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Invited review

The role of root decomposition in global mangrove and saltmarsh carbon budgets

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ABSTRACT

This study aims to determine the drivers of root decomposition and its role in carbon (C) budgets in mangroves and saltmarsh. We review the patterns of root decomposition, and its contribution to C budgets, in mangroves and saltmarsh: the impact of climatic (temperature and precipitation), geographic (latitude), temporal (decay period) and biotic (ecosystem type) drivers using multiple regression models. Best-fit models explain 50% and 48% of the variance in mangrove and saltmarsh root decay rates, respectively. A combination of biotic, climatic, geographic and temporal drivers influences root decay rates. Rainfall and latitude have the strongest influence on root decomposition rates in saltmarsh. For mangroves, forest type is the most important; decomposition is faster in riverine mangroves than other types. Mangrove species *Avicennia marina* and saltmarsh species *Spartina maritima* and *Phragmites australis* have the highest root decomposition rates. Root decomposition rates of mangroves were slightly higher in the Indo-west Pacific region (average 0.16% day^{-1}) than in the Atlantic-east Pacific region (0.13% day^{-1}). Mangrove root decomposition rates also show a negative exponential relationship with porewater salinity. In mangroves, global root decomposition rates are 0.15% day^{-1} based on the median value of rates in individual studies (and 0.14% day^{-1} after adjusting for area of mangroves at different latitudes). In saltmarsh, global root decomposition rates average 0.12% day^{-1} (no adjustment for area with latitude necessary). Our global estimate of the amount of root decomposing is 10 Tg C yr^{-1} in mangroves (8 Tg C yr^{-1} adjusted for area by latitude) and 31 Tg C yr^{-1} in saltmarsh. Local root C burial rates reported herein are 51–54 g C m^{-2} yr^{-1} for mangroves (58–61 Tg C yr^{-1} adjusted for area by latitude) and 191 g C m^{-2} yr^{-1} for saltmarsh. These values account for 24.1–29.1% (mangroves) and 77.9% (saltmarsh) of the reported sediment C accumulation rates in these habitats. Globally, dead root C production is the significant source of stored sediment C in mangroves and saltmarsh.

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1. Introduction

Coastal wetlands, including mangroves and saltmarsh, are blue carbon (C) ecosystems that provide numerous benefits and services important in climate change adaptation Atwood et al. (2015). These habitats typically sequester C several times faster than terrestrial ecosystems, and are therefore important despite occupying a smaller area of the earth's surface (Breithaupt et al., 2012; Mcleod et al., 2011). Globally, these habitats, along with macroalgae, are estimated to contribute 50% of the C sequestration in marine sediments (Duarte et al., 2013). The role of mangroves in global C cycling and storage has been thoroughly reviewed, and led to the identification of significant unknown processes, e.g. the fate of dissolved inorganic C (DIC) from decomposition (Bouillon et al., 2008). For saltmarsh, although sequestration rates are known (Mcleod et al., 2011), their overall role in C cycling has not yet been fully described, despite a scale-up study of C cycling in saltmarshes on the U.S. East (Atlantic) Coast (Wang et al., 2016). For both habitats, syntheses of their roles have to date failed to incorporate the contribution of plant root decay to sediment C budgets. Assessing the contribution of mangrove and saltmarsh root production will be a significant step towards fully quantifying sediment C storage in these habitats.

Organic matter (OM) accumulation in mangroves and saltmarsh is dependent on the balance between the production and decomposition of below-ground biomass, in addition to above-ground production and import/export determined by the hydrological regime. Production and decomposition of below-ground roots and rhizomes in mangroves and saltmarsh are known to contribute to soil fertility through the formation of humic substances. However, it is their significant contribution to C storage and peat formation (Huxham et al., 2010; McKee et al., 2007; Ouyang and Lee, 2014) that we focus on here, because this drives sediment supply, sediment accretion, OM accumulation and influences responses to rising sea levels in coastal wetlands (Lovelock et al., 2015). Root and rhizome decomposition also produces significant greenhouse gases, predominantly from aerobic oxidation and sulphate reduction, which are the main pathways of OM degradation in coastal sediments (Alongi, 2009; Penha-Lopes et al., 2010). Even so, there exist other pathways of microbial OM decomposition, including manganese and iron reduction, which are among the sources of benthic DIC and alkalinity and thereby C sinks in the coastal zone (Krumins et al., 2013; Ovalle et al., 1990).

Little attention has been paid to the patterns of root decomposition in mangroves and saltmarsh, despite the expected significant role of root decomposition. Substrate quality and the presence and abundance of fauna are known to influence the decay rate of leaf litter in mangrove forests (e.g. Kristensen et al., 2008). A wide range of factors may influence the root decomposition processes. Different environmental, hydrological and climatic conditions can affect below-ground microbial activities and oxygen concentrations (Alongi, 2009; Gonzalez-Alcaraz et al., 2012; Sousa et al., 2010a), and thus the decomposition rate. Sediment porewater salinity might also modulate microbial decomposition of roots. Davidson and Janssens (2006) proposed that hydrological factors and substrate quality are the chief constraints on decomposition rates in wetlands. These factors potentially interact with an assumed response of decomposition rates to temperature. Although there is a growing literature on root decomposition in coastal wetlands, there has been no global synthesis of root decay rates in mangroves and saltmarsh. The integration of the influence of climatic, geographic, biotic and other drivers of root decay is a significant step in understanding the ecological function of these estuarine habitats and their capacity for blue C.

This study quantifies the contribution of root decay to global C budgets in mangroves and saltmarsh and assesses factors that may cause variation in reported rates. We analyse the nexus between root decay rates and climatic (temperature and precipitation), geographic (latitude), temporal (decay period), biogeochemical (sampling depth) as well as biotic (ecosystem type) factors. Then we investigate differences in root decay rates among ecosystem types, significant factors in the model, and with porewater salinity, as well as species. Global root decomposition rates are estimated by averaging individual rates in mangroves and saltmarsh, and also by integrating mangrove area with decay rates in latitudinal ranges. Then we examine how much C is mineralised in the root decay process and how much is buried in sediments. This is the first comprehensive global review synthesizing the fate of mangrove and saltmarsh root C production. The findings will contribute to an improved understanding of below-ground OM mineralisation and accumulation in mangrove and saltmarsh sediments, and its implications for C budgets in coastal wetlands.

2. Materials and methods

2.1. Data collection and collation

Decomposition rates of roots and/or rhizomes in mangroves and saltmarsh were compiled from the literature. We conducted a literature search in http://www.sciencedirect.com/ and http://pcs.webofknowledge.com/, using 'carbon OR decomposition' combined with either 'mangrove' or 'saltmarsh OR salt marsh' in 'Abstract, title and Keywords' or 'Topic, title'. These terms cover root and/or rhizome decomposition in mangroves and saltmarsh. In total, 2611 and 2427 results were found for mangrove and saltmarsh studies, respectively. Our careful sifting through these papers for studies containing primary data on root decomposition of mangroves and saltmarsh reduced the number to 36 for the two habitats.

Individual studies investigate root decomposition by quantifying the variation of root mass at intervals during the whole decay period. Specifically, in all studies replicates (the number depends on sampling intervals and duration of the whole decay period) of a known amount of roots were put in sediment in the field, retrieved at intervals and then re-weighed. The loss of root mass is calculated as the difference between the initial and remaining mass, and is a function of the decomposition rate.

When decomposition rates were not reported directly in individual studies, they were calculated from the decay period and the decay rate constant, as estimated by the linear or negative exponential model (remaining biomass ~ decay period). The selection of a linear or exponential model depended on which explained more variance in the dependent variable. For studies measuring remaining biomass over a series of decay periods, only root decay rates corresponding to the final decay period were used. Overall, the data from the 36 studies covered a latitudinal range from 38.3°S to 26.1°N for mangroves and 38.3°S to 51.4°N for saltmarsh (Fig. 1, and Table S1 in Appendix A). Root decomposition rates (% day^{-1}) are derived from Eqs. (1) and (3) for the linear model, to Eqs. (2) and (3) for the exponential model.

$$M_t = k_c t + b \quad (1)$$

$$M_t = \exp(k_c t + b) \quad (2)$$

$$\text{decomposition rate} = 100 \times \frac{M_0 - M_t}{M_0 T} \quad (3)$$

Where M_t is the remaining root mass (in g) at the specific decomposition period t (days), g; k_c is decay rate constant, g day^{-1}; b is the intercept in the regression models, g; M_0 is the initial root mass, g; T is the overall decomposition period in days.

