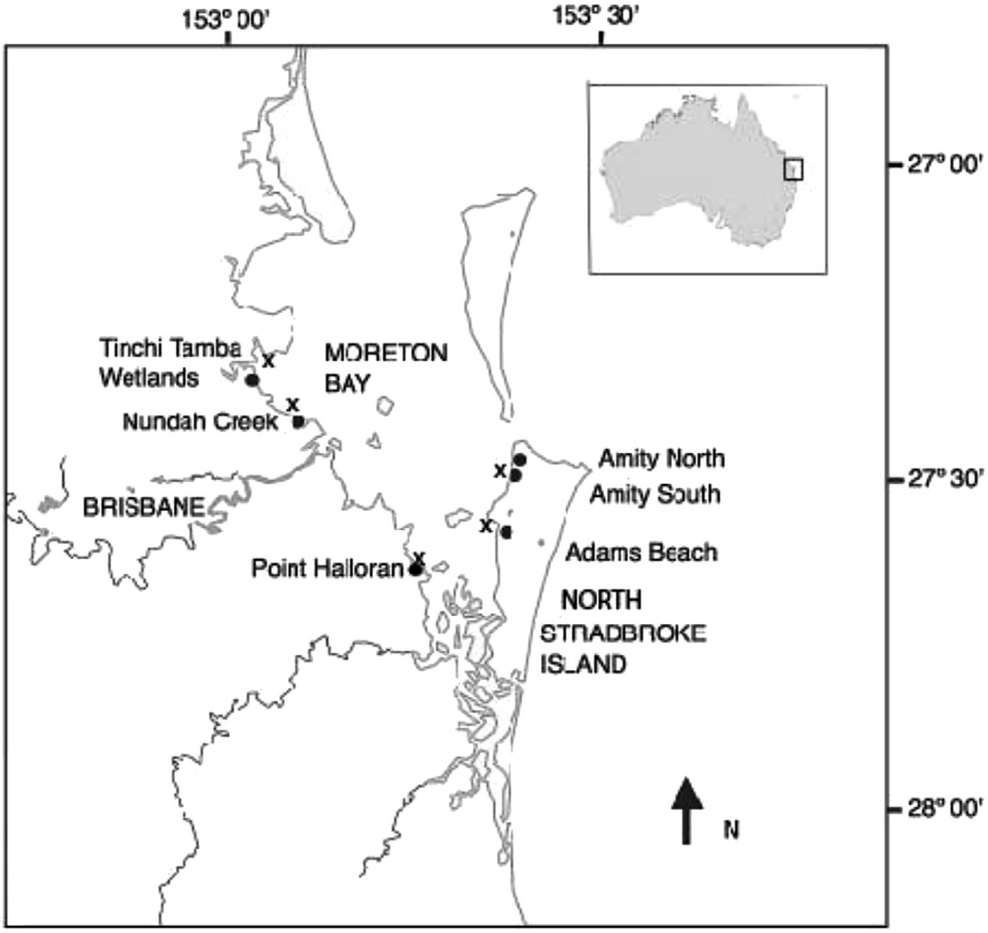

Fig. 1. Map of the location of the study sites within Moreton Bay, Queensland, Australia. Surface elevation table sites are marked with a filled circle and turbidity monitoring sites with crosses.

September. Mean annual rainfall in Moreton Bay is 1050 mm/year (Australian Bureau of Meteorology, Brisbane Airport station, record from 1949 to 2000, http,//www.bom.gov.au/) but rainfall is seasonal with the highest rainfall in the warmer months (November to March, 95–175 mm/month) and lower rainfall in the cooler months (April–October, 35–90 mm/month). Heavy rainfall events lead to sediment delivery through rivers and creeks to Moreton Bay (Dennison and Abal, 1999). Additionally, in Australia, ENSO strongly influences sea level (Aubrey and Emery, 1986; Feng et al., 2008) and rainfall (Hughes, 2003). Extreme El Niño events can give rise to reductions in sea level that can be up to 44 cm below mean sea level (recorded in Guam), which influences a range of ecological processes (Glynn, 1988). On the east coast of Australia El Niño (when the Southern Oscillation index, SOI is low), sea levels are low and lower than normal rainfall results in drought conditions. In contrast, during la Niña phases, sea levels are higher and rainfall is also higher, with concomitant increases in the availability of suspended sediment in coastal waters (Wolanski et al., 2008).

The mangrove forests of Moreton Bay are exposed to variable environmental conditions due to variable geomorphology within the bay and natural variation in climate and sea level and the influence of the city of Brisbane. On the western shore (near the city of Brisbane), mangrove forests grow on fine sediments (Morelli et al., 2012) that have high organic carbon contents (8%)and bulk density 0.46–0.55 g cm^{-3} (Lovelock et al., 2014). These forests are exposed to freshwater inputs associated with creeks and rivers, as well as sediments and nutrients from flood plumes that are trapped in-shore by the prevailing south east winds and currents (Dennison and Abal, 1999). Additionally, wind driven waves resuspend fine sediments, increasing suspended sediment concentrations in the western bay (You, 2005). In contrast, on the eastern shores (on the shores of the high sand islands), mangroves grow in sandy sediments where turbidity and nutrients are low, similar to oceanic conditions, and tidal currents are strong (Dennison and Abal, 1999). Sediments in the eastern bay have a bulk density of approximately 1 g cm^{-3} and an organic carbon content of 1% (Lovelock et al., 2014). Over the duration of our experiment, variation in rainfall, stream flow to the bay, sea level and the turbidity of the bay waters were high (Supplementary material Figure S2).

2.2. Surface elevation gains

We measured mangrove surface elevation with the rod surface elevation table – marker horizon (RSET-MH) approach developed by Cahoon et al. (2002a and b). Eighteen RSET-MH stations were installed in mangrove forests between February and June of 2007 and monitored until 2012. Three sites were chosen on both the eastern and western bay. Western bay sites were located within the Tinchi Tamba Wetlands Reserve (Brisbane City Council), Nundah Creek (Boondall Wetlands Park) and in the south at Halloran Reserve (Redlands Shire Council) (Lovelock et al., 2011). At each site three RSET-MHs were installed in the mangrove forests fringing the creek, within 20 m of the creek bank and 30–50 m apart. Mangrove forests at Tinchi Tamba and Nundah Creek were comprised of

