Carbon Balance in Salt Marsh and Mangrove Ecosystems: A Global Synthesis

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Abstract: Mangroves and salt marshes are among the most productive ecosystems in the global coastal ocean. Mangroves store more carbon (739 Mg C\textsubscript{ORG} ha\textsuperscript{-1}) than salt marshes (334 Mg C\textsubscript{ORG} ha\textsuperscript{-1}), but the latter sequester proportionally more (24%) net primary production (NPP) than mangroves (12%). Mangroves exhibit greater rates of gross primary production (GPP), aboveground net primary production (AGNPP) and plant respiration (R\textsubscript{C}), with higher P\textsubscript{GPP}/R\textsubscript{C} ratios, but salt marshes exhibit greater rates of below-ground NPP (BGNPP). Mangroves have greater rates of subsurface DIC production and, unlike salt marshes, exhibit active microbial decomposition to a soil depth of 1 m. Salt marshes release more CH\textsubscript{4} from soil and creek waters and export more dissolved CH\textsubscript{4}, but mangroves release more CO\textsubscript{2} from tidal waters and export greater amounts of particulate organic carbon (POC), dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC), to adjacent waters. Both ecosystems contribute only a small proportion of GPP, R\textsubscript{E} (ecosystem respiration) and NEP (net ecosystem production) to the global coastal ocean due to their small global area, but contribute 72% of air–sea CO\textsubscript{2} exchange of the world’s wetlands and estuaries and contribute 34% of DIC export and 17% of DOC + POC export to the world’s coastal ocean. Thus, both wetland ecosystems contribute disproportionately to carbon flow of the global coastal ocean.

Keywords: biogeochemistry; carbon; carbon balance; ecosystem; ecosystem processes; mangrove; salt marsh; wetland

1. Introduction

Salt marshes and mangrove forests are intertidal ecosystems comparable \textit{sensu lato} in that they both occupy the coastal land–sea interface; the former mostly in sheltered temperate and high-latitude coastlines, the latter along quiescent subtropical and tropical shores [1]. Both ecosystems are characterized by a rich mixture of terrestrial and marine organisms, forming unique estuarine food webs, and play an important role in linking food webs, inorganic and organic materials, and biogeochemical cycles between the coast and adjacent coastal zone. Structurally simple compared to other ecosystems, salt marshes and mangroves harbor few plant species, but they are functionally complex, having ecosystem attributes analogous to those of other grasslands and forests, respectively, but also functioning in many ways like other estuarine and coastal ecosystems [1–3].

Drivers such as salinity, geomorphology, and tidal regime impose structural and functional constraints and foster adaptations and physiological mechanisms to help these wetland plants subsist in waterlogged saline soils. Tides and waves (to a much lesser extent) are an auxiliary energy subsidy that allows both ecosystems to store and transport newly fixed carbon, sediments, food and nutrients, and to do the work of exporting wastes, heat, gases and solutes to the atmosphere and adjacent coastal zone. This subsidized energy is used indirectly by organisms to shunt more of their own energy into growth and reproduction, making tidal power one of the main drivers regulating these intertidal systems [1]. Tidal circulation is complex, as marsh and forest topography and morphology and the
tidal prism regulate the degree of mixing and trapping of water and suspended matter within adjacent tidal waters and the wetland communities [1].

Food webs within these wetlands are composed of mixtures of terrestrial, estuarine and marine fauna and flora that help to actively cycle nutrients and carbon. Plankton communities in adjacent creeks and waterways are productive and abundant, and well-adapted to complex hydrology and water chemistry. These opaque tidal waters host organisms ranging in size from viruses to reptiles, such as alligators and crocodiles.

Salt marshes and mangrove forests are carbon-rich ecosystems that are perceived to play a role in climate regulation, biogeochemical cycling, and in capturing and preserving large amounts of carbon that counterbalance anthropogenic CO₂ emissions [4–6]. It is unclear to what extent both ecosystems constitute a significant carbon sink in the global coastal ocean, and whether restoring and replanting new marshes and mangroves will assist in ameliorating climate change. Thus, an improved understanding of carbon allocation and balance within these ecosystems is urgently needed. In this synthesis, similarities and differences in carbon cycling in both ecosystems are identified to better understand how they function, especially with regard to their role in carbon cycling in the global coastal ocean.

2. Allocation of Carbon Stocks

Salt marshes and mangrove forests both store large quantities of organic carbon (C_{ORG}) in soils and, to a lesser extent, in plant biomass (Figure 1). On average, soil C_{ORG} to a depth of 1 m comprises 77% and 95% of the total C_{ORG} stocks in mangrove forests and salt marshes, respectively.