Methods used by the studies to estimate the decomposition rate were categorised into four types: litter bags, litter tubes, unbagged litter and coring method. Litter bags are used to investigate root decomposition by enclosing a known amount of roots in permeable bags, and the mass loss from roots in the bags over time is an estimate of decomposition rate. Litter tubes are similar to litter bags but enclose roots in tubes, the end of which is closed with permeable mesh screens. In contrast to

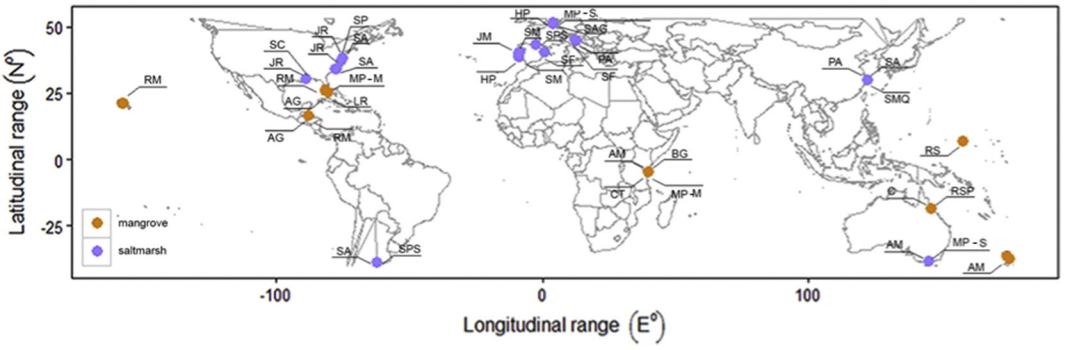

Fig. 1. Distribution of mangrove and saltmarsh species at sampling sites from our collated references. Full names of species abbreviations in the figure are as below. (1) mangrove species: AG – *Avicennia germinans*, AM – *Avicennia marina*, BG – *Bruguiera gymnorhiza*, CT – *Ceriops tagal*, C – *Ceriops*, LR- *Laguncularia racemosa*, RM – *Rhizophora mangle*, RSP – *Rhizophora* spp., RS – *Rhizophora stylosa*, MP-M – mixed species, (2) saltmarsh species: HP – *Halimione portulacoides*, SA – *Spartina alterniflora*, SAG – *Spartina anglica*, SC – *Spartina cynosuroides*, JM - *Juncus maritimus*, JR – *Juncus roemerianus*, PA – *Phragmites australis*, SF – *Suaeda fruticosa*, SM – *Spartina maritima*, SP – *Spartina patens*, SPS – *Sarcocornia perennis*, SMQ – *Scirpus mariqueter*, MP-S – mixed species. Mangroves and saltmarsh species, as a whole, are distinguished by different colours. Species abbreviations were denoted in the figure where different species labels were clearly overlapped.

litter bags or tubes, the unbagged litter method does not enclose roots in mesh bags or tubes but roots are put into a bundle and fixed at the end to living roots. As for the coring method, after roots are weighed and put belowground for a certain period, the sediment is cored and sieved, and then roots are picked out to examine the variation of root mass over the decay period. Litter bags were the most commonly employed method, accounting for 83.9% of measurements, and the other methods were all employed only in a very small number of studies. In terms of sample treatment, some studies directly utilised oven-dried samples, while others air-dried samples or air-dried before oven-drying samples at higher temperatures.

We combined root decay rates, global mangrove and saltmarsh areas, and dead root C production, to estimate the global contribution of root C to C budgets. Dead root C production was root C production multiplied by turnover rates. Root C production data and turnover rates were collected from two avenues: two reviews (Alongi, 2014 and Bouillon et al., 2008) and additional individual studies that report data from specific regions. The ranges of the unit-area root decay rates, turnover rates and root C production were propagated using the "uncertainty propagation" approach of Ouyang and Lee (2014). We define decayed root C as the portion of annual dead root C production decomposed in the root decay process. Global decayed root C was estimated as the product of root decay rates, dead root C production and global area of the habitats. To estimate the contribution of root C to sediment C stock in mangroves and saltmarsh, local root C burial rate was also calculated as the difference between average unit-area dead root C production and decayed root C.

The factor Sediment Depth was categorised into surface or buried (range of depths from 3 to 30 cm, where values are available). Mangrove forests were classified into five types: basin, fringe, overwash, riverine and scrub mangroves (Lugo and Snedaker, 1974). Saltmarsh was classified into three types: high, mid and low marsh. Decomposition rates potentially vary with root size class at the same site. However, there is a general lack of information on and inconsistency in size classes in our collected data. Some studies did not report root size classes. Some reported ambiguous sizes, such as >0.4 mm (1 mm, 1.25 mm, 1.6 mm) or 1–4 mm, which could not be sorted into either fine or coarse roots. Others used mixed fine and coarse roots, and the proportion of fine and coarse roots varies in related studies. Therefore, although root size class is a potential confounding factor, its influence on decomposition rates could not be analysed in our study.

We collected long-term climate records from meteorological stations nearest to the sampling sites (usually within a few km, and always <100 km) because root decomposition rates might vary with climatic conditions. Average precipitation and daily air temperature values over the original experimental period were obtained and used in the analysis.

2.2. Data analysis

The central statistical analyses were multiple linear regressions on root decomposition rates, separately for mangroves and saltmarsh. Six independent variables were included in the starting model (Table 1). Species identity would have been of interest but was omitted from the multiple regression model because only limited data were available for several mangrove and saltmarsh species, and their inclusion would have resulted in the loss of significant degrees of freedom in the regression models. We separately evaluated the difference in root decomposition rates among species with a Kruskal-Wallis rank sum test, followed by non-parametric Mann-Whitney *U* tests. For the single-factor tests (among species and among vegetation types) we had to use subsets of the data from studies with identifiable species/types; these data consisted of uncontrolled combinations of other factors (latitude, temperature), which were not well balanced, and thus the multivariate analysis used for the main analysis was not applicable here. For saltmarsh, the numbers of root decay rates for individual species are 4 (*Halimione portulacoides*), 11 (*Juncus roemerianus*), 3 (*Phragmites australis*), 17 (*Spartina alterniflora*), 11 (*Spartina anglica*), and 5 (*Spartina maritima*). For mangrove, the numbers of root decay rates for individual species are 6 (*Avicennia germinans*), 35 (*Avicennia marina*), 8 (*Bruguiera gymnorhiza*), 6 (*Ceriops tagal*), 3 (*Laguncularia racemosa*), and 24 (*Rhizophora mangle*). The numbers of root decay rates for other species are <3. In addition, mangrove species belong to different biogeographic regions, i.e. Indo-west-Pacific (IWP) and Atlantic-east-Pacific (AEP). *Avicennia marina*, *Ceriops tagal* and *Bruguiera gymnorhiza* distribute in IWP while *Laguncularia racemosa*, *Rhizophora mangle* and *Avicennia germinans* distribute in AEP. Interactions among the explanatory variables were explored using Pearson correlation analysis. The models contain all the explanatory variables and their possible interactions. Based on the above data exploration, the initial model for mangrove data is: root decay rate ≈ rainfall + decay period + T + latitude + T:latitude + sampling depth + mangrove type, while that of saltmarsh data is: root decay rate ≈ T + latitude + T:latitude + rainfall + rainfall:latitude + rainfall:T + decay period + sampling depth + saltmarsh type. In the regression models, T is air temperature, and 'T:latitude' is the interaction between T and latitude. Homoscedasticity was verified by plotting residuals versus fitted values of root decay rates. Normality was tested using the Shapiro-Wilk normality test. When assumptions were not met, data were transformed (e.g. square root).

Table 1
Independent variables assessed in regression analyses, and those included in the final models.

Factors	Independent variables	Variable type	Variables included in FINAL regression model?
Temporal	Decay period	Continuous	Yes
Climatic	Air temperature	Continuous	Yes
	Precipitation	Continuous	Yes, in saltmarsh model
Geographic	Latitude	Continuous	Yes, covaries with air temperature and precipitation (saltmarsh)
Biogeochemical	Sampling depth	Categorical: buried, surface	No
Local	Ecosystem type	Categorical: Mangrove: basin, fringe, overwash, riverine, scrub	Yes
		Saltmarsh: high, mid, low	No

Collinearity was checked by variance inflation factor values. All values are lower than 3, suggesting no collinearity problem (Quinn and Keough, 2002).

Unusually influential values, as measured by Cook distance, were removed from the data set. Step-wise regression analysis was conducted with ecosystem type and buried depth included as dummy variables, with one level of each variable selected as the reference (see Table 1, Quinn and Keough, 2002). For a subset of studies on mangroves that measured soil porewater salinity, the relationship between root decay rates and salinity was explored by exponential regression in a separate analysis because the inclusion of salinity in the multiple regression model would result in the loss of significant degrees of freedom. Pearson correlation test was conducted to find the correlation coefficients of interactions among explanatory variables in the regression models.

All analyses were conducted using the R programming language (R Core Team, 2014). The R package 'relaimpo' (Grömping, 2006) was employed to determine the relative importance of independent variables. The R packages 'ggmap' (Kahle and Wickham, 2013) was used to visualise the sampling sites on a world map, and 'ggplot2' (Wickham, 2009) was used to plot other figures.

As mangrove forest type was a significant factor in the final models, differences in root decay rates among mangrove types were further tested with Kruskal-Wallis rank sum test (the assumption of normality could not be met). After a significant treatment effect, non-parametric Mann-Whitney *U* tests were used to detect difference among group means. Non-parametric Mann-Whitney *U* tests were also used to compare root decay rates of different biogeographic regions.

Global root decomposition rates of mangrove and saltmarsh were estimated as the respective central values of individual root decay rates. Decay rates, turnover rates and unit-area production values were checked for normality using the Shapiro-Wilk normality test, in order to estimate global root C production of mangroves and saltmarsh. When raw or transformed data (e.g. log-transformed) violated the normality assumption, the median of global root decay rates, root turnover rates or root C production was reported. When data met the normality assumption, the mean of individual data was used. Further, the geometric mean was employed when the transformed data had a normal distribution.

