Review

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_{ORG} ha^{-1}) than salt marshes (334 Mg C_{ORG} ha^{-1}), but the latter sequester proportionally more (24%) net primary production (NPP) than mangroves (12%). Mangroves exhibit greater rates of gross primary production (GPP), above-ground net primary production (NPP) and plant respiration (R_C) with higher P_{GPP}/R_C ratios, but salt marshes exhibit greater rates of below-ground NPP. Mangroves have greater rates of subsurface DIC production and, unlike salt marshes, exhibit significant microbial decomposition to a soil depth of 1 m. Salt marshes release more soil CH_4 and export more dissolved CH_4, but mangroves release more CO_2 from tidal waters and export greater amounts of POC, DOC and DIC to adjacent waters. Both ecosystems contribute only a small proportion of GPP, R_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_2 exchange from 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

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1. Introduction

Salt marshes and mangrove forests are intertidal ecosystems comparable *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 nearshore waters. 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 new 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].

Food webs are composed of mixtures of terrestrial, estuarine, and marine fauna and flora that help to actively cycle nutrients and carbon. Plankton communities are as productive and abundant as those within marshes and mangroves and are equally well-adapted to the complex hydrology and chemistry of opaque tidal creeks and waterways. These tidal waters are also host to organisms ranging in size from viruses to reptiles. 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 waters and wetlands [1].

Salt marshes and mangrove forests are carbon-rich ecosystems that are perceived to play a role in climate regulation, biogeochemical cycling, and capturing and preserving large amounts of carbon to help counterbalance anthropogenic CO_2 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, 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 regarding 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 (CORG) in soils and, to a lesser extent, in plant biomass (Figure 1). On average, soil CORG comprises 77% and 95% of total

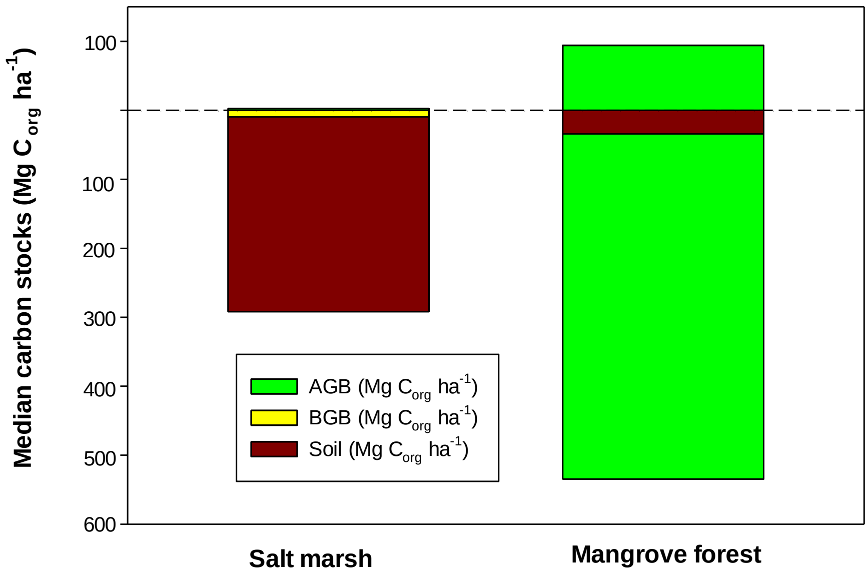

Figure 1. Median organic carbon stocks vested in above- and belowground plant biomass and in soils to a depth of 1 m in salt marshes and mangrove forests on a per hectare basis. Mean (± 1 standard error) values and references are listed in Table 1.

carbon stocks in mangroves and salt marshes; above-ground biomass CORG accounts for 15% and 1% of total CORG in mangroves and salt marshes, respectively. Mangrove below-ground biomass CORG accounts for twice (8%) the total carbon stocks than in salt marshes (4%). Total CORG stock in mangrove forests is twice as great as in salt marshes on a per hectare basis (Table 1). Globally, mangrove CORG stocks (6.17 Pg) are on average three times greater than salt marshes (1.84 Pg) due to greater stocks on both an areal 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 geographic, climatic, and environmental factors.

Table 1. Comparison of mean carbon stocks between salt marsh and mangrove ecosystems. Units = Mg CORG ha^{-1}. Median values are in parentheses and in Figure 1. Mangrove data from [6]. Salt

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marsh g dry weight (DW) biomass was converted to g CORG using percent CORG 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 (54,950 km²) from [49].

