

Deconstructing the mangrove carbon cycle: Gains, transformation, and losses

M. F. Adame¹  | N. Cormier² | P. Taillardat^{3,4} | N. Iram^{1,4}  |
A. Rovai⁵  | T. M. Sloey⁶ | E. S. Yando⁶  | J. F. Blanco-Libreros⁷ |
M. Arnaud⁸  | T. Jennerjahn⁹  | C. E. Lovelock¹⁰ | D. Friess¹¹ |
G. M. S. Reithmaier¹² | C. A. Buelow¹ | S. M. Muhammad-Nor^{13,14} |
R. R. Twilley⁵  | R. A. Ribeiro⁵

¹Australian Rivers Institute, Centre for Marine and Coastal Research, Griffith University, Nathan, Queensland, Australia

²School of Natural Sciences, Macquarie University, Sydney, New South Wales, Australia

³Environmental Research Institute, National University of Singapore, Singapore

⁴Department of Biological Sciences, Faculty of Science, Centre for Nature-Based Climate Solutions, National University of Singapore, Singapore

⁵Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, Louisiana, USA

⁶Department of Biological Sciences, Old Dominion University, Norfolk, Virginia, USA

⁷Faculty of Exact and Natural Sciences, Institute of Biology, Universidad de Antioquia, Medellin, Colombia

⁸Institute of Ecology and Environmental Sciences (IEES), UMR 7618, CNRS-Sorbonne University-INRAE-UPEC-IRD, Paris, France

⁹Leibniz Centre for Tropical Marine Research (LZM), Bremen, Germany

¹⁰School of Environmental Sciences, The University of Queensland, St Lucia, Queensland, Australia

¹¹School of Science and Engineering, Tulane University, New Orleans, Louisiana, USA

¹²Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden

¹³Faculty of Science and Marine Environment, Universiti Malaysia Terengganu, Kuala Nerus, Terengganu, Malaysia

¹⁴East Coast Environmental Research Institute, Universiti Sultan Zainal Abidin, Kuala Nerus, Terengganu, Malaysia

Correspondence

M. F. Adame

Email: f.adame@griffith.edu.au

Funding information

Department of Science, Information Technology and Innovation, Queensland Government (Advance Queensland Industry Fellowship)

Handling Editor: Robert J. Miller

Abstract

Mangroves are one of the most carbon-dense forests on the Earth and have been highlighted as key ecosystems for climate change mitigation and adaptation. Hundreds of studies have investigated how mangroves fix, transform, store, and export carbon. Here, we review and synthesize the previously known and emerging carbon pathways in mangroves, including gains (woody biomass accumulation, deadwood accumulation, soil carbon sequestration, root and litterfall production), transformations (food web transfer through herbivory, decomposition), and losses (respiration as CO₂ and CH₄, litterfall export, particulate and dissolved carbon export). We then review the technologies available to measure carbon fluxes in mangroves, their potential, and their limitations. We also synthesize and compare mangrove net ecosystem

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

productivity (NEP) with terrestrial forests. Finally, we update global estimates of carbon fluxes with the most current values of fluxes and global mangrove area. We found that the contributions of recently investigated fluxes, such as soil respiration as CH_4 , are minor ($<1 \text{ Tg C year}^{-1}$), while the contributions of deadwood accumulation, herbivory, and lateral export are significant ($>35 \text{ Tg C year}^{-1}$). Dissolved inorganic carbon exports are an order of magnitude higher than the other processes investigated and were highly variable, highlighting the need for further studies. Gross primary productivity (GPP) and ecosystem respiration (ER) per area of mangroves were within the same order of magnitude as terrestrial forests. However, ER/GPP was lower in mangroves, explaining their higher carbon sequestration. We estimate the global mean mangrove NEP of $109.1 \text{ Tg C year}^{-1}$ ($7.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) or through a budget balance, accounting for lateral losses, a global mean of $66.6 \text{ Tg C year}^{-1}$ ($4.5 \text{ Mg C ha}^{-1} \text{ year}^{-1}$). Overall, mangroves are highly productive, and despite losses due to respiration and tidal exchange, they are significant carbon sinks.

KEYWORDS

blue carbon, litterfall, productivity, roots, sequestration, tidal export, wetlands

INTRODUCTION

A decade ago, mangroves gained global attention as they were identified as one of the most carbon-dense ecosystems on Earth (Donato et al., 2011). They have high productivity and exchange large quantities of carbon with the atmosphere and terrestrial, freshwater, and marine ecosystems through regular tidal inundation (Adame & Lovelock, 2011). The carbon fixed by mangroves can be stored as plant biomass or soil organic matter, transformed through herbivore consumption and microbial decomposition, or exported through tidal exchange (Bouillon et al., 2008; Figure 1).

The fate of mangrove-derived carbon has numerous implications; initially, exports from mangroves were considered important for their role in coastal productivity (Dittmar & Lara, 2001; Lee, 1995). More recently, understanding the carbon cycle within mangroves is beyond ecological importance. The carbon stored in mangroves, known as “Blue Carbon,” can be managed to reduce losses or increase sequestration through avoided habitat loss, restoration, and improved management practices (Macreadie et al., 2021). Policy and funding incentives are increasingly in place for such practices, as these could achieve significant climate change adaptation and mitigation benefits.

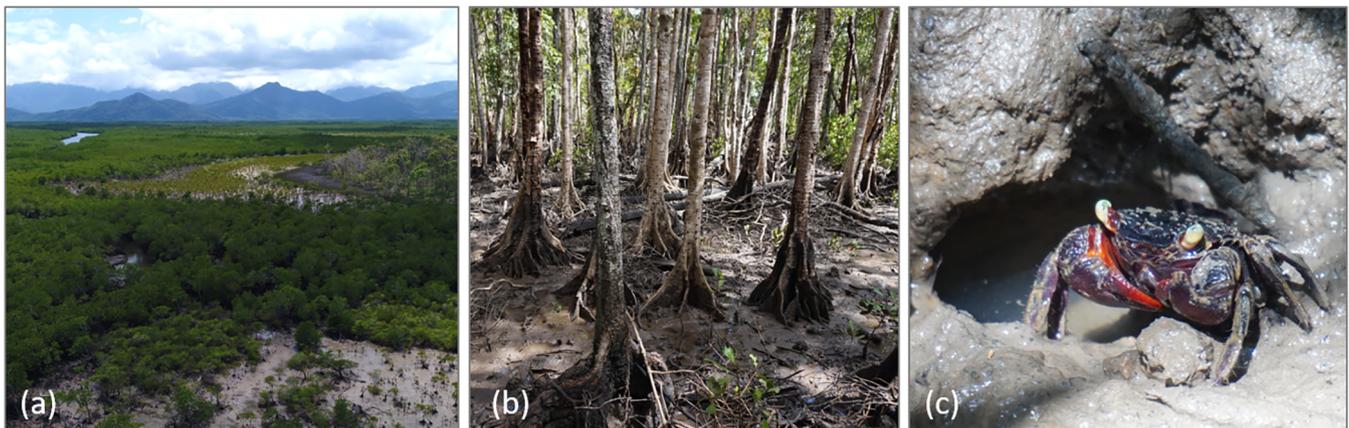


FIGURE 1 (a) Mangroves are frequently inundated by the tides and continually exchange carbon with the coastal zone; (b) mangroves produce woody aboveground and belowground carbon as roots; (c) a large portion of the litterfall can be consumed by herbivores, such as crabs. Photo credit: M. F. Adame.

For instance, restoring mangroves in Australia through tidal reintroduction will contribute to national emission reductions (Lovelock et al., 2022), while Indonesia has set ambitious short-term mangrove restoration targets, partly from Blue Carbon projects (Sidik et al., 2023).

There has been an exponential growth of studies on the mangrove carbon cycle in the past years (Duarte de Paula & Macreadie, 2022), including comprehensive reviews that have provided invaluable frameworks (Alongi, 2020; Bouillon et al., 2008; Twilley et al., 2017). Here, we build on these studies to provide an updated and holistic estimation of the carbon cycle of mangroves. First, we reviewed recent literature on carbon fluxes, including those that were not previously included, such as deadwood accumulation and export, rhizodeposition, food web transfer through herbivory, soil and tree methane (CH₄) emissions, and dissolved inorganic carbon (DIC) export through tidal exchange. Second, we provide information on emerging technologies to measure carbon fluxes, their potential, and limitations. Third, we compared mangrove net ecosystem productivity (NEP) with that of terrestrial forests. Fourth, we updated global estimations with the most current global datasets of the mangrove area (Bunting et al., 2022). Finally, we provide recommendations and guidance on future studies to fill critical knowledge gaps.

This study is divided into seven sections: (1) carbon accumulation from aboveground (woody growth, deadwood, and litter production) and belowground production (root production and soil carbon accumulation), (2) carbon transformation as food web transfer through herbivory and decomposition, (3) carbon losses as lateral export (litterfall, particulate organic carbon [POC], and dissolved organic carbon [DOC] and DIC) and respiration, (4) net ecosystem primary productivity (NPP), gross primary productivity (GPP), and ecosystem respiration (ER), (5) comparison of mangrove carbon NEP with terrestrial forests, (6) updated global mangrove carbon budgets, and (7) knowledge gaps, future directions, and management implications. Sites for the reviewed papers and details of the review process for each section, including search strings, are found in Appendix S1: Figure S1. Values are shown as mean \pm SE (range) unless otherwise stated.

CARBON GAINS

Aboveground production

Woody growth

Mangrove aboveground biomass has been studied for decades. Woody biomass globally has an average of

164 Mg ha⁻¹ or 78.7 Mg C ha⁻¹, with variation not clearly explained by latitude but by regional climate and hydroperiod (Rovai et al., 2021). Woody biomass accumulation in mangroves or tree growth can be measured as changes in diameter at breast height (dbh) or changes in biomass with time. Mangrove tree biomass can be estimated through allometric equations, usually from measurements of tree height and dbh (Komiya et al., 2008). Gains in wood biomass are often converted to carbon units by multiplying biomass by 0.48, which is the average carbon content in mangrove wood (Kauffman & Donato, 2012).

A review of 556 observations showed that mangroves grow (as incremental increases of dbh) at an average of 0.31 cm year⁻¹, ranging from 0.0 to 1.84 cm year⁻¹ (Xiong et al., 2019). At regional scales, mangrove tree growth is mainly influenced by precipitation during the driest time of the year. Within regions of lower precipitation, species composition significantly influenced biomass increments, with *Laguncularia racemosa* growing faster than other species (Xiong et al., 2019). At local scales, tree growth rates are also influenced by geomorphic settings; for instance, in Micronesia, mangroves grow seven times faster in riverine and interior zones compared with fringing zones (Krauss et al., 2007).

In contrast, tree basal area growth is mainly determined by the initial dbh, with larger trees accumulating more biomass than smaller ones (Xiong et al., 2019). Dbh growth is also influenced by tree age, with tree volume in undisturbed tropical mangroves reaching its maximum growth rate after 35 years (e.g., Sillanpää et al., 2017). Overall, mangroves can accumulate woody biomass at a rate from 0.28 to 45.5 Mg ha⁻¹ year⁻¹, with a mean of 8.27 Mg ha⁻¹ year⁻¹, corresponding to 4.0 (0.13–21.8) Mg C ha⁻¹ year⁻¹ (Xiong et al., 2019).

Litterfall production

Litterfall production is the input to the forest floor of senescent leaves, stipules, flower parts (e.g., sepals and buds), propagules, and small branches (<2-cm diameter; Riascos & Blanco-Libreros, 2019; Saenger & Snedaker, 1993; Zhang et al., 2014). Leaves are a significant component of annual litterfall production, accounting for up to 80% of the total (e.g., Alongi, 2011; Félix-Pico et al., 2006; Utrera-López & Moreno-Casasola, 2008). Reproductive structures are the second largest contributor to total litterfall, particularly for trees with large-sized propagules, such as *Rhizophora mucronata* and *Xylocarpus* spp. (Van der Stocken et al., 2019).

Litterfall production can be measured in the field with mesh baskets or traps hanging from the trees or attached to fixed structures placed high enough to avoid

tidal overwash (e.g., Cortés et al., 2019). Trap design varies among studies in the area ($0.25\text{--}1\text{ m}^2$), shape (rounded vs. squared), and framing material (polyvinyl chloride tubes or wooden frames). Changes in the litterfall deposited on the forest floor (standing stock) can be measured by periodically collecting litter accumulated within an established area, such as within a quadrat (Cortés et al., 2019). The combination of litterfall production and changes in standing stock on the forest floor provides information on aboveground productivity, herbivory, decomposition, and lateral fluxes (Ouyang et al., 2023; Zhao et al., 2021).

Mangroves produce litter year-round because they are evergreen forests. However, the volume of litter tends to vary seasonally, with some locations having higher falls during the dry season and others during the wet season (Riascos & Blanco-Libreros, 2019; Ribeiro et al., 2019). Litterfall is not strongly predicted by annual precipitation

but tends to increase where mean annual temperatures are above 25°C (Figure 2). Litterfall production is also associated with the minimum temperature of the coldest quarter, minimum precipitation of the driest quarter, and potential evapotranspiration (Ribeiro et al., 2019). The lowest litterfall values in the subtropics can also be explained by freeze temperatures at higher latitudes, which limit mangrove distribution. Finally, litterfall production can be strongly affected by short or episodic strong disturbances such as storms, wind throws, freezes, droughts, and lightning strikes, events that produce significant falls (Krauss & Osland, 2020; Zhao et al., 2021). At the forest scale, litter productivity is affected by inundation frequency and duration (Hughes et al., 2019).