Avicennia marina trees that were 10–13 m in height. *Avicennia marina* was dominant at Halloran Reserve, though *Rhizophora stylosa* was abundant. In the eastern bay three sites were chosen along the western side of North Stradbroke Island. Two sites were north of the town of Dunwich, between Myora Light and Amity Point (Amity North and Amity South) and one was south of Dunwich (Adams Beach). RSET-MH stations were within 30–50 m of the shoreline and at least 50 m apart. In the eastern bay mangrove forests were 10–15 m in height and were comprised of both *A. marina* and *R. stylosa*. During RSET installation benchmark rods were driven to refusal. The depth to which they were driven was variable on the western bay (from 4 m rods hit bed rock to 15 m at Tinchi Tamba). In the eastern bay rods were driven to a uniform depth of 12 m. The vertical position of each RSET-MH within the intertidal zone was determined by measuring the water depth covering the site at high tide using dyed cotton strips as recorders, which were deployed temporarily on stakes at the site (English et al., 1997). Sites on the eastern bay were lower in the intertidal than those on the western bay, with a position of 1.36 ± 0.01 m relative to the lowest astronomical tide (LAT, ~0.09 m above mean sea level) compared to 1.87 ± 0.06 m relative to LAT (0.6 m above mean sea level) in the western bay. In the western bay mangroves occur within estuaries (associated with tidal creeks), while in the east the mangroves form a band along the shore.

We assessed changes in soil surface elevation over each measurement interval at each RSET as the mean of 36 measurements made over four cardinal directions around the RSET benchmark and then expressed as a rate of change per month. For the first 18 months of the study RSET-MHs were measured every 3–4 months after which sampling intervals were lengthened to approximately 6 months to encompass the winter, dry (April–November) and summer, wet seasons (November–April). We evaluated the mean rates of change for each RSET from April 2007 to November, 2011, which encompassed variation in the SOI (Figure S2), by fitting a linear regression over time to observations for the 12 measurement intervals. Mean coefficient of determination (R^2 ± SE) for the regression of surface elevation change over time for individual RSETs was 0.713 ± 0.05.

Vertical surface accretion was assessed at the same time as surface elevation by measuring the depth of sediment over a white powdered feldspar clay layer that in the marker horizon which accompanied each RSET (Cahoon and Turner, 1989). Marker horizons were sampled using a small (1.5 cm diameter) transparent corer. Three cores per marker horizons were extracted. On each core, three measurements (equidistant around the core) of the sediment depth accreted on top of the marker horizon were made using a ruler giving nine measurements, which were averaged per RSET station and normalized to an accretion rate per month for each measurement interval. Shallow subsidence was calculated as surface accretion minus surface elevation change. Thus, if surface elevation change is mainly due to surface accretion, the values of surface elevation and surface accretion will be approximately the same; if surface elevation change exceeds surface accretion, then subsurface expansion is occurring, and conversely, if surface elevation is less than surface accretion, shallow subsidence (autocompaction) over the depth of the benchmark is occurring.

Digital sea level data for Moreton Bay was obtained from https//www.bodc.ac.uk for station PSM 21764 on Bishop Island at the mouth of the Brisbane River (GLOSS number 58). We calculated the anomaly in sea level in each of our measurement periods from 2007 to 2012, as the difference between the mean sea level during the measurement period and the mean sea level between 1984 and 2012. The sea level anomaly varied between −34 mm and +150 mm (see Supplementary material Figure S2). Turbidity, expressed as Nephelometric Turbidity Units (NTU), of the coastal waters for Moreton Bay was available from the Environmental Health Monitoring Program (EHMP, Queensland Government). Mean turbidity of EHMP monitoring stations that were closest to our study sites (Fig. 1) were obtained for each of the measurement intervals during the study period. Values used in the analysis were means for three EHMP stations on either side of the bay (west stations 4500, 900 and 922; east stations 502 and 531).

2.3. Root production

Root production was measured using five root ingrowth bags per RSET plot (McKee et al., 2007) at two measurement intervals (wet period from Nov 2010 to May 2011 and a dry period from May 2011 until November 2011). In-growth bags were 5 cm in diameter and 20 cm long, made of nylon mesh (2 mm) and filled with root-free natural sediment or material closely approximating the natural sediments. Root bags were filled with sand obtained at the RSET sites in the eastern bay and filled bags with commercial peat moss and coconut fibre packed to a dry bulk density measured as 0.12 g cm^{-3} in the western side of the bay. The bulk density of the peat moss mix was lower than the natural organic soils (~0.4 g cm^{-3}), but we chose this approach as we could not obtain naturally root-free mangrove soil in the western bay without major disturbance to the sites. Root bags were collected after six months and roots extracted by wet sieving over a 1 mm mesh. Roots were dried at 60 °C and weighed to give a total root biomass per root bag. The volume of fresh roots was assessed by volume displacement of water using graduated cylinders for a subset of the root samples. The relationship between root weight and root volume where root volume (cm^3) = (root weight (g) × 11.932) − 0.0792 was used to calculate the root volume produced over each sampling interval. The volume of roots produced per unit soil surface area (20.25 cm^2 area of root bag) was converted to potential contribution to soil elevation gain as volume of roots divided by surface area of root bag.

2.4. Data analyses

We used regression analyses to assess the relationship between the Southern Oscillation Index (SOI) and the sea level anomaly in Moreton Bay. To assess the relationships among 1) sea level anomaly and turbidity; 2) sea level anomaly and soil surface elevation and surface accretion; and 3) turbidity and soil surface elevation and surface accretion we used analysis of co-variance, where the factor "bay" (eastern or western bay) was included as a fixed effect in the model. Data consisted of measurements for each RSET installation for each time interval (12 intervals with measurements of 9 RSET on either side of the bay). We used a repeated measures, nested ANOVA to test for differences in soil surface elevation change and surface accretion over seasons using five years of data where both wet and dry season data were available. In the model, "bay" and "season" were fixed effects in the model and with "sites" (random) nested in "bay". We analysed differences in the slope of the cumulative change in soil elevation with a nested ANOVA where "bay" was a fixed effect in the model and with "sites" (random) nested in "bay". Differences in root production across the bay and between measurement intervals were assessed using nested ANOVA, where sites were nested within the factor "bay". Significant differences between means were assessed using least significant difference tests. Analysis of the relationship between the contribution of root volume to soils and soil subsidence over seasons and with location in the bay was done using ANCOVA, where the contribution of root volume to soils was a continuous random variable and "season" and "bay" were fixed effects in the model. Homogeneity of the variances of the data was assessed using Levene tests. Root production and turbidity

(NTU) were log transformed prior to analysis to satisfy the homogeneity of variance criteria when using linear models. All analyses were performed using the statistical package Data Desk 7 (Data Descriptions Inc., Ithaca, NY).

