

Carbon Cycling in Mangrove Ecosystems

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The carbon cycle in mangrove ecosystems is an important biogeochemical pathway in understanding the links between this forest ecosystem and both the atmosphere and the adjacent coastal ocean. Mangroves are a major habitat in the coastal zone for storing carbon in the soils of their deep forest floor, and for exporting to adjacent coastal seas significant quantities of dissolved inorganic carbon (DIC). The large export of DIC is sufficient to result in adjacent coastal waters becoming a source of carbon dioxide to the atmosphere in tropical and subtropical latitudes.

Keywords: Carbon ; Mangroves ; Biogeochemistry ; Carbon cycling ; Forests ; Coastal ecology

1. Mangrove Forests

Mangrove forests have the largest organic carbon (C_{ORG}) stocks of any tropical terrestrial or marine ecosystem ^{[1][2]}, with a global mean total forest stock of 738.9 ± 27.9 (± 1 standard error, SE) $Mg\ C_{ORG}\ ha^{-1}$, of which 76.5% is stored in the soil, 14.8% vested in aboveground biomass and the remaining 8.7% vested in belowground roots ^[3]. These large amounts of organic carbon reflect high mangrove primary productivity, equal to those of tropical humid evergreen forests and coral reefs ^[2] and rapid rates of soil accretion on the forest floor.

Mangroves function like other forested ecosystems in exchanging gases with the atmosphere but are like other coastal tidal wetlands in exchanging gases and dissolved and particulate materials with adjacent coastal waters. Mangrove ecosystems are thus tightly linked to land, ocean, and atmosphere, yet still, store vast quantities of C_{ORG} and other elements in their soils and forest biomass. While mangroves have some features of both terrestrial and coastal ecosystems, they do have a number of unique ecological and physiological characteristics ^[4] that enable them to efficiently utilize and sequester carbon and nutrient elements, especially nitrogen, phosphorus, iron, and copper ^{[5][6]}.

2. The Biogeochemical Connections

The biogeochemical connections between mangroves and adjacent tidal waters are complex, with variable concentrations of dissolved organic and inorganic solutes and particulates imported and exported by both tides, porewater pumping, and subsurface groundwater advection ^[7]. Tidal circulatory processes, such as a pronounced asymmetry between ebb and flood tides (with the ebb tide being shorter in duration but with stronger current velocity than the flood tide); friction, flow resistance, drag of tidal waters due to the presence of aboveground and belowground structures, lateral trapping (water flowing in and out of a waterway is temporarily retained in the forest to be returned to the main channel later), and lateral gradients due to high evapotranspiration ^[8]. Interrelated processes exert control over sediment transport and deposition: (1) tidal pumping, (2) baroclinic circulation, (3) particle trapping in the turbidity maximum, (4) flocculation, (5) the mangrove tidal prism, (6) physiochemical reactions that destroy cohesive flocs, and (7) microbial production of mucus. Sedimentation of particles is often rapid in quiescent mangrove environments, resulting in a global mean carbon sequestration rate of $179.6 \pm 16.4\ gC\ m^{-2}\ a^{-1}$ ^[3]. Over decades, after initial colonization of a mudflat, the forest develops and the floor builds up further, adjusting to sea-level, subsidence, and uplift, with the net result being several meters of soil ^[9]. Over time, these deposits are penetrated further by mangrove trees and their extensive root systems, various other flora (e.g., microalgae) and fauna, especially burrowing crabs, and highly abundant and productive microbial communities ^[10]. The forest floor is thus ordinarily pockmarked with mounds, burrows, tubes, cracks, fissures, coarse and fine living and dead roots and root hairs, and layered with decayed wood, litter, crawling epifauna, and various forms of micro- and macroalgae. Mangrove deposits contribute about 30% to carbon storage on the coastal margins in subtropical and tropical latitudes ^[11]

Mangrove ecosystems similarly contribute a disproportionate share of various forms of carbon to the coastal ocean in low latitudes. Although they occupy only 1.5% of the world's subtropical and tropical coastal ocean area, mangroves account for about 5% of net primary production and 12% of ecosystem respiration. How much mangrove particulate carbon (i.e., litter) is exported to adjacent waters is well-known ^{[7][12]}, but how much mangrove ecosystems contribute to dissolved

inorganic carbon (DIC) discharging into low latitude coastal waters is unclear ^[11], as are the amounts of carbon gases released from mangrove waters to the atmosphere. How much soil carbon is mineralized throughout the entire soil horizon is poorly understood, with the current knowledge based mostly on measurements of oxygen consumption and DIC and CO₂ production at the surface soil-air/water interface. The functional link between these processes within the forest floor and the adjacent coastal zone has remained similarly unquantified until only very recently ^[13].