The geomorphic setting is also a good predictor of litterfall production. The lowest litterfall production can be found at lagoonal and carbonate settings with 7.9 ± 0.4 and $8.6 \pm 0.5\text{ Mg C ha}^{-1}\text{ year}^{-1}$, respectively,

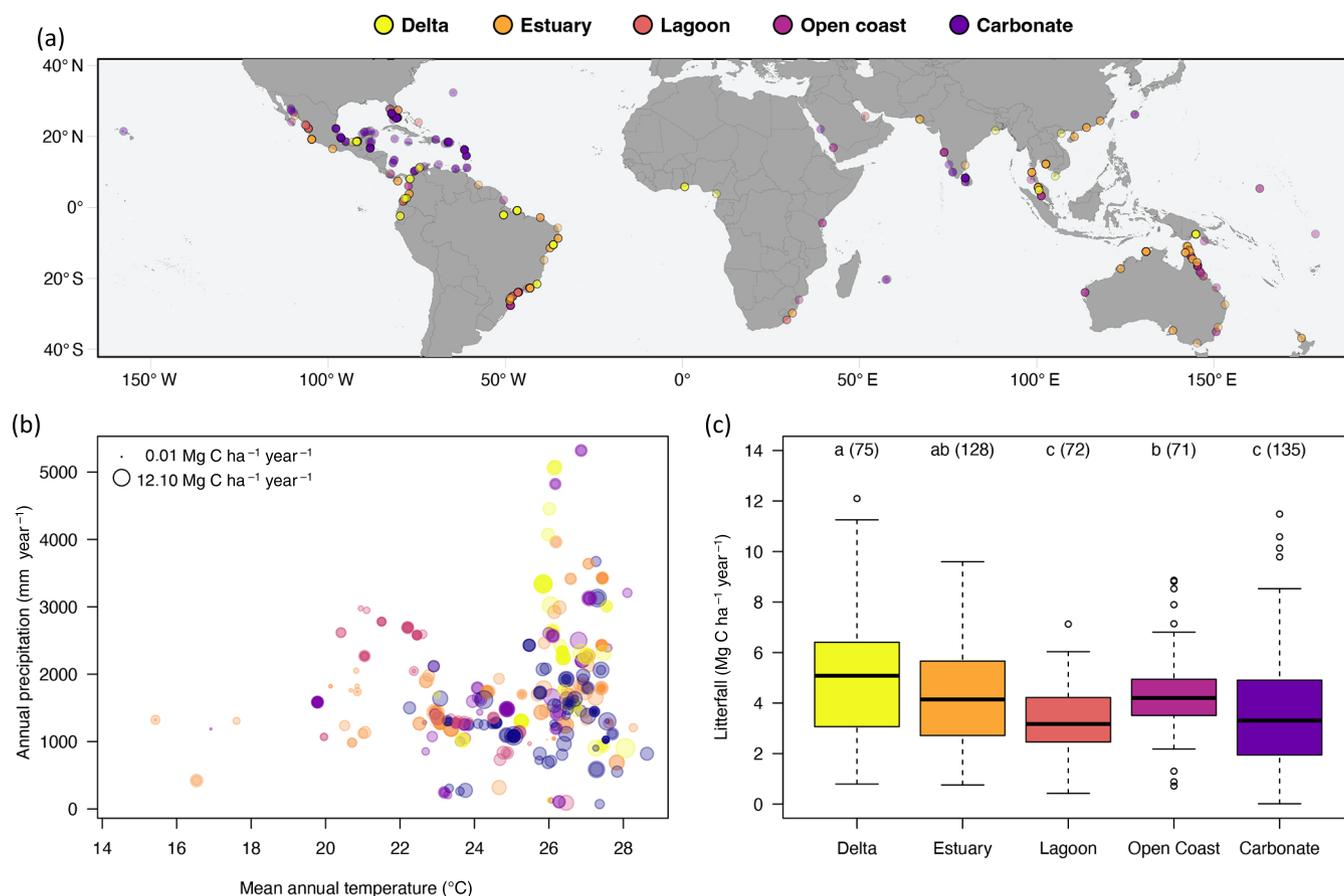


FIGURE 2 (a) Global distribution and (b) variability of mangrove litterfall productivity rates (in megagrams of carbon per hectare per year) relative to mean annual temperature and annual precipitation, and (c) across coastal geomorphic settings. Colors in panels (a) and (b) represent distinct coastal geomorphic settings. The sizes of circles in panel (b) are proportional to productivity rates, and transparency was added to facilitate visualization of overlapping data points. Lowercase letters on top of boxplots show significant statistical differences ($p < 0.05$) and within brackets are the number of observations. Boxplots show the median (thicker middle bar within boxes), the first and third quartiles (bottom and top of boxes), minimum and maximum values (bottom and top whiskers), and outliers (open circles, defined as values below $Q1 - 1.5IQR$ or above $Q3 + 1.5IQR$ where $Q1$, $Q3$, and IQR are the first and third quartiles, and IQR is the interquartile range). Biomass was converted to carbon with a ratio of 0.43 (based on Rodrigues et al., 2015).

which can be explained by reduced or absent riverine inputs and substantial nutrient limitations (Adame et al., 2013). Estuarine and open coast mangroves have intermediate litterfall rates at 10.0 ± 0.4 and 10.5 ± 0.5 Mg ha⁻¹ year⁻¹, respectively, and deltas have the highest rates at 12.2 ± 0.7 Mg ha⁻¹ year⁻¹. High litterfall in deltas is associated with rivers that have low salinity and high nutrients (Twilley et al., 2019), such as in the Atrato River Delta in the Southern Caribbean (Riascos & Blanco-Libreros, 2019) and Sarawak, Malaysia (16.4 Mg ha⁻¹ year⁻¹; Hoque et al., 2015). Expanding on previous reviews (Bouillon et al., 2008; Ribeiro et al., 2019; Saenger & Snedaker, 1993), here, we estimate a global mean litterfall production rate of 9.7 ± 0.2 (0.1–29) Mg ha⁻¹ year⁻¹ corresponding to 4.7 ± 0.1 (0.05–13.9) Mg C ha⁻¹ year⁻¹ ($n = 481$, Figure 2).

Deadwood accumulation

Deadwood contributes to about 2% of the total carbon stocks of mangroves worldwide (Kauffman et al., 2020). However, its long-term contribution to soil carbon stocks is uncertain. A proportion of the deadwood will be buried and incorporated into the soil organic pool, while the rest will be either decomposed on the forest floor or exported through tidal exchange, for instance, during strong storms (Krauss & Osland, 2020).

Deadwood can be measured from standing trees or from wood deposited on the forest floor (downed) with transects, where the number, size, and consistency (hard vs. decomposed) of the wood are measured (Kauffman & Donato, 2012). The deadwood can be converted to biomass by measuring the specific gravity of hard and decomposing wood samples, then converted to carbon units by multiplying biomass by a local value or a default factor of 0.5 (Kauffman & Donato, 2012).

Globally, mangrove deadwood stock calculated from a review of 76 sites has a mean of 16.9 ± 25.4 and 29.9 ± 36.7 Mg ha⁻¹ or 8.4 ± 12.7 and 15.0 ± 18.4 Mg C ha⁻¹ for standing and downed wood, respectively (Mugi et al., 2022). Deadwood accumulates on the forest floor at rates of 3.2 (1.6–5.7) Mg C ha⁻¹ year⁻¹, with the lowest contributions in forests where wood is harvested for either fuel or fishing equipment (Mugi et al., 2022).

Belowground production

Root production and rhizodeposition

Root production is the incremental growth in root mass or length over time. In mangroves, root production

includes aboveground aerial and belowground roots, but here we focus on belowground roots. Root production is a significant control of mangrove soil surface elevation and, thus, essential to understanding mangrove resilience to sea level rise (McKee et al., 2007). Root production is also a central component of the carbon cycle in mangroves, with trees allocating about 30%–40% of their total ecosystem production to roots (Alongi, 2014; Bouillon et al., 2008), although in some locations, allocation can be as high as 70% (Santos et al., 2017). Root production has been less studied than aboveground production (Cormier, 2021).

Direct and indirect techniques can measure mangrove root production. Standard direct techniques include the root ingrowth-core method (>80% of measurements) and the sequential coring method (Arnaud et al., 2023). Ingrowth and sequential coring techniques tend to exclude large roots (>20 mm diameter; Adame et al., 2017), and only a few of these studies include measurements of roots below 50 cm in depth or are conducted for longer than a year (Adame et al., 2017). Indirect techniques include calculating productivity as a percentage of aboveground rates (Clough, 1998), allometric equations, and mass balance approaches (e.g., Lovelock, 2008). These indirect methods are accessible as they do not require intensive fieldwork, but they carry uncertainties; for instance, the root:shoot ratios assumed from allometric equations are inappropriate in some climatic settings (Adame et al., 2017). Finally, new techniques, such as minirhizotrons, are promising, as they can directly analyze root turnover through image software, improving accuracy (Arnaud et al., 2021).

Mangrove fine root (<5 mm) production is 7.7 ± 2.0 (0.46–31.0) Mg ha⁻¹ year⁻¹ or 3.0 ± 0.8 (0.2–12.1) Mg C ha⁻¹ year⁻¹, with variability at the global scale explained by geomorphic settings, air temperature, and precipitation (Arnaud et al., 2023). Stressors, such as nutrient availability and high salinity, can also be significant drivers of root production, although no clear global trends have been found (Arnaud et al., 2023). High salinity may increase carbon allocation to roots, increasing root growth in field experiments (Adame et al., 2014; Ball, 1988) but greenhouse experiments have shown little or no effect (e.g., Ball & Pidsley, 1995; Nguyen et al., 2015). Mangrove root productivity increases with soil nitrogen at the global scale (Arnaud et al., 2023) but not always at the local scale (e.g., Castañeda-Moya et al., 2011; Hayes, Jesse, Tabet, et al., 2017; Lovelock et al., 2009).

Other controlling factors on root production include tree species (Arnaud et al., 2023; Gleason & Ewel, 2002; Pongparn et al., 2016) and stand age, with rapid production rates in young trees and slower rates in adult trees

(Arnaud et al., 2021; Pérez-Ceballos et al., 2018). Mangrove root production increases with precipitation in some locations (Hayes, Jesse, Tabet, et al., 2017; Muhammad-Nor et al., 2019) and drastically decreases following storm damage (Cahoon et al., 2003; Radabaugh et al., 2020). An important regulating factor is tidal inundation duration and frequency, which can increase or decrease root production (Krauss et al., 2013).

Still unaccounted in the carbon cycle is rhizodeposition, which is the organic carbon released into the soil by live roots as exudates, sloughed cells, and mucilage (Dijkstra et al., 2021). Root exudates can represent between 1% and 20% of the net primary productivity of terrestrial forests (Aoki et al., 2012; Phillips et al., 2008) and are disproportionately abundant in coastal wetlands, such as seagrasses (Sogin et al., 2022). Root exudates may increase dissolved carbon in the porewater (Abril & Borges, 2019) and increase carbon trapped as microbial biomass (Dijkstra et al., 2021). In laboratory experiments, root exudates have been measured in mangrove roots of seedlings grown in the laboratory (Haoliang et al., 2007; Liu et al., 2022). Root exudates in mangroves have yet to be measured *in situ*, as they could contribute significantly to the soil carbon dynamics (Arnaud et al., 2023).

Soil organic carbon accumulation

One of the most extensive and permanent carbon stocks in mangroves is in their soils. Mangrove soils have high local (autochthonous) and external (allochthonous) inputs of organic matter, which can be preserved under their anoxic conditions (Bouillon et al., 2003). Soil organic carbon can account for between 50% and almost 100% of the total mangrove carbon stock (Kauffman et al., 2020). Soil organic carbon can be stored for centuries or even millennia (e.g., Adame et al., 2021), making mangrove soils a long-term carbon sink. Soil organic carbon is reported as stock (i.e., concentration per unit area) and less often as a carbon accumulation rate (CAR, i.e., accumulation per unit area and time). A stock measurement is a proxy of the potential carbon to be released as CO₂ upon mangrove degradation or if converted to another land use. In contrast, a CAR reports how much carbon accumulates in the soil over time or the accumulation potential lost. The former is, therefore, a quantitative measure of the “vulnerability” potential of remineralization of organic matter, while the latter is a measure of the “mitigation” potential of mangroves (Jennerjahn, 2020).

A commonly used method to describe soil carbon characteristics from mangroves is measuring stocks through sediment coring and analyses of organic soil

carbon content and bulk density. It is technically relatively easy, requires moderate financial resources, and can be conducted following internationally standardized protocols (e.g., Kauffman & Donato, 2012). Additionally, the measurement of carbon stocks through time or space-for-time substitution (i.e., plots with different ages, e.g., Adame et al., 2018) can be used to estimate soil carbon sequestration.

Measuring CAR can be done by age-dating soil cores, mainly through costly analyses of radioactive isotopes (²¹⁰Pb, ¹³⁷Cs, ¹⁴C). Moreover, age dating may not be possible in all geomorphic settings due to the concentrations of isotopes below detection limits, sites with high sediment mixing or erosion, or in sites with deep soil subsidence (for an overview of methods and constraints, see Arias-Ortiz et al., 2018). Other techniques for measuring CAR include the assessment of soil accumulated over known event horizons (e.g., a volcanic ash layer; Adame et al., 2015) and the use of surface elevation tables that measure soil accumulation at annual-decadal time scales from a fixed benchmark (Lovelock et al., 2014). Because of methodological constraints and costs, there is much less global CAR than carbon stock data.

Globally, carbon stocks are similar among geographical regions and continents, but significant differences are observed among coastal geomorphic settings (Hayes, Jesse, Hawke, et al., 2017; Kusumaningtyas et al., 2019; Figure 3). Carbon stocks are significantly lower in deltas of large rivers and higher in carbonate settings (Twilley et al., 2018). However, most available estimates are based on the first top meter of soil, but deltaic mangroves may have much deeper soils (Kauffman et al., 2020). CAR is also higher in the Indo-West Pacific compared with the Atlantic East Pacific region (Figure 3b). Similar to carbon stocks, CAR is better explained by geomorphic settings, with lower rates in arid settings and high rates in small deltas and tidal systems. Global reviews have obtained similar CAR averages of 2.3 (0.1–6) Mg C ha⁻¹ year⁻¹ (Jennerjahn, 2020) and 2.4 Mg C ha⁻¹ year⁻¹ (MacKenzie et al., 2021).

The differences in carbon stocks and CAR among geomorphic settings depend on the supply and deposition of external mineral sediment (Breithaupt et al., 2012; Taillardat, 2022). Mineral sediment dilutes carbon concentration in the deposits but also leads to high sedimentation, bulk density, and burial rates, which can result in high carbon stocks (MacKenzie et al., 2016). Therefore, carbon density tends to be lower and CAR higher in deltaic and tidal systems because of high external inputs and sedimentation rates (Jennerjahn, 2020). Contrastingly, carbon density tends to be higher and CAR lower in lagoons and carbonate settings because of the low external input of mineral sediments.

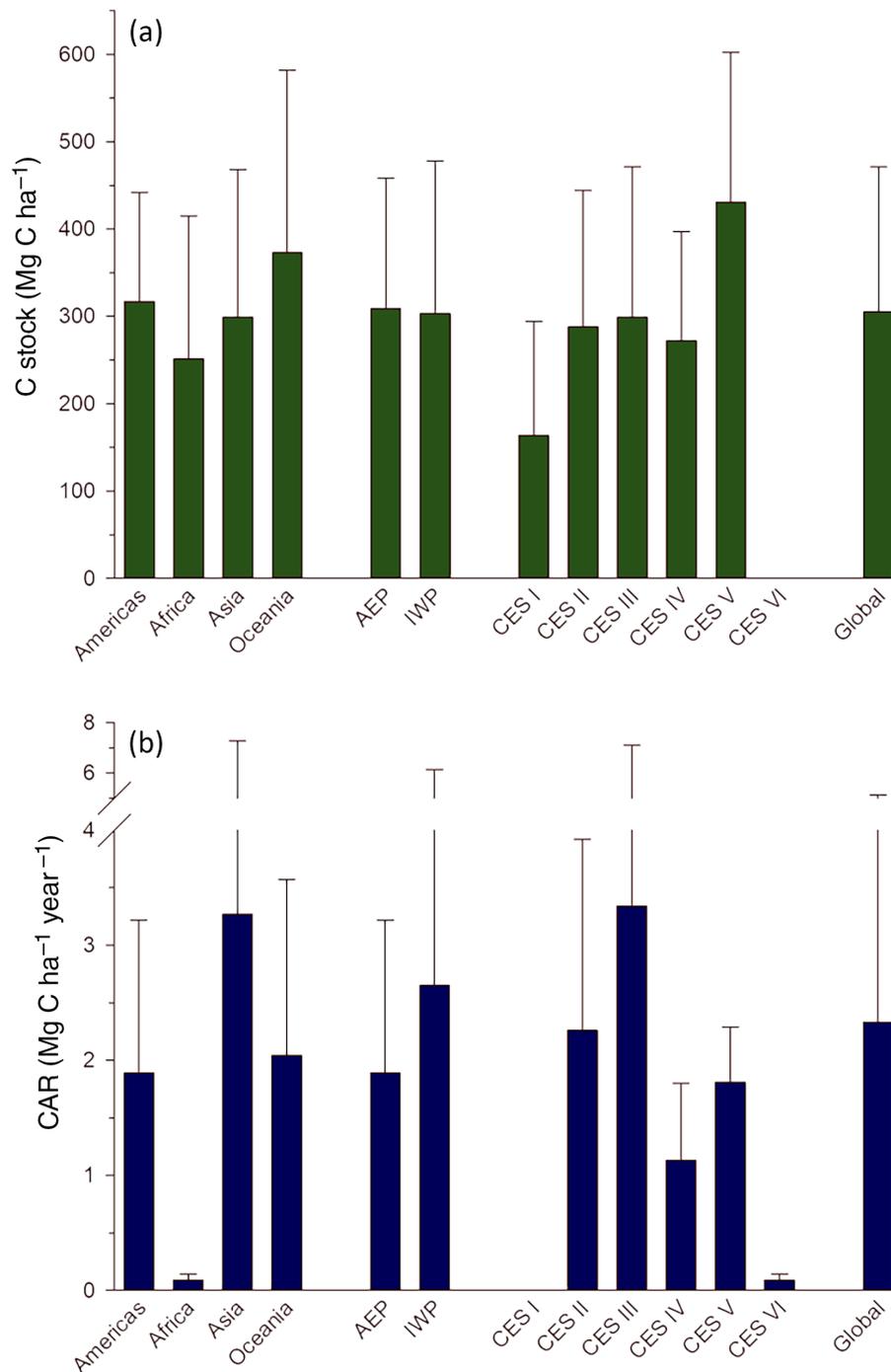


FIGURE 3 (a) Carbon stocks (upper 1 m) and (b) carbon accumulation rates (CARs) of mangrove sediments of the world listed by continent, biogeographic region and coastal geomorphic setting, and global averages. AEP, Atlantic East Pacific; CES, coastal geomorphic setting (I, deltas; II, small deltas; III, tidal systems; IV, lagoons; V, carbonate; and VI, arctic); IWP, Indo-West Pacific. Values are mean + SD. No data are available for C stocks for CES VI and CAR for CES I. Modified from Jennerjahn (2020).