Component	Mangrove forests	Salt marshes
Above-ground biomass (AGB)	109.3 ± 5.0 (94.1)	4.3 ± 0.10 (2.4)
Below-ground biomass (BGB)	80.9 ± 9.5 (34.2)	12.9 ± 1.2 (9.6)
Soil (0-1 m depth)	565.4 ± 25.7 (500.5)	317.2 ±19.1 (282.2)
Total C stock (Mg C_{org} ha^{-1})	738.9 ± 27.9 (702.5)	334.4 ± 3.5 (294.2)
Global area (km²)	83,495	54,951
Global C stock (Pg C_{org})	6.17	1.84

Median CORG 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 CORG content undoubtedly reflects different geomorphological, climate, environmental factors and ecosystem age, species composition and hydrology. Similarly, C:N ratios are highly variable for the same reasons, varying within both marshes and mangroves from 5:1 to 60:1 [50-51].

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 humid forests [52]. Median rates of gross primary production (GPP), above-ground net primary production (NPP) 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.

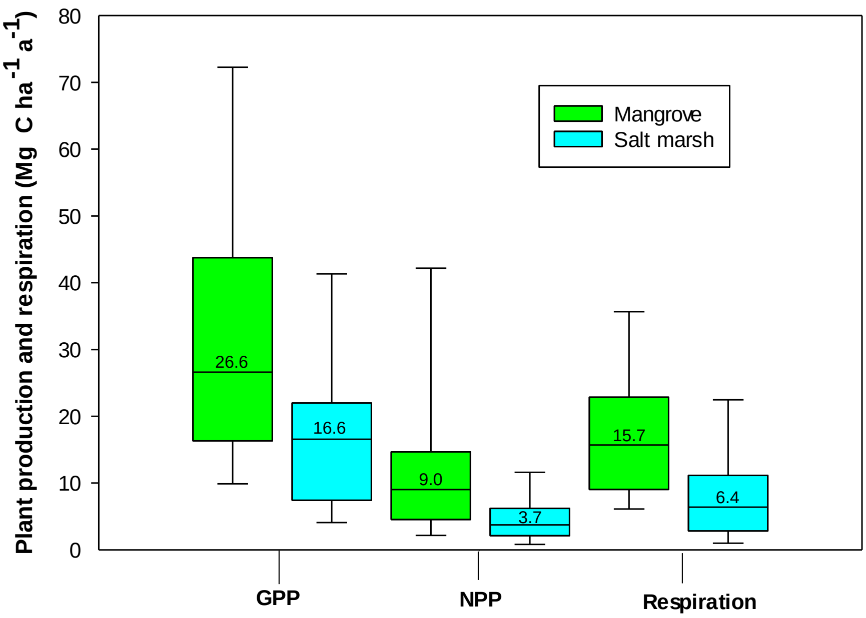

Figure 2. Rates of gross (GPP) and above-ground net (NPP) primary production and plant respiration for mangroves (green bars) and salt marshes (blue bars). Vertical line in each box

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denotes the median and the boxes encompass the 25th and 75th percentiles and the outer bars denote the 5th and 95th percentiles. Data from Table 2.

Rates of mangrove GPP, above-ground NPP and canopy respiration (Table 2) are significantly greater than those for salt marshes (one-way ANOVA on ranks; $p < 0.001$). However, below-ground root production is 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}/R_C 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].

Table 2. Comparison of rates of gross (GPP) and above- and below-ground net (NPP) primary production, canopy respiration (R_C) and benthic microalgal GPP and NPP between salt marsh and mangrove ecosystems. Units = Mg C_{ORG} 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 C_{ORG} using percent C_{ORG} 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 below ground production data from [54-85 and earlier references within] and microalgal production data from [86-93].

Component	Mangrove forests	Salt Marshes
GPP	36.5 ± 6.0 (26.6)	17.7 ± 1.9 (16.6)
Above -ground NPP	13.7 ± 1.7 (9.0)	5.0 ± 0.3 (3.7)
Below-ground NPP	5.4 ± 4.4 (5.1)	12.6 ± 1.1 (9.4)
R_C	23.1 ± 4.9 (15.7)	8.4 ± 1.2 (6.4)
Microalgal GPP	4.6 ± 2.2 (3.3)	1.7 ± 0.8 (1.3)
Microalgal NPP	2.2 ± 0.7 (1.8)	1.4 ± 0.2 (1.1)
P_{GPP}/R_C	1.8 ± 0.1 (1.5)	1.0 ± 1.3

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 are penetrated by roots and rhizomes and pieces of dead plant material. Having similar C and nutrient contents (section 2), it is not surprizing 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 2); these oxygen fluxes are significantly less than those for DIC and CO_2 [94].