3. Carbon Flow through the World's Mangrove Ecosystems and Contributions to the Coastal Ocean

The supersaturation of mangrove waters leads to significant CO₂ (40 Tg C a⁻¹) and CH₄ (0.19 Tg C a⁻¹) release to the atmosphere. The rates of soil mineralization imply that the turnover time of the entire soil C_{ORG} pool is on the order of 25 years. This time frame is supported by empirical findings that mangrove roots decompose slowly ^[14] and that mangrove soil organic matter is composed mostly of allochthonous, highly-refractory, plant-derived material that is high in lignocellulose, and hemicellulose derived mostly from leaves ^[15] that decompose slowly ^[16]. About 58% of soil carbon is mangrove-derived, a value that comes from stable isotope signatures of mangrove soils ^[17], and about one-third of the total soil carbon pool is composed of dead roots ^{[2][10]} that also decompose slowly ^[14]. Assuming that 4 Tg C a⁻¹ of litter is buried and that all POC export is derived from litter, then the remaining 16 Tg a⁻¹ of litter produced must fall to the forest floor where it is presumably incorporated into detritus food webs and eventually mineralized in situ. Wood that falls to the forest floor may be eventually incorporated into the soil pool, but decomposition is very slow ^[18] and likely a minor flux, so it is not included in the mass balance; also not included are benthos and zooplankton production and chemical defenses. The total soil mineralization equates to approximately 140% of mangrove NPP. This anomaly suggests that: (1) inputs from allochthonous marine and terrestrial sources are necessary to balance the mineralization outputs (158 Tg C a⁻¹); (2) a large proportion of the soil pool and its subsequent decomposition is derived from the intertidal mudflat prior to mangrove colonization; (3) wood, algae, and fauna contribute to the soil pool; and/or (4) the subsurface soil mineralization rates and subsequent export data are overestimated. It is also conceivable that root production is underestimated given that the empirical dataset (mostly for estimates of fine roots) is small and that there are some methodological shortcomings in deriving production estimates ^{[10][19]}.

Analysis of the origin of mangrove soil organic matter indicates that about 42% of the organic matter may be derived from external sources ^{[20][17]}. Measurements of radiogenic and stable isotopes in a subtropical Australian mangrove indicate that century-old sequestered carbon is still susceptible to remineralization and tidal export ^[21], supporting the idea that organic carbon deposited prior to mangrove colonization continues to be decomposed, as all mangroves colonize intertidal mudflats that have considerable amounts of soil C_{ORG} ^[6]. Mangrove DIC export contributes nearly 60% of DIC, and 27% of DOC discharged from the world's tropical rivers to the coastal ocean, based on comparison with tropical riverine export values in Huang et al. ^[22]. Mangroves inhabit only 0.3% of global coastal ocean area but contribute 55% of air-sea exchange compared with the global average ^[23], 28% of DIC export, 14% of C burial, and 13% of DOC + POC export, compared to global averages in ^[24] for the world's coastal ocean. Mangrove ecosystems thus contribute a disproportionate share to carbon cycling in tropical seas and in the global coastal ocean.

The mass balance model is only a tool to identify the major and minor pathways of carbon flow in mangrove ecosystems and is not meant to be absolute as it does not distinguish known site-specific differences in soil type, forest composition and age, tidal exchange, bioturbation, and rates of forest productivity. As noted in the tables and figures, there are considerable variations in the mean of most measurements that are not represented in the model. Nevertheless, the model is helpful in suggesting where more research is needed, such as in more measurements of canopy GPP and respiration, preferably using the eddy covariance method, root production, estimates of DOC, CH₄, and especially DIC export, as well as more empirical measurements of subsurface DIC production as well as a clearer understanding of the contribution of groundwater derived from upland and inputs from allochthonous sources, such as the adjacent catchment and coastal zone.

Net ecosystem production (NEP), derived by subtracting all respiratory losses (ecosystem respiration, R_E = R_C + R_S + R_{WATER} + R_{MICROALGAE}) from all mangrove, algal, and phytoplankton gross primary production (GPP) is 628 g C m⁻² a⁻¹ and 54 Tg C a⁻¹ for the world's mangroves. Phytoplankton GPP and R in mangrove tidal creeks and waterways (total area = 7208 km² assuming a forest: waterway area ratio of 12 ^[10]) averaged 1524.4 and 846.9 mg C m⁻² d⁻¹ ^[10]. Subsurface soil respiration was excluded from the ecosystem respiration estimate because (1) the core incubation method used to measure subsurface respiration is crude and may be an overestimate; (2) it is unclear how much porewater DIC is actually derived from groundwater; and (3) the proportional amounts of dissolved carbon derived from

groundwater and from subsurface respiration is unknown.) R_E was $3558 \text{ g C m}^{-1} \text{ a}^{-1}$ for a global R_E of 306 Tg C a^{-1} , and total GPP was $4186 \text{ g C m}^{-2} \text{ a}^{-1}$ for a global GPP of 360 Tg C a^{-1} . The ratio of P_{GPP}/R_E averaged 1.18, indicating that mangrove ecosystems are net autotrophic.

4. Conclusions

The mangrove forest floor is unique, with cracks, fissures, extensive roots, burrows, tubes, and drainage channels, and its dynamic nature facilitates non-steady-state early diagenesis of organic matter in the soil. Rate processes and edaphic conditions (e.g., temperature, redox status, salinity) oscillate in synchrony with tidal flushing and inundation and other factors such as the extent of bioturbation and weather. Rates of soil C_{ORG} mineralization and belowground C_{ORG} stocks are high, indicating rapid accumulation and recycling of organic matter within the deep ($>1 \text{ m}$) soil horizon. On average, carbon respiration across the surface soil-air/water interface equates to only 25% of total carbon mineralized within the entire soil horizon as most respired carbon is released in a dissolved form via advective porewater exchange and/or lateral transport and subsurface tidal pumping to adjacent tidal waters. A revised carbon budget for the world's mangrove ecosystems indicates that subsurface respiration is the second-largest respiratory flux after canopy respiration. The amounts of dissolved carbon released to adjacent tidal waters are sufficient to cause pCO_2 oversaturation of the water column, leading to tropical coastal waters being a source of CO_2 to the atmosphere. Mangrove DIC and DOC discharge contribute disproportionately to dissolved carbon discharge from the world's low latitude rivers to the tropical coastal ocean and contribute 55% of air-sea exchange, 28% of DIC export, 14% of C burial, and 13% of DOC + POC export from the world's wetlands and estuaries to the coastal ocean.

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