3. Results

The mean sea level anomaly in Moreton Bay was correlated with the mean SOI for each measurement interval, although in some measurement intervals mean sea level was much lower than described by the regression (Supplementary materials Figure S3). Additionally, the mean sea level anomaly and cumulative rainfall for each measurement period had a significant positive relationship with the turbidity of coastal water close to our sites in the western bay, but not in the eastern bay (Supplementary materials, Figure S4, Sea level anomaly × bay interaction, $F_{1,68} = 5.174$, $P = 0.021$; rainfall × bay interaction, $F_{1,68} = 6.042$, $P = 0.016$), reflecting the co-variation of rainfall and the sea level anomaly with turbidity.

Mean soil surface elevation gains at our sites over the entire monitoring period (2007–2012) were significantly higher in the eastern bay compared to the western bay (Table 1, factor bay, $F_{1,4} = 31.88$, $P = 0.0048$). Surface elevation gains tended to vary with season, although more strongly in some years than others (season × year interaction $F_{4,16} = 3.467$, $P = 0.032$). There was significant variation in surface elevation gains among sites ($F_{4.96} = 4.250$, $P = 0.009$) that also varied in strength among the years of the study (sites × year × season interaction, $F_{16.96} = 3.933$, $P < 0.0001$). Analysis of the effect of seasonality on surface accretion over the study found that accretion was higher in the wet/warm season than in the dry/cool season ($F_{1,16} = 8.947$, $P = 0.0403$), the strength of this trend varied among years (season × year interaction $F_{4,16} = 7.357$, $P = 0.0015$), but the side of the bay was not a significant factor determining rates of surface accretion.

Over the duration of the study, surface elevation gains were positively related to the sea level anomaly in the western bay, but not in the eastern bay (Fig. 2, Sea level anomaly × bay interaction, $F_{1,197} = 9.313$, $P = 0.003$). Surface accretion above the marker horizons was also significantly positively related to the sea level anomaly, but this was not statistically different on either side of the bay (Fig. 3, sea level anomaly, $F_{1,192} = 8.096$, $P = 0.005$).

Assessment of the effect of variation in turbidity on soil surface elevation gains and surface accretion found that as turbidity increased soil surface elevation ($F_{1,197} = 13.529$, $P = 0.0003$) and accretion on the soil surface ($F_{1,192} = 4.006$, $P = 0.0468$) also increased, but the data were highly variable about these relationships (Fig. 4).

Table 1
Mean rates of soil surface elevation change, surface accretion over the entire study ($N = 9$) and seasonally ($N = 45$), and root production ($N = 9$) (+standard error) for mangrove forests in the western and eastern Moreton Bay, Queensland between 2007 and 2012. Root production (g m^{-2} mo^{-1}) was measured in root bags deployed in the top 20 cm of soil in either the dry season or wet season of 2011. Different letters after the mean for each row indicate values are significantly different at $P < 0.05$ determined using a least significant difference test.

	Western bay	Eastern bay
Cumulative rates (mm y^{-1})		
Mean surface elevation change	1.72 ± 0.53^a	5.78 ± 0.71^b
Mean surface accretion	9.23 ± 1.00^a	7.95 ± 0.76^a
Surface elevation change (mm mo^{-1})		
Dry season	0.010 ± 0.029^a	0.208 ± 0.036^b
Wet season	0.200 ± 0.050^b	0.201 ± 0.046^b
Surface accretion (mm mo^{-1})		
Dry season	0.254 ± 0.037^a	0.263 ± 0.071^a
Wet season	0.542 ± 0.047^b	0.403 ± 0.079^b
Shallow subsidence (mm mo^{-1})		
Dry season	0.228 ± 0.039^a	0.048 ± 0.079^b
Wet season	0.287 ± 0.053^a	0.206 ± 0.009^a
Root production (g m^{-2} mo^{-1})		
Dry season	2.9 ± 0.9^a	16.6 ± 1.6^b
Wet season	18.8 ± 5.8^b	84.2 ± 3.3^c

We tested whether surface accretion could account for the gains in soil surface elevation across the study sites (Fig. 5). We found a weak but significant positive relationship among soil surface elevation gains and surface accretion in the western bay, but no significant relationship in the eastern bay (bay × accretion interaction $F_{1,191} = 9.415$, $P = 0.0025$, Fig. 5A). Additionally we found that surface elevation gains were significantly negatively related to shallow subsidence on both sides of the bay ($F_{1,196} = 51.389$, $P < 0.0001$, Fig. 5B).

We assessed the potential contribution that root production could make to surface elevation gains by assessing root volume increases in root ingrowth bags during two measurement periods. We found that mean root production (g m^{-2} mo^{-1}) was higher in the eastern bay than in the western bay ($F_{1,4} = 35.3$, $P = 0.0040$) and higher in the wet/warm period compared to the cool/dry period ($F_{1,4} = 43.7$, $P = 0.0027$) (Table 1). Root production in the top 20 cm of soil could account for the maintenance of up to 13 mm $year^{-1}$ of surface elevation gain in the eastern bay compared to 6 mm $year^{-1}$ in the western bay (Fig. 6). Potential root contributions to surface elevation in the dry period were much lower than measured in the wet period, particularly in the western bay. We did not find a

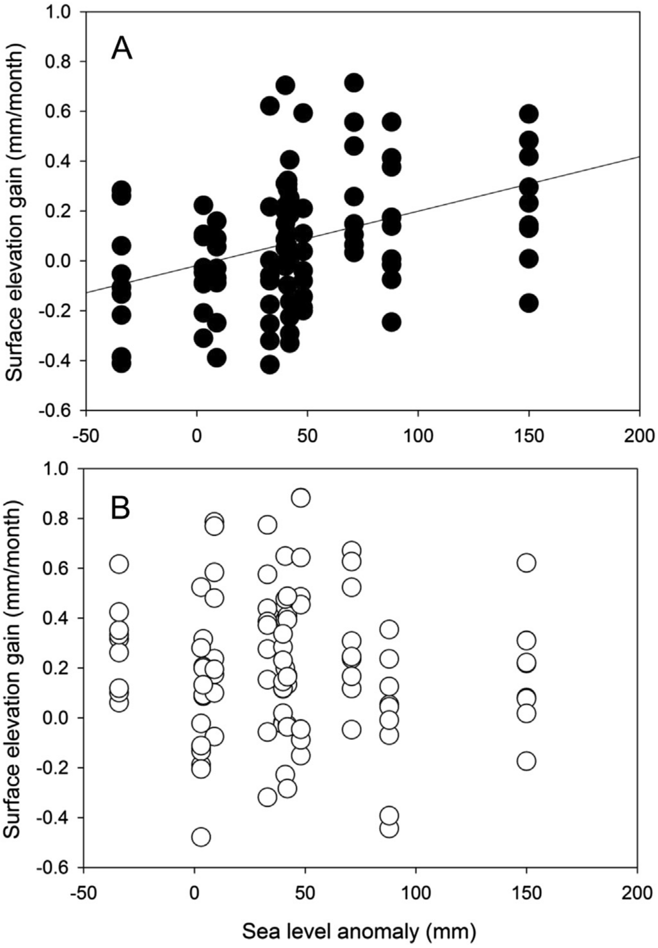

Fig. 2. The relationship between soil surface elevation gain and the sea level anomaly in the western (panel A), and eastern bay (panel B). The regression line in panel A is of the form $Y = -0.0186 + 0.00218 * X$, $R^2 = 0.133$, $P = 0.0002$. There was no significant relationship in panel B.