In contrast, rates of CH_4 release are, on average, 9 times greater from salt marsh soils than from mangrove deposits (Table 2). 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 are irregular and even peak at various depths to 1 m [94]. In salt marsh soils, rates of sulfate, iron and manganese reduction decrease over the upper 10-20 cm and presumably methanogenesis then becomes the dominant diagenetic pathway in deeper soils [86].

Table 2. Comparison of rates of soil respiration, DIC production, CH_4 release and C_{org} burial between mangrove and salt marsh ecosystems. Units = Mg C ha^{-1} a^{-1}. Soil respiration data averages measurements taken during air exposure and tidal inundation and includes both gas (O_2 and CO_2) and solute (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].

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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].

Component	Mangrove forests	Salt Marshes
Soil respiration	6.39 ± 0.62 (DIC, CO_2) 3.88 ± 0.29 (DO, O_2)	5.61 ± 0.63 (3.66)
Soil DIC production	18.94 ± 2.30 (15.5)	6.91 ± 1.61 (3.8)
Soil CH_4 release	0.015 ± 0.006 (0.004)	0.14 ± 0.02 (0.07)
C_{org} burial	1.71 ± 0.27 (1.03)	2.12 ± 0.28 (1.84)

4.2. Soil DIC production

In mangrove soils, respired carbon as DIC (and 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 0-100 cm profiles [94]. These continuously high rates are likely sustained by decomposition of deep roots, release of root exudates, activites of deep-dwelling crabs, and recycling of an extraordinarily large pool of 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 2). 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 2). 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 CORG burial in soils

Rates of CORG burial in salt marsh soils are slightly greater than rates in mangrove soils (Table 2), 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 tidal waters (Table 3) are significantly greater than those from salt marsh waterways (one-way ANOVA on ranks; $p < 0.05$), likely reflecting higher rates of bacterioplankton production and plankton metabolism in warmer waters [52]. However, rates of CH_4 emissions were identical, with both ecosystems showing a net release to the atmosphere.

Table 3. Comparison of rates of water-air CO_2 and CH_4 emissions between mangrove and salt marsh ecosystems. Units = Mg C ha^{-1} a^{-1}. Median values are in parentheses. Mangrove data from [94]. Salt marsh data from [139-152].

Component	Mangrove forests	Salt Marshes
Water-air CO_2 release	4.79 ± 0.49 (3.04)	2.81 ± 0.33 (1.55)
Water-air CH_4 release	0.023 ±0.003 (0.011)	0.023 ± 0.008 (0.004)

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5.2 Carbon export

Rates of 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 4). Similarly, DOC export is more than twice the rate in mangroves than in salt marshes (Table 4); DIC export is nearly three times greater in mangroves than in salt marshes (Table 4). 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 soil CH_4 release (Table 2).

Table 4. Comparison of rates of POC, 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 [75,91,140,144,159-186].

Export component	Mangrove forests	Salt Marshes
POC	1.83 ± 0.23 (1.76)	0.60 ± 0.11 (0.31)
DOC	6.16 ± 1.95 (1.43)	2.63 ± 0.55 (1.33)
DIC	14.88 ± 2.26 (10.82)	5.31 ± 1.212 (3.995)
CH_4	0.029 ± 0.0135 (0.026)	0.112 ± 0.0786 (0.0081)

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 [86]. A recent study indicates that deep (30-100 cm deep) salt marsh soils can produce high rates of methane [187]. In a Korean *Phragmites australis* tidal marsh, rates of methane production were rapid in deep soil layers compared to surface (0-30 cm deep) soils. As *Phragmites australis* is a deep-root plant, the high subsurface emission rates were attributed to increased DOC release from marsh roots and reduced competition between sulfate reducers and methanogens as porewater sulfate and its subsequent reduction were depleted in deeper soil layers [187].