![Figure 1](image_url)

**Figure 1.** Median organic carbon stocks vested in above- and belowground plant biomass and in soils to a depth of 1 m in salt marshes and mangrove forests on a per hectare basis. Mean (±1 standard error) values and references are listed in Table 1.

Carbon stocks in mangroves and salt marshes; above-ground biomass C_{ORG} accounts for 15% and 1% of total C_{ORG} in mangroves and salt marshes, respectively. Mangrove below-ground biomass C_{ORG} accounts for twice (8%) the total carbon stocks of salt marshes (4%). Total C_{ORG} stock in mangrove forests is twice as great as in salt marshes on a per hectare basis (Table 1). Globally, mangrove C_{ORG} stocks (6.17 Pg) are, on average, three times greater than salt marshes (1.84 Pg) due to greater stocks on both a per area basis and the fact that there are 1.5 times more mangrove forests than salt marshes worldwide (Table 1). Of course, carbon stocks vary greatly within both ecosystems as a function of ecosystem age, intertidal position, and species composition, as well as in terms of geographic, climatic and environmental factors.
Table 1. Comparison of mean (±1 standard error, SE) carbon stocks between salt marsh and mangrove ecosystems. Units = Mg C_{ORG} ha^{-1}. Median values are in parentheses and in Figure 1. Mangrove data from [6]. Salt marsh g dry weight (DW) biomass was converted to g C_{ORG} using percent C_{ORG} content in roots + rhizomes (41.5 ± 1.2%) and shoots (38.5 ± 0.7%) of various species [7–15]. Salt marsh above-and below ground biomass data (from [16–47] and earlier references within). Global mangrove area (86,495 km²) from [48] and salt marsh global area (54,951 km²) from [49].

<table>
<thead>
<tr>
<th>Component</th>
<th>Mangrove Forests</th>
<th>Salt Marshes</th>
</tr>
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<tbody>
<tr>
<td>Aboveground biomass (AGB)</td>
<td>109.3 ± 5.0 (94.1)</td>
<td>4.3 ± 0.10 (2.4)</td>
</tr>
<tr>
<td>Belowground biomass (BGB)</td>
<td>80.9 ± 9.5 (34.2)</td>
<td>12.9 ± 1.2 (9.6)</td>
</tr>
<tr>
<td>Soil (0–1 m depth)</td>
<td>565.4 ± 25.7 (500.5)</td>
<td>317.2 ± 19.1 (282.2)</td>
</tr>
<tr>
<td>Total C stock (Mg C_{ORG} ha^{-1})</td>
<td>738.9 ± 27.9 (702.5)</td>
<td>334.4 ± 3.5 (294.2)</td>
</tr>
<tr>
<td>Global area (km²)</td>
<td>86,495</td>
<td>54,951</td>
</tr>
<tr>
<td>Global C stock (Pg C_{ORG})</td>
<td>6.17</td>
<td>1.84</td>
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</table>

Median C_{ORG} content in salt marsh (5.8%) soils is greater than in mangrove soils (2.6%), but there is a wide spread of values in both wetland types, varying from 0.1% to 30% [50,51]. The wide range of soil C_{ORG} content undoubtedly reflects different geomorphological, climatic and environmental factors, as well as ecosystem age, species composition and hydrology. Similarly, C/N ratios are highly variable for the same reasons, varying within both marshes and mangroves, by 5/1 to 60/1 [50,51], respectively.

3. Primary Production and Plant Respiration

Rates of gross and net primary production in salt marshes and mangrove forests are among the highest for aquatic ecosystems and are within the range of rates for terrestrial grasslands and humid forests [32]. Median rates of gross primary production (GPP), aboveground net primary production (AGNPP) and canopy (plant) respiration (R_{C}) are greater for mangroves than salt marshes (Figure 2), although there is significant variation in rates reflecting species-specific differences in production among salt marsh and mangrove plants; nutrient status; wetland age; and other factors such as soil salinity, location, hydrology, intertidal position and temperature.

Figure 2. Median rates of gross (GPP) and aboveground net (AGNPP) primary production and plant respiration for mangroves (green bars) and salt marshes (blue bars). Vertical line in each box denotes the median (values presented in each box), and the boxes encompass the 25th and 75th percentiles and the outer bars denote the 5th and 95th percentiles. Data from Table 2.
Table 2. Comparison of mean (±1SE) GPP and above- and belowground net (NPP) primary production, canopy respiration (RC) and benthic microalgal GPP and NPP between salt marsh and mangrove ecosystems. Units = Mg CORG ha⁻¹ a⁻¹. Median values are in parentheses. Mangrove data from [6,52,53]. Salt marsh g dry weight (DW) production converted to g CORG using percent CORG content in roots + rhizomes (41.5 ± 1.2%) and shoots (38.5 ± 0.7%) of various species (references in Table 1). Salt marsh above- and belowground production data from ([54–85] and earlier references within) and microalgal production data from [86–93].