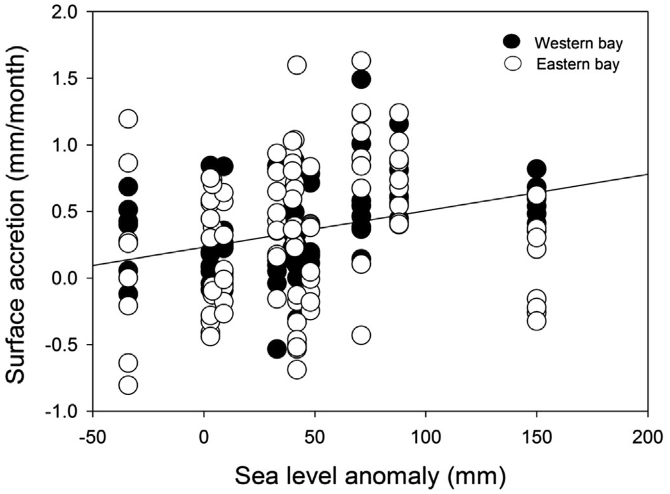

Fig. 3. Relationship between soil surface accretion and sea level anomaly in the western (filled circles) and eastern bay (open circles). The regression line for all data is of the form, $Y = 0.255 + 0.00195 * X$, $R^2 = 0.040$, $P = 0.005$.

significant relationship between root production and soil surface elevation gains across our sites in the two measurement intervals of our root growth study, however we observed that root production negatively associated with subsidence such that when root production increased subsidence decreased (Table 1, Fig. 7). The relationship between the root contributions to soil volume and subsidence was significantly influenced by season and side of the bay (season × root contributions × bay interaction, $F_{1,28} = 6.210$, $P = 0.0189$) indicating that reductions in root contributions have a greater effect on subsidence in the dry season than the wet season and in the western than the eastern bay.

4. Discussion

The increase in soil surface accretion and elevation with increasing size of the sea level anomaly and with high levels of turbidity in the western bay is consistent with models of increasing wetland soil elevation with increasing sediment availability and sea level (Allen, 2000; Temmerman and Govers, 2004; Kirwan and Murray, 2007), although these relationships are based on correlations and thus should be interpreted cautiously. The high level of variation about the linear relationships likely reflects differences among sites in the depth of flooding (Adame et al., 2010; Lovelock et al., 2011), site to site variation in hydrology, which influences the velocity of tidal flows, and variation in grain size of sediments and trapping efficiency of sediment by the vegetation structure (Kirwan and Murray, 2007). Differences in the strength of the relationships between soil surface elevation gains and sea level anomaly and turbidity in the eastern and western bay (Figs. 2 and 4), but similarity in the relationship between sea level anomaly and surface accretion (Fig. 3) suggests that the differences between the eastern and western bay will influence their behaviour with sea level rise. Sand is abundant in the eastern bay and is pushed into mangroves by strong long-shore currents and waves (Eberhardt, 1978). The resuspension of sand in the water column requires high levels of energy and often occurs only after a certain wave energy threshold is reached (Dick et al., 1994). Thus, accretion of sandy sediments in mangroves in the eastern bay may be influenced more strongly by oceanographic conditions including waves or extreme events (e.g. Smoak et al., 2013) than by the factors associated with enhanced turbidity in the western bay which may be more strongly influenced by rainfall stream flow and delivery of sediments from the land (Figure S1).

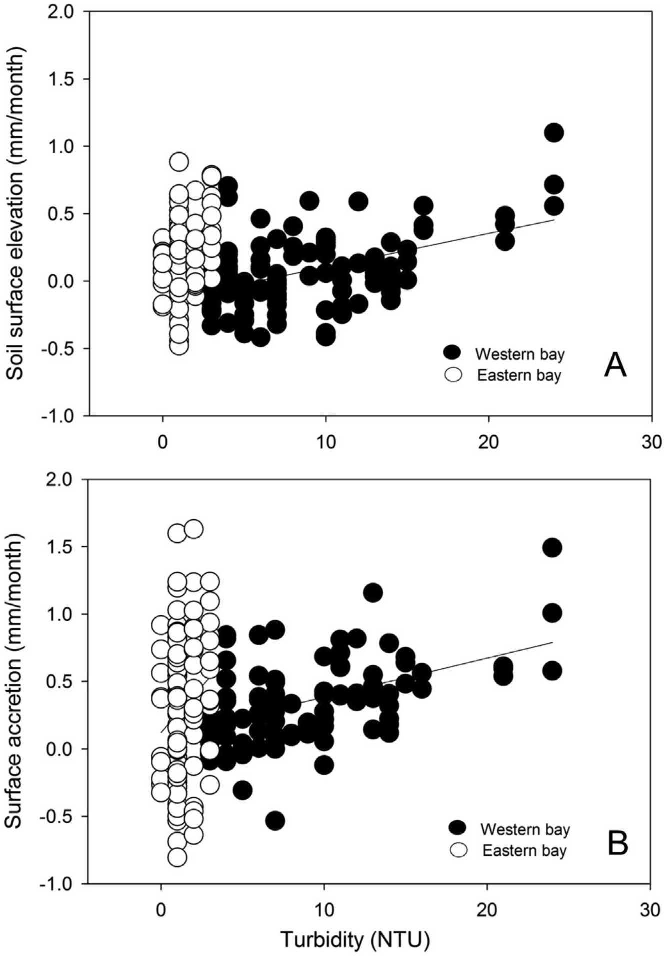

Fig. 4. A) The relationship between soil surface elevation change and turbidity (NTU) of coastal waters for the western (filled symbols) and eastern (open symbols) side of Moreton Bay, Queensland. The regression line for the western bay is of the form, $Y = -0.144 + 0.0249 * X$, $R^2 = 0.216$, $P < 0.0001$. B) The relationship between surface accretion and turbidity of coastal waters for the western (filled symbols) and eastern (open symbols) side of Moreton Bay, Queensland. The regression line for the western bay is of the form, $Y = 0.261 + 0.0160 * X$, $R^2 = 0.038$, $P = 0.0064$.