CARBON TRANSFORMATIONS

Food web transfer through herbivory

Herbivory is an essential component within the mangrove carbon cycle; without its inclusion, primary productivity and detrital export can be underestimated

(Robertson, 1986). Herbivory occurs in leaves but also in propagules, wood (Feller, 2002), and roots (Cannicci et al., 2008; Figure 4). Herbivory can occur before or after the leaves or propagules fall, with losses before leaf fall ranging from 3% to 20%, similar to rates in some tropical rainforests (Feller & Chamberlain, 2007; Johnstone, 1981). Severe defoliation of mangrove leaves by



FIGURE 4 Herbivory of mangrove trees, deadwood, and leaf litter in mangrove forests by fungi, termites, and mollusks. Photo credit: A. Rovai.

caterpillars (larval *Lepidoptera*) has been observed in *Avicennia marina* stands in Queensland, Australia (West & Thorogood, 1985), Hong Kong (Anderson & Lee, 1995), Singapore (Murphy, 1990), and in forests of *Excoecaria agallocha* in Indonesia (Whitten & Damanik, 1986). Pre-fall herbivory may differ among mangrove species, age of the leaf material, temperature, and the feeding ecology of the herbivores present (Feller & Chamberlain, 2007) and has been estimated in forests in tropical Australia at $0.11 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (Robertson & Duke, 1987).

After fall, leaf consumption averages 4.1 ± 2.2 (0.1–15) $\text{Mg ha}^{-1} \text{ year}^{-1}$ or 2.0 ± 1.1 (0.3–7.2) $\text{Mg C ha}^{-2} \text{ year}^{-1}$, with the highest values found in mangroves where sesarmid crabs are abundant, which can consume up to 87% of the total litterfall of the forest floor (Lee, 1998; Malley, 1978; Thongtham et al., 2008; Table 1). Similar to pre-fall herbivory, the herbivory of fallen leaves differs by litter age; for example, the diet of the crab *Aratus pisonii* is dominated by fresh, not senescent, *Rhizophora mangle* leaves (Sandoval et al., 2022).

Although the most conspicuous herbivory occurs on the leaves, many propagules can also be consumed. For instance, 5%–60% of mangrove propagules can be eaten by insects before dispersing or establishing (Sousa et al., 2003; Yando et al., 2021; Appendix S1: Table S1). Thus, some of the mangrove production may be consumed by organisms, while another portion (e.g., crab faces, exoskeletons) is accumulated in the

forests as organic matter (Chen & Ye, 2010), and the rest is exported to the coastal zone (Ouyang et al., 2023; Yando et al., 2021).

Root and leaf decomposition

Decomposition is the breakdown of organic tissue, resulting in the loss of organic material in the form of CO_2 , CH_4 , POC, and DOC, some of which can be transferred into porewater and exported to the coastal zone (Kristensen & Alongi, 2006). Organic matter decomposition is associated with climate, with the highest decomposition rates when temperatures exceed 25°C (Ouyang et al., 2023). Decomposition rates are also affected by benthic macrofauna, which can increase decomposition, and by phenolic compounds of litter, which can slow it (Friesen et al., 2018).

Decomposition is measured as the difference in biomass of a known quantity of plant material over time. The plant material can be left on site on the soil surface, submerged or buried (Middleton & McKee, 2001; Simpson et al., 2023). Studies of decomposition in mangroves have been conducted in leaves, roots, and downed wood, with leaves decomposing the fastest, especially when they are not buried (Simpson et al., 2023). Although poorly studied, leaf decomposition appears not to be influenced by latitude but by leaf composition (Simpson et al., 2023).

TABLE 1 Litterfall consumption rates and percentage of total litterfall consumed by detritivores in mangrove ecosystems.

Dominant detritivore	Litterfall consumption (Mg ha ⁻¹ year ⁻¹)	Litterfall consumed (% total)	Source
<i>Sesarma</i> spp.	1.5	27	Robertson (1986)
<i>Ucides cordatus</i>	14.9 ^a	81.3	Nordhaus et al. (2006)
<i>Sesarma meinerti</i>	2.8	43.6	Emmerson and McGwynne (1992)
<i>Aratus pisonii</i>	n.a.	2.2–5.4	Faraco and Da Cunha Lana (2004)
Sesarmid	4.8 ^a		Chen and Ye (2008)
<i>Helograpsus haswellianus</i>	0.66 ^a	9.4	Imgraben and Dittmann (2008)
Sesarmid	n.a.	79	Ashton (2002)
Sesarmid	n.a.	87	Thongtham et al. (2008)
n.a.	0.11	2.1	Robertson and Duke (1987)

Note: n.a. = species that caused the herbivory were not identified.

^aDaily data extrapolated to annual values.

Root decomposition is sensitive to porewater salinity, with rates declining exponentially with increasing salinity (Ouyang et al., 2017). Also, larger diameter coarse roots decompose slower than fine roots (Huxham et al., 2010; Zhang et al., 2021). Root decomposition is similar throughout the sediment column (0–40 cm; Middleton & McKee, 2001; Poret et al., 2007) but varies among species. In mangroves in Gazi Bay, Kenya, the roots of *A. marina* lose a greater proportion of the mean dry weight of roots (76%) than *Bruguiera gymnorrhiza* (47%) and *Ceriops tegal* (44%) after one year of burial (Huxham et al., 2010).

Mangrove root decomposition tends to increase with nutrient availability. In the Florida Everglades, USA, roots tend to decompose faster where phosphorus and inundation frequency are higher (Poret et al., 2007), while in Kenya, the roots of *B. gymnorrhiza* that were enriched with nitrogen decomposed faster than unenriched control roots (Huxham et al., 2010). Finally, the decomposition of roots is explained by the soil density, with slower decomposition in dense soils (Ola & Lovelock, 2021).

The factors influencing root decomposition are relatively new areas for investigation. Classifying roots according to their functions (absorptive vs. transportive) could improve our estimations of production and decomposition, as different root types may grow and decay differently (Zhang et al., 2021). Additionally, the site-specific effects of decay rates have been observed; thus, more studies would help identify global trends in root decomposition.

Mass loss during root decomposition ranges from 10% to 76% of initial mass loss one year after burial (Huxham et al., 2010; Middleton & McKee, 2001), corresponding to a mean and range of 1.6 (0.06–14.1) Mg C ha⁻¹ year⁻¹ (based on mean root production under section “Root

production and rhizodeposition” and decomposition rates of 0.08%–0.26% per day by Ouyang et al., 2017). However, these values have been estimated from a small dataset, so should be taken cautiously. For leaf decomposition, rates are difficult to calculate as most of the litter in mangroves is likely to be exported or consumed and the proportion of leaves remaining on the forest floor to decompose is unknown. Nevertheless, mean decay roots of leaf litter are estimated at 0.009 ± 0.0005 (Simpson et al., 2023).

CARBON LOSSES

Lateral carbon export

A portion of the carbon fixed in mangroves will not be consumed or stored but exported into the coastal ocean (Adame & Lovelock, 2011). Some of this carbon will be in the form of litter, and some will be POC, DOC and DIC. Additionally, very large materials, such as trunks of trees, can also be exported after extreme weather events, such as tropical storms (Krauss & Osland, 2020). The fate of each one of these components, whether burial or consumption, will differ based on the characteristics of the material (e.g., size, composition) and the receiving environment (e.g., anoxic vs. oxic; Lovelock et al., 2017).

Lateral carbon export is generally measured by sampling water as it moves in and out of the forests. Early studies used flumes, island enclosures, incubation chambers, and porewater profiles (Adame & Lovelock, 2011). Recent studies quantified lateral carbon export at larger spatial scales, such as creeks, estuaries, or whole catchments (Reithmaier et al., 2020; Santos et al., 2019; Sippo et al., 2016). The most used method to quantify exchange between small mangrove creeks and the coastal ocean is

the Eulerian method, which integrates changes in dissolved carbon concentrations and water discharge volume over time (e.g., Ohtsuka et al., 2020; Taillardat et al., 2018). In large estuaries, the Lagrangian method is used, which follows the particle movement measuring concentrations along transects (Ho et al., 2017). In combination with Eulerian and Lagrangian methods, isotope mass balances, for example, using ^{13}C and ^{222}Rn , have been used to estimate mangrove porewater contributions to lateral dissolved carbon fluxes (e.g., Ray et al., 2020; Reithmaier et al., 2020; Santos et al., 2019). The findings obtained in such different spatial areas complicate the extrapolation of fluxes at the forest scale (Adame & Lovelock, 2011) but provide clear evidence of carbon export as a key process in mangroves.

Export of litterfall and POC

Litterfall and POC exported from mangroves are evident forms of carbon loss in mangroves. POC results from litterfall decomposition and the accumulation of organic matter, such as algal detritus. Mangrove litter has low value as a food source, and despite the original claims that it fuels coastal productivity, it is mostly recalcitrant (e.g., Baker et al., 2021). The fate of mangrove litter and POC in the coastal zone is a challenge that needs to be quantified, but it appears to be strongly driven by tidal currents (Hyndes et al., 2014). Stable isotope approaches have been commonly used to trace mangrove litter and POC movements in the coast, but better outcomes have resulted from combining multiple tracers, including organic markers and eDNA (He et al., 2016; Reef et al., 2017).

Litterfall exports can be assessed through changes in litterfall on the forest floor or continuous measurements of litter and POC mass as it is flushed out of the forest during ebb tides (Adame & Lovelock, 2011). However, these methodologies do not allow to distinguish among the portion of litter that is consumed, decomposed, or exported. Litterfall can be separated from POC by filtering water samples (e.g., 0.7- μm filters; Kristensen, Bouillon, et al., 2008) and retaining the accumulated POC material on a filter, which can be analyzed for carbon content (mass per volume). Fluxes of litter and POC over time can be obtained from estimates of the area and frequency of tidal inundation.

Similar to litterfall production, there are spatial variations in the export of litter and POC. Litterfall export is usually higher in mangroves in regions with high mean annual temperatures and low precipitation, such as in arid climates (Adame & Lovelock, 2011). Comparatively, POC export varies with tidal flushing, geomorphology,

watershed size, currents, and storms (Krauss & Osland, 2020; Romigh et al., 2006; Taillardat et al., 2018), with the tidal range being a crucial driving force (Dittmar & Lara, 2001). Temporal variations in litter and POC export are also evident. For instance, in the Philippines, 42% of carbon outflow as POC occurs during a few months of the wet season (Ray et al., 2021), and some forests have very low or even POC imports during the dry season (Akhand et al., 2021; Ayukai et al., 1998). Globally, POC export is estimated at 0.59 ± 0.42 (import of 0.001 to export of 1.4) $\text{Mg C ha}^{-1} \text{ year}^{-1}$, and litter export at 1.0 ± 0.76 ($0.001\text{--}2.4$) $\text{Mg C ha}^{-1} \text{ year}^{-1}$ (Adame & Lovelock, 2011).

DOC and DIC export

DIC and DOC are produced from the decomposition of organic matter (Kristensen, Bouillon, et al., 2008), for example, through the leaching of root compounds into pore water (Kristensen & Alongi, 2006), which can be exported to surface waters and subsequently to the coastal ocean during tidal exchange (Maher et al., 2013). DOC could be important for fuelling coastal production (Then et al., 2020), although a significant fraction of the DOC exported is not consumed but remains trapped within coastal sediments (Duarte et al., 2005; Maher et al., 2018). However, the exact proportion of DOC that is sequestered versus consumed is currently unknown.

Exported inorganic carbon constitutes primarily of carbonate alkalinity (mostly as HCO_3^- at $\text{pH} < 8$) and pCO_2 . Exported carbonate alkalinity increases the buffer capacity and represents a long-term carbon sink (>1000 years; Fakhraee et al., 2023; Reithmaier et al., 2023; Sippo et al., 2016). In contrast, exported pCO_2 can partly be outgassed back to the atmosphere or form carbonic acid (H_2CO_3^-), which can then dissociate into bicarbonate (HCO_3^-), acidifying surrounding waters but also acting as a long-term carbon store in the ocean. The fractions of each of these processes remain to be quantified.

Dissolved carbon concentrations change throughout the tidal cycle, with the highest concentrations measured during low tides of cycles of large amplitudes (Taillardat et al., 2018). Exports vary seasonally (Belliard et al., 2022; Liu & Lai, 2019), and episodic rain events can increase DIC but decrease DOC exports (Reithmaier et al., 2021). The patterns of DIC and DOC exports cannot be explained solely by temperature, precipitation, tidal amplitude, or carbon stocks (Alongi, 2020). However, DOC export decreases with increased nutrients in the water, probably due to increased microbial consumption (Adame et al., 2012). Globally, mangroves export 0.27 ± 0.88 $\text{Mg C ha}^{-1} \text{ year}^{-1}$ of DOC, ranging from an import of 0.67 to an export of

1.4 Mg C ha⁻¹ year⁻¹ (Adame & Lovelock, 2011). Lateral DIC export rates ($n = 26$ sites) are an order of magnitude higher, ranging from an import of 4.2 to an export of 46 Mg C ha⁻¹ year⁻¹, with a global average of 6.8 ± 2.1 Mg C ha⁻¹ year⁻¹ and median of 3.6 Mg C ha⁻¹ year⁻¹ (Reithmaier et al., 2023). However, the data set has a significant variance, with many outliers, underlining the need for more lateral export measurements.

Respiration

Soil respiration, either as CO₂ or CH₄, is the release of gaseous carbon in the atmosphere from the chemical oxidation of organic matter and the respiration of microbes, live roots, or fauna (Malerba et al., 2022). Soil respiration in mangroves is commonly measured through one of the following methods: (1) enclosed chambers, (2) micrometeorological data, (3) laboratory experiments, and (4) spaceborne measurements.

The enclosed chamber method involves deploying a box or cylinder on the soil surface, leaving a headspace for gas accumulation. The efflux of CO₂ and CH₄ is analyzed externally by gas chromatography or through a nondispersive infrared (NDI) sensor. This method allows detailed small-scale data (Oertel et al., 2016) but may not capture ebullition events that may account for a large proportion of the CH₄ emitted. The chamber method, although relatively simple, can be time-consuming and cannot directly distinguish between autotrophic (roots) or heterotrophic (microbial) respiration. A way to overcome this limitation is to simultaneously measure locations with and without plants or with and without evident microbial communities (e.g., cyanobacterial mats; Lovelock, 2008).

