

Carbon Cycling and Storage in Mangrove Forests

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Abstract

Mangroves are ecologically and economically important forests of the tropics. They are highly productive ecosystems with rates of primary production equal to those of tropical humid evergreen forests and coral reefs. Although mangroves occupy only 0.5% of the global coastal area, they contribute 10–15% (24 Tg C y⁻¹) to coastal sediment carbon storage and export 10–11% of the particulate terrestrial carbon to the ocean. Their disproportionate contribution to carbon sequestration is now perceived as a means for conservation and restoration and a way to help ameliorate greenhouse gas emissions. Of immediate concern are potential carbon losses to deforestation (90–970 Tg C y⁻¹) that are greater than these ecosystems' rates of carbon storage. Large reservoirs of dissolved inorganic carbon in deep soils, pumped via subsurface pathways to adjacent waterways, are a large loss of carbon, at a potential rate up to 40% of annual primary production. Patterns of carbon allocation and rates of carbon flux in mangrove forests are nearly identical to those of other tropical forests.

INTRODUCTION

Mangroves are the only woody plants occupying the margin between land and sea in low latitudes. First appearing on the shores of the Tethys Sea, mangroves diverged from terrestrial relatives during the Late Cretaceous–Early Tertiary (Ricklefs et al. 2006). Today, approximately 70 genetically diverse species constitute the mangrove flora (Spaulding et al. 2010). These tidal forests inhabit approximately 138,000 km² (Giri et al. 2010) of mostly sheltered subtropical and tropical coastlines, and are disappearing at an alarming rate and facing an uncertain future (Polidoro et al. 2010, Van Lavieren et al. 2012). Structurally simple compared with terrestrial forests, mangrove forests harbor few tree species and usually lack an understory, but they are functionally complex, having ecosystem attributes analogous to those of other forests but also functioning like other estuarine and marine ecosystems in myriad ways (Feller et al. 2010).

The biomass of mangrove forests peaks at equatorial latitudes. Their global mean biomass [247 tonnes per hectare (t ha⁻¹)] equals the global average biomass of tropical humid evergreen forests (Alongi 2009, Camacho et al. 2011, Donato et al. 2012). Drivers such as salinity, geomorphology, and tidal regime impose structural and functional constraints and foster adaptations (e.g., aerial roots, viviparous embryos, and efficient nutrient-retention mechanisms) as well as physiological mechanisms to help mangroves subsist in waterlogged saline soils. Most mangrove carbon is stored in soil and sizable belowground pools of dead roots (Alongi et al. 2003, 2004b), which helps to conserve and recycle nutrients beneath the forest.

Tides and (to a lesser extent) waves constitute an auxiliary energy subsidy that allows mangrove forests to store and transport new fixed carbon, sediments, food, and nutrients and to do the work of exporting wastes, heat, and refractory compounds to the atmosphere and adjacent coastal waters (Vo-Luong & Massel 2008, Barr et al. 2013). Organisms that make use of this subsidized energy can shunt more of their own energy to growth and reproduction, thus making tides one of the primary drivers structuring and regulating mangrove ecosystems (Wolanski et al. 1992).

Forest food webs are composed of a mixture of arboreal and soil fauna and flora that actively cycle carbon (Scharler 2011, Sousa & Dangremond 2011). Equally productive are highly diverse plankton communities that are well adapted to the complex chemistry and physics of opaque tidal waters. Mangrove creeks and waterways are important habitats for estuarine and marine organisms ranging in size from viruses to crocodiles. Tidal circulation is highly complex, as forest topography and morphology and the tidal prism control the extent of mixing and trapping of water and suspended matter within the forest and adjacent waterways (Wolanski et al. 1992). These phenomena are responsible for the tendency of most, but not all, mangroves to passively and actively accumulate sediments (Wolanski 1995).

Mangroves are increasingly seen as carbon-rich ecosystems that warrant preservation and restoration (Van Lavieren et al. 2012), not so much because they are ecologically and economically important as because they are perceived as able to play a role in climate regulation, capturing and preserving significant amounts of carbon to help counterbalance anthropogenic CO₂ emissions (McLeod et al. 2011, Siikamäki et al. 2012). It is unclear, however, whether they constitute a significant carbon sink in the coastal ocean, or whether management plans to replant and create new forests will make a difference in ameliorating climate change (see sidebar, Blue Carbon and Climate Change Mitigation). Here, I review what is known about carbon cycling in mangroves, especially their capacity to capture and store carbon, as well as aspects of these processes that are not fully understood but may nevertheless provide new insights into the fate of mangrove carbon.