In addition, global root decomposition rates of mangroves were estimated by another method, which integrated mangrove area in different latitudinal ranges and the associated decomposition rates. This method was used because the vast distribution of mangroves in the tropics suggests that the mean or median value of global individual root decomposition rates may not account for the bias in mangrove distribution. This is corroborated by data extracted from Giri et al. (2011), who show that the total mangrove area in the latitudinal range 0–20° account for around 82% of global mangrove area. Specifically, we estimated root decomposition rates at intervals of 10° in the range 0–40°, and extracted mangrove area also at 10° intervals. Root decomposition rates at each latitudinal interval were estimated as the representative central values, similar to the above estimate of the central tendency of global root decay rates. Then they were propagated to global root decomposition rates by integrating root decomposition rates with mangrove area at the latitudinal intervals. Coordinates of global mangroves were extracted from Giri et al. (2011) via ArcGIS, and were divided into different latitudinal intervals, corresponding to root decay rates at latitudinal intervals.

3. Results

3.1. Drivers of root decay rates

A total of 110 valid independent decomposition rates were included in the analysis for mangroves. Multiple regression analysis showed that there was a highly significant relationship between root decay rates and a combination of temperature, latitude, decay period and ecosystem type ($p < 0.001$, Table 2a). This combination of factors explained half of the variance in decay rates ($R^2 = 0.50$). In particular, latitude interacted with temperature ('T:latitude' in the regression model, $R = -0.8$, $p < 0.001$) to influence mangrove root decay rates. Mangrove

Table 2
The relationship between root decay rates and climatic, geographic as well as temporal factors as examined by multiple regression. Decay rates were expressed as % yr^{-1} in multiple regression.

a) Mangrove
Final model: Root decay rates ≈ T × latitude + decay period + type

Variables	Estimate	SE	t value	*p*
(Intercept)	−414.082	177.572	−2.332	*
T	17.713	6.533	2.711	**
latitude	11.813	4.604	2.566	*
decay period	−28.387	8.697	−3.264	**
typebasin	11.823	9.947	1.189	>0.05
typefringe	26.606	9.577	2.778	**
typeoverwash	11.662	9.962	1.171	>0.05
typeriverine	29.093	8.047	3.615	***
T:latitude	−0.409	0.173	−2.363	*
$R^2 = 0.50$, $p < 0.001$				

b) Saltmarsh
Final model: Root decay rates ≈ decay period + precipitation × latitude + T^2 × latitude

Variables	Estimate	SE	t value	*p*
(Intercept)	283.828	47.686	5.952	***
decay period	−15.719	6.654	−2.362	*
precipitation	−92.744	19.962	−4.646	***
latitude	−5.230	1.147	−4.559	***
T^2	0.675	0.281	2.407	*
precipitation:latitude	2.241	0.535	4.192	***
latitude:T^2	−0.016	0.007	−2.234	*
$R^2 = 0.48$, $p < 0.001$				

T denotes air temperature. T × latitude equals 'T + latitude + T:latitude'. T:latitude represents the interaction between T and latitude.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

type, however, was the most important individual explanatory variable (17% of variance).

For saltmarsh, 66 decomposition rates were included. There was a highly significant relationship between saltmarsh root decay rates and precipitation, latitude, temperature and decay period ($p < 0.001$, Table 2b). The combined factors explained nearly half of the variance in saltmarsh root decay rates ($R^2 = 0.48$); with combined precipitation and latitude being the most important factors (33%). Latitude interacted with both precipitation ($R = -0.63$, $p < 0.001$) and temperature ($R = -0.62$, $p < 0.001$) to modulate saltmarsh root decay rates.

There were clear differences in root decay rates among different mangrove forest types (K-W $\chi^2(4) = 16.14$, $p < 0.01$, Fig. 2). Decomposition rates were fastest in riverine mangroves, intermediate in fringe and scrub, and lowest in basin and overwash forest types (Fig. 2).

There were also clear differences in root decay rates among different mangrove and saltmarsh species (K-W $\chi^2(6) = 27.5$, $p < 0.001$ and K-W $\chi^2(6) = 20.79$, $p < 0.01$, respectively, Fig. 3). Decomposition rates were highest for *Avicennia marina* (mangroves), *Spartina maritima* and *Phragmites australis* (saltmarsh). In combination with root decay rates of species in different biogeographic regions, root decay rates of IWP were estimated to be

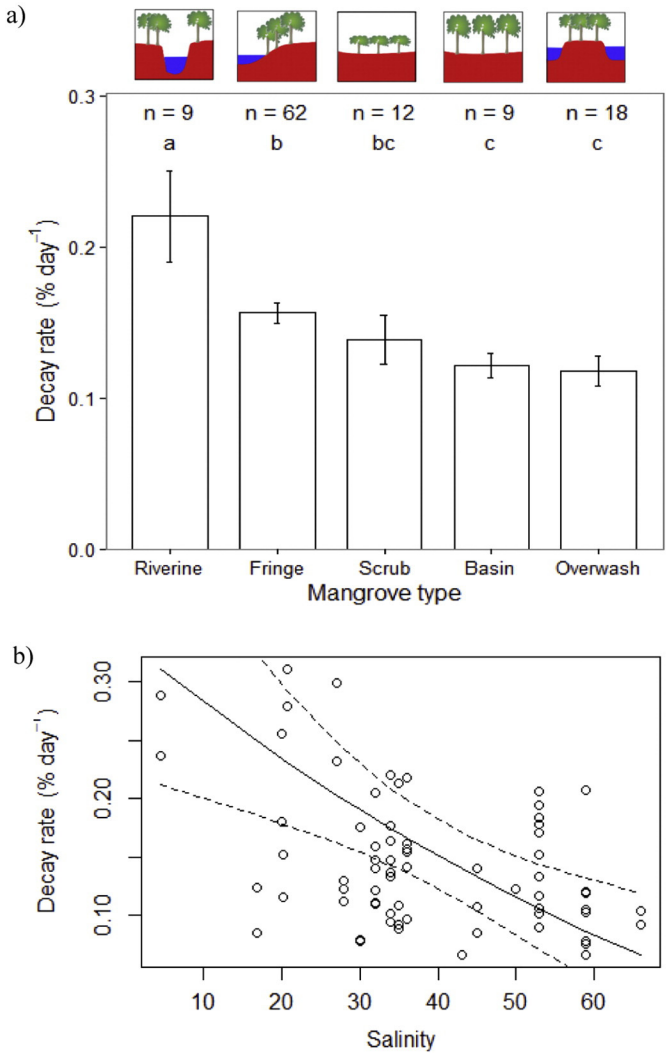

Fig. 2. (a) Variation of root decay rates among mangrove types and (b) the relationship between soil porewater salinity and mangrove root decay rates. Values with different letters in (a) are significantly different from each other. The dotted lines in (b) are 95% confidence intervals.

0.162 ± 0.008% day^{-1}, not significantly different from those of AEP (0.134 ± 0.012% day^{-1}) (M-W test, W = 827.5, $p > 0.05$).

For the mangrove studies that included porewater salinity ($n = 72$), regression analysis showed that decay rates declined exponentially with porewater salinity ($R^2 = 0.16$, $p < 0.001$, Fig. 2). There were too few salinity data in saltmarsh studies to allow a meaningful analysis.

3.2. Global estimates of decomposed root carbon in mangroves and saltmarsh

Both the area-averaged value of mangrove root decay rates at the latitudinal ranges and the median value of individual rates were used to represent the central tendency of global mangrove root decay rates, as described above. For the area-averaged rates, root decomposition rates of all latitudinal ranges meet the normality assumption except rates at 20–30°, which were represented by the geometrical mean since they meet the assumption after log-transformation. Root decomposition rates at latitudinal ranges were estimated (Fig. 4) as below: 0.141 ± 0.007% day^{-1} (0–10°), 0.111 ± 0.011% day^{-1} (10–20°), 0.152% day^{-1} (20–30°, geometrical mean), 0.201 ± 0.013% day^{-1} (30–40°). Saltmarsh root decay rates were found to meet the assumption of normality (Shapiro-Wilk normality test, $p > 0.05$) after log-transformation and the geometrical mean value was therefore used. Globally, root decay rates of mangroves were 0.135 (the area-averaged rate) and 0.152% day^{-1} (the median value of individual rates), while root decay rates of saltmarsh were 0.119% day^{-1} (Table 3).

The aforementioned global root decay rates were used to estimate global decayed root C in combination with root C production and turnover rates by the 'uncertainty propagation' approach. Firstly, the unit area of root C production was scaled up to 135.3 and 1425.8 g C m^{-2} yr^{-1}, using data from the 5th and the 95th percentiles, respectively, of the collated saltmarsh data. Global root C production data (75 and 82 Tg C yr^{-1}) from reviews of Alongi (2014) and Bouillon et al. (2008) were directly applied to estimate global decayed root C in mangroves. Dividing by the low and high global mangrove area estimates (138,000 and 160,000 km^2) used in their estimate of root C production, mangrove root C production was estimated to reach 544 (estimated from Alongi, 2014) and 513 g C m^{-2} yr^{-1} (estimated from Bouillon et al., 2008), respectively. Secondly, the root decay rate of mangroves was propagated from 0.076 (the 5th percentile) to 0.262% day^{-1} (the 95th percentile), while that of saltmarsh ranged from 0.052 to 0.278% day^{-1}. Likewise, the root turnover rates of mangroves and saltmarsh were propagated to range from 0.048 to 0.51 yr^{-1} and from 0.219 to1.857 yr^{-1}, respectively.