Micrometeorological techniques include eddy covariance measurements and open-path Fourier transform infrared spectroscopy (FTIR). The eddy covariance is a tower deployed on-site with a gas analyzer and a 3D ultrasonic anemometer that continuously measures fluxes over an area of square kilometers (see *NEP*, *GPP*, and *ER*). The FTIR is an instrument containing a radiation source that emits an infrared spectrum modified by CO₂ and CH₄ fluxes from the soil. A telescope receives these modified signals and generates gas emission data (Griffith et al., 2012). Eddy covariance towers can provide long-term and continuous data, but do not distinguish among different pathways of uptake or emissions and can be expensive and difficult to maintain.

Laboratory experiments quantify the effect of one or more parameters, for example, moisture or nutrients, under controlled conditions. However, the disturbance to the soil physical structure and changes in microbial communities while transporting and manipulating the data

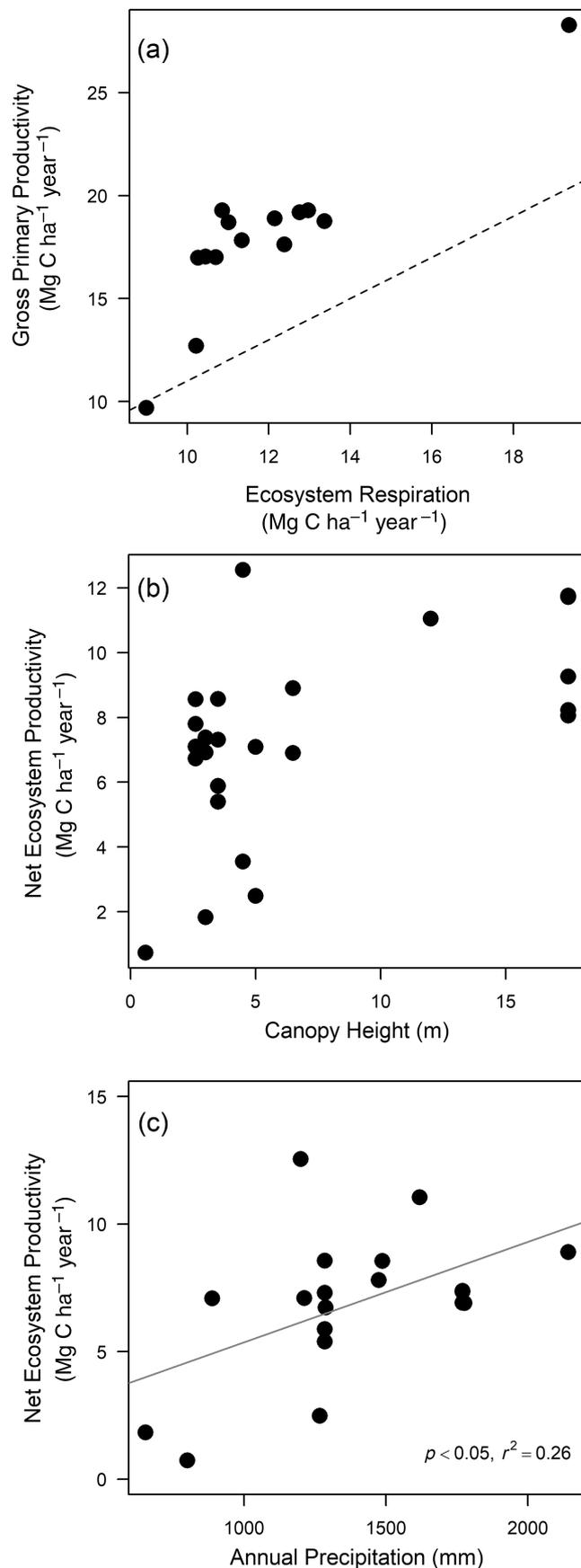
can affect the emissions rates (Oertel et al., 2016). Finally, satellite remote sensing can continuously measure CO₂ and CH₄ fluxes over large spatial scales (Frankenberg et al., 2005). Nevertheless, this method may require on-ground measurement validation to achieve realistic results (Oertel et al., 2016).

Soil respiration is regulated by the soil-atmosphere gas concentration gradient and environmental factors, including temperature, humidity, vegetation, and the soil carbon-to-nitrogen ratio (Oertel et al., 2016). From these parameters, the canopy leaf area index—which reflects forest productivity and soil moisture are important factors influencing CO₂ fluxes at the ecosystem scale (Leopold et al., 2015; Lovelock et al., 2014). Soil CO₂ emissions are usually lower in seaward than in landward mangroves (Cameron et al., 2019). Temperature also moderates CO₂ emissions, which can be doubled with slight temperature increases (e.g., from 28 to 30°C; Pongpam et al., 2009; Van Vinh et al., 2019). Finally, soil disturbance, such as modifications of flooding regimes, erosion, and direct excavations, can increase the oxygen of the soil and promote root and soil organic matter degradation, causing increased emissions (Bulmer et al., 2017; Lovelock et al., 2011).

The soil CH₄ fluxes in mangroves decrease with salinity, biomass, NEP, and carbon-to-nitrogen ratio while increasing with organic matter content (Al-Haj & Fulweiler, 2020). At the local scale, salinity is one of the most critical drivers of CH₄ emissions as high sulfate levels in marine water leads to sulfate-reducing bacteria outcompeting methanogens and methanogenesis for substrate uptake (Malerba et al., 2022; Rosentreter, Borges, et al., 2021). Additionally, an important microbial pathway is anaerobic CH₄ oxidation to CO₂ in mangrove soils, which may reduce CH₄ emissions (Zhang et al., 2022). Plants can also be essential transport conduits for CO₂ and CH₄ fluxes (Van Vinh et al., 2019), with their importance varying among mangrove species; for instance, the branches and roots of *A. marina* increased CH₄ fluxes from the soil (Jeffrey et al., 2019; Kreuzwieser et al., 2003). Finally, crab burrows can facilitate CH₄ efflux by increasing the sediment-air contact area (Kristensen, Flindt, et al. 2008; Pülmanns et al., 2014). Globally, mangrove mean soil respiration is 3.9 ± 1.1 (2.2–9.6) Mg C ha⁻¹ year⁻¹ of CO₂ and 0.04 ± 0.19 (0.06 to 0.86) Mg C ha⁻¹ year⁻¹ of CH₄ (Rosentreter, Borges, et al., 2021; Shiau & Chiu, 2020).

NEP, GPP, AND ER

Fluxes of gaseous carbon (CO₂ or CH₄) from mangroves can be used to determine ecosystem carbon balance with eddy covariance flux towers. These micrometeorological stations are installed above the mangrove canopy to



measure continuously turbulent fluxes as variations in gas concentrations. The eddy covariance technique measures the total vertical exchange of carbon at the ecosystem scale surrounding the tower, which includes GPP and the sum of all ER from plants (i.e., autotrophic; R_a), soil organic matter decomposition (i.e., heterotrophic; R_h) but also from fauna, and open water—if present within the tower footprint. The net ecosystem exchange (NEE) equates to its overall CO₂ balance ($NEE = ER - GPP$). The NEP also equates to an overall CO₂ balance, but the two variables of the equation are reversed ($NEP = GPP - ER$). Hence, a negative NEE and a positive NEP mean that the ecosystem is absorbing more CO₂ than what it releases to the atmosphere (Chapin et al., 2006). The net ecosystem carbon balance (NECB) can also be calculated as the sum of NEP minus aquatic carbon exports and the net CH₄ balance. These continuous measurements help determine the daily, seasonal, and interannual variations of carbon fluxes.

Annual ecosystem carbon fluxes from mangroves have been obtained globally (Figure 5) with a median NEP of 7.4 Mg C ha⁻¹ year⁻¹ ($n = 32$). The NEP ranges from 0.74 Mg C ha⁻¹ year⁻¹ in a semiarid, hypersaline mangrove of New Caledonia (Leopold et al., 2017) to 12.6 Mg C ha⁻² year⁻¹ in a subtropical estuarine mangrove in China (Zhu et al., 2021). The lowest values for GPP and ER are in New Caledonia, which has a tenth of the median global carbon uptake of mangroves. The highest GPP and ER values of 28.3 and 19.4 Mg C ha⁻² year⁻¹ were measured in a subtropical mangrove near Hong Kong, dominated by *Kandelia obovata* and *A. marina* (Liu & Lai, 2019). The high GPP at this site was explained by high freshwater and nutrient inputs from the adjacent rivers and the ability of *K. obovata* to use diffuse radiation efficiently (Liu & Lai, 2019). Besides these two extreme sites, GPP values from other sites range between 16 and 20 Mg C ha⁻² year⁻¹ with an ER between 10 and 15 Mg C ha⁻² year⁻¹. Despite geomorphic, climatic variability, disturbance by insect outbreaks (Lu et al., 2019) and hurricanes (Barr et al., 2012), all forests analyzed so far suggest that mangroves are net annual carbon sinks (Figure 5).

Annual precipitation explains some of the variability in CO₂ fluxes, with higher precipitation associated with

FIGURE 5 (a) Annual gross primary production (GPP) and annual ecosystem respiration (ER). The dashed line represents $GPP = ER$. All points above this line have net ecosystem carbon uptake ($GPP > ER$). (b) Net ecosystem productivity ($NEP = GPP - ER$) against canopy height and (c) annual precipitation. Linear regressions were only conducted on data that were normally distributed.

taller trees and higher NEP (Figure 5c,d). However, this trend is not statistically significant, probably because of scarce data from mangroves near the Equator, where trees are the tallest and most productive (11.5° N and 21° S). Nevertheless, rainfall has been identified as the key driver explaining the distribution of mangrove carbon stocks globally (Sanders et al., 2016). High rainfall is thought to stimulate both primary productivity (above- and belowground biomass) but also minimize organic matter decomposition in the oxygen-depleted soils and potentially increase root production and respiration (Arnaud et al., 2023). Air temperature and vapor pressure deficit also affect CO₂ fluxes, increasing soil respiration (Van Vinh et al., 2019). High temperature and vapor deficit values reduce stomatal conductance and, thus, photosynthesis (Niu et al., 2012). Like terrestrial forests, the relationship between NEP, vapor pressure deficit, and air temperature in mangroves follows a convex pattern. The most favorable vapor pressure deficit conditions are between 1.4 and 2.3 kPa, depending on the mangrove species, and between 26.8 and 29.8°C (Leopold et al., 2017; Liu & Lai, 2019; Zhu et al., 2021).

Tidal inundation also affects CO₂ fluxes, with lower ER values during neap tides and when the mangroves are inundated (Gnanamoorthy et al., 2020; Liu & Lai, 2019; Zhu et al., 2021). Lower ER is a function of reduced oxygen availability, favoring heterotrophic respiration and reducing gas diffusion (Kristensen, Bouillon, et al., 2008). Moreover, in some sites, GPP is greatest during high tides, such as in semiarid, hypersaline mangroves, where tidal inundation increases productivity (Leopold et al., 2017). The GPP is also highest in tropical mangroves with high nutrient inputs, which facilitate high rates of primary production (Liu & Lai, 2019).

The seasonal variability of CO₂ fluxes is complex. Two sites (Yucatan, Mexico and Pichavaram, India) had net CO₂ emissions (GPP < ER) during dry periods (Alvarado-Barrientos et al., 2021; Gnanamoorthy et al., 2020), which could be explained by high salinity that

causes water stress, reducing plant productivity. In comparison, other sites had lower CO₂ emissions during the dry season (Leopold et al., 2017; Liu & Lai, 2019). These results suggest that mangroves could overcome water stress during dry periods if they have frequent tidal inundation. Additionally, increased microbial activity, thus, increased ER could counteract high GPP during wet periods (Saleska et al., 2003), resulting in lower NEP than expected. Greater DIC, pCO₂, and CO₂ efflux of some mangroves during the wet season suggest a high microbial activity, resulting in high ER values (Linto et al., 2014; Taillardat et al., 2018).

COMPARISON WITH TERRESTRIAL FORESTS

Terrestrial NPP is the balance between GPP and autotrophic respiration (Ra). Terrestrial NPP, including trees plus fine roots, ranges from 4.2 to 16.5 Mg C ha⁻¹ year⁻¹ (Malhi et al., 2011), which is within the same range as our estimates of mangrove NEP of 0.7–12.6 Mg C ha⁻¹ year⁻¹. Similarly, the GPP and ER of mangroves are within the same order of magnitude as terrestrial forests (Figure 5a, Table 2). However, the ratio ER/GPP is lower in mangroves (0.65) compared with other terrestrial forests (>0.76), which explains higher carbon sequestration. There are little data for tropical mangroves close to the Equator, suggesting that the most productive mangroves were not included; thus, our global NEP, GPP, and ER are likely underestimated.

Similar to NEP, other carbon cycle components differ between terrestrial forests and mangroves. For instance, litterfall production in deltaic, estuarine, and open coast mangroves is higher than for tropical terrestrial forests, although litterfall in lagoonal and carbonate settings is lower in mangroves (Anderson-Teixeira et al., 2016; Anderson-Teixeira et al., 2021). In terrestrial tropical forests, the production of woody biomass ranged between 0.6 and

TABLE 2 Annual median ± SD (min–max) of net ecosystem productivity (NEP), gross primary productivity (GPP), and ecosystem respiration (ER) of evergreen terrestrial forests (Luyssaert et al., 2007) compared with mangroves (this study).

Ecosystem	NEP (Mg C ha ⁻² year ⁻¹)	GPP (Mg C ha ⁻² year ⁻¹)	ER (Mg C ha ⁻² year ⁻¹)	ER/GPP
Boreal humid evergreen	1.31 ± 0.79	9.73 ± 0.83	8.24 ± 1.12	0.88 ± 0.09
Boreal semiarid evergreen	0.40 ± 0.30	7.73 ± 0.35	7.34 ± 0.37	0.97 ± 0.04
Mediterranean semiarid evergreen	3.80 ± 0.73	14.78 ± 1.36	11.12 ± 0.10	0.76 ± 0.10
Temperate humid evergreen	3.98 ± 0.42	17.62 ± 0.56	13.36 ± 0.57	0.77 ± 0.03
Temperate semiarid evergreen	1.33 ± 0.47	12.28 ± 2.86	11.04 ± 2.60	0.87 ± 0.22
Tropical humid evergreen	4.03 ± 1.02	35.51 ± 1.60	30.61 ± 1.62	0.88 ± 0.04
Mangroves	7.35 (0.74–12.55)	18.71 (9.70–28.27)	11.17 (900–1937)	0.65 (0.56–0.93)

10.8 Mg C ha⁻¹ year⁻¹, while belowground production ranged between 1.1 and 6.8 Mg C ha⁻¹ year⁻¹ (Malhi et al., 2011). These values are lower than mangrove wood production at 0.1–21.8 Mg C ha⁻¹ year⁻¹ but similar to mangrove root production of 0.2–4.8 Mg C ha⁻¹ year⁻¹.

UPDATED GLOBAL C BUDGETS

Early estimates of mangrove carbon budgets were focused only on aboveground components, including woody biomass and litterfall production (Twilley et al., 1992). Because of scarce data at the time, they either did not include belowground root contributions (Jennerjahn & Ittekkot, 2002; Twilley et al., 1992) or used only a limited number of datasets (Bouillon et al., 2008; Ouyang et al., 2017). At the time, Bouillon et al. (2008) discovered that half of the carbon was unaccounted for to balance the total budget and suggested that the missing flux was the lateral export of dissolved carbon. The following reviews

(Along, 2022) incorporated lateral fluxes but did not include deadwood accumulation, herbivory, or root decomposition (Tables 3 and 4).

Our revised estimate of the mangrove global NEP is 109 Tg C year⁻¹ using eddy covariance methods (Table 3). These estimates are comparable to 114 Tg C year⁻¹ (Alongi, 2020) but lower than the 218 ± 72 Tg C year⁻¹ by Bouillon et al. (2008; Table 4). When adding all components of the mangrove carbon budget, we estimate gains of 251.8 Tg C year⁻¹ from tree uptake, downed wood accumulation, root and litterfall production, and soil accumulation. Losses are estimated at 185.2 Tg C year⁻¹ from, litterfall, POC, DOC, and DIC export and soil respiration. Thus, the total mangrove carbon uptake from a budget balance is -66.6 Tg C year⁻¹ (4.5 Mg C ha⁻¹ year⁻¹), lower than previous estimates, probably due to the inclusion of lateral exports.