BLUE CARBON AND CLIMATE CHANGE MITIGATION

Blue carbon refers to the preservation of carbon within aquatic ecosystems, especially in their soils and sediments (see Related Resources at the end of this article). The term is increasingly used to describe projects aimed at enhancing carbon storage by expanding mangrove coverage in particular, based on the fact that carbon sequestration by mangroves is disproportionate to their area. Blue carbon is almost certainly a moniker through which projects to restore, conserve, and create mangroves will be conducted. The expectation of nongovernmental organizations and governments is that restoring mangroves will help to ameliorate climate change. However, this notion is an oversimplification, as global expansion of mangroves is unlikely to significantly redress the global CO₂ imbalance; even if replanting the current global mangrove area were able to double the global mangrove carbon sequestration rate of 24 Tg C y⁻¹ in a year, the amount of carbon sequestered would remain minuscule compared with the annual rate of CO₂ emissions (30.6 Gt) to the atmosphere (Farmer & Cook 2013). Although the presence of more mangroves does mean more coastal carbon storage, the short- and medium-term value of such conservation projects seems to lie mainly in the restoration of the many other valuable ecosystem services that mangroves offer to the tropical coastal zone and its inhabitants.

CAPTURING CARBON

Shallow-water aquatic ecosystems acquire carbon by photosynthesis and by import of allochthonous carbon from adjacent land, sea, and sky. Although various types of algae grow on mangrove surfaces, the trees manufacture the vast bulk of carbon fixed from the atmosphere (Alongi 2009). The second-largest carbon input comes from macroalgae colonizing aboveground roots and microalgae carpeting portions of the forest floor. The third-largest carbon input comes from transport and deposition of materials from upstream and from the adjacent coastal zone. The relative contributions of terrestrial and marine sources depend mainly on forest location and the rate of river discharge in relation to the strength of tidal pulses; over the long term, most carbon is produced in situ and stored belowground, eventually as peat (Krauss et al. 2010, Ray et al. 2011, Osland et al. 2012). Atmospheric carbon deposition may be significant in places where fires are widespread and where concentrations of black carbon from smoke and dust may be seasonally intense, such as Indonesia (Jurado et al. 2008). However, no data are available on this phenomenon in mangrove environments.

Primary Production

Like other trees, mangroves assimilate atmospheric CO₂ into organic compounds to manufacture new leaves, roots, branches, and stem tissue; maintain existing tissue; create storage reserves; and develop chemical defenses. Living in salty, anoxic soils, mangroves use an advantageous strategy of minimizing water loss and maximizing carbon gain by being highly efficient in water use and transpiration and by exhibiting physiological plasticity in relation to changes in environmental conditions (Ball 1996, Krauss & Ball 2013).

Maximum CO₂ assimilation rates in mangrove leaves may exceed 25 μmol m⁻² s⁻¹, but most values range from 5 to 20 μmol m⁻² s⁻¹, as saturation at comparatively low light levels is due to low stomatal conductance and intercellular CO₂ levels (Alongi 2009). Despite constraints such as soil salinity and anoxia, mangroves tend to have higher mean rates of leaf photosynthesis

Gross primary production (GPP):

the rate at which an ecosystem's producers capture and store chemical energy as biomass

Respiration (R): the rate at which organisms release heat energy produced by work

Net primary production (NPP):

the rate at which an ecosystem's producers store net chemical energy ($GPP - R = NPP$)

($12 \mu\text{mol m}^{-2} \text{s}^{-1}$) than leaves of tropical humid evergreen trees ($7 \mu\text{mol m}^{-2} \text{s}^{-1}$), although shade-intolerant species have equivalent rates (Alongi 2009).

There have been few measurements of dark respiration by mangrove leaves, but the mean rate for mangroves ($0.6 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) is roughly equal to that for tropical humid trees ($0.4 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) (Alongi 2009). Using these data, we obtain average ratios of gross primary production (GPP) to ecosystem respiration (R) of 17.9 and 14.3 for mangrove leaves and tropical humid leaves, respectively. Root respiration measurements are also rare, with the few estimates for mangroves being low but varying widely ($0.5\text{--}10 \text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$) compared with those for other tropical trees ($3\text{--}55 \text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$) (Ball 1996). The differences in these data do not forecast differences in rates of GPP or net primary production (NPP) among forest types, as the data are limited and there is great variability among all forests.

Mangroves are among the most productive plants in the sea, yet considerable uncertainty remains about rates of mangrove canopy production owing to the shortcomings of methods adapted from terrestrial forest ecology. For instance, rates of primary production based on canopy measurements of gas exchange or light attenuation overestimate what are considered to be more realistic rates of NPP based on actual growth measurements over time (Alongi 2009). The most reliable forest estimates are derived from measures of litterfall (as a proxy for foliage production) and increases in stem girth (as a proxy for wood production). Using these data for mangroves, Alongi (2009) estimated a mean aboveground NPP rate of $11.1 \text{Mg C ha}^{-1} \text{y}^{-1}$. There is considerable scatter in the data owing to variations among forests in tree age structure, species composition, climate, and