Although the western bay was the environmental setting in which turbidity and surface accretion was most strongly related to soil surface elevation gains, shallow subsidence had a strong influence on surface elevation gains in both the western and eastern bay. The influence of shallow subsidence on the soil surface elevation of tidal wetland soils has been recognized in many studies (e.g. Krauss et al., 2003; Rogers and Saintilan, 2008; McKee, 2011; Lovelock et al., 2011), but the proposed causes of subsidence vary (Cahoon et al., 2006). Compaction of soil profiles can occur due to reductions in groundwater (e.g. Whelan et al., 2005; Rogers and Saintilan, 2008); decomposition of soil organic matter (e.g. Cahoon et al., 2003; McKee et al., 2007); loss of living root biomass (Cahoon et al., 2003; Krauss et al., 2014) and consolidation of the mineral components (Allen, 2000). In our study we found a relationship between root production and shallow subsidence which suggests levels of shallow subsidence may be linked to changes in belowground productivity as well as to physical processes.

In our study, rates of root production were in the range (300–600 g C m^{-2} y^{-1}) of those measured using root bag methods in mangroves in Florida (McKee and Faulkner, 2000) and also in Belize (McKee et al., 2007). In the eastern bay during the warm/wet

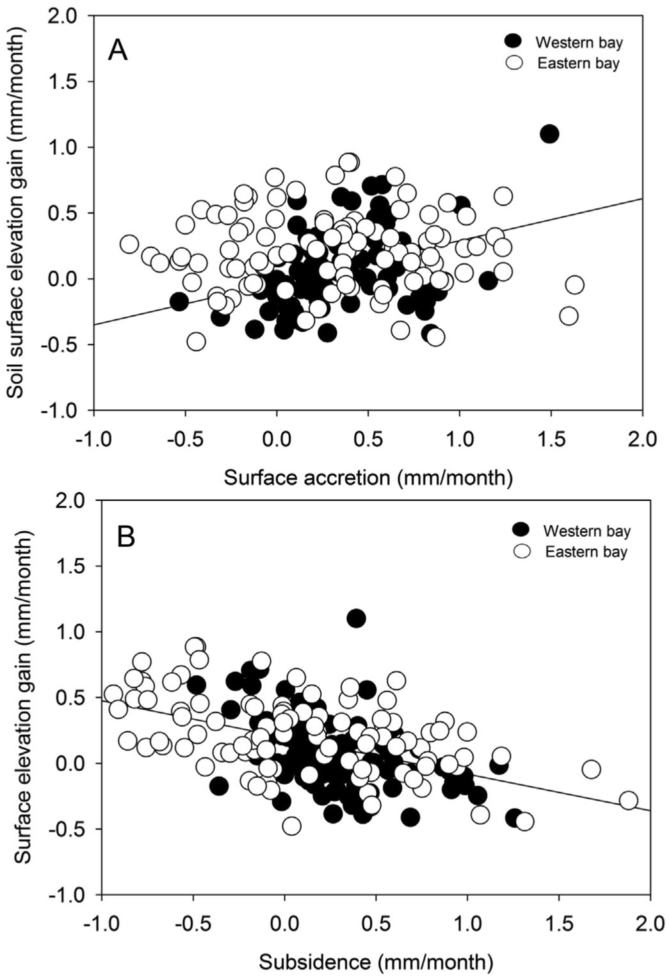

Fig. 5. The relationship between surface elevation and surface accretion (panel A) and surface elevation and shallow subsidence (panel B). Data are from the western (filled symbols) and eastern (open symbols) sides of Moreton Bay, Queensland. The regression in panel A for the western bay is of the form, $Y = -0.144 + 0.0249 * X$, $R^2 = 0.216$, $P < 0.0001$. The regression for panel B for both the eastern and western bay is of the form, $Y = 0.261 + 0.0160 * X$, $R^2 = 0.038$, $P = 0.0064$.

measurement interval, root production exceeded those reported for Micronesia (Gleason and Ewel, 2002; Cormier, 2003), but were similar to estimations derived from total belowground carbon allocation (~1200 g m^{-2} y^{-1}, assuming biomass is ~50% carbon, Lovelock, 2008). In the western bay root production rates were low compared to the eastern bay and to those reported in other studies, particularly in the dry/cool period. High nutrient concentrations in soils of the western bay may reduce allocation to roots in these forests (Castenada et al., 2011). Additionally, the differences in tree species in either side of the bay as well as the differences in the position in the intertidal zone (eastern bay forests were lower in the intertidal zone at approximately the level of mean sea level while those in the western bay are 0.6 m above mean sea level) may also contribute to difference in root production. In the western bay *Avicenna marina* is dominant, while in the eastern bay, *Rhizophora stylosa*, which is in the same genus as *R. mangle*, a species that produces peat (McKee et al., 2007), is also abundant. Trees lower in the intertidal may allocate a greater proportion of biomass to roots as an adaptation to longer inundation periods (Krauss et al., 2014) which may also contribute to differences in root production over the bay.

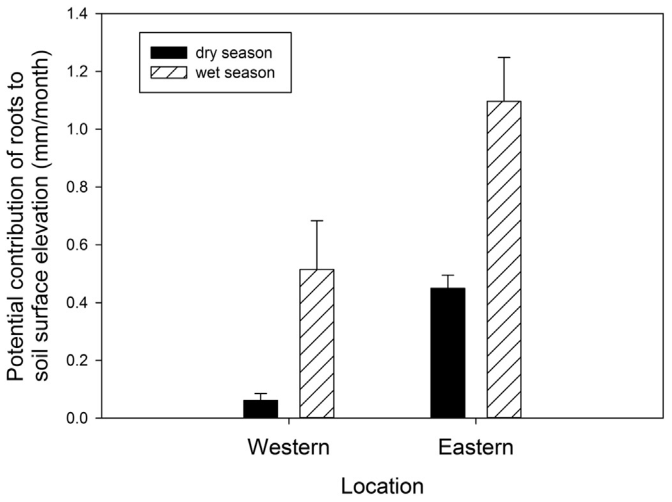

Fig. 6. The potential contribution of root growth to soil surface elevation in Moreton Bay in either the dry season (black bars) and wet season (dashed bars). The potential root contribution was calculated as the volume of roots grown within root bags in the top 20 cm of soil. Values are means of three sites ± standard errors. Different letters indicate significantly different values ($P < 0.05$) determined using a least significant difference test.