The mangrove budget (inputs–outputs) from the average flux values in this study appears to be balanced (Figure 6, Table 3). However, the budget is unbalanced (higher exports than what is available for export) when

TABLE 3 Mangrove mean (range) stocks and fluxes as (1) gross primary productivity (GPP), ecosystem respiration (ER), and net ecosystem productivity (NEP), carbon gains from aboveground biomass (AB) growth, belowground biomass (BG) growth, deadwood accumulation, soil organic carbon (SOC) accumulation, and litterfall production, (2) carbon transformations as herbivory, and (3) losses as export of litter, particulate organic carbon (POC), dissolved organic carbon (DOC), and dissolved inorganic carbon (DIC) export, root decomposition, and soil respiration.

Stock/flux	Component	Stock (Mg C ha ⁻¹)/ flux (Mg C ha ⁻¹ year ⁻¹)	Reference
Stocks	AB	115 (33–261)	Kauffman et al. (2020)
	BG	16.1 (2.9–41)	Adame et al. (2017)
	SOC	741 (199–1218)	Kauffman et al. (2020)
	Deadwood	Standing (29.9) Downed (16.9)	Mugi et al. (2022)
Ecosystem productivity	GPP	16–20	This study
	ER	10–15	This study
	NEP	7.4 (0.7–12.6)	This study
Gains	AB growth	4.0 (0.1–21.8)	Xiong et al. (2019)
	BG growth	3.0 (0.2–12.1)	Arnaud et al. (2023)
	Deadwood accumulation	3.2 (1.6–5.7)	Mugi et al. (2022)
	SOC accumulation	2.3 (0.1–6.0)	Jennerjahn (2020)
	Litter production	4.7 (0.1–13.9)	This study
Transformation	Herbivory	2.0 (0.3–7.2)	This study
	Root decomposition	1.6 (0.06–14.1)	This study and Ouyang et al. (2017)
Losses	Litterfall export	0.97 (0.001–2.4)	Adame and Lovelock (2011)
	POC export	0.59 (–0.001–2.9)	Adame and Lovelock (2011)
	DOC export	0.27 (–0.7 – 1.4)	Adame and Lovelock (2011)
	DIC export	6.8 (–4.2–46)	Reithmaier et al. (2023)
	Soil respiration	0.04 (0.06–0.86) CH ₄ 3.9 (2.2–9.6) CO ₂	This study

TABLE 4 Comparison of global carbon fluxes across studies (in teragrams of carbon per year).

Flux type	Process	Bouillon et al. (2008)	Twilley et al. (2017)	Alongi (2020)	This study
	Mangrove area (ha)	16,000,000	14,735,899	8,649,500	14,735,899
	NEP		58.9	114	109.1
	GPP			305	265.3
	ER			246	184.2
	Algal GPP			38	
Gains	Tree wood	67	42.4	32	58.5
	Deadwood downed				46.4
	Root production	82		45	44.2
	Litterfall production	68	42.4	37	68.8
	Soil accumulation	18.4	33.0	14	33.9
Transformation	Herbivory				29.2
	Root decomposition				23.7
Loses	Litterfall export				14.3
	POC export	21		15	8.7
	DOC export	24	36.8	51	
	DIC export		36.8	124	100.2
	Soil respiration (CO ₂)	42		53	57.5
	Soil respiration (CH ₄)			0.02	0.59

Note: Fluxes from Twilley et al. (2017) and this study were estimated using the latest (2020) global mangrove area estimation (Bunting et al., 2022). Abbreviations: DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; ER, ecosystem respiration; GPP, gross primary productivity; NEP, net ecosystem productivity; POC, particulate organic carbon.

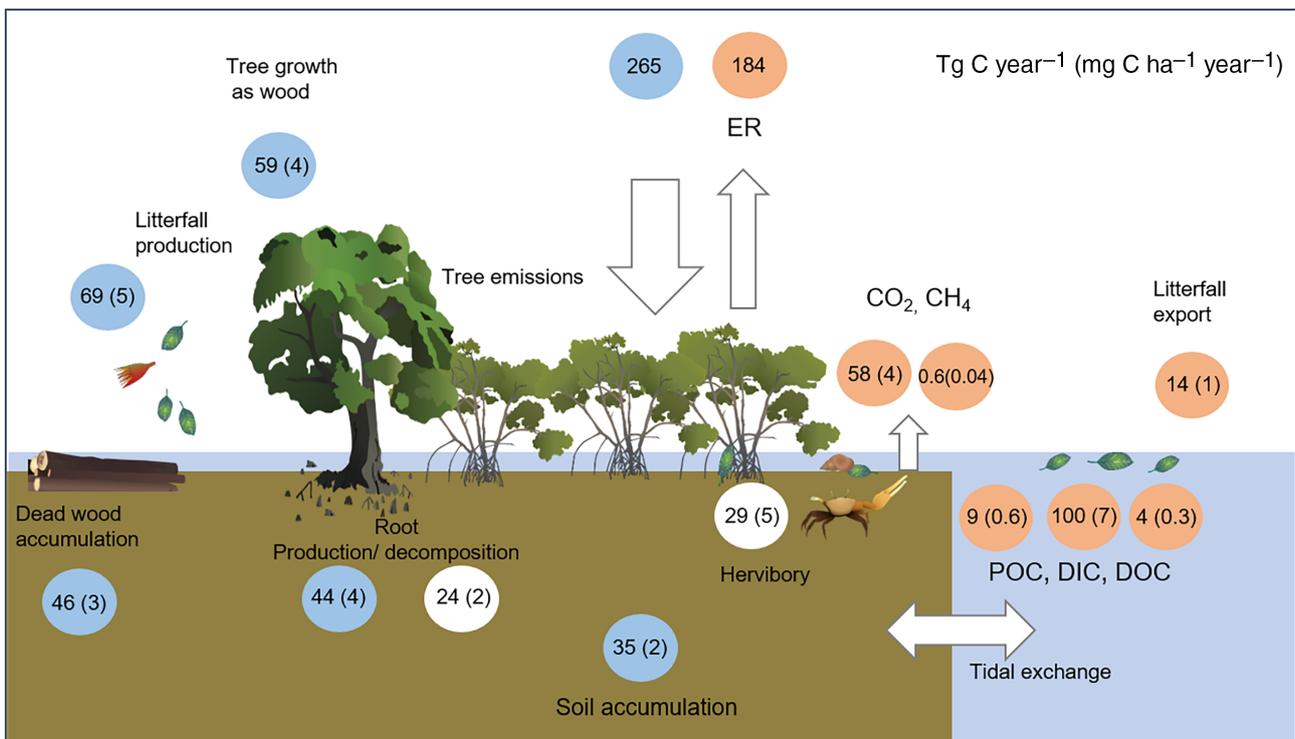


FIGURE 6 Mangrove global carbon fluxes exchange (in teragrams of carbon per year) and per area (in megagrams of carbon per hectare per year); blue circles are gains, orange circles are losses, and white circles are transformations. The mangrove area used to calculate global rates was obtained from Bunting et al. (2022) (14,735,899 ha). DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; ER, ecosystem respiration; GPP, gross primary productivity; POC, particulate organic carbon.

the highest DIC export values are used. For instance, the DIC export of $46 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ is larger than the maximum GPP recorded in mangroves so far ($20 \text{ Mg C ha}^{-1} \text{ year}^{-1}$). Thus, future refinement of DIC export and their attribution to a specific mangrove area are needed to improve our estimations.

Finally, we identified the relative importance of previously unaccounted carbon fluxes in mangroves. Soil respiration as CH_4 was minor ($<0.05 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, or $<1 \text{ Tg C year}^{-1}$), probably because globally most mangroves are saline, which suppress CH_4 emissions (Rosentreter, Al-Haj, et al., 2021; Rosentreter, Borges, et al., 2021). However, dead downed wood accumulation and herbivory were significant ($\geq 2 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, $\geq 30 \text{ Tg C year}^{-1}$; Figure 6), and are likely to have important implication in some locations, for example, in old forests or where sesarmid crabs are abundant.

KNOWLEDGE GAPS, FUTURE DIRECTIONS, AND MANAGEMENT IMPLICATIONS

There have been great advances in our understanding of the carbon cycle of mangroves in the past 30 years. Here, we have collated information on all the fluxes that have been described, showing that despite losses due to tidal exchange and soil respiration, all mangroves are carbon sinks. On average, global mangroves accumulate 33.9 Tg in the soil and 58.5 Tg as woody biomass, providing climate mitigation benefits. Additionally, lateral carbon export of mangroves as DIC (100.2 Tg) may increase nearshore carbon sequestration through increased alkalinity in the coastal ocean.

We identified challenges in current methodologies. First, fluxes are measured at different scales; root and tree growth, litterfall production, and soil carbon accumulation occur at the forest scale, while carbon export is measured at the creek or estuary scale. Temporal scales among flux studies are also highly variable; soil carbon accumulation is measured at decadal, centennial, or millennial scales, while trees grow in seasonal or decadal periods. On the contrary, lateral fluxes can vary daily depending on tidal amplitude or seasonally depending on rainfall and are usually only conducted for a few tidal cycles. This time and space discrepancy complicates comparing fluxes (Adame & Lovelock, 2011) and adds uncertainties to our budget calculations. For instance, DIC exports are an order of magnitude higher than any other fluxes and are highly variable, partly due to discrepancies in scale comparisons but also due to data scarcity. This data gap is essential, as DIC export can be higher than soil carbon sequestration (Maher et al., 2018).

Furthermore, studies on the fate of exported material, either dissolved or particulate, need further exploration.

Soil gas fluxes also were hampered by high spatiotemporal variability. For instance, fluxes increase due to mangrove roots and the presence of microphytobentos (Leopold et al., 2013; Lovelock, 2008). Soil gas fluxes are also primarily measured during the daytime, although emissions can be significantly higher at night (Dutta et al., 2019). This review found that CH_4 emissions from mangrove soils are minor compared with CO_2 fluxes (0.6 vs. 58 Tg year^{-1}). However, most studies on CH_4 fluxes are conducted with portable gas chambers, which do not capture ebullition events that may account for a significant portion of total emissions.

We also identified areas of study that have improved, such as information on root growth, which has steadily increased in the past decade. New methods, such as minirhizotrons, have improved the measurement accuracy of root production. However, field sampling needs to include coarse and deep roots and incorporate both intensive and extensive measurements to improve root production estimations. Additionally, data on root mortality and decomposition are still scarce.

Herbivory appears to be a significant component of mangrove carbon fluxes. However, data were few and variable, and additional empirical studies are needed to quantify this carbon flux. Observational studies (Feller & Chamberlain, 2007), controlled field experiments (e.g., propagule tethering), or stable isotopes and mesocosm experiments (e.g., Sandoval et al., 2022) could be helpful. More studies are also needed that couple litterfall and downed wood with breakdown and its sequestration in the soil, their consumption or export through tidal exchange (Cragg et al., 2020; Van der Stocken et al., 2017, 2019).

Spaceborne tools and UAVs are used increasingly and promise to overcome many challenges of working in mangroves by decreasing costs and expanding the spatial scale of measurements. However, they still have significant challenges as they must be verified in the field and be able to balance the need for consistent global maps with local studies that require high resolution at the local scale. While there is no best method, combined approaches covering site-scale measurements, modeling techniques, and spatial analyses are ideal.

Finally, we found biogeographic and climatic gaps in some of the carbon fluxes in mangroves. Data on some fluxes are scarce in the east and west of the southern Atlantic (South America and West Africa) and areas within the Pacific (e.g., Papua New Guinea and smaller islands). Root productivity, soil carbon sequestration, and herbivory studies are particularly rare. NEP is scarce in some of the most productive mangroves or those near the Equator, where trees are very tall, where the installation of eddy

covariance towers is challenging. Arid mangroves, urban mangroves, and those under the limits of mangrove distribution are poorly represented in the literature. Finally, long-term monitoring programs are required to understand the current carbon fluxes of mangroves and their impending changes due to El Niño-Southern Oscillation patterns, extreme events, and ongoing climate change.

Carbon offsets through mangrove restoration and conservation (blue carbon) are expanding globally. Local data are not always available for these projects, and entire carbon flux budgets are unlikely to be conducted for every location with limited resources and time constraints for projects to occur. This review advances our understanding and provides realistic ranges of carbon sequestration potential and the drivers of each carbon flux, which can inform the management of mangroves for climate change mitigation and adaptation, even for regions where data are scarce.

ACKNOWLEDGMENTS

We thank Jackie Raw for inputs in early versions of this manuscript. Open access publishing facilitated by Griffith University, as part of the Wiley - Griffith University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study.