<table>
<thead>
<tr>
<th>Component</th>
<th>Mangrove Forests</th>
<th>Salt Marshes</th>
</tr>
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<tbody>
<tr>
<td>GPP</td>
<td>35.3 ± 6.0 (26.6)</td>
<td>17.7 ± 1.9 (16.6)</td>
</tr>
<tr>
<td>Aboveground NPP</td>
<td>13.2 ± 1.7 (9.0)</td>
<td>5.0 ± 0.3 (3.7)</td>
</tr>
<tr>
<td>Belowground NPP</td>
<td>5.2 ± 4.4 (5.1)</td>
<td>12.6 ± 1.1 (9.4)</td>
</tr>
<tr>
<td>RC</td>
<td>22.3 ± 4.9 (15.7)</td>
<td>8.4 ± 1.2 (6.4)</td>
</tr>
<tr>
<td>Microalgal GPP</td>
<td>4.4 ± 2.2 (3.3)</td>
<td>1.8 ± 0.8 (1.3)</td>
</tr>
<tr>
<td>Microalgal NPP</td>
<td>2.1 ± 0.7 (1.8)</td>
<td>1.5 ± 0.2 (1.1)</td>
</tr>
<tr>
<td>P_{GPP}/RC</td>
<td>1.6 ± 0.1 (1.5)</td>
<td>1.0 ± 1.3 (1.0)</td>
</tr>
</tbody>
</table>

Rates of belowground root production (Table 2) are significantly greater in salt marshes (one-way ANOVA on ranks; p < 0.05), although mangrove root production has most likely been greatly underestimated due to problems with methodology and the lack of empirical measurements [53]. Rates of benthic microalgal productivity in both salt marshes and mangroves (Table 2) are not significantly different (one-way ANOVA on ranks; p > 0.05). P_{GPP}/RC ratios are significantly greater in mangrove forests than in salt marshes (one-way ANOVA on ranks; p < 0.001) and are equivalent to those estimated for tropical terrestrial forests [52].

4. Soil Carbon Biogeochemistry

4.1. Soil-Air/Water Fluxes

Salt marsh and mangrove soils are waterlogged and saline and inundated for a part of every day. Usually but not always composed of silt and clay particles, soil of both ecosystems is penetrated by roots, rhizomes, and pieces of dead plant material. Having similar C and nutrient contents (Section 2), it is not surprising that they have rates of soil respiration that are not significantly different (one-way ANOVA on ranks; p > 0.05), except for significantly lower rates of oxygen uptake in mangrove soils (Table 3); these oxygen fluxes are significantly lower than those of dissolved inorganic carbon (DIC) and CO₂ [94].

Table 3. Comparison of mean (±1SE) rates of soil respiration, dissolved inorganic carbon (DIC) production (to a depth of 1 m), CH₄ release and C_{org} burial between mangrove and salt marsh ecosystems. Units = Mg C ha⁻¹ a⁻¹. Soil respiration data averages measurements taken at the soil surface during air exposure and tidal inundation and includes both gas (O₂ and CO₂) and solute (dissolved oxygen (DO) and DIC) measurements together for salt marshes and separately for mangroves. Mangrove oxygen and carbon fluxes are kept separate because of significant differences [94]. Median values are in parentheses. Mangrove data from [94]. Burial rates for both ecosystems from [4]. Salt marsh data from [56,58,76,95–138].

<table>
<thead>
<tr>
<th>Component</th>
<th>Mangrove Forests</th>
<th>Salt Marshes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil respiration</td>
<td>6.13 ± 0.62 (DIC, CO₂); 3.88 ± 0.29 (DO, O₂)</td>
<td>5.64 ± 0.63 (3.66)</td>
</tr>
<tr>
<td>Soil DIC production</td>
<td>18.27 ± 2.30 (15.5)</td>
<td>6.92 ± 1.61 (3.8)</td>
</tr>
<tr>
<td>Soil CH₄ release</td>
<td>0.015 ± 0.006 (0.004)</td>
<td>0.142 ± 0.02 (0.07)</td>
</tr>
<tr>
<td>C_{org} burial</td>
<td>1.62 ± 0.67 (1.33)</td>
<td>3.82 ± 0.58 (1.84)</td>
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</table>