Subsequently, the uncertainty of global decayed root C was propagated by multiplying the unit area root C production by turnover rates, root decay rates and global mangrove/saltmarsh area. Specifically, the low-end estimate of global decayed root C in mangroves was estimated by combining the low-end of global area (138,000 km^2), the 5th percentile root decay rate (0.076% day^{-1}) and turnover rate (0.048 yr^{-1}), and the low-end of root C production (513 g C m^{-2} yr^{-1}). The high-end estimate of global decayed root C was estimated by combining the high-end of global area (160,000 km^2), the 95th percentile root decay rate (0.262% day^{-1}) and turnover rate (0.51 yr^{-1}), and the high-end of root C production (544 g C m^{-2} yr^{-1}). Integrating data from individual studies, the unit-area root C production in saltmarsh met the normality assumption after transformation. The geometric mean of the unit-area root production was estimated as 525 g C m^{-2} yr^{-1} (for precision estimate see Table 3). This estimation resulted in the global decayed root C in mangroves ranging from 0.9 to 42.4 Tg C yr^{-1}. Likewise, the global decayed root C in saltmarsh was propagated to be 0.5–395.5 Tg C yr^{-1}. Combining reported global mangrove and saltmarsh area with root decay rates of the median (or area averaged) or geometrical mean, turnover rates, and the unit-area root production rate, global decayed root C for

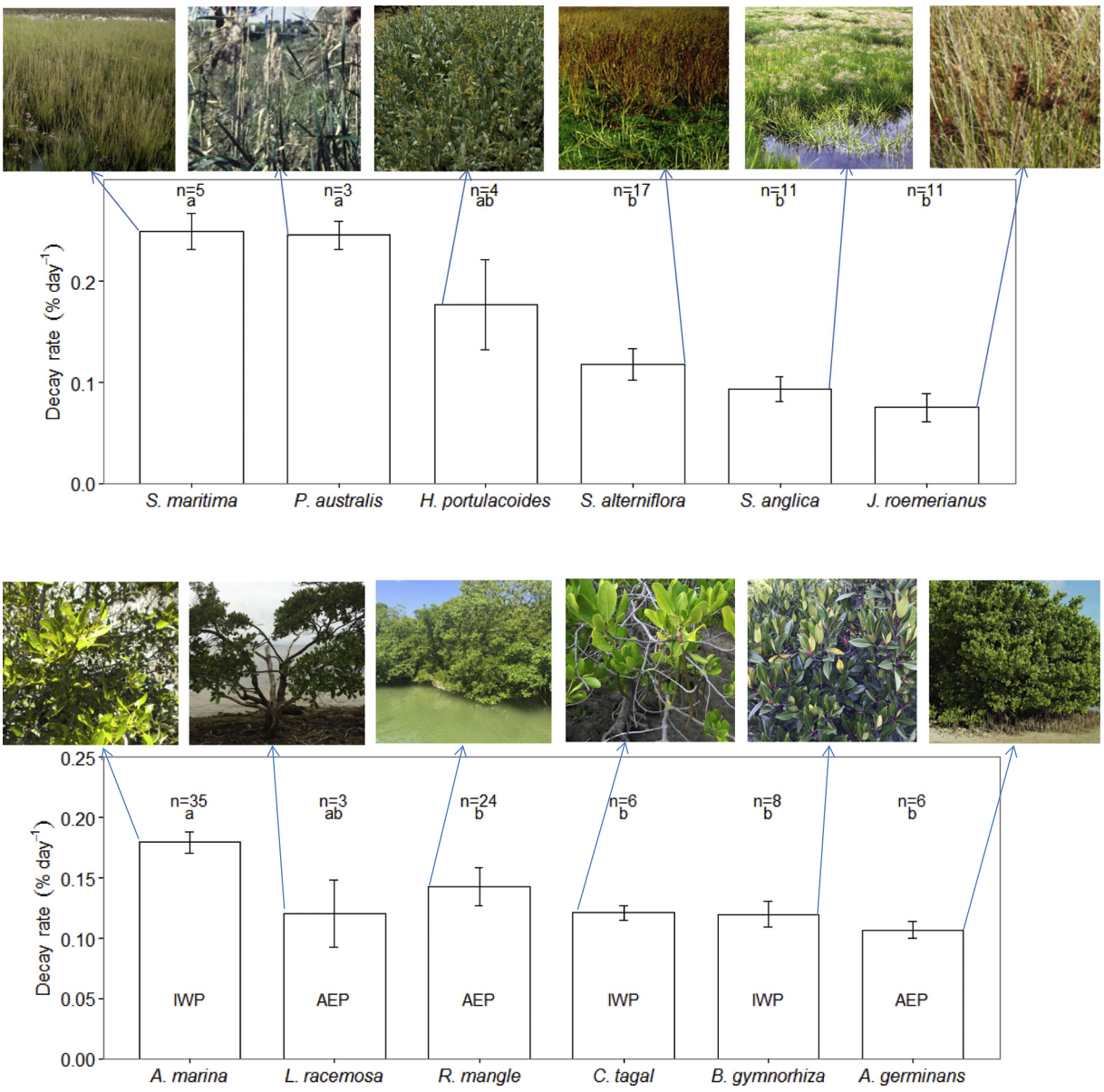

Fig. 3. Variation of root decay rates among saltmarsh (upper) and mangrove (lower) species. Values with different letters are significantly different from each other. Mangroves are labelled with respect to different biogeographic regions, i.e. Indo-west Pacific (IWP) and Atlantic-east Pacific (AEP). Photos of species come from us and Global Invasive Species Database (2016a, 2016b), Ellison et al. (2010), Duke et al. (2010), Waysel (1972), Virginia Institute of Marine Science GBIF Secretariat and http://www.dpi.qld.au.

mangroves and saltmarsh was estimated to be 10 (8) Tg C yr^{-1} and 31 Tg C yr^{-1}, respectively (Table 3). The area-averaged root decay rates were not estimated for saltmarsh since the latitudinal distribution of global saltmarsh is not available. Root C burial rate was estimated at 51–54 g C m^{-2} yr^{-1} (estimated from the median value of individual root decomposition rates) or 58–61 g C m^{-2} yr^{-1} (estimated from the area-averaged root decomposition rate) for mangroves, and 191 g C m^{-2} yr^{-1} for saltmarsh (Table 4).

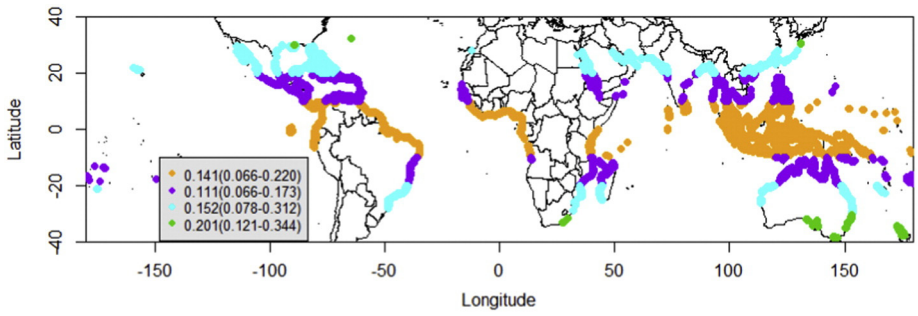

Fig. 4. Mangrove root decay rates (% day^{-1}) among latitudinal ranges of 0–40° at an interval of 10°. Numbers before and in the brackets are the mean values and ranges of root decay rates, respectively. Geometric mean was used to represent the root decay rate at the latitudinal range 20–30°.

Table 3
Global decayed C stock in root production of mangroves and saltmarsh.

Ecosystem	Root production (Tg C yr^{-1})	Root decay rate (% day^{-1})	Unit-area root production (g C m^{-2} yr^{-1})	Root turnover rate (yr^{-1})	Unit-area dead root production (g C m^{-2} yr^{-1})	Global area (km^2)	Global C decayed (Tg C yr^{-1})	References
Mangroves	75[a]	0.152[c] (0.076–0.262)	513[a]	0.222 (0.048–0.51)	114[d] (24.6–21.6)	138,000–160,000	10[e] (0.9–42.4)	1–5
	82[b]	0.135[c]	544[b]		121[d] (26.1–277.4)	152,308	8[e] (1.7–21.8)	
Saltmarsh	NA	0.119 (0.052–0.278)	525 (135.3–1425.8)	0.642 (0.219–1.857)	337[d] (29.6–2647.7)	22,000–400,000 200,000 41,657	31[e] (0.5–395.5)	6–21

[a,b] The estimates of root production from Alongi (2014) and Bouillon et al. (2008) are based on mangrove area of 138, 000 km^2 and 160, 000 km^2, respectively.
[c] These rates represent estimates of root decomposition rates in mangroves via two methods, i.e. 0.152% day^{-1} (the median value of individual rates) and 0.135% day^{-1} (the area-averaged rate).
[d] Unit-area dead root production = Unit-area root production × Root turnover rate.
[e] These values are estimated as the combined geometrical mean/median value of root decay rates, unit-area dead root production and global area. Global C decayed = Unit-area dead root production × Root decay rate × 365 × Global area × 106 / 1012, 365 is used to transform decay rate from % day^{-1} to % yr^{-1}.
References: 1. Alongi (2014); 2. Mcleod et al. (2011); 3. Spalding et al. (2010); 4. Bouillon et al. (2008); 5. Castañeda-Moya et al. (2011); 6. Ouyang and Lee (2014); 7. Chmura (2013); 8. Gonzalez-Alcaraz et al. (2012); 9. Cai (2011); 10. Sousa et al. (2010a); 11. Sousa et al. (2010b); 12. Palomo and Niell (2009); 13. Liao et al. (2007); 14. Edwards and Mills (2005);15. Blum and Christian (2004); 16. Blum (1993); 17. Hackney and Armando (1986); 18. Howes et al. (1985); 19. Smith et al. (1979); 20. Duarte et al. (2010); 21. da Cunha Lana et al. (1991).