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 mangrove mass balance is derived from [94], revised from an earlier iteration [188]. This revised model shows that about 63% of GPP is respired by the mangrove canopy and 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 was 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] indicate 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 and result 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 estimates that salt marshes sequester proportionally more C_{ORG} in soils than mangroves.

C_{ORG} decomposition in mangrove soils to a depth of 1m (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; (2) other sources of allochthonous carbon, such as marine and terrestrial inputs are required to balance carbon flow; or (3) centuries-old C_{ORG} is also being mineralized, perhaps C_{ORG} buried prior to when the mangroves inhabited the unvegetated mudflat. As the export of DIC, DOC and 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 C_{ORG} mineralization (158 Tg C a^{-1}), it is likely that allochthonous sources of carbon are important in mangrove carbon flow. Further, buried C_{ORG} is likely to be a source of respired carbon as measurements of isotopes in a subtropical Australian mangrove indicate that carbon deposited centuries ago is still susceptible to decomposition and subsequent tidal export [190].

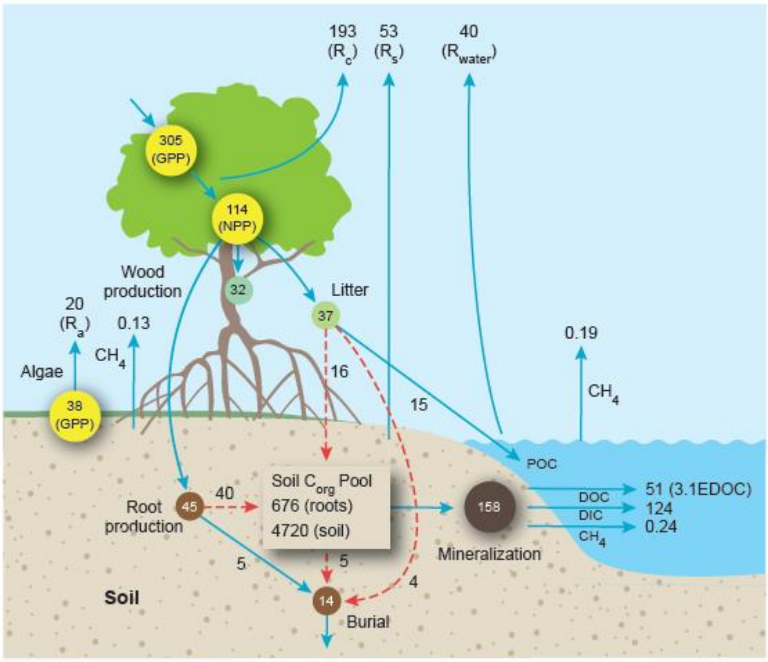

Figure 3. Mass balance of carbon flow through the world's mangrove forests. Units are Tg C a^{-1}. The budget assumes a global mangrove area of 86,495 km^2 [94]. Solid blue arrows depict mean values based on empirical data (see text for explanation and references). Dashed red arrows represent mean values estimated indirectly by difference. The C_{ORG} pool (both roots and soils) in soils to a depth of 1 m is presented in a box in the forest floor with units of Tg C_{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_{WATER} = waterway respiration; POC = particulate organic carbon derived from litter and exported to tidal waters; DIC = dissolved inorganic carbon; DOC = dissolved organic carbon; CH_4 = methane; EDOC = exchangeable dissolved organic carbon.

In both ecosystems, pCO_2 and pCH_4 supersaturation of adjacent tidal waters leads to significant CO_2 and CH_4 release to the atmosphere. The mean rates of total soil mineralization imply that the turnover time of the entire soil C_{ORG} pool (including dead and live roots) is on 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

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organic matter is composed of higher plant-derived material high in lignocellulose and hemicellulose that decomposes slowly [189].