Differences in the material used in the root bags in the east and western bay, which were used to reflect differences in the soil on either side of the bay, could also contribute to the differences in root production in the eastern and western bay. Root growth is usually higher in low bulk density compared to high bulk density soils (e.g. Vocanson et al., 2006), and thus we may expect root production in the western bay (where we used peat moss/coconut fibre as substrate, to reflect the high levels of organic matter and low bulk density at the site) should actually be higher than in the natural soils. However, the low bulk density of the artificial soil in the root bags may also have altered hydrological properties, which could have contributed to low root production in the western mangrove forests. Lower root production in the dry/cool months compared to the warm/wet months is likely to reflect temperature constraints on mangrove growth in subtropical environments (Mackay et al., 1993), seasonally lower sea level (Supplementary material Figure S1, Kirwan and Guntenspergen, 2012) and

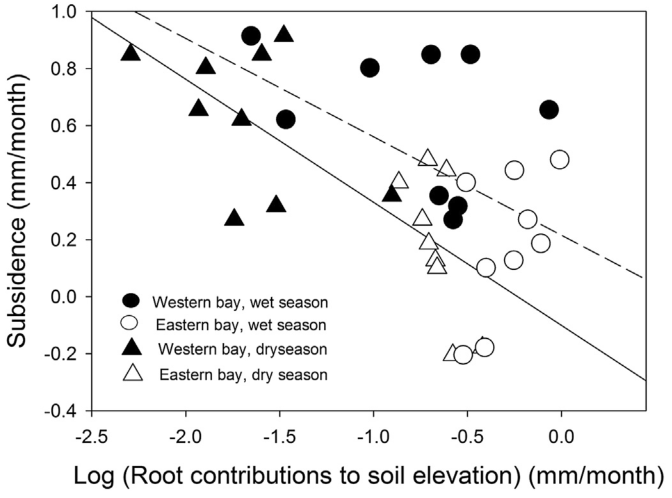

Fig. 7. The relationship between shallow soil subsidence (mm mo^{-1}) and the potential contributions to soil surface elevation by root growth for the western (filled symbols) and eastern (open symbols) Moreton Bay, Queensland. Measurements were made in a low rainfall period (triangles) and a high rainfall period (circles). The lines are the regression for the dry period, $Y = -0.101 + (-0.432) * X$, $R^2 = 0.576$ (solid line) and the wet period, $Y = 0.216 + (-0.345) * X$, $R^2 = 0.212$ (dashed line). Negative subsidence indicates a subsurface increase in soil volume.

possibly higher salinity of soils due to lower rainfall and freshwater and tidal inputs into mangrove habitats.

The volume of roots produced was not correlated with soil surface elevation gains at our sites in Moreton Bay. This contrasts with the important role of root production in sustaining soil surface elevation gains in settings with low levels of sediment inputs (McKee, 2011). Although we did not find a significant relationship between soil surface elevation gains and root production, we did find a significant relationship between root production and decreasing rates of shallow subsidence (Fig. 7). The generally higher rates of shallow subsidence in the western than eastern bay may occur because of high rates of compaction of low bulk density soils when they are loaded with tidal water during inundation and/or due to changes in the availability of groundwater or organic matter decomposition (Lovelock et al., 2011). However, because mangrove roots preferentially use old root channels and other macropores in soils to maximize nutrient capture (McKee, 2001), root production may limit subsidence of soils by filling macropores within soils, thereby reducing compaction of soils. The high level of subsidence observed in the western bay is consistent with low bulk density soils and low levels of root production, which could be a response to reduced requirement for nutrient conservation because of nutrient pollution (Dennison and Abal, 1999). But we also found that subsidence tended to be lower in the cool/dry season compared to the warm/wet season, which is the reverse of what might be expected if root production was the only factor determining subsidence (Table 1). More detailed knowledge of root growth, turnover, soil structure and decomposition of soil organic matter is required to fully understand the influences of roots on soil subsidence in this ecosystem.

Sea level rise in Moreton Bay is likely to increase rates of accretion in the western bay mangrove forests if suspended sediment concentrations are maintained. Decreases in rainfall are predicted for the region for the next century (Hughes, 2003) which may decrease sediment supply delivered in flood events (Fabricius et al., 2013). However, rainfall is predicted to occur in heavier pulses, which could maintain sediment loads if upstream erosion is enhanced. Our results indicate that declines in sediment run-off to Moreton Bay could have negative consequences for the ability of mangrove forest soils to keep up with sea level rise in the western bay. Re-suspension of fine sediments that have been deposited over the last century (You et al., 2005; Morelli et al., 2012) due to wind and waves could also continue to deliver sediments to mangroves in western Moreton Bay into the future, but this is likely to occur mostly in the northern bay where the fetch is greater compared to the southern bay.

5. Conclusion

Our study indicates that mangrove forests are likely to accrete with sea level rise where sediment supply is high, as predicted by models of tidal marsh surface elevation (Allen, 2000; Temmerman et al., 2004; Kirwan and Murray, 2007). Other forces, for example currents and waves, are likely to be more important in determining accretion in settings where sediments are coarse (e.g. MacDonald and O'Connor, 1996). We also found some evidence that root growth could be important in maintaining soil surface elevation in mineral settings due to its link to reduced soil subsidence. Current models do not consider the role of soil macropores and the consequences of their collapse on soil surface elevation dynamics, yet in mangroves, where boles and roots of trees are woody, this could be an important process. Climate change is resulting in rising sea level, but there is co-variation with sediment supply and rainfall that will have complex, interacting effects on intertidal wetland ecosystems. On balance, our study suggests predicted climate change for the region will have a negative effect on mangrove soil surface elevation gains in the western bay, and other mangrove forests that are dependent on sediments delivered during rainfall events, because of reductions in sediment supply, but effects on mangroves of the eastern bay are less certain. Our results indicate that both surface (sedimentation) and subsurface (root growth) processes can influence mangrove capacity to keep pace with sea level rise within the same geographic location, and that current models of tidal marsh responses to sea level rise capture the major feature of the response of mangroves where fine, but not coarse, sediments are abundant.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2014.11.026.