4. Discussion

4.1. Drivers of root decomposition

Biotic drivers strongly regulate root decay rates. Root decay rates vary among different mangrove forest types, including fringe, overwash, riverine, basin, dwarf and hammock mangroves (Lugo and Snedaker, 1974). Root decay is slowest for overwash mangroves, accumulate substrate slowly and only through autochthonous input (Middleton and McKee, 2001). The low substrate supply, and thereby nutrient limitation, may be responsible for the lower root decay rates in these isolated mangroves. Among the other mangrove types, riverine mangroves demonstrate the highest rates of root decomposition. These mangroves dominate along river and creek drainages and receive regular freshwater dilution of tidal water and thus alleviated salinity stress which promotes root decomposition. In addition, sediments of riverine mangroves can have higher nutrients (e.g. phosphorus) than scrub mangroves (Castañeda-Moya et al., 2011). The higher nutrient supply may also lead to faster root decomposition rates in riverine mangroves. Mangrove roots on average decay slightly faster than saltmarsh roots (0.152 vs. 0.119% day^{-1}, Table 3), except for overwash mangroves, for which the lower rate is probably due to limited substrate supply.

Species identity is another biotic driver of root decomposition rates. Species differences in root decay rates may be attributed to differences in biochemistry and physiology. Overall, our results for saltmarsh illustrate that root decay rates of *Spartina maritima* are higher than the rates of *Juncus* spp. *Spartina maritima* aerates the sediment through their roots (Hackney and de La Cruz, 1980), resulting in faster root decay, compared with roots of *Juncus* spp. that lack oxygen transport from above-ground parts. For mangroves, root decay rates of *Avicennia marina* are high compared to other species. The presence of pneumatophores increases oxygenation of the sediment and the general permeability of their root system (Leopold et al., 2013). Although *Avicennia germinans* also has pneumatophores which allow oxygen transport to roots, this species in our collated studies generally occurred in water-logged conditions, limiting oxygen transport and root decay.

Apart from oxygen transport, different species can be distinguished in the stoichiometry of root litter such as lignin contents and C:N ratios, resulting in the difference in root decay rates (Blum and Christian, 2004; Tam et al., 1998). The metabolic activity of the microbial community was found to rise directly, responding to increased initial litter N content, while the inhibition of decomposition by lignin is attributable to its chemical structure which makes it resistant to microbial attack (Hemminga and Buth, 1991). *Phragmites australis* roots may have relatively low C:N and lignin:N ratios compared to *Spartina* species (Liao et al., 2008), facilitating root decomposition. Likewise, roots of *Avicennia marina* are described as having lower C:N ratios than both *Ceriops tagal* and *Bruguiera gymnorhiza* (Huxham et al., 2010).

Root decay rates generally vary with climatic and geographic conditions. Our results show that root decay rates generally increase with latitude for mangroves, except the higher decay rates at 0–10° than 10–20° latitudinal intervals, and decrease marginally with latitude for saltmarsh. Decay rates increase with temperature for both mangroves and saltmarsh. Although there is a strong negative correlation between latitude and temperature, latitude is not exclusively a proxy for temperature, since it also mirrors other parameters such as sediment C accumulation rate, which was found to increase with latitude from the equator to mid-latitude and then decrease with latitude from mid-latitude to the poles in saltmarsh (Ouyang and Lee, 2014). As sediment C provides substrate for root decomposition, this may have contrasting effects on root decomposition compared with temperature, which increases consistently with latitude.

Specifically, latitude relates to temperature and length of the growth season. Firstly, high temperatures may speed up sediment microbial decomposer activities and primary production. Net primary production of mangroves has been found to decrease with increasing latitudes, when measured by the modified light attenuation method (Alongi, 2009). This pattern has also been detected in North American saltmarsh

Table 4
Local C burial attributed to root production of mangroves and saltmarsh.

Ecosystem	Global root decay rate (% day^{-1})	Unit-area dead root production (g C m^{-2} yr^{-1})	Local root C burial[a] (g C m^{-2} yr^{-1})	Reported local C accumulation rate[b] (g C m^{-2} yr^{-1})	Local root C burial/Reported local C accumulation rate	Reference
Mangroves	0.152	114–121	51–54	211	24.1–25.5%	1
	0.135		58–61		27.4–29.1%	
Saltmarsh	0.119	337	191	244.7	77.9%	2

[a] Local root C burial = Unit-area dead root production × (1 − 365 × global root decay rate).
[b] 1. Alongi (2014); 2. Ouyang and Lee (2014). The references provided reported local C accumulation rates.

(Kirwan et al., 2009). Likewise, decomposition of root matter is correlated with temperature. Benner et al. (1986) found that the mineralisation rates of *Spartina alterniflora* lignocellulose in sediments were positively correlated with temperature. Higher temperature fuels microbial heterotrophy by increasing production of exudates such as ethanol from living roots (Fogel, 1985). In addition, root decomposition by microbial communities depends on the availability of energy supply. Sediment C peaks at mid-latitude and is generally lower in low or high latitudinal zones in saltmarsh (Ouyang and Lee, 2014). This variation of sediment C accumulation with latitude could partly counteract the temperature effect on root decay rates, and explain the low partial regression coefficient of latitude in the saltmarsh analysis. Secondly, sediment salinity may also demonstrate a latitudinal trend owing to differences in the trade-off between rainfall and evaporation (Ouyang and Lee, 2014), and offset the temperature effect on root decay rates in mangroves. These factors, combined, may underpin the increase in mangrove root decay rates with latitude. Nevertheless, there are compounding factors in root decomposition rates that could not be attributed to latitude, including seasonality (e.g. monsoon seasons), and wet and dry tropics.

Precipitation may regulate root decay processes by influencing oxygen supply to, and thus the redox potential of, sediments, as well as their salinity. Precipitation is more variable in the saltmarsh studies analysed here, the range of averages among individual study locations fluctuating between 2 and 7 mm day^{-1}, compared to the variation between 3 and 4 mm day^{-1} in mangrove studies (except one study, from Micronesia (Ono et al., 2015), which showed high precipitation, but as a significant outlier was excluded from our analysis). An increase in precipitation may result in sustained water-logging conditions, which may hinder root decay. The effect of precipitation on mangrove root decay cannot be fully resolved here because of the small differences in precipitation among mangrove locations available for analysis. No studies were available, for example, from arid zone mangroves.

4.2. Local effects

Porewater salinity indirectly affects mangrove root decay through regulating microbial degradation of root/rhizome material, providing an important link between sediment biogeochemistry and greenhouse gas production (Chen et al., 2010; Maher et al., 2015). The weak, but significant, relationship we detected between decomposition rates and porewater salinity is mirrored in the small proportion of variation in soil respiration attributable to porewater salinity in mangroves (Lovelock et al., 2014). The negative direction of the relationship between decay rates and porewater salinity may be due to microbial activities being constrained under high salinities.

4.3. Implications for global C budget in mangroves and saltmarsh

Based on the geometrical mean (or area averaged) root decomposition rate, our estimates of root C mineralisation in mangroves account for 1.6% (1.3%) of the total global mangrove gross primary production (635 Tg C yr^{-1}) estimated by Alongi (2014). The mineralised root C can emerge in porewater as inorganic (DIC) and organic C (DOC), and is potentially exported to other nearshore environments. Some C may be released as CO_2 or CH_4 gases, the balance of which is strongly influenced by salinity and the availability of sulphate. Further, as estimated by Alongi (2014), belowground sediment C gas released is 38 Tg C yr^{-1} while DIC (including CO_2 and CH_4) and DOC export rates are 86 and 15 Tg C yr^{-1} in mangroves. Therefore, released C gases, DIC and DOC account for 27.3%, 61.9%, and 10.8% of mangrove belowground C mineralisation. The C sinks (DIC + DOC) are significantly higher (10×) than C emissions associated with mangrove root decomposition. The remaining root C in mangroves (8 (9) Tg C yr^{-1}, range 0.7–13.3 (7.9–9.3) Tg C yr^{-1}) and saltmarsh (40 Tg C yr^{-1}, range 0.2–79 Tg C yr^{-1}) was estimated as the difference between total dead root C production and decayed root C. This part contributes to sediment C burial (see Fig. 5).