ORCID

M. F. Adame  <https://orcid.org/0000-0001-9620-9252>

N. Iram  <https://orcid.org/0000-0002-2128-5020>

A. Rovai  <https://orcid.org/0000-0003-4117-2055>

E. S. Yando  <https://orcid.org/0000-0002-8786-6178>

M. Arnaud  <https://orcid.org/0000-0003-4001-6499>

T. Jennerjahn  <https://orcid.org/0000-0003-1022-5126>

R. R. Twilley  <https://orcid.org/0000-0002-6173-6033>

REFERENCES

- Abril, G., and A. V. Borges. 2019. "Ideas and Perspectives: Carbon Leaks from Flooded Land: Do We Need to Replumb the Inland Water Active Pipe?" *Biogeosciences* 16: 769–784.
- Adame, M. F., S. Cherian, R. Reef, and B. Stewart-Koster. 2017. "Mangrove Root Biomass and the Uncertainty of Belowground Carbon Estimations." *Forest Ecology and Management* 403: 52–60.
- Adame, M. F., and C. E. Lovelock. 2011. "Carbon and Nutrient Exchange of Mangrove Forests with the Coastal Ocean." *Hydrobiologia* 663: 23–50.
- Adame, M. F., N. S. Santini, O. Torres-Talamante, and K. Rogers. 2021. "Mangrove Sinkholes (Cenotes) of the Yucatan Peninsula, a Global Hotspot of Carbon Sequestration." *Biology Letters* 17: 20210037. <https://doi.org/10.1098/rsbl.2021.0037>.
- Adame, M. F., C. Teutli, N. S. Santini, J. P. Caamal, A. Zaldívar-Jiménez, R. Hernandez, and J. A. Herrera-Silveira. 2014. "Root Biomass and Production of Mangroves Surrounding a Karstic Oligotrophic Coastal Lagoon." *Wetlands* 34: 479–488.
- Adame, M. F., A. Zaldívar-Jiménez, C. Teutli, J. P. Caamal, M. T. Andueza, A. Lopez-Adame, R. Cano, H. A. Hernandez-Arana, R. Torres-Lara, and J. A. Herrera-Silveira. 2013. "Drivers of Mangrove Litterfall within a Karstic Region Affected by Frequent Hurricanes." *Biotropica* 45: 147–154.
- Adame, M. F., M. F., R. Reef, J. A. Herrera-Silveira, and C. E. Lovelock. 2012. "Sensitivity of Dissolved Organic Carbon Exchange and Sediment Bacteria to Water Quality in Mangrove Forests." *Hydrobiologia* 691: 239–253.
- Adame, N. S., C. Santini, A. Tovilla, L. C. Vázquez-Lule, and M. Guevara. 2015. "Carbon Stocks and Soil Sequestration Rates of Tropical Riverine Wetlands." *Biogeosciences* 12: 3805–18.
- Adame, R. M., B. Zakaria, V. C. Fry, Y. H. A. T. Chong, C. J. Brown, and S. Y. Lee. 2018. "Loss and Recovery of Carbon and Nitrogen after Mangrove Clearing." *Ocean and Coastal Management* 161: 117–126.
- Akhand, A., K. Watanabe, A. Chanda, T. Tokoro, K. Chakraborty, H. Moki, T. Tanaya, J. Ghosh, and T. Kuwae. 2021. "Lateral Carbon Fluxes and CO₂ Evasion from a Subtropical Mangrove-Seagrass-Coral Continuum." *Science of the Total Environment* 752: 142190.
- Al-Haj, A. N., and R. W. Fulweiler. 2020. "A Synthesis of Methane Emissions from Shallow Vegetated Coastal Ecosystems." *Global Change Biology* 26: 2988–3005.
- Alongi, D. M. 2011. "Patterns of Mangrove Wood and Litter Production within a Beach Ridge-Fringing Reef Embayment, Northern Great Barrier Reef Coast." *Estuaries and Coasts* 34: 32–44.
- Alongi, D. M. 2014. "Carbon Cycling and Storage in Mangrove Forests." *Annual Review of Marine Science* 6: 195–219.
- Alongi, D. M. 2020. "Carbon Balance in Salt Marsh and Mangrove Ecosystems: A Global Synthesis." *Journal of Marine Science and Engineering* 8: 1–21.
- Alvarado-Barrientos, M. S., H. López-Adame, H. E. Lazcano-Hernández, J. Arellano-Verdejo, and H. A. Hernández-Arana. 2021. "Ecosystem-Atmosphere Exchange of CO₂, Water, and Energy in a Basin Mangrove of the Northeastern Coast of the Yucatan Peninsula." *Journal of Geophysical Research: Biogeosciences* 126: e2020JG005811.
- Anderson, C., and S. Y. Lee. 1995. "Defoliation of the Mangrove *Avicennia marina* in Hong Kong: Cause and Consequences." *Biotropica* 27: 218–226.
- Anderson-Teixeira, K. J., V. Herrmann, R. B. Morgan, B. Bond-Lamberty, S. C. Cook-Patton, A. E. Ferson, H. C. Muller-Landau, and M. M. H. Wang. 2021. "Carbon Cycling in Mature and Regrowth Forests Globally." *Environmental Research Letters* 16: 053009.
- Anderson-Teixeira, K. J., M. M. H. Wang, J. C. Mcgarvey, and D. S. Lebauer. 2016. "Carbon Dynamics of Mature and Regrowth Tropical Forests Derived from a Pantropical Database (TropForC-db)." *Global Change Biology* 22: 1690–1709.

- Aoki, M., K. Fujii, and K. Kitayama. 2012. "Environmental Control of Root Exudation of Low-Molecular Weight Organic Acids in Tropical Rainforests." *Ecosystems* 15: 1194–1203.
- Arias-Ortiz, A., P. Masqué, J. Garcia-Orellana, O. Serrano, I. Mazarrasa, N. Marbá, C. E. Lovelock, P. S. Lavery, and C. M. Duarte. 2018. "Reviews and Syntheses: ²¹⁰Pb-Derived Sediment and Carbon Accumulation Rates in Vegetated Coastal Ecosystems – Setting the Record Straight." *Biogeosciences* 15: 6791–6818.
- Arnaud, M., S. Krause, R. J. Norby, T. H. Dang, N. Acil, N. Kettridge, V. Gauci, and S. Ullah. 2023. "Global Mangrove Root Production, Its Controls and Roles in the Blue Carbon Budget of Mangroves." *Global Change Biology* 29: 3256–70.
- Arnaud, M., P. J. Morris, A. J. Baird, H. Dang, and T. T. Nguyen. 2021. "Fine Root Production in a Chronosequence of Mature Reforested Mangroves." *New Phytologist* 232: 1591–1602.
- Ashton, E. C. 2002. "Mangrove Sesarimid Crab Feeding Experiments in Peninsular Malaysia." *Journal of Experimental Marine Biology and Ecology* 273: 97–119.
- Ayukai, T., D. Miller, E. Wolanski, and S. Spagnol. 1998. "Fluxes of Nutrients and Dissolved and Particulate Organic Carbon in Two Mangrove Creeks in Northeastern Australia." *Mangroves and Salt Marshes* 2: 223–230.
- Baker, R., K. Abrantes, and I. C. Feller. 2021. "Stable Isotopes Suggest Limited Role of Wetland Macrophyte Production Supporting Aquatic Food Webs across a Mangrove-Salt Marsh Ecotone." *Estuaries and Coasts* 44: 1619–27.
- Ball, M. 1988. "Salinity Tolerance in the Mangroves *Aegiceras corniculatum* and *Avicennia marina* I. Water Use in Relation to Growth, Carbon Partitioning, and Salt Balance." *Australian Journal of Plant Physiology* 15: 447–464.
- Ball, M. C., and S. M. Pidsley. 1995. "Growth Responses to Salinity in Relation to Distribution of Two Mangrove Species, *Sonneratia alba* and *S. lanceolata*, in Northern Australia." *Functional Ecology* 9: 77–85.
- Barr, J. G., V. Engel, T. J. Smith, and J. D. Fuentes. 2012. "Hurricane Disturbance and Recovery of Energy Balance, CO₂ Fluxes and Canopy Structure in a Mangrove Forest of the Florida Everglades." *Agricultural and Forest Meteorology* 153: 54–66.
- Belliard, J. P., S. Hernandez, S. Temmerman, R. H. Suello, L. E. Dominguez-Granda, A. M. Rosado-Moncayo, J. A. Ramos-Veliz, et al. 2022. "Carbon Dynamics and CO₂ and CH₄ Exchange in the Mangrove Dominated Guayas River Delta, Ecuador." *Estuarine, Coastal and Shelf Science* 267: 107766.
- Bouillon, S., A. V. Borges, E. Castañeda-Moya, K. Diele, T. Dittmar, N. C. Duke, E. Kristensen, et al. 2008. "Mangrove Production and Carbon Sinks: A Revision of Global Budget Estimates." *Global Biogeochemical Cycles* 22: 1–12.
- Bouillon, S., F. Dahdouh-Guebas, A. Rao, N. Koedam, and F. Dehairs. 2003. "Sources of Organic Carbon in Mangrove Sediments: Variability and Possible Ecological Implications." *Hydrobiologia* 495: 33–39.
- Breithaupt, J. L., J. M. Smoak, T. J. S. Iii, C. J. Sanders, and A. Hoare. 2012. "Organic Carbon Burial Rates in Mangrove Sediments: Strengthening the Global Budget." *Global Biogeochemical Cycles* 26: 1–11.
- Bulmer, R. H., L. Schwendenmann, A. M. Lohrer, and C. J. Lundquist. 2017. "Sediment Carbon and Nutrient Fluxes from Cleared and Intact Temperate Mangrove Ecosystems and Adjacent Sandflats." *Science of the Total Environment* 599–600: 1874–84.
- Bunting, P., A. Rosenqvist, L. Hilarides, R. M. Lucas, N. Thomas, T. Tadono, T. A. Worthington, M. Spalding, and N. J. Murray. 2022. "Global Mangrove Extent Change 1996–2020: Global Mangrove Watch Version 3.0." *Remote Sensing* 14: 3657.
- Cahoon, D. R., P. Hensel, J. Rybczyk, K. L. McKee, C. E. Proffitt, and B. C. Perez. 2003. "Mass Tree Mortality Leads to Mangrove Peat Collapse at Bay Islands, Honduras after Hurricane Mitch." *Journal of Ecology* 91: 1093–1105.
- Cameron, C., L. B. Hutley, and D. A. Friess. 2019. "Estimating the Full Greenhouse Gas Emissions Offset Potential and Profile between Rehabilitating and Established Mangroves." *Science of the Total Environment* 665: 419–431.
- Cannicci, S., D. Burrows, S. Fratini, T. J. Smith, J. Offenberg, and F. Dahdouh-Guebas. 2008. "Faunal Impact on Vegetation Structure and Ecosystem Function in Mangrove Forests: A Review." *Aquatic Botany* 89: 186–200.
- Castañeda-Moya, E., R. R. Twilley, V. H. Rivera-Monroy, B. D. Marx, C. Coronado-Molina, S. M. L. Ewe, E. Castañeda-Moya, et al. 2011. "Patterns of Root Dynamics in Mangrove Forests along Environmental Gradients in the Florida Coastal Everglades, USA." *Ecosystems* 14: 1178–95.
- Chapin, F. S., G. M. Woodwell, J. T. Randerson, E. B. Rastetter, G. M. Lovett, D. D. Baldocchi, D. A. Clark, et al. 2006. "Reconciling Carbon-Cycle Concepts, Terminology, and Methods." *Ecosystems* 9: 1041–50.
- Chen, G. C., and Y. Ye. 2008. "Leaf Consumption by *Sesarma plicata* in a Mangrove Forest at Jiulongjiang Estuary, China." *Marine Biology* 154: 997–1007.
- Chen, G. C., and Y. Ye. 2010. "Changes in Properties of Mangrove Sediment Due to Foraging on *Kandelia obovata* Leaves by Crabs *Parasesarma plicatum* (Grapsidae: Sesarminae)." *Marine Ecology Progress Series* 419: 137–145.
- Clough, B. 1998. "Mangrove Forest Productivity and Biomass Accumulation in Hinchinbrook." *Mangroves and Salt Marshes* 2: 191–98.
- Cormier, N. 2021. "Getting to the Root of the Problem: Improving Measurements of Mangrove Belowground Production and Carbon Sequestration." *New Phytologist* 232: 1525–27.
- Cortés, J., H. A. Oxenford, B. I. van Tussenbroek, E. Jordán-Dahlgren, A. Cróquer, C. Bastidas, and J. C. Ogden. 2019. "The CARICOMP Network of Caribbean Marine Laboratories (1985–2007): History, Key Findings, and Lessons Learned." *Frontiers in Marine Science* 5: 519.
- Cragg, S. M., D. A. Friess, L. G. Gillis, S. M. Trevathan-Tackett, O. M. Terrett, J. E. M. Watts, D. L. Distel, and P. Dupree. 2020. "Vascular Plants Are Globally Significant Contributors to Marine Carbon Fluxes and Sinks." *Annual Review of Marine Science* 12: 16.1–16.29.
- Dijkstra, F. A., B. Zhu, and W. Cheng. 2021. "Root Effects on Soil Organic Carbon: A Double-Edged Sword." *New Phytologist* 230: 60–65.
- Dittmar, T., and R. J. Lara. 2001. "Driving Forces behind Nutrient and Organic Matter Dynamics in a Mangrove Tidal Creek in North Brazil." *Estuarine, Coastal and Shelf Science* 52: 249–259.
- Donato, D. C., J. B. Kauffman, D. Murdiyarsa, S. Kurnianto, M. Stidham, and M. Kanninen. 2011. "Mangroves among the

- Most Carbon-Rich Forests in the Tropics.” *Nature Geoscience* 4: 293–97.
- Duarte, C., J. Middelburg, and N. Caraco. 2005. “Major Role of Marine Vegetation on the Oceanic Carbon Cycle C.” *Biogeosciences* 2: 1–8.
- Duarte de Paula Costa, M., and P. I. Macreadie. 2022. “The Evolution of Blue Carbon Science.” *Wetlands* 42: 109.
- Dutta, M. K., S. Kumar, R. Mukherjee, N. Sharma, A. Acharya, P. Sanyal, R. Bhusan, and S. K. Mukhopadhyay. 2019. “Diurnal Carbon Dynamics in a Mangrove-Dominated Tropical Estuary (Sundarbans, India).” *Estuarine, Coastal and Shelf Science* 229: 106426.
- Emmerson, W. D., and L. E. McGwynne. 1992. “Feeding and Assimilation of Mangrove Leaves by the Crab *Sesarma meinerti* de Man in Relation to Leaf-Litter Production in Mgazana, a Warm-Temperate Southern African Mangrove Swamp.” *Journal of Experimental Marine Biology and Ecology* 157: 41–53.
- Fakhraee, M., N. Planavsky, and C. Reinhard. 2023. “Ocean Alkalinity Enhancement through Blue Carbon Ecosystem Restoration.” *Nature Sustainability* 6: 1087–94.
- Faraco, L. F. D., and P. Da Cunha Lana. 2004. “Leaf-Consumption Levels in Subtropical Mangroves of Paranaguá Bay (SE Brazil).” *Wetlands Ecology and Management* 12: 115–122.
- Félix-Pico, E. F., O. E. Holguín-Quiñones, A. Hernández-Herrera, and F. Flores-Verdugo. 2006. “Mangrove Primary Production at El Conchalito Estuary in La Paz Bay (Baja California Sur, Mexico).” *Ciencias Marinas* 32: 53–63.
- Feller, I. C. 2002. “The Role of Herbivory by Wood-Boring Insects in Mangrove Ecosystems in Belize.” *Oikos* 97: 167–176.
- Feller, I. C., and A. Chamberlain. 2007. “Herbivore Responses to Nutrient Enrichment and Landscape Heterogeneity in a Mangrove Ecosystem.” *Oecologia* 153: 607–616.
- Frankenberg, C., J. F. Meirink, M. Van Weele, U. Platt, and T. Wagner. 2005. “Assessing Methane Emissions from Global Spaceborne Observations.” *Science* 308: 1010–14.
- Friesen, S. D., C. Dunn, and C. Freeman. 2018. “Decomposition as a Regulator of Carbon Accretion in Mangroves: A Review.” *Ecological Engineering* 114: 173–78.
- Gleason, S. M., and K. C. Ewel. 2002. “Organic Matter Dynamics on the Forest Floor of a Micronesian Mangrove Forest: An Investigation of Species Composition Shifts.” *Biotropica* 34: 190–98.
- Gnanamoorthy, P., V. Selvam, P. K. Deb Burman, S. Chakraborty, A. Karipot, R. Nagarajan, R. Ramasubramanian, Q. Song, Y. Zhang, and J. Grace. 2020. “Seasonal Variations of Net Ecosystem (CO₂) Exchange in the Indian Tropical Mangrove Forest of Pichavaram.” *Estuarine, Coastal and Shelf Science* 243: 106828.
- Griffith, D. W. T., N. M. Deutscher, C. Caldwell, G. Kettlewell, M. Riggenbach, and S. Hammer. 2012. “A Fourier Transform Infrared Trace Gas and Isotope Analyzer for Atmospheric Applications.” *Atmospheric Measurement Techniques* 5: 2481–98.
- Haoliang, L., Y. Chongling, and L. Jingchun. 2007. “Low-Molecular-Weight Organic Acids Exuded by Mangrove (*Kandelia candel* (L.) Druce) Roots and Their Effect on Cadmium Species Change in the Rhizosphere.” *Environmental and Experimental Botany* 61: 159–166.
- Hayes, M. A., A. Jesse, B. Hawke, J. Baldock, B. Tabet, D. Lockington, and C. E. Lovelock. 2017. “Dynamics of Sediment Carbon Stocks across Intertidal Wetland Habitats of Moreton Bay, Australia.” *Global Change Biology* 23: 4222–34.
- Hayes, M. A., A. Jesse, B. Tabet, R. Reef, J. A. Keuskamp, and C. E. Lovelock. 2017. “The Contrasting Effects of Nutrient Enrichment on Growth, Biomass Allocation and Decomposition of Plant Tissue in Coastal Wetlands.” *Plant and Soil* 416: 193–204.
- He, D., B. R. T. Simoneit, B. Jara, and R. Jaffé. 2016. “Compositions and Isotopic Differences of Iso- and Anteiso-Alkanes in Black Mangroves (*Avicennia germinans*) across a Salinity Gradient in a Subtropical Estuary.” *Environmental Chemistry* 13: 623–630.
- Ho, D. T., S. Ferrón, V. C. Engel, W. T. Anderson, P. K. Swart, R. M. Price, and L. Barbero. 2017. “Dissolved Carbon Biogeochemistry and Export in Mangrove-Dominated Rivers of the Florida Everglades.” *Biogeosciences* 14: 2543–59.
- Hoque, M. M., A. H. M. Kamal, M. H. Idris, O. H. Ahmed, A. T. M. R. Hoque, and M. M. Billah. 2015. “Litterfall Production in a Tropical Mangrove of Sarawak, Malaysia.” *Zoology and Ecology* 25: 157–165.
- Hughes, M. G., K. Rogers, and L. Wen. 2019. “Saline Wetland Extents and Tidal Inundation Regimes on a Micro-Tidal Coast, New South Wales, Australia.” *Estuarine, Coastal and Shelf Science* 227: 106297.
- Huxham, M., J. Langat, F. Tamooh, H. Kennedy, M. Mencuccini, M. W. Skov, and J. Kairo. 2010. “Decomposition of Mangrove Roots: Effects of Location, Nutrients, Species Identity and Mix in a Kenyan Forest.” *Estuarine, Coastal and Shelf Science* 88: 135–142.
- Hyndes, G. A., I. Nagelkerken, R. J. Mcleod, R. M. Connolly, P. S. Lavery, and M. A. Vanderklift. 2014. “Mechanisms and Ecological Role of Carbon Transfer within Coastal Seascapes.” *Biological Reviews* 89: 232–254.
- Imgraben, S., and S. Dittmann. 2008. “Leaf Litter Dynamics and Litter Consumption in Two Temperate South Australian Mangrove Forests.” *Journal of Sea Research* 59: 83–93.
- Jeffrey, L. C., G. Reithmaier, J. Z. Sippo, S. G. Johnston, D. R. Tait, Y. Harada, and D. T. Maher. 2019. “Are Methane Emissions from Mangrove Stems a Cryptic Carbon Loss Pathway? Insights from a Catastrophic Forest Mortality.” *New Phytologist* 224: 146–154.
- Jennerjahn, T. C. 2020. “Relevance and Magnitude of “Blue Carbon” Storage in Mangrove Sediments: Carbon Accumulation Rates vs. Stocks, Sources vs. Sinks.” *Estuarine, Coastal and Shelf Science* 247: 107027.
- Jennerjahn, T. C., and V. Ittekkot. 2002. “Relevance of Mangroves for the Production and Deposition of Organic Matter along Tropical Continental Margins.” *Naturwissenschaften* 89: 23–30.
- Johnstone, I. M. 1981. “Consumption of Leaves by Herbivores in Mixed Mangrove Stands.” *Biotropica* 13: 252–59.
- Kauffman, J., M. F. Adame, V. B. Arifanti, L. M. Schile-Beers, A. F. Bernardino, R. K. Bhomia, D. C. Donato, et al. 2020. “Total Ecosystem Carbon Stocks of Mangroves across Broad Global Environmental and Physical Gradients.” *Ecological Monographs* 90: e01405.
- Kauffman, J. B., and D. C. Donato. 2012. “Protocols for the Measurement, Monitoring and Reporting of Structure, Biomass and Carbon Stocks in Mangrove Forests.” Working Paper 86. Bogor.
- Komiyama, A., J. E. On, S. Pongparn, J. E. Ong, and S. Pongparn. 2008. “Allometry, Biomass, and Productivity of Mangrove Forests: A Review.” *Aquatic Botany* 89: 128–137.