In contrast, rates of CH₄ release are, on average, nine times greater from salt marsh soils than from mangrove deposits (Table 3). Methanogenesis is not a large decomposition pathway in mangrove
soils [50], probably due to the vertically depth-elongated zones of sulfate, iron and manganese reduction, in which rates vary irregularly and even peak at various depths to 1 m [94]. In salt marsh soils, rates of sulfate, iron, and manganese reduction decline over the upper 10–20 cm and presumably methanogenesis then becomes the dominant diagenetic pathway in deeper soils [86]. Methanogenesis in mangrove soils is ordinarily low, but high rates of methanogenic activity have been measured in organically polluted mangroves, and otherwise competitive sulfate-reducing and methanogenic bacteria can coexist if there is sufficient labile organic matter [50]. In salt marsh soils, measured CH$_4$ production rates vary considerably depending on the dominance of sulfate and iron-reduction but are often measurable in deep (30–100 cm) soils [86].

4.2. Soil DIC Production

In mangrove soils, respired carbon as DIC (and dissolved organic carbon (DOC) and CH$_4$) is produced to a depth of at least 1 m [94] and perhaps to greater depths considering that there is no indication of a clear decline in production rates measured over surface–100 cm profiles [94]. These continuously high rates are likely sustained by decomposition of deep roots, release of root exudates, activities of deep-dwelling crabs and recycling of an extraordinarily large pool of dead roots and subsurface bacterial biomass [1,52]. Due to a number of geophysical and geochemical factors [94], early diagenesis of soil organic matter in mangroves is unlikely to be in steady-state, as it is in most subtidal coastal and marine sediments [1]. This phenomenon results in a discrepancy between decomposition processes in surface and subsurface soils, in which rates of respiration across the soil–water/air interface are not directly linked to respiratory processes in deeper soil layers. As a result, rates of surface soil respiration equate to only about one-third of subsurface respiration, as measured by DIC release from incubated soils (Table 3). In salt marshes, in contrast, early diagenesis of organic matter is probably in steady-state as surface respiration rates are equivalent to subsurface DIC production rates (Table 3). Oxygen, carbon dioxide and DIC fluxes across the soil surface/air–water interface have long been presumed to represent total carbon decomposition, assuming steady-state diffusion of gases and solutes from within the entire soil profile [1]. As discussed in Section 6, it may be that subsurface and surface respiration in soil marsh soils are similarly spatially separated, helping to account for export of DIC, DOC and CH$_4$.

4.3. $C_{ORG}$ Burial in Soils

Rates of $C_{ORG}$ burial in salt marsh soils are greater than rates in mangrove soils (Table 3), although the differences are not significant (one-way ANOVA on ranks, $p > 0.05$). There are wide variations in burial rates among locations, depending on a variety of factors, such as geomorphology, intertidal position, climate, extent of terrestrial and marine input, habitat age, species composition and soil texture [4,6]. Along with seagrasses, salt marshes and mangrove forests sequester more organic carbon on a per area basis than all other terrestrial and marine ecosystems (see Table 3 in reference [6]).

5. Carbon Biogeochemistry in Tidal Waters

5.1. CO$_2$ and CH$_4$ Emissions

Rates of CO$_2$ emissions from mangrove and salt marsh tidal waters (Table 4) are equivalent (one-way ANOVA on ranks; $p < 0.05$), but rates of CH$_4$ emissions (Table 4) are significantly greater from salt marsh waters (one-way ANOVA on ranks; $p < 0.05$), probably reflecting the higher rates of methanogenesis in marsh soils (Table 3).
Table 4. Comparison of mean (±1SE) rates of water–air CO$_2$ and CH$_4$ emissions between mangrove and salt marsh ecosystems, including open water estuaries containing mangrove and salt marsh habitats. Units = Mg C ha$^{-1}$ a$^{-1}$. Median values are in parentheses. Mangrove data from [94,139]. Salt marsh data from [139–152] and references within.