Our results also suggest higher root C burial relative to sediment C accumulation rate in saltmarsh (ratio: 0.78) than mangroves (ratio: 0.24 (0.27)–0.25 (0.29), Table 4). The discrepancy may lie in the fact that saltmarsh plants are perennial while mangroves are mainly trees and it takes a long time for their roots to turnover. However, the estimates may deviate from the actual values. Sediment C stocks in mangroves and saltmarsh may be lost through anthropogenic (e.g. reclamation and aquaculture development) or natural processes (e.g. shoreline erosion) (Donato et al., 2011; Ouyang and Guo, 2016; Theuerkauf et al., 2015). The different components of sediment C stock, including root, leaf litter and allochthonous sources, can be released through disturbance during sediment erosion. Further, in addition to in situ root and litter production, there are a range of other factors regulating sediment accretion and thus C accumulation, including autocompaction (Allen, 2000). Hence, the reported sediment C accumulation rate is not expected to be the simple aggregation of root burial rate and the burial rate of other sources. The C storage capacity of mangroves and saltmarsh may be mitigated by anthropogenic and natural forces. Theuerkauf et al. (2015) explained how saltmarsh in North Carolina could shift from C sinks to C sources if shoreline erosion expands uncontrolled; organic C may be removed or transported by water or wind as peat erosion, which accounts for considerable organic C loss from organic soils (Verheijen et al., 2009).

The mangrove root C burial rate reported herein, i.e. 51–54 (58–61) g C m^{-2} yr^{-1} (Table 4), is higher than that (36.2 g C m^{-2} yr^{-1}) estimated by Alongi (2014). On the one hand, the difference may lie in the fact that only fine root burial was considered by Alongi (2014). Fine roots were estimated to contribute 24%, 45% and 42% of total root biomass for *Rhizophora mucronata*, *Sonneratia alba* and *Avicennia marina*, respectively (Tamooh et al., 2008), and contribute only 2.2% of total root biomass of *Ceriops tagal* (Komiyama et al., 2000). McKee et al. (2007) suggested that both fine and coarse root accumulation are important; the decomposition rate of coarse roots is less than one half that of fine roots. Nevertheless, root turnover rates also contribute to the difference in fine and coarse root C burial rate. The turnover rate of fine roots averaged 0.33 yr^{-1} (0.23–0.6 yr^{-1}), which was suggested to be more than doubled that of coarse roots (mean: 0.09 yr^{-1}, range: 0.04–0.15 yr^{-1}, Castañeda-Moya et al., 2011). Both the relatively low biomass and high decomposition rate of fine roots hamper fine root burial, overriding the facilitative effect on burial of the rapid turnover rate of fine roots. This can explain why the estimated mangrove root C burial rate is much higher than the reported fine root C burial rate. It is possible, nonetheless, that the discrepancy may imply that some other C sink pathways have been overestimated in the global mangrove C budget. For instance, the DIC export (86 Tg C yr^{-1}), calculated by the difference between C sources and sinks by (Alongi, 2014), approximately doubled in comparison with a recent estimate (43.2 Tg C yr^{-1}) (Sippo et al., 2016).

Compared with leaf litter C burial (72.5 g C m^{-2} yr^{-1} based on 10 Tg yr^{-1}) in Alongi (2014), mangrove root C burial is the same order of magnitude. However, different processes contribute differently to the variation from C production to C burial for leaf litter and roots. On the one hand, global syntheses of mangrove primary production demonstrate C production of roots is generally higher than that of litterfall (Alongi, 2014; Bouillon et al., 2008), irrespective of allochthonous OM import which can contribute to sediment C accumulation. Similarly, below-ground production of saltmarsh tends to be much higher than aboveground production (Chmura et al., 2011). Further, mangrove leaf litter is, to varying extents, exported by tides or shredded by crabs (Lee, 1995; Lee et al., 2014) and other detritivores while there is no direct evidence that crabs ate mangrove roots (Van and Attiwill, 1984), accounting for the loss of C production for leaf litter. Field investigations provide evidence for this inference; mangrove peat was found to consist primarily of root fragments and fine roots, and only occasionally, leaf

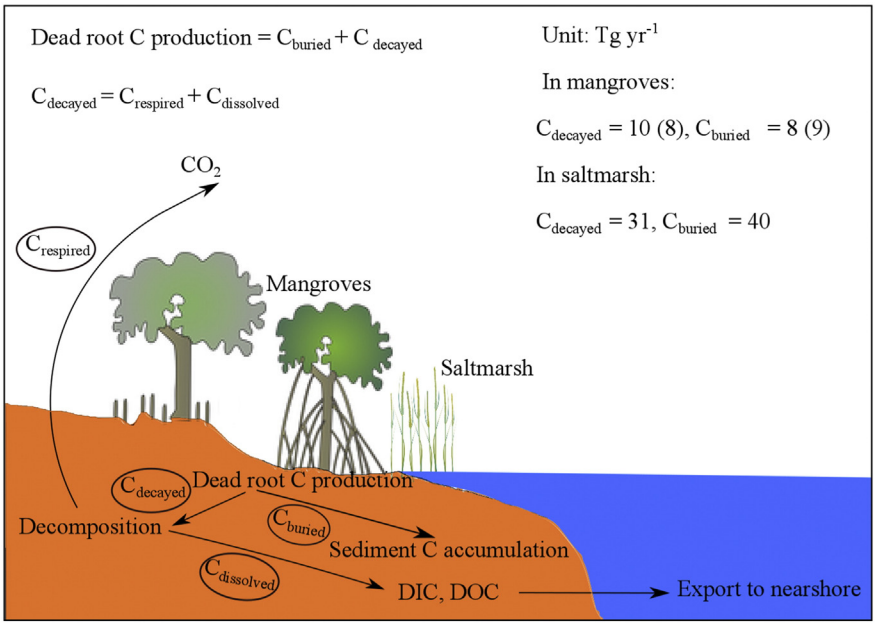

Fig. 5. Global fate of root C in mangroves and saltmarsh. Data outside and inside brackets were calculated from the median and area-averaged root decomposition rates in mangroves, respectively. Saltmarsh can occur adjacent to or mixed with mangroves but only saltmarsh exists in temperate zones. This figure does not represent all settings of mangroves and saltmarsh.

litter (McKee and Faulkner, 2000). In saltmarsh, above-ground litter is also more readily decomposable than roots (Pozo and Colino, 1992; Van and Attiwill, 1983), owing to the difference in chemical composition (Buth, 1987; Hemminga et al., 1988) and oxygen availability. In addition, below-ground environmental conditions are harsher for root decomposition; the more saline and anoxic conditions in sediment generally hamper microbial activities (Van and Attiwill, 1983). On the other hand, mangrove root turnover rate is rather low (0.222 yr^{-1}, Table 3), and results in the low dead root production, which is more than discounted.

Nevertheless, only the contribution of dead root production to sediment C is considered in our study, while live roots may exudate organic matter (Luglia et al., 2013) and also contribute to sediment C accumulation. Since this study focuses on the decomposition of dead roots, the contribution of live roots to sediment C burial could not be accounted for. Nonetheless, the major contribution of root production (dead + live roots) to sediment C burial is corroborated by stable C isotope analysis in mangroves, showing that roots predominate in below-ground C accumulation (Saintilan et al., 2013). Saltmarsh below-ground production is closely associated with total C in sediments (Palomo and Niell, 2009), aligning with the dominant contribution of roots to sediment C sequestration. Our results are the first to evaluate the contribution of mangrove and saltmarsh underground primary production to sediment C burial.

4.4. Uncertainties of root decay rates and decayed root C production

Errors and differences in collection and treatment process of root litter samples would be partly responsible for the variation of reported root decay rates. Air-drying before initiating the litter experiment alters the microbial population of the root litter, thereby indirectly changing root decay rates. Nonetheless, air-drying seems to be better than drying at much higher temperatures (e.g. >100 °C), which results in loss of the volatile components (Hackney and de La Cruz, 1980). Moreover, with respect to the coring method, it is impossible to remove a sediment core without disrupting the sediment microbial community. It also takes considerable time for sediment biogeochemical processes to return to normal rates.

Root decay rates of mangrove and saltmarsh species depend on the type of root/rhizome material selected for measurement, e.g. dead and live roots, or fine and coarse roots. However, there are methodological issues in distinguishing dead from live roots in mixed root samples in earlier studies (e.g. Hackney and de La Cruz, 1980). Likewise, simple selection of fine roots from various sizes of root samples may also generate uncertainties. Dead plant tissues generally are more resistant to decomposition than live plant materials (Hodson et al., 1984). Any uncertainty about the proportion of dead to live root litter introduces incidental variation in decay rates.

Several factors contributed to the large variability of our estimates of root decomposition rates and decayed root C. Firstly, because there is a wide range of reported root decay rates, the 95th percentile root decay rates are an order of magnitude higher than the 5th percentile decay rates for both mangroves and saltmarsh. Secondly, estimates of the global area of mangroves and saltmarsh are highly variable, especially for the latter (the high-end of reported area is almost 20× of the low-end). The precision of our estimate is expected to be improved by studies on global area of current coastal wetlands using GIS technology, e.g. Giri et al. (2011) and Spalding et al. (2010). Thirdly, our estimated root decay rates among latitudinal ranges could not account for the differences from specific countries, such as mangroves in Indonesia, where no root decomposition data are available. The use of root decomposition rates at available sites to represent the missing data from the same latitudinal ranges may ignore the differences in other aspects, such as biogeography. In addition, the specific ecotones in the global mangrove map cannot be apportioned into different mangrove types, one of the important factors in estimating mangrove root decomposition rates. We were thus not able to use the regression model for mangroves to validate the root decomposition rates of propagated data (e.g. for Indonesia) from available data among the same latitudinal ranges (e.g. Kenya). Last but not least, no studies reported root production, C burial rate and root decomposition rates simultaneously in our collated literature. Future studies would provide a better perspective if these processes are measured concurrently at the same locations.