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Supplementary material

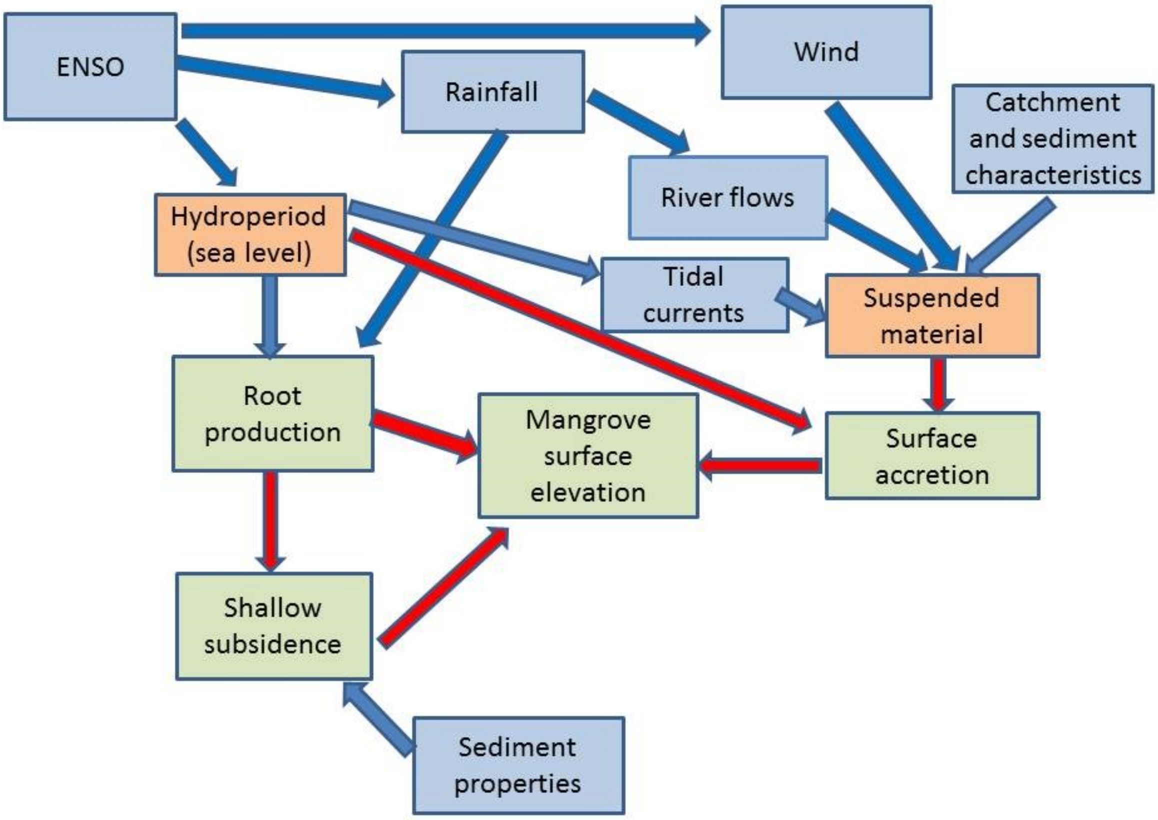

Figure S1. Conceptual framework for this study based on Figure 4 of Allen (2000). Parameters in green are measured in this study for twelve time periods between 2007 and 2011. The role of suspended material (using turbidity as an indicator) and hydroperiod (sea level) in orange and their relationship to surface accretion (arrows in red) are assessed in this study.

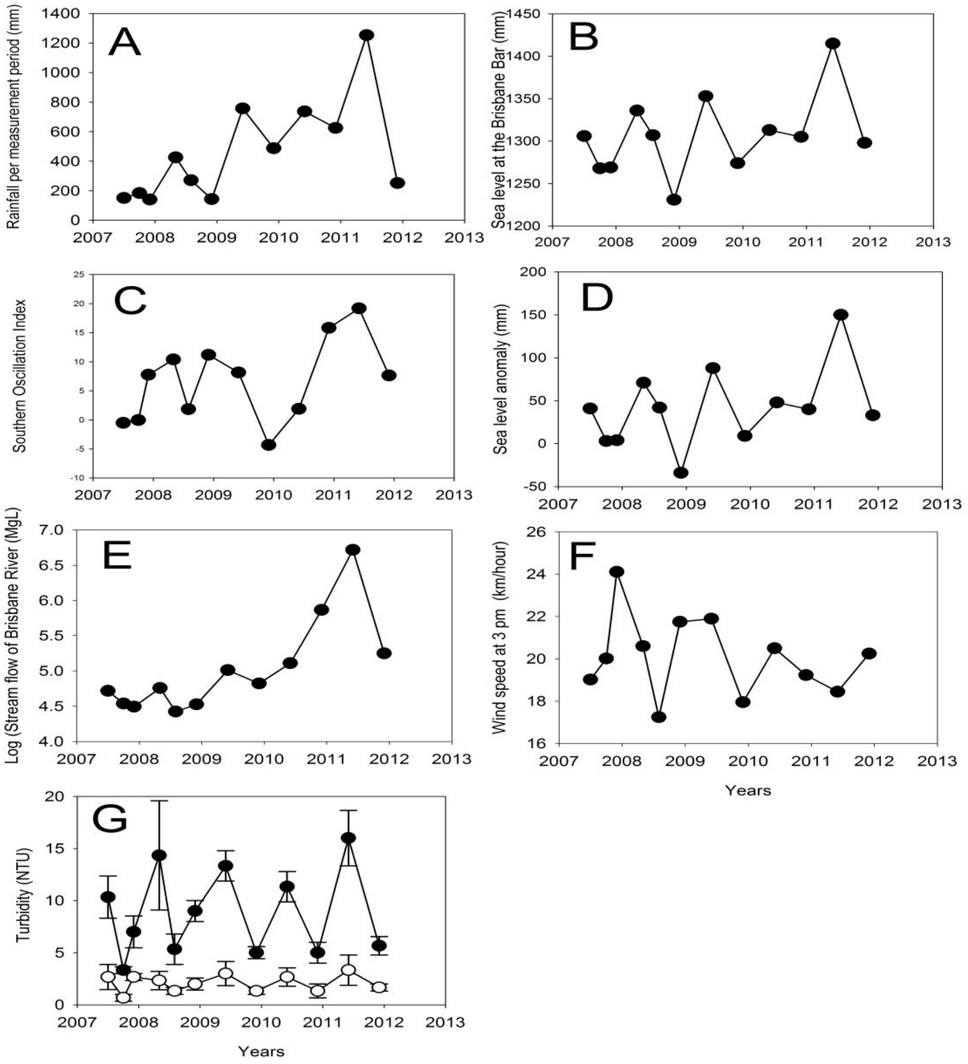

Figure S2. Variation in climatic and oceanographic variables over the study period from March 2007 to November 2011. A) rainfall; B) sea level at the Brisbane Bar; C) Southern Oscillation Index; D) sea level anomaly; E) stream flow of the Brisbane River (log transformed); F) wind speed at 3 pm (Brisbane Airport); and G) turbidity of coastal waters adjacent to the study sites in either eastern or western Moreton Bay. Rainfall, stream flow, wind speed and the SOI were sourced from the Australian Bureau of Meteorology. Sea level was obtained from https,//www.bodc.ac.uk for station PSM 21764 on Bishop Island at the mouth of the Brisbane River (GLOSS number 58). Sea level anomaly was the difference between the sea level during the measurement period and the mean sea level from 1984 to 2012. Turbidity was sourced from the Environmental Health Monitoring Program (EHMP, Queensland Government).