<table>
<thead>
<tr>
<th>Component</th>
<th>Mangrove Forests</th>
<th>Salt Marshes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water-air CO$_2$ release</td>
<td>3.35 ± 0.35 (2.19)</td>
<td>2.981 ± 0.33 (1.55)</td>
</tr>
<tr>
<td>Water-air CH$_4$ release</td>
<td>0.0116 ± 0.003 (0.01)</td>
<td>0.104 ± 0.047 (0.006)</td>
</tr>
</tbody>
</table>

5.2. Carbon Export

Rates of particulate organic carbon (POC) export to adjacent tidal waters are three times greater (one-way ANOVA on ranks, $p < 0.05$) in mangroves than in salt marshes (Table 5). Similarly, DOC export is more than twice the rate in mangroves than in salt marshes (Table 5); DIC export is nearly three times greater in mangroves than in salt marshes (Table 5). However, export of dissolved CH$_4$ is four times greater in salt marshes than in mangroves; methanogenesis is likely to be greater in deeper salt marsh soils than in mangroves, as reflected in the higher rates of CH$_4$ release from soils and tidal waters (Tables 3 and 4). The greater rates of organic carbon export from mangroves probably reflect the higher rates of primary production, litter production and soil mineralization in deep soils. Monsoonal rainfall in the tropics may facilitate greater export during the wet season.

Table 5. Comparison of mean (±1SE) rates of particulate organic carbon (POC), dissolved organic carbon (DOC), DIC and CH$_4$ export from mangrove and salt marsh ecosystems to adjacent tidal waters. Units = Mg C ha$^{-1}$ a$^{-1}$. Median values are in parentheses. Mangrove data from [52,94,153–158]. Salt marsh data from [75,91,140,144,159–187].

<table>
<thead>
<tr>
<th>Export Component</th>
<th>Mangrove Forests</th>
<th>Salt Marshes</th>
</tr>
</thead>
<tbody>
<tr>
<td>POC</td>
<td>1.73 ± 0.23 (1.76)</td>
<td>0.60 ± 0.11 (0.31)</td>
</tr>
<tr>
<td>DOC</td>
<td>5.90 ± 1.95 (1.43)</td>
<td>2.55 ± 0.55 (1.33)</td>
</tr>
<tr>
<td>DIC</td>
<td>14.34 ± 2.26 (10.82)</td>
<td>5.28 ± 1.212 (3.995)</td>
</tr>
<tr>
<td>CH$_4$</td>
<td>0.0277 ± 0.0135 (0.026)</td>
<td>0.109 ± 0.0786 (0.0081)</td>
</tr>
</tbody>
</table>

6. Whole-Ecosystem Carbon Mass Balance

Sufficient data exist to construct carbon mass balance models of mangrove (Figure 3) and salt marsh (Figure 4) ecosystems. The salt marsh model is derived from the data in this review, while the mangrove mass balance is derived from [94], revised and updated from an earlier iteration [188]. This revised mangrove model shows that about 63% of GPP is respired by the forest canopy. The salt marsh budget indicates that about 47% of GPP is respired by salt marsh plants. Mangrove NPP is vested nearly equally in litter, wood and belowground roots, with about 40% of litter exported to adjacent tidal waters; salt marsh NPP is vested mostly in belowground roots (72%). Unlike in the mangrove mass balance, salt marsh below- and aboveground NPP are inexplicably greater than GPP, implying that either below- and/or aboveground production are overestimates or that GPP is underestimated by about 30%. The standard deviation of the salt marsh GPP data is 73% of the mean with a range of 45 Mg C ha$^{-1}$ a$^{-1}$ (GPP mean = 17.7 Mg C ha$^{-1}$ a$^{-1}$), suggesting that these data have a wide margin of error. Pre-eddy covariance data [143] estimate GPP, plant R and NPP for salt marshes of 112, 10.7 and 11.5 Tg C a$^{-1}$, respectively, which nearly balance assuming that the estimate for root production (69 Tg C a$^{-1}$) is correct. However, plant R would be too low, equating to only 9.5% of GPP, resulting in an extraordinarily high P$_{GPP}$/R$_C$ ratio of 10.5; both values are highly unlikely compared to those estimated for other vegetated ecosystems [1]. In both ecosystems, most roots produced (90% for mangroves, 78% for salt marshes) are shunted into the soil C$_{ORG}$ pool for eventual decomposition; the remainder is buried (estimates from [189]). The balance of buried carbon is derived equally from litter and the soil pool. About 12% of mangrove NPP and 22% of marsh NPP is
eventually sequestered in soils, supporting the estimate that salt marshes sequester proportionally more \( \text{C}_{\text{ORG}} \) in soils than mangroves.