- Krauss, K., K. McKee, C. E. Lovelock, D. Cahoon, N. Saintilan, R. Reef, and L. Chen. 2013. "How Mangrove Forests Adjust to Rising Sea Level." *New Phytologist* 202: 19–34.
- Krauss, K. W., B. D. Keeland, J. A. Allen, K. C. Ewel, and D. J. Johnson. 2007. "Effects of Season, Rainfall, and Hydrogeomorphic Setting on Mangrove Tree Growth in Micronesia." *Biotropica* 39: 161–170.
- Krauss, K. W., and M. J. Osland. 2020. "Tropical Cyclones and the Organization of Mangrove Forests: A Review." *Annals of Botany* 125: 213–234.
- Kreuzwieser, J., J. Buchholz, and H. Rennenberg. 2003. "Emission of Methane and Nitrous Oxide by Australian Mangrove Ecosystems." *Plant Biology* 5: 423–431.
- Kristensen, E., and D. M. Alongi. 2006. "Control by Fiddler Crabs (*Uca vocans*) and Plant Roots (*Avicennia marina*) on Carbon, Iron, and Sulfur Biogeochemistry in Mangrove Sediment." *Limnology and Oceanography* 51: 1557–71.
- Kristensen, E., S. Bouillon, T. Dittmar, and C. Marchand. 2008. "Organic Carbon Dynamics in Mangrove Ecosystems: A Review." *Aquatic Botany* 89: 201–219.
- Kristensen, E., M. R. Flindt, S. Ulomi, A. V. Borges, G. Abril, and S. Bouillon. 2008. "Emission of CO₂ and CH₄ to the Atmosphere by Sediments and Open Waters in Two Tanzanian Mangrove Forests." *Marine Ecology Progress Series* 370: 53–67.
- Kusumaningtyas, M. A., A. A. Hutahaean, H. W. Fischer, M. Pérez-Mayo, D. Ransby, and T. C. Jennerjahn. 2019. "Variability in the Organic Carbon Stocks, Sources, and Accumulation Rates of Indonesian Mangrove Ecosystems." *Estuarine, Coastal and Shelf Science* 218: 310–323.
- Lee, S. Y. 1995. "Mangrove Outwelling: A Review." *Hydrobiologia* 295: 203–212.
- Lee, S. Y. 1998. "Ecological Role of Grapsid Crabs in Mangrove Ecosystems: A Review." *Marine and Freshwater Research* 49: 335–343.
- Leopold, A., C. Marchand, J. Deborde, and M. Allenbach. 2015. "Temporal Variability of CO₂ Fluxes at the Sediment-Air Interface in Mangroves (New Caledonia)." *Science of the Total Environment* 502: 617–626.
- Leopold, A., C. Marchand, J. Deborde, C. Chaduteau, and M. Allenbach. 2013. "Influence of Mangrove Zonation on CO₂ Fluxes at the Sediment-Air Interface (New Caledonia)." *Geoderma* 202–203: 62–70.
- Leopold, A., C. Marchand, A. Renchon, J. Deborde, T. Quiniou, and M. Allenbach. 2017. "Net Ecosystem CO₂ Exchange in the "Coeur de Voh" Mangrove, New Caledonia: Effects of Water Stress on Mangrove Productivity in a Semi-Arid Climate." *Agricultural and Forest Meteorology* 232: 711–12.
- Linto, N., J. Barnes, R. Ramachandran, J. Divia, P. Ramachandran, and R. C. Upstill-Goddard. 2014. "Carbon Dioxide and Methane Emissions from Mangrove-Associated Waters of the Andaman Islands, Bay of Bengal." *Estuaries and Coasts* 37: 381–398.
- Liu, B., L. Wu, P. Pan, R. Li, and B. Lin. 2022. "Response of Root Exudates of *Bruguiera gymnorrhiza* (L.) to Exposure of Polycyclic Aromatic Hydrocarbons." *Frontiers in Environmental Science* 9: 1–10.
- Liu, J., and D. Y. F. Lai. 2019. "Subtropical Mangrove Wetland Is a Stronger Carbon Dioxide Sink in the Dry than Wet Seasons." *Agricultural and Forest Meteorology* 278: 107644.
- Lovelock, C., I. C. Feller, R. Reef, and R. Ruess. 2014. "Variable Effects of Nutrient Enrichment on Soil Respiration in Mangrove Forests." *Plant and Soil* 379: 135–148.
- Lovelock, C. E. 2008. "Soil Respiration and Belowground Carbon Allocation in Mangrove Forests." *Ecosystems* 11: 342–354.
- Lovelock, C. E., M. F. Adame, J. Bradley, S. Dittmann, V. Hagger, S. M. Hickey, L. Hutley, et al. 2022. "An Australian Blue Carbon Method to Estimate Climate Change Mitigation Benefits of Coastal Wetland Restoration." *Restoration Ecology* 31: e13739.
- Lovelock, C. E., M. C. Ball, K. C. Martin, and I. C. Feller. 2009. "Nutrient Enrichment Increases Mortality of Mangroves." *PLoS One* 4: e5600.
- Lovelock, C. E., J. W. Fourqurean, and J. T. Morris. 2017. "Modeled CO₂ Emissions from Coastal Wetland Transitions to Other Land Uses: Tidal Marshes, Mangrove Forests, and Seagrass Beds." *Frontiers in Marine Science* 4: 143.
- Lovelock, C. E., R. W. Ruess, and I. C. Feller. 2011. "CO₂ Efflux from Cleared Mangrove Peat." *PLoS One* 6: e21279.
- Lu, W., J. Xiao, X. Cui, F. Xu, G. Lin, and G. Lin. 2019. "Insect Outbreaks Have Transient Effects on Carbon Fluxes and Vegetative Growth but Longer-Term Impacts on Reproductive Growth in a Mangrove Forest." *Agricultural and Forest Meteorology* 279: 107747.
- Luyssaert, S., I. Inglima, M. Jung, A. D. Richardson, M. Reichstein, D. Papale, S. L. Piao, et al. 2007. "CO₂ Balance of Boreal, Temperate, and Tropical Forests Derived from a Global Database." *Global Change Biology* 13: 2509–37.
- MacKenzie, R., S. Sharma, and A. R. Rovai. 2021. "Environmental Drivers of Blue Carbon Burial and Soil Carbon Stocks in Mangrove Forests." In *Dynamic Sedimentary Environments of Mangrove Coasts*, edited by F. Sidik and D. A. Friess, 275–294. Amsterdam: Elsevier.
- MacKenzie, R. A., P. B. Foulk, J. Val Klump, K. Weckerly, J. Purbospito, D. Murdiyarto, D. C. Donato, and V. N. Nam. 2016. "Sedimentation and Belowground Carbon Accumulation Rates in Mangrove Forests that Differ in Diversity and Land Use: A Tale of Two Mangroves." *Wetlands Ecology and Management* 24: 245–261.
- Macreadie, P. I., D. P. Costa, T. B. Micheli, D. A. Atwood, J. J. Friess, H. Kelleway, C. E. Kennedy, O. Lovelock, and C. D. Serrano. 2021. "Blue Carbon as a Natural Climate Solution." *Nature Reviews Earth and Environment* 2: 826–839.
- Maher, D. T., M. Call, I. R. Santos, and C. J. Sanders. 2018. "Beyond Burial: Lateral Exchange Is a Significant Atmospheric Carbon Sink in Mangrove Forests." *Biology Letters* 14: 20180200. <https://doi.org/10.1098/rsbl.2018.0200>.
- Maher, D. T., I. R. Santos, J. Gleeson, B. D. Eyre, L. Golsby-Smith, J. Gleeson, and B. D. Eyre. 2013. "Groundwater-Derived Dissolved Inorganic and Organic Carbon Exports from a Mangrove Tidal Creek: The Missing Mangrove Carbon Sink?" *Limnology and Oceanography* 58: 475–488.
- Malerba, M. E., D. A. Friess, M. Peacock, A. Grinham, P. Taillardat, J. A. Rosentreter, J. Webb, N. Iram, A. N. Al-Haj, and P. I. Macreadie. 2022. "Methane and Nitrous Oxide Emissions Complicate the Climate Benefits of Teal and Blue Carbon Wetlands." *One Earth* 5: 1336–41.
- Malhi, Y., C. Doughty, and D. Galbraith. 2011. "The Allocation of Ecosystem Net Primary Productivity in Tropical Forests." *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 3225–45.

- Malley, D. F. 1978. "Degradation of Mangrove Leaf Litter by the Tropical Sesamid Crab *Chiromantes onychophorum*." *Marine Biology* 49: 377–386.
- McKee, K. L., D. R. Cahoon, and I. C. Feller. 2007. "Caribbean Mangroves Adjust to Rising Sea Level through Biotic Controls on Change in Soil Elevation." *Global Ecology and Biogeography* 6: 545–556.
- Middleton, B. A., and K. L. McKee. 2001. "Degradation of Mangrove Tissues and Implications for Peat Formation in Belizean Island Forests." *Journal of Ecology* 89: 818–828.
- Mugi, L. M., D. Kiss, J. G. Kairo, and M. R. Huxham. 2022. "Stocks and Productivity of Dead Wood in Mangrove Forests: A Systematic Literature Review." *Frontiers in Forests and Global Change* 5: 1–12.
- Muhammad-Nor, S. M., M. Huxham, Y. Salmon, S. J. Duddy, A. Mazars-Simon, M. Mencuccini, P. Meir, and G. Jackson. 2019. "Exceptionally High Mangrove Root Production Rates in the Kelantan Delta, Malaysia; an Experimental and Comparative Study." *Forest Ecology and Management* 444: 214–224.
- Murphy, D. 1990. "The Natural History of Insect Herbivory on Mangrove Trees in and near Singapore." *Raffles Bulletin of Zoology* 38: 119–203.
- Nguyen, H. T., D. E. Stanton, N. Schmitz, G. D. Farquhar, and M. C. Ball. 2015. "Growth Responses of the Mangrove *Avicennia marina* to Salinity: Development and Function of Shoot Hydraulic Systems Require Saline Conditions." *Annals of Botany* 115: 397–407.
- Niu, S., Y. Luo, S. Fei, W. Yuan, D. Schimel, B. E. Law, C. Ammann, et al. 2012. "Thermal Optimality of Net Ecosystem Exchange of Carbon Dioxide and Underlying Mechanisms." *New Phytologist* 194: 775–783.
- Nordhaus, I., M. Wolff, and K. Diele. 2006. "Litter Processing and Population Food Intake of the Mangrove Crab *Ucides cordatus* in a High Intertidal Forest in Northern Brazil." *Estuarine, Coastal and Shelf Science* 67: 239–250.
- Oertel, C., J. Matschullat, K. Zurba, F. Zimmermann, and S. Erasmí. 2016. "Greenhouse Gas Emissions from Soils – A Review." *Chemie der Erde* 76: 327–352.
- Ohtsuka, T., T. Onishi, S. Yoshitake, M. Tomotsune, M. Kida, Y. Iimura, M. Kondo, et al. 2020. "Lateral Export of Dissolved Inorganic and Organic Carbon from a Small Mangrove Estuary with Tidal Fluctuation." *Forests* 11: 1–15.
- Ola, A., and C. E. Lovelock. 2021. "Decomposition of Mangrove Roots Depends on the Bulk Density They Grew In." *Plant and Soil* 460: 177–187.
- Ouyang, X., E. Kristensen, M. Zimmer, C. Thornber, Z. Yang, and S. Y. Lee. 2023. "Response of Macrophyte Litter Decomposition in Global Blue Carbon Ecosystems to Climate Change." *Global Change Biology* 13: 3806–20.
- Ouyang, X., S. Y. Lee, and R. M. Connolly. 2017. "The Role of Root Decomposition in Global Mangrove and Saltmarsh Carbon Budgets." *Earth-Science Reviews* 166: 53–63.
- Pérez-Ceballos, R., K. Rivera-Rosales, A. Zaldívar-Jiménez, J. Canales-delgadillo, R. Brito-Pérez, L. A. Del Ángel, and M. Merino-Ibarra. 2018. "Effect of Hydrological Restoration on the Productivity of Underground Roots in the Mangroves of Laguna de Terminos, Mexico." *Botanical Sciences* 96: 569–581.
- Phillips, R. P., Y. Erlitz, R. Bier, and E. S. Bernhardt. 2008. "New Approach for Capturing Soluble Root Exudates in Forest Soils." *Functional Ecology* 22: 990–99.
- Poret, N., R. Twilley, V. Rivera-Monroy, and C. Coronado-Molina. 2007. "Belowground Decomposition of Mangrove Roots in Florida Coastal Everglades." *Estuaries and Coasts* 30: 491–96.
- Poungparn, S., T. Charoenphonphakdi, T. Sangtiewan, and P. Patanaponpaiboon. 2016. "Fine Root Production in Three Zones of Secondary Mangrove Forest in Eastern Thailand." *Trees Structure and Function* 30: 467–474.
- Poungparn, S., A. Komiya, A. Tanaka, T. Sangtiewan, C. Maknual, S. Kato, P. Tanapermpool, and P. Patanaponpaiboon. 2009. "Carbon Dioxide Emission through Soil Respiration in a Secondary Mangrove Forest of Eastern Thailand." *Journal of Tropical Ecology* 25: 393–400.
- Pülmanns, N., K. Diele, U. Mehlig, and I. Nordhaus. 2014. "Burrows of the Semi-Terrestrial Crab *Ucides cordatus* Enhance CO₂ Release in a North Brazilian Mangrove Forest." *PLoS One* 9: e109532.
- Radabaugh, K. R., R. P. Moyer, A. R. Chappel, E. E. Dontis, C. E. Russo, K. M. Joyse, M. W. Bownik, A. H. Goeckner, and N. S. Khan. 2020. "Mangrove Damage, Delayed Mortality, and Early Recovery Following Hurricane Irma at Two Landfall Sites in Southwest Florida, USA." *Estuaries and Coasts* 43: 1104–18.
- Ray, R., T. Miyajima, A. Watanabe, M. Yoshikai, C. M. Ferrera, I. Orizar, T. Nakamura, M. L. San Diego-McGlone, E. C. Herrera, and K. Nadaoka. 2021. "Dissolved and Particulate Carbon Export from a Tropical Mangrove-Dominated Riverine System." *Limnology and Oceanography* 66: 3944–62.
- Ray, R., G. Thouzeau, R. Walcker, V. Vantrepotte, G. Gleixner, S. Morvan, J. Devesa, and E. Michaud. 2020. "Mangrove-Derived Organic and Inorganic Carbon Exchanges between the Sinnamary Estuarine System (French Guiana, South America) and Atlantic Ocean." *Journal of Geophysical Research Biogeosciences* 125: e2929JG005739.
- Reef, R., T. B. Atwood, J. Samper-Villarreal, M. F. Adame, E. M. Sampayo, and C. E. Lovelock. 2017. "Using eDNA to Determine the Source of Organic Carbon in Seagrass Meadows." *Limnology and Oceanography* 62: 1254–65.
- Reithmaier, G. M. S., A. Cabral, A. Akhand, M. J. Bogard, A. Borges, S. Bouillon, D. J. Burdige, et al. 2023. "Carbonate Chemistry and Carbon Sequestration Driven by Inorganic Carbon Outwelling from Mangroves and Saltmarshes." *Nature Communications* 14: 8196.
- Reithmaier, G. M. S., X. Chen, I. R. Santos, M. J. Drexler, C. Holloway, M. Call, P. G. Álvarez, S. Euler, and D. T. Maher. 2021. "Rainfall Drives Rapid Shifts in Carbon and Nutrient Source-Sink Dynamics of an Urbanized, Mangrove-Fringed Estuary." *Estuarine, Coastal and Shelf Science* 249: 107064.
- Reithmaier, G. M. S., D. T. Ho, S. G. Johnston, and D. T. Maher. 2020. "Mangroves as a Source of Greenhouse Gases to the Atmosphere and Alkalinity and Dissolved Carbon to the Coastal Ocean: A Case Study from the Everglades National Park, Florida." *Journal of Geophysical Research: Biogeosciences* 125: 1–16.
- Riascos, J. M., and J. F. Blanco-Libreros. 2019. "Pervasively High Mangrove Productivity in a Major Tropical Delta throughout an ENSO Cycle (Southern Caribbean, Colombia)." *Estuarine, Coastal and Shelf Science* 227: 106301.
- Ribeiro, R. D. A., A. S. Rovai, R. R. Twilley, and E. Castañeda-Moya. 2019. "Spatial Variability of Mangrove Primary Productivity in the Neotropics." *Ecosphere* 10: e02841.
- Robertson, A. I. 1986. "Leaf-Burying Crabs: Their Influence on Energy Flow and Export from Mixed Mangrove Forests