Anthropogenic pollution, e.g. aquaculture and domestic wastewater (Ouyang et al., 2015), and pollution-induced N deposition from the atmosphere by human activities (Howarth, 2008) are significant N sources in coastal wetlands, and may have a significant effect on root

decay. At this stage, however, a lack of data prevents an evaluation of the fertiliser effect on decay rates. Nitrogen is regarded as a widespread limiting factor for decay of litter and plant roots, especially fine roots (Berg and McClaugherty, 2003). Nitrogen enrichment may result in higher initial root decay rates by increasing the nutrient content of roots.

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Appendix A. Data sources

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.earscirev.2017.01.004.

References

Allen, J.R.L., 2000. Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. Quat. Sci. Rev. 19, 1155–1231.
Alongi, D.M., 2009. The Energetics of Mangrove Forests. Springer, New York, USA.
Alongi, D.M., 2014. Carbon cycling and storage in mangrove forests. Annu. Rev. Mar. Sci. 6, 195–219.
Atwood, T.B., Connolly, R.M., Ritchie, E.G., Lovelock, C.E., Heithaus, M.R., Hays, G.C., Fourqurean, J.W., Macreadie, P.I., 2015. Predators help protect carbon stocks in blue carbon ecosystems. Nat. Clim. Chang. 5, 1038–1045.
Benner, R., Maccubbin, A., Hodson, R.E., 1986. Temporal relationship between the deposition and microbial degradation of lignocellulosic detritus in a Georgia salt marsh and the Okefenokee Swamp. Microb. Ecol. 12, 291–298.
Berg, B., McClaugherty, C., 2003. Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. Springer-Verlag, Berlin, Germany.
Blum, L.K., 1993. *Spartina alterniflora* root dynamics in a Virginia marsh. Mar. Ecol. Prog. Ser. 102, 697178.
Blum, L.K., Christian, R.R., 2004. Belowground production and decomposition along a tidal gradient in a Virginia salt marsh. The Ecogeomorphology of Tidal Marshes, pp. 47–73.
Bouillon, S., Borges, A.V., Castañeda-Moya, E., Diele, K., Dittmar, T., Duke, N.C., Kristensen, E., Lee, S.Y., Marchand, C., Middelburg, J.J., Rivera-Monroy, V.H., Smith III, T.J., Twilley, R.R., 2008. Mangrove production and carbon sinks: a revision of global budget estimates. Glob. Biogeochem. Cycles 22, GB2013.
Breithaupt, J.L., Smoak, J.M., Smith, T.J., Sanders, C.J., Hoare, A., 2012. Organic carbon burial rates in mangrove sediments: strengthening the global budget. Glob. Biogeochem. Cycles 26, GB3011. http://dx.doi.org/10.1029/2012GB004375.
Buth, G.J.C., 1987. Decomposition of roots of three plant communities in a Dutch salt marsh. Aquat. Bot. 29, 123–138.
Cai, W.J., 2011. Estuarine and coastal ocean carbon paradox: CO_2 sinks or sites of terrestrial carbon incineration? Annu. Rev. Mar. Sci. 3, 123–145.
Castañeda-Moya, E., Twilley, R.R., Rivera-Monroy, V.H., Marx, B.D., Coronado-Molina, C., Ewe, S.M., 2011. Patterns of root dynamics in mangrove forests along environmental gradients in the Florida Coastal Everglades, USA. Ecosystems 14, 1178–1195.
Chen, G.C., Tam, N.F.Y., Ye, Y., 2010. Summer fluxes of atmospheric greenhouse gases N_2O, CH_4 and CO_2 from mangrove soil in South China. Sci. Total Environ. 408:2761–2767. http://dx.doi.org/10.1016/j.scitotenv.2010.03.007.
Chmura, G.L., 2013. What do we need to assess the sustainability of the tidal salt marsh carbon sink? Ocean Coast. Manag. 83, 25–31.
Chmura, G.L., Kellman, L., Guntenspergen, G.R., 2011. The greenhouse gas flux and potential global warming feedbacks of a northern macrotidal and microtidal salt marsh. Environ. Res. Lett. 6, 1–6.
da Cunha Lana, P., Guiss, C., Disaró, S.T., 1991. Seasonal variation of biomass and production dynamics for above-and belowground components of a *Spartina alterniflora* marsh in the euhaline sector of Paranaguá Bay (SE Brazil). Estuar. Coast. Shelf Sci. 32, 231–241.
Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.
Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kumianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. Nat. Geosci. 4, 293–297.
Duarte, B., Caetano, M., Almeida, P.R., Vale, C., Caçador, I., 2010. Accumulation and biological cycling of heavy metal in four salt marsh species, from Tagus estuary (Portugal). Environ. Pollut. 158, 1661–1668.
Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I., Marbà, N., 2013. The role of coastal plant communities for climate change mitigation and adaptation. Nat. Clim. Chang. 3, 961–968.
Duke, N., Kathiresan, K., Salmo III, S.G., Fernando, E.S., Peras, J.R., Sukardjo, S., Miyagi, T., 2010. Ceriops tagal. The IUCN Red List of Threatened Species 2010: e.T178822A7617531 (http://dx.doi.org/10.2305/IUCN.UK.2010-2.RLTS.T178822A7617531.en).
Edwards, K.R., Mills, K.P., 2005. Aboveground and belowground productivity of *Spartina alterniflora* (Smooth Cordgrass) in natural and created Louisiana salt marshes. Estuaries 28, 252–265.
Ellison, A., Farnsworth, E., Moore, G., 2010. Laguncularia racemosa. The IUCN Red List of Threatened Species 2010: e.T178798A7609219 (http://dx.doi.org/10.2305/IUCN.UK.2010-2.RLTS.T178798A7609219.en).
Fogel, R., 1985. Roots as primary producers in below-ground ecosystems. Special Publications Series of the British Ecological Society.
Giri, C., Ochieng, E., Tieszen, L.L., Zhu, Z., Singh, A., Loveland, T., Masek, J., Duke, N., 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. Glob. Ecol. Biogeogr. 20, 154–159.
Global Invasive Species Database, 2016a. Species profile: *Spartina anglica*. (Downloaded from). http://www.iucngisd.org/gisd/species.php?sc=76.
Global Invasive Species Database, 2016b. Species profile: *Spartina alterniflora*. (Downloaded from). http://www.iucngisd.org/gisd/species.php?sc=792.
Gonzalez-Alcaraz, M.N., Egea, C., Jimenez-Carceles, F.J., Parraga, I., Maria-Cervantes, A., Delgado, M.J., Alvarez-Rogel, J., 2012. Storage of organic carbon, nitrogen and phosphorus in the soil-plant system of *Phragmites australis* stands from a eutrophicated Mediterranean salt marsh. Geoderma 185:61–72. http://dx.doi.org/10.1016/j.geoderma.2012.03.019.
Grömping, U., 2006. Relative importance for linear regression in R: the package relaimpo. J. Stat. Softw. 17, 1–27.
Hackney, C.T., Armando, A., 1986. Belowground productivity of roots and rhizomes in a giant cordgrass marsh. Estuaries 9, 112–116.
Hackney, C.T., de La Cruz, A.A., 1980. In situ decomposition of roots and rhizomes of two tidal marsh plants. Ecology 226–231.
Hemminga, M., Buth, G., 1991. Decomposition in salt marsh ecosystems of the SW Netherlands: the effects of biotic and abiotic factors. Vegetatio 92, 73–83.
Hemminga, M.A., Kok, C.J., Munck, W.d., 1988. Decomposition of *Spartina anglica* roots and rhizomes in a salt marsh of the Westerschelde Estuary. Mar. Ecol. Prog. Ser. 48, 175–184.
Hodson, R.E., Christian, R.R., Maccubbin, A.E., 1984. Lignocellulose and lignin in the salt marsh grass *Spartina alterniflora*: initial concentrations and short-term, post-depositional changes in detrital matter. Mar. Biol. 81, 1–7.
Howarth, R.W., 2008. Coastal nitrogen pollution: a review of sources and trends globally and regionally. Harmful Algae 8, 14–20.
Howes, B.L., Dacey, J.W., Teal, J.M., 1985. Annual carbon mineralization and belowground production of *Spartina alterniflora* in a New England salt marsh. Ecology 595–605.
Huxham, M., Langat, J., Tamooh, F., Kennedy, H., Mencuccini, M., Skov, M.W., Kairo, J., 2010. Decomposition of mangrove roots: effects of location, nutrients, species identity and mix in a Kenyan forest. Estuar. Coast. Shelf Sci. 88, 135–142.
Kahle, D., Wickham, H., 2013. ggmap: spatial visualization with ggplot2. R J. 5, 144–161.
Kirwan, M.L., Guntenspergen, G.R., Morris, J.T., 2009. Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. Glob. Chang. Biol. 15, 1982–1989.
Komiyama, A., Havanond, S., Srisawatt, W., Mochida, Y., Fujimoto, K., Ohnishi, T., Ishihara, S., Miyagi, T., 2000. Top/root biomass ratio of a secondary mangrove (*Ceriops tagal* (Perr.) CB Rob.) forest. For. Ecol. Manag. 139, 127–134.
Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: a review. Aquat. Bot. 89, 201–219.
Krumins, V., Gehlen, M., Arndt, S., Van Cappellen, P., Regnier, P., 2013. Dissolved inorganic carbon and alkalinity fluxes from coastal marine sediments: model estimates for different shelf environments and sensitivity to global change. Biogeosciences 10, 371–398.
Lee, S.Y., 1995. Mangrove outwelling: a review. Hydrobiologia 295, 203–212.
Lee, S.Y., Primavera, J.H., Dahdouh-Guebas, F., McKee, K., Bosire, J.O., Cannicci, S., Diele, K., Fromard, F., Koedam, N., Marchand, C., Mendelssohn, I., Mukherjee, N., Record, S., 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. Glob. Ecol. Biogeogr. 23:726–743. http://dx.doi.org/10.1111/geb.12155.
Leopold, A., Marchand, C., Deborde, J., Chaduteau, C., Allenbach, M., 2013. Influence of mangrove zonation on CO_2 fluxes at the sediment–air interface (New Caledonia). Geoderma 202, 62–70.
Liao, C., Luo, Y., Jiang, L., Zhou, X., Wu, X., Fang, C., Chen, J., Li, B., 2007. Invasion of *Spartina alterniflora* enhanced ecosystem carbon and nitrogen stocks in the Yangtze Estuary, China. Ecosystems 10, 1351–1361.
Liao, C.Z., Luo, Y.Q., Fang, C.M., Chen, J.K., Li, B., 2008. Litter pool sizes, decomposition, and nitrogen dynamics in *Spartina alterniflora*-invaded and native coastal marshlands of the Yangtze Estuary. Oecologia 156, 589–600.
Lovelock, C.E., Feller, I.C., Reef, R., Ruess, R.W., 2014. Variable effects of nutrient enrichment on soil respiration in mangrove forests. Plant Soil 379:135–148. http://dx.doi.org/10.1007/s11104-014-2036-6.
Lovelock, C.E., Cahoon, D.R., Friess, D.A., Guntenspergen, G.R., Krauss, K.W., Reef, R., Rogers, K., Saunders, M.L., Sidik, F., Swales, A., 2015. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. Nature 526:559–563. http://dx.doi.org/10.1038/nature15538.
Luglia, M., Criquet, S., Sarrazin, M., Ziarelli, F., Guiral, D., 2013. Functional patterns of microbial communities of rhizospheric soils across the development stages of a young mangrove in French Guiana. Microb. Ecol. 67, 302–317.
Lugo, A.E., Snedaker, S.C., 1974. The ecology of mangroves. Annu. Rev. Ecol. Syst. 39–64.
Maher, D.T., Cowley, K., Santos, I.R., Macklin, P., Eyre, B.D., 2015. Methane and carbon dioxide dynamics in a subtropical estuary over a diel cycle: insights from automated in situ radioactive and stable isotope measurements. Mar. Chem. 168, 69–79.
McKee, K.L., Faulkner, P.L., 2000. Mangrove peat analysis and reconstruction of vegetation history at the Pelican Cays, Belize. Atoll Res. Bull. 468, 46–58.