**Figure 3.** Mass balance of mean carbon flow through the world’s mangrove forests. Units are Tg C a\(^{-1}\). The budget assumes a global mangrove area of 86,495 km\(^2\) [94]. Solid blue arrows depict mean values based on empirical data (see text for explanation and references). Dashed red arrows represent mean values estimated indirectly by difference. The \( \text{C}_{\text{ORG}} \) pool (both live and dead roots and other organic matter) in soils to a depth of 1 m is presented in a box in the forest floor with units of Tg \( \text{C}_{\text{ORG}} \). Abbreviations: GPP = gross primary production; NPP = net primary production; \( R_a \) = algal production at soil surface and aboveground biomass; \( R_c \) = canopy respiration; \( R_s \) = soil respiration at soil surface; \( R_{\text{WATER}} \) = waterway respiration; POC = particulate organic carbon derived from litter and exported to tidal waters; DIC = dissolved inorganic carbon; DOC = dissolved organic carbon; \( \text{CH}_4 \) = methane; EDOC = exchangeable dissolved organic carbon.

\( \text{C}_{\text{ORG}} \) decomposition in mangrove soils to a depth of 1 m (158 Tg C yr\(^{-1}\)) is greater than NPP (114 Tg C a\(^{-1}\)), implying that (1) the measurements of below-ground microbial decomposition are overestimates (due to methodological shortcomings; variable incubation times, etc.); (2) other sources of allochthonous carbon, such as marine and terrestrial inputs are required to balance carbon flow; and/or (3) centuries-old \( \text{C}_{\text{ORG}} \) is also being mineralized, such as \( \text{C}_{\text{ORG}} \) buried prior to when the mangroves inhabited the unvegetated mudflat. As the export of DIC, DOC and \( \text{CH}_4 \) from mangrove subsurface soils to adjacent tidal waters (175 Tg C a\(^{-1}\)) is within the error estimate of the measured rates of total soil \( \text{C}_{\text{ORG}} \) mineralization (158 Tg C a\(^{-1}\)), it is likely that allochthonous sources of carbon are important in mangrove carbon flow, such as imports from adjacent seagrass beds and coastal plankton. Additionally, the budget does not account for carbon fixed by benthic cyanobacterial mats and other nitrogen-fixing biota on the forest floor, roots and rhizomes, tree stems, litter and downed wood; these are very productive assemblages but too patchy in distribution to extrapolate beyond a square meter.
Further, buried C\textsubscript{ORG} is likely to be a source of respired carbon since measurements of isotopes in a subtropical Australian mangrove indicate that carbon deposited centuries ago is still susceptible to decomposition and subsequent tidal export [190]. Incubation experiments with coastal wetlands have also indicated the potential for sea-level rise to increase remineralization of previously buried carbon [191].

![Mass balance of mean carbon flow through the world’s salt marshes](image)

**Figure 4.** Mass balance of mean carbon flow through the world’s salt marshes. Units are Tg C a\(^{-1}\). The budget assumes a global salt marsh area of 54,951 km\(^2\) [49]. Solid blue arrows depict mean values based on empirical data (see text for explanation and references). Dashed red arrows represent mean values estimated indirectly by difference. The C\textsubscript{ORG} pool (both live and dead roots and other organic matter) in soils to a depth of 1 m is presented in a box in the marsh floor with units of Tg C\textsubscript{ORG}. Abbreviations: GPP = gross primary production; NPP = net primary production; RA = algal production at soil surface and aboveground biomass; Rc = canopy respiration; Rs = soil respiration at soil surface; Rw\textsubscript{WATER} = waterway respiration; POC = particulate organic carbon derived from litter and exported to tidal waters; DIC = dissolved inorganic carbon; DOC = dissolved organic carbon; CH\textsubscript{4} = methane.

In both ecosystems, pCO\textsubscript{2} and pCH\textsubscript{4} supersaturation of adjacent tidal waters leads to significant CO\textsubscript{2} and CH\textsubscript{4} release to the atmosphere. The mean rates of total soil mineralization imply that the turnover time of the entire soil C\textsubscript{ORG} pool (including dead and live roots) is in the order of 25 years for mangroves and 20 years for salt marshes, which is in agreement with the fact that mangrove roots decompose more slowly than marsh plant roots [189] and that most mangrove and salt marsh soil organic matter is composed of higher plant-derived material high in lignocellulose and hemicellulose that decomposes slowly [189].