- (*Rhizophora* spp.) in Northeastern Australia.” *Journal of Experimental Marine Biology and Ecology* 102: 237–248.
- Robertson, A. I., and N. C. Duke. 1987. “Insect Herbivory on Mangrove Leaves in North Queensland.” *Australian Journal of Ecology* 12: 1–7.
- Rodrigues, D. P., C. Hamacher, G. C. D. Estrada, and M. L. G. Soares. 2015. “Variability of Carbon Content in Mangrove Species: Effect of Species, Compartments and Tidal Frequency.” *Aquatic Botany* 120: 346–351.
- Romigh, M. M., S. E. Davis, V. H. Rivera-Monroy, and R. R. Twilley. 2006. “Flux of Organic Carbon in a Riverine Mangrove Wetland in the Florida Coastal Everglades.” *Hydrobiologia* 569: 505–516.
- Rosentreter, J. A., A. N. Al-Haj, R. W. Fulweiler, and P. Williamson. 2021. “Methane and Nitrous Oxide Emissions Complicate Coastal Blue Carbon Assessments.” *Global Biogeochemical Cycles* 35: e2020GB006858.
- Rosentreter, J. A., A. V. Borges, B. R. Deemer, M. A. Holgerson, S. Liu, C. Song, J. Melack, et al. 2021. “Half of Global Methane Emissions Come from Highly Variable Aquatic Ecosystem Sources.” *Nature Geoscience* 14: 225–230.
- Rovai, A. S., R. R. Twilley, E. Castañeda-Moya, S. R. Midway, D. A. Friess, C. C. Trettin, J. J. Bukoski, et al. 2021. “Macroecological Patterns of Forest Structure and Allometric Scaling in Mangrove Forests.” *Global Ecology and Biogeography* 30: 1000–1013.
- Saenger, P., and S. C. Snedaker. 1993. “Pantropical Trends in Mangrove Aboveground Biomass and Annual Litterfall.” *Oecologia* 96: 293–99.
- Saleska, S. R., S. D. Miller, D. M. Matross, M. L. Goulden, S. C. Wofsy, H. da Rocha, P. B. De Camargo, et al. 2003. “Carbon in Amazon Forests: Unexpected Seasonal Fluxes and Disturbance-Induced Losses.” *Science* 302: 1554–58.
- Sanders, C. J., D. T. Maher, D. R. Tait, D. Williams, C. Holloway, J. Z. Sippo, and I. R. Santos. 2016. “Are Global Mangrove Carbon Stocks Driven by Rainfall?” *Journal of Geophysical Research: Biogeosciences* 121: 2600–2609.
- Sandoval, L. A., J. E. Mancera-Pineda, A. Delgado-Huertas, J. F. Blanco-Libreros, and J. Leal-Flórez. 2022. “Leaf Consumption and Experimental Discrimination of Stable Isotopes between Mangrove Leaves and the Tree-Climbing Crab (Brachyura: Sesamidae: *Aratus pisonii*).” *Estuarine, Coastal and Shelf Science* 274: 107906.
- Santos, D. M. C., G. C. D. Estrada, V. Fernandez, M. R. M. Estevam, B. T. de Souza, and M. L. G. Soares. 2017. “First Assessment of Carbon Stock in the Belowground Biomass of Brazilian Mangroves.” *Anais da Academia Brasileira de Ciências* 89: 1579–89. <https://doi.org/10.1590/0001-3765201720160496>.
- Santos, I. R., D. T. Maher, R. Larkin, J. R. Webb, and C. J. Sanders. 2019. “Carbon Outwelling and Outgassing vs. Burial in an Estuarine Tidal Creek Surrounded by Mangrove and Saltmarsh Wetlands.” *Limnology and Oceanography* 64: 996–1013.
- Shiau, Y. J., and C. Y. Chiu. 2020. “Biogeochemical Processes of C and N in the Soil of Mangrove Forest Ecosystems.” *Forests* 11: 1–15.
- Sidik, F., A. Lawrence, T. Wagey, F. Zamzani, and C. E. Lovelock. 2023. “Blue Carbon: A New Paradigm of Mangrove Conservation and Management in Indonesia.” *Marine Policy* 147: 105388.
- Sillanpää, M., J. Vantellingen, and D. A. Friess. 2017. “Vegetation Regeneration in a Sustainably Harvested Mangrove Forest in West Papua, Indonesia.” *Forest Ecology and Management* 390: 137–146.
- Simpson, L. T., S. K. Chapman, L. M. Simpson, and J. A. Cherry. 2023. “Do Global Change Variables Alter Mangrove Decomposition? A Systematic Review.” *Global Ecology and Biogeography* 32: 1874–92.
- Sippo, J. Z., D. T. Maher, D. R. Tait, C. Holloway, and I. R. Santos. 2016. “Are Mangroves Drivers or Buffers of Coastal Acidification? Insights from Alkalinity and Dissolved Inorganic Carbon Export Estimates across a Latitudinal Transect.” *Global Biogeochemical Cycles* 30: 753–766.
- Sogin, E. M., D. Michellod, H. R. Gruber-Vodicka, P. Bourceau, B. Geier, D. V. Meier, M. Seidel, et al. 2022. “Sugars Dominate the Seagrass Rhizosphere.” *Nature Ecology and Evolution* 6: 866–877.
- Sousa, W. P., P. G. Kennedy, and B. J. Mitchell. 2003. “Propagule Size and Predispersal Damage by Insects Affect Establishment and Early Growth of Mangrove Seedlings.” *Oecologia* 135: 564–575.
- Taillardat, P. 2022. “Going Local: How Coastal Environmental Settings Can Help Improve Global Mangrove Carbon Storage and Flux Estimates.” *Geophysical Research Letters* 49: e2022GL101979.
- Taillardat, P., P. Willemsen, C. Marchand, D. A. Friess, D. Widory, P. Baudron, V. V. Truong, T. N. Nguyễn, and A. D. Ziegler. 2018. “Assessing the Contribution of Porewater Discharge in Carbon Export and CO₂ Evasion in a Mangrove Tidal Creek (Can Gio, Vietnam).” *Journal of Hydrology* 563: 303–318.
- Then, A. Y. H., M. F. Adame, B. Fry, V. C. Chong, P. M. Riekenberg, R. Mohammad Zakaria, and S. Y. Lee. 2020. “Stable Isotopes Clearly Track Mangrove Inputs and Food Web Changes along a Reforestation Gradient.” *Ecosystems* 24: 939–954.
- Thongtham, N., E. Kristensen, and S. Y. Puangprasan. 2008. “Leaf Removal by Sesamid Crabs in Bangrong Mangrove Forest, Phuket, Thailand; with Emphasis on the Feeding Ecology of *Neopisesarma versicolor*.” *Estuarine, Coastal and Shelf Science* 80: 573–580.
- Twilley, R., E. Castañeda-Moya, V. Rivera-Monroy, and A. Rovai. 2017. “Productivity and Carbon Dynamics in Mangrove Wetlands.” In *Mangrove Ecosystems: A Global Biogeographic Perspective: Structure, Function, and Services*, edited by V. H. Rivera-Monroy, S. Y. Lee, E. Kristensen, and R. R. Twilley, 113–162. Cham: Springer.
- Twilley, R. R., R. H. Chen, and T. Hargis. 1992. “Carbon Sinks in Mangroves and Their Implications to Carbon Budget of Tropical Coastal Ecosystems.” *Water, Air and Soil Pollution* 64: 265–288.
- Twilley, R. R., V. H. Rivera-Monroy, A. S. Rovai, E. Castañeda-Moya, and S. Davis. 2019. “Mangrove Biogeochemistry at Local to Global Scales Using Ecogeomorphic Approaches.” In *Coastal Wetlands: An Integrated Ecosystem Approach*, 2nd ed., edited by G. M. E. Perillo, E. Wolanski, D. R. Cahoon, and C. S. Hopkinson, 717–785. Amsterdam: Elsevier.

- Twilley, R. R., A. S. Rovai, and P. Riul. 2018. "Coastal Morphology Explains Global Blue Carbon Distributions." *Frontiers in Ecology and the Environment* 16: 503–8.
- Utrera-López, M. E., and P. Moreno-Casasola. 2008. "Mangrove Litter Dynamics in La Mancha Lagoon, Veracruz, Mexico." *Wetlands Ecology and Management* 16: 11–22.
- Van der Stocken, T., J. López-Portillo, and N. Koedam. 2017. "Seasonal Release of Propagules: Assessment of Current Data." *Aquatic Botany* 138: 92–99.
- Van der Stocken, T., A. K. S. Wee, D. J. R. De Ryck, B. Vanschoenwinkel, D. A. Friess, F. Dahdouh-Guebas, M. Simard, N. Koedam, and E. L. Webb. 2019. "A General Framework for Propagule Dispersal in Mangroves." *Biological Reviews* 94: 1547–75.
- Van Vinh, T., M. Allenbach, A. Joanne, and C. Marchand. 2019. "Seasonal Variability of CO₂ Fluxes at Different Interfaces and Vertical CO₂ Concentration Profiles within a *Rhizophora* Mangrove Forest (Can Gio, Vietnam)." *Atmospheric Environment* 201: 301–9.
- West, R., and C. Thorogood. 1985. "Mangrove Dieback in Hunter River Caused by Caterpillars." *Australian Fisheries* 44: 27–28.
- Whitten, A. J., and S. J. Damanik. 1986. "Mass Defoliation of Mangroves in Sumatra, Indonesia." *Biotropica* 18: 176.
- Xiong, Y., R. Cakir, S. M. Phan, A. Ola, K. W. Krauss, and C. E. Lovelock. 2019. "Global Patterns of Tree Stem Growth and Stand Aboveground Wood Production in Mangrove Forests." *Forest Ecology and Management* 444: 382–392.
- Yando, E. S., S. F. Jones, and M. W. Hester. 2021. "Limited Mangrove Propagule Retention at a Latitudinal Range Limit: Spatiotemporal Patterns at the Patch Scale." *Estuaries and Coasts* 44: 834–845.
- Zhang, H., W. Yuan, W. Dong, and S. Liu. 2014. "Seasonal Patterns of Litterfall in Forest Ecosystem Worldwide." *Ecological Complexity* 20: 240–47.
- Zhang, M., Y. Dai, P. Dai, Z. Sun, X. Lin, Z. He, and Y. Tian. 2022. "Finding the Pieces for the Anaerobic Methane Oxidation Jigsaw Puzzle in Mangrove Wetlands." *International Biodeterioration and Biodegradation* 168: 105375.
- Zhang, Y., L. Xiao, D. Guan, Y. Chen, M. Motelica-Heino, Y. Peng, and S. Y. Lee. 2021. "The Role of Mangrove Fine Root Production and Decomposition on Soil Organic Carbon Component Ratios." *Ecological Indicators* 125: 107525.
- Zhao, X., V. H. Rivera-Monroy, L. M. Farfán, H. Briceño, E. Castañeda-Moya, R. Travieso, and E. E. Gaiser. 2021. "Tropical Cyclones Cumulatively Control Regional Carbon Fluxes in Everglades Mangrove Wetlands (Florida, USA)." *Scientific Reports* 11: 1–17.
- Zhu, X., Z. Qin, and L. Song. 2021. "How Land-Sea Interaction of Tidal and Sea Breeze Activity Affect Mangrove Net Ecosystem Exchange?" *Journal of Geophysical Research: Atmospheres* 126: e2020JD034047.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Adame, M. F., N. Cormier, P. Taillardat, N. Iram, A. Rovai, T. M. Sloey, E. S. Yando, et al. 2024. "Deconstructing the Mangrove Carbon Cycle: Gains, Transformation, and Losses." *Ecosphere* 15(3): e4806. <https://doi.org/10.1002/ecs2.4806>