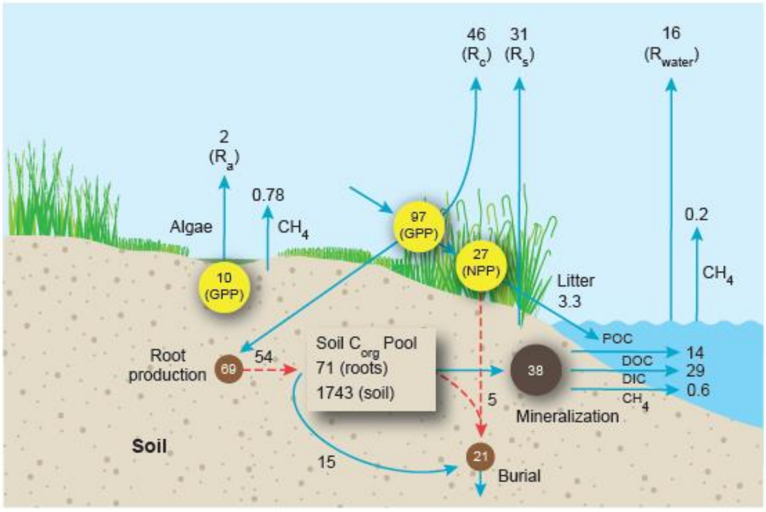

Figure 4. Mass balance of carbon flow through the world's salt marshes. Units are Tg C a^{-1}. The budget assumes a global salt marsh area of 54, 951 km^2 [49]. Solid blue arrows depict mean values based on empirical data (see text for explanation and references). Dashed red arrows represent mean values estimated indirectly by difference. The C_{ORG} pool (both roots and soils) in soils to a depth of 1 m is presented in a box in the forest floor with units of Tg C_{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_{WATER} = waterway respiration; POC = particulate organic carbon derived from litter and exported to tidal waters; DIC = dissolved inorganic carbon; DOC = dissolved organic carbon; CH_4 = methane.

Mangrove DIC discharge contributes nearly 60% of DIC and 27% of DOC export from the world's tropical rivers to the coastal ocean, based on comparing the river export data in Huang et al. [191]. 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_2 exchange from the world's wetlands and estuaries [192]. 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 [193]. 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, $R_E = R_C + R_S + R_{WATER} + R_{MICROALGAE}$) 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 5). 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 5).

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).

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 5). 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. 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, above-ground NPP and canopy respiration with higher P_{GPP}/R_C ratios, whereas salt marshes exhibit greater rates of below-ground root production. Mangroves have greater rates of subsurface DIC production and, unlike salt marshes, exhibit significant microbial decomposition to a soil depth of 1 m. Salt marshes exhibit greater rates of soil CH_4 release and greater export of dissolved CH_4, perhaps reflecting greater rates of subsurface methanogenesis, as competing sulfate reducers decline in activity below about the 20-40 cm soil horizon. Mangroves have greater rates of CO_2 release from tidal waters and greater amounts of POC, DOC and DIC export to adjacent waters. Mangroves have net ecosystem production (628 g C m^{-2} a^{-1}) greater than 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 air-sea CO_2 exchange from the world's estuaries and 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 in the global coastal ocean.

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Table 5. Contribution of salt marshes and mangroves to carbon balance in the global coastal ocean compared with the contributions of other marine ecosystems. Global seagrass area from [194], macroalgae area from [195] and area of other ecosystems from [188], except the global coastal ocean [193] which encompasses estuaries, wetlands, estuaries, and continental shelves. Seagrass data [188] updated from [196-209] and macroalgae data from [210-235]. Plankton GPP and R in salt marshes from [236] and in mangroves from [52]. All other data from [188], except global coastal ocean data from [193]. Percentage contribution 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: R_E= ecosystem respiration ($R_C + R_S + R_{WATER} + R_{MICROALGAE}$; GPP = gross primary production; NEP = net ecosystem production (GPP-R_E).

Ecosystem	Area (10^{10} m^2)	R_E (g C m^{-2} a^{-1})	Global R_E (Tg C a^{-1})	GPP (g C m^{-2} a^{-1})	Global GPP (Tg C a^{-1})	Mean P_{GPP}/R_E	NEP (g C m^{-2} a^{-1})	Global NEP (Tg C a^{-1})
Salt marsh	5.5	1,727	95	2,109	116	1.22	382	21
Mangrove	8.6	3,558	306	4,186	360	1.18	628	54
Seagrass	16.0	2,133	342	2,752	441	1.29	619	99
Macroalgae	354.0	1,572	5,565	2,159	7,643	1.37	587	2,078
Coral reef	60.0	1,572	943	1,720	1,032	1.09	148	84
Global coastal ocean	2,750	1,034	28,435	1,028	28,270	0.98	-6	-165
Salt marsh contribution	0.20%	—	0.33%	—	0.47%	—	—	1.0%
Mangrove contribution	0.31%	—	1.08%	—	1.27%	—	—	2.4%

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