Mangrove discharge of dissolved carbon contributes nearly 60% of DIC and 27% of DOC export from the world’s tropical rivers to the coastal ocean, based on comparison with the river export data in Huang et al. [192]. Salt marshes and mangrove forests each inhabit only about 0.3% of global coastal ocean area, but, respectively, contribute 17% and 55% for a combined contribution of 72% of air–sea CO\textsubscript{2} exchange from the world’s wetlands and estuaries [193]. Salt marshes and mangrove ecosystems, respectively, export 6% and 28% of DIC export and 4% and 13% of DOC + POC export to the world’s coastal ocean [194]. Thus, both wetland ecosystems contribute disproportionately to carbon flow in the global coastal ocean.
As defined in [53], net ecosystem production (NEP) can be derived by subtracting all respiratory losses (ecosystem respiration, $R_E = RC + RS + RWATER + RMICROALGAE$) from all salt marsh/mangrove, benthic algal and plankton gross primary production (GPP). NEP is 54 Tg C a$^{-1}$ for mangroves and 21 Tg C a$^{-1}$ for salt marshes (Table 6). Both ecosystems contribute only a small proportion of GPP and $R_E$ to the global coastal ocean due to their small global area, but mangroves are more productive in terms of NEP on a per area basis than the other coastal habitats (Table 6). Macroalgae contribute nearly 94% of NEP to total NEP (2217 Tg C a$^{-1}$), the latter derived by summing the NEP of the global benthic coastal ocean (~165 Tg C a$^{-1}$) and all the other habitats (2382 Tg C a$^{-1}$). Seagrass meadows also contribute a larger share to total NEP (4.5%) than either mangroves (2.4%) or salt marshes (1.0%) due to their larger global area. On a per area basis, mangroves produce and respire more carbon than the other coastal habitats. Coral reefs are on average less productive in terms of GPP than their coastal ocean counterparts but have roughly equivalent global NEP to seagrasses. All vegetated ecosystems are net autotrophic ($P_{GPP}/R_E = 1.09–1.37$), with macroalgae being the most autotrophic; the global coastal ocean is net heterotrophic ($P_{GPP}/R_E = 0.98$).

Table 6. Contribution of salt marshes and mangroves to carbon balance in the global coastal ocean compared with other marine ecosystems. Global seagrass area from [195], macroalgae area from [196] and area of other ecosystems from [188], except the global coastal ocean [194], which encompasses estuaries, other wetlands, and continental shelves. Seagrass data [188] updated from [197–210] and macroalgae data from [211–236]. Plankton GPP and R in salt marshes from [237] and in mangroves from [52]. All other data from [188], except global coastal ocean data from [194]. Percentage contributions of salt marsh and mangrove NEP are based on comparison with sum of all ecosystem NEP plus the negative global coastal ocean NEP (= 2217 Tg C a$^{-1}$). Percentage contributions of salt marsh and mangrove $R_C$ and GPP are based on comparison only with global coastal ocean $R_E$ and GPP. Abbreviations and units: $R_E$ (g C m$^{-2}$ a$^{-1}$) = ecosystem respiration ($RC + RS + RWATER + RMICROALGAE$); GPP (g C m$^{-2}$ a$^{-1}$) = gross primary production; NEP (g C m$^{-2}$ a$^{-1}$) = net ecosystem production. Units = area ($10^10$ m$^2$); global $R_E$, global GPP and global NEP (Tg C a$^{-1}$).

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>Area</th>
<th>$R_E$</th>
<th>Global $R_E$</th>
<th>GPP</th>
<th>Global GPP</th>
<th>Mean $P_{GPP}/R_E$</th>
<th>NEP</th>
<th>Global NEP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salt marsh</td>
<td>5.5</td>
<td>1727</td>
<td>95</td>
<td>2109</td>
<td>116</td>
<td>1.22</td>
<td>382</td>
<td>21</td>
</tr>
<tr>
<td>Mangrove</td>
<td>8.6</td>
<td>3558</td>
<td>306</td>
<td>4186</td>
<td>360</td>
<td>1.18</td>
<td>628</td>
<td>54</td>
</tr>
<tr>
<td>Seagrass</td>
<td>16.0</td>
<td>2133</td>
<td>342</td>
<td>2752</td>
<td>441</td>
<td>1.29</td>
<td>619</td>
<td>99</td>
</tr>
<tr>
<td>Macroalgae</td>
<td>354.0</td>
<td>1572</td>
<td>5665</td>
<td>2159</td>
<td>7643</td>
<td>1.37</td>
<td>587</td>
<td>2078</td>
</tr>
<tr>
<td>Coral reef</td>
<td>60.0</td>
<td>1572</td>
<td>943</td>
<td>1720</td>
<td>1032</td>
<td>1.09</td>
<td>148</td>
<td>84</td>
</tr>
<tr>
<td>Global coastal ocean</td>
<td>2750</td>
<td>1034</td>
<td>28,435</td>
<td>1028</td>
<td>28,270</td>
<td>0.98</td>
<td>–6</td>
<td>–165</td>
</tr>
<tr>
<td>Salt marsh contribution</td>
<td>0.20%</td>
<td>-</td>
<td>0.33%</td>
<td>-</td>
<td>0.47%</td>
<td>-</td>
<td>-</td>
<td>1.0%</td>
</tr>
<tr>
<td>Mangrove contribution</td>
<td>0.31%</td>
<td>-</td>
<td>1.08%</td>
<td>-</td>
<td>1.27%</td>
<td>-</td>
<td>-</td>
<td>2.4%</td>
</tr>
</tbody>
</table>