McKee, K.L., Cahoon, D.R., Feller, I.C., 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Glob. Ecol. Biogeogr. 16, 545–556.
Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Front. Ecol. Environ. 9, 552–560.
Middleton, B.A., McKee, K.L., 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. J. Ecol. 89:818–828. http://dx.doi.org/10.1046/j.0022-0477.2001.00602.x.
Ono, K., Hiradate, S., Morita, S., Hiraide, M., Hirata, Y., Fujimoto, K., Tabuchi, R., Lihpai, S., 2015. Assessing the carbon compositions and sources of mangrove peat in a tropical mangrove forest on Pohnpei Island, Federated States of Micronesia. Geoderma 245, 11–20.
Ouyang, X., Guo, F., 2016. Paradigms of mangroves in treatment of anthropogenic wastewater pollution. Sci. Total Environ. 544:971–979. http://dx.doi.org/10.1016/j.scitotenv.2015.12.013.
Ouyang, X., Lee, S.Y., 2014. Updated estimates of carbon accumulation rates in coastal marsh sediments. Biogeosciences 11:5057–5071. http://dx.doi.org/10.5194/bg-11-5057-2014.
Ouyang, X., Guo, F., Shan, D., Yu, H., Wang, J., 2015. Development of the integrated fuzzy analytical hierarchy process with multidimensional scaling in selection of natural wastewater treatment alternatives. Ecol. Eng. 74:438–447. http://dx.doi.org/10.1016/j.ecoleng.2014.11.006.
Ovalle, A.R.C., Rezende, C.E., Lacerda, L.D., Silva, C.A.R., 1990. Factors affecting the hydrochemistry of a mangrove tidal creek, Sepetiba Bay, Brazil. Estuar. Coast. Shelf Sci. 31:639–650. http://dx.doi.org/10.1016/0272-7714(90)90017-l.
Palomo, L., Niell, F.X., 2009. Primary production and nutrient budgets of *Sarcocornia perennis ssp alpini* (Lag.) Castroviejo in the salt marsh of the Palmones River estuary (Southern Spain). Aquat. Bot. 91, 130–136.
Penha-Lopes, G., Kristensen, E., Flindt, M., Mangion, P., Bouillon, S., Paula, J., 2010. The role of biogenic structures on the biogeochemical functioning of mangrove constructed wetlands sediments–a mesocosm approach. Mar. Pollut. Bull. 60, 560–572.
Pozo, J., Colino, R., 1992. Decomposition processes of *Spartina maritima* in a salt marsh of the Basque County. Hydrobiologia 231, 165–175.
Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.
R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
Saintilan, N., Rogers, K., Mazumder, D., Woodroffe, C., 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuar. Coast. Shelf Sci. 128, 84–92.
Sippo, J.Z., Maher, D.T., Tait, D.R., Holloway, C., Santos, I.R., 2016. Are mangroves drivers or buffers of coastal acidification? Insights from alkalinity and dissolved inorganic carbon export estimates across a latitudinal transect. Glob. Biogeochem. Cycles 30, 753–766.
Smith, K.K., Good, R.E., Good, N.F., 1979. Production dynamics for above and belowground components of a New Jersey *Spartina alterniflora* tidal marsh. Estuar. Coast. Mar. Sci. 9, 189–201.
Sousa, A.I., Lillebo, A.I., Pardal, M.A., Cacador, I., 2010a. The influence of *Spartina maritima* on carbon retention capacity in salt marshes from warm-temperate estuaries. Mar. Pollut. Bull. 61, 215–223.
Sousa, A.I., Lillebo, A.I., Pardal, M.A., Cacador, I., 2010b. Productivity and nutrient cycling in salt marshes: contribution to ecosystem health. Estuar. Coast. Shelf Sci. 87, 640–646.
Spalding, M., Kainuma, M., Collins, L., 2010. World Atlas of Mangroves: Earthscan, London, UK. pp. 47–52.
Tam, N.F.Y., Wong, Y.S., Lan, C.Y., Wang, L.N., 1998. Litter production and decomposition in a subtropical mangrove swamp receiving wastewater. J. Exp. Mar. Biol. Ecol. 226, 1–18.
Tamooh, F., Huxham, M., Karachi, M., Mencuccini, M., Kairo, J., Kirui, B., 2008. Belowground root yield and distribution in natural and replanted mangrove forests at Gazi bay, Kenya. For. Ecol. Manag. 256, 1290–1297.
Theuerkauf, E.J., Stephens, J.D., Ridge, J.T., Fodrie, F.J., Rodriguez, A.B., 2015. Carbon export from fringing saltmarsh shoreline erosion overwhelms carbon storage across a critical width threshold. Estuar. Coast. Shelf Sci. 164:367–378. http://dx.doi.org/10.1016/j.ecss.2015.08.001.
Van der valk, A.G., Attiwill, P.M., 1983. Above- and below-ground litter decomposition in an Australian salt marsh. Aust. J. Ecol. 8, 441–447.
Van der valk, A.G., Attiwill, P.M., 1984. Decomposition of leaf and root litter of *Avicennia marina* at Westernport Bay, Victoria, Australia. Aquat. Bot. 18, 205–221.
Verheijen, F.G.A., Jones, R.J.A., Rickson, R.J., Smith, C.J., 2009. Tolerable versus actual soil erosion rates in Europe. Earth Sci. Rev. 94:23–38. http://dx.doi.org/10.1016/j.earscirev.2009.02.003.
Virginia Institute of Marine Science, n.d. Field guide to Virginia salt and brackish marsh plants. Virginia, USA, http://ccrm.vims.edu/.
Wang, Z.A., Kroeger, K.D., Ganju, N.K., Gonneea, M.E., Chu, S.N., 2016. Intertidal salt marshes as an important source of inorganic carbon to the coastal ocean. Limnol. Oceanogr. 61, 1916–1931.
Waysel, Y., 1972. Biology of Halophytes. Academic Press Inc., New York, USA.
Wickham, H., 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.