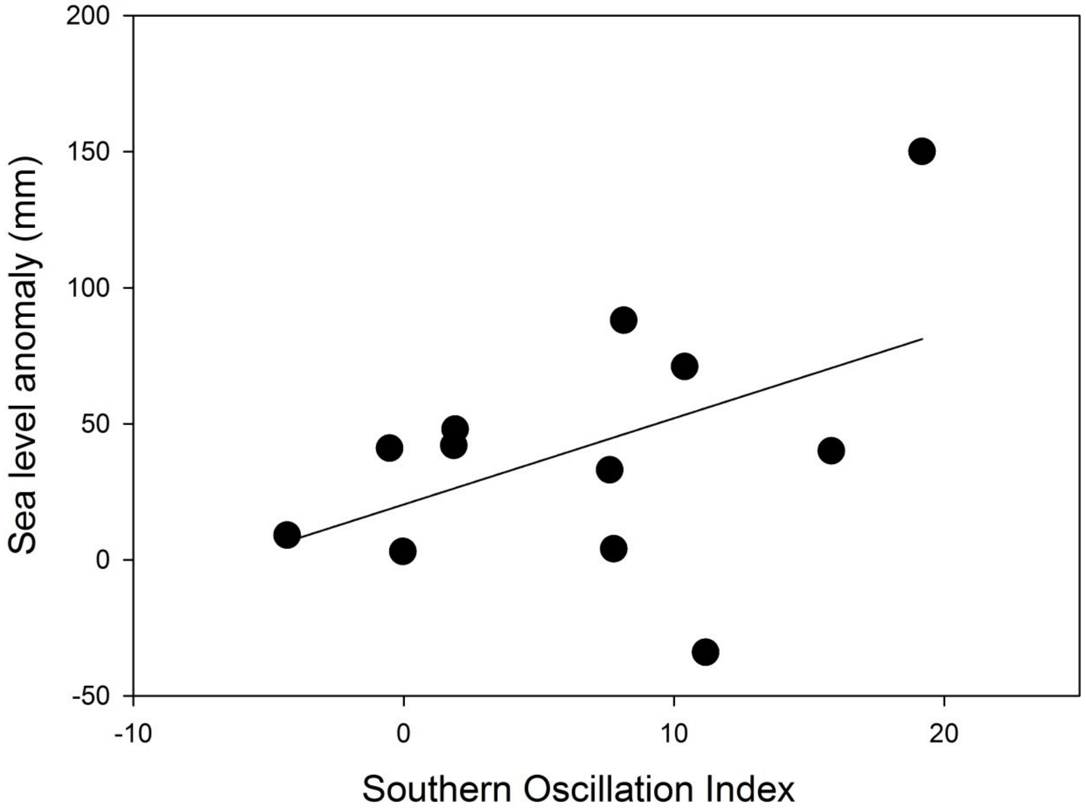

Figure S3. Variation in the sea level anomaly (mean value for the measurement interval – mean sea level from 1984-2012) with the Southern Oscillation Index (sourced from the Australian Bureau of Meteorology). The line is the regression of the form: Y = 20.2 + 3.17 * X, $R^2 = 0.22$.

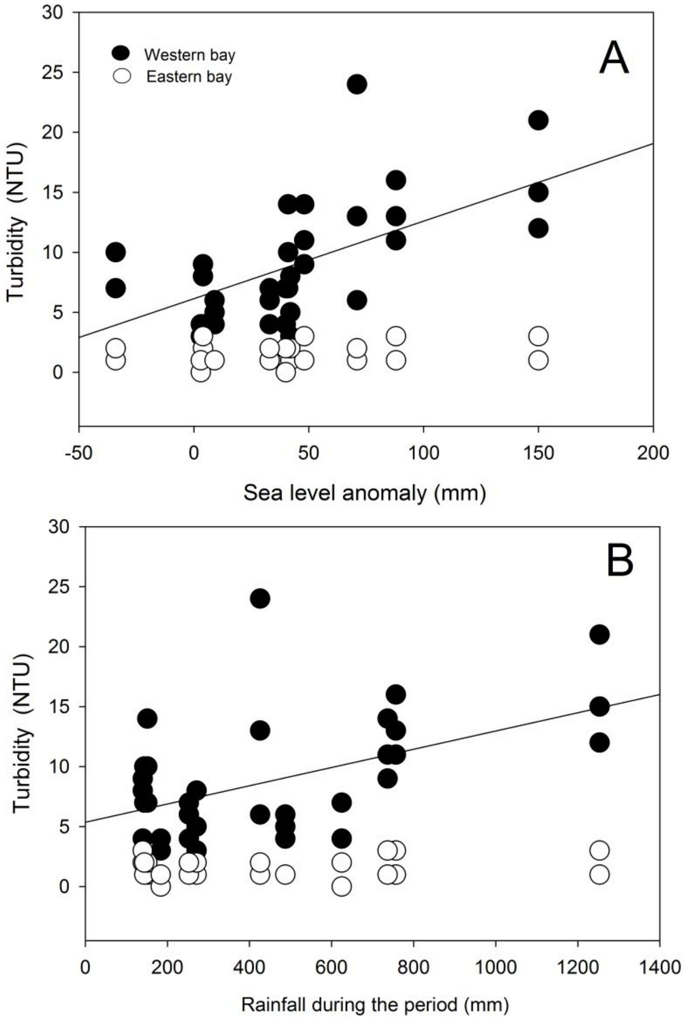

Figure S4. The relationship between A) turbidity and sea level anomaly; and B) turbidity and cumulative rainfall for each measurement period in Moreton Bay for the western side of the bay (filled symbols) and the eastern side of the bay (open symbols). The line for the western bay in panel A is the regression of the form, $Y = 6.14 + 0.065 * X$, $R^2 = 0.346$, $P < 0.0001$ and for panel B is $Y = 5.50 + 0.0065 * X$, $R^2 = 0.140$, $P = 0.014$.