The sum of plant respiration, surface and subsurface soil respiration, and respiration in tidal waterways equates to about 82% of salt marsh and 85% of mangrove GPP (Table 6). The remaining carbon, including that fixed by algae, is stored in vegetation and soil and, to a smaller but vital extent, is probably lost to fisheries, food webs, birds, and other organisms, including humans.

7. Data Refinements and Future Needs

Both carbon budgets reveal some important shortcomings in the databases. For both ecosystems, there is a need for more or greater

- Clarity of their global area, as areal estimates vary greatly;
- Estimates of ecosystem GPP, NPP and R, using eddy covariance technology;
- Estimates of belowground root production;
- Quantification and extrapolation of algal mat production and carbon fixation of nitrogen fixers on tree stems, downed wood and plant debris (litter; leaves);
• Quantification of allochthonous inputs from marine and terrestrial sources, such as adjacent seagrass beds, other estuary producers and advection from offshore;
• Estimates of DIC, DOC and CH$_4$ exchange between these wetlands and adjacent waters;
• Estimates of CO$_2$ and CH$_4$ release from associated tidal creeks and waterways;
• Estimates of benthic microalgal GPP;
• Estimates of soil C stocks and fluxes deeper than 50 cm, especially in salt marshes;
• Reconciling rates of soil respiration at the surface and in subsurface deposits and their linkage;
• Quantification of groundwater export of dissolved carbon in relation to porewater advection of mineralized carbon within deep mangrove and marsh soils;
• Quantification of the fate of roots and their productivity;
• Understanding of C$_{ORG}$ differences between within-site and between-site locations (e.g., differences with intertidal position);
• Clarification of links among roots, litter and the soil C$_{ORG}$ pool in relation to mineralization rates;
• Clarification of the contributions of litter, dead plants, wood and the soil C$_{ORG}$ pool to carbon burial.

These are just some of the high priority shortcomings and needs to construct more accurate and balanced carbon budgets for these two ecosystems.

The impact of climate change will likely have a large impact on ecosystem C fluxes and stocks. For instance, sea-level rise will result in die-off of established plant communities with an increase in export and burial of plant debris; burial rates will concomitantly increase. It has already been observed that the encroachment of mangroves into salt marshes has resulted in an increase in storage of C$_{ORG}$ [238,239]. Increases in temperature and atmospheric carbon dioxide concentrations will likely result in increased mangrove and salt marsh productivity and respiration [240–242], altering the carbon balance of these ecosystems.

8. Summary and Conclusions

Mangroves and salt marshes are important storage sites for organic carbon and are among the most productive ecosystems on Earth. Mangroves store, on average, twice as much C$_{ORG}$ as salt marshes, although marshes have greater rates of C$_{ORG}$ burial. Mangroves exhibit greater rates of GPP, aboveground NPP, and canopy respiration with higher P$_{GPP}$/R$_C$ ratios, whereas salt marshes exhibit greater rates of belowground root production. Mangroves have greater rates of subsurface DIC production and, unlike salt marshes, exhibit active microbial diagenesis to a soil depth of 1 m. Salt marshes exhibit greater rates of soil CH$_4$ release and greater export of dissolved CH$_4$, reflecting greater rates of subsurface methanogenesis, as competing sulfate reducers decline in activity below about the 20–50 cm soil horizon. Mangroves release greater amounts of CO$_2$ from tidal waters to the atmosphere and greater amounts of POC, DOC and DIC export to adjacent waters. Mangrove net ecosystem production (628 g C m$^{-2}$ a$^{-1}$) is greater than in salt marshes (382 g C m$^{-2}$ a$^{-1}$).

Both ecosystems contribute only a small proportion of GPP and R$_E$ (ecosystem respiration) to the global coastal ocean due to their small global area, but contribute 72% of the air–sea CO$_2$ exchange of the world’s estuaries, 34% of the DIC export and 17% of DOC + POC export to the world’s coastal ocean. Thus, both wetland ecosystems contribute disproportionately to carbon flow in the global coastal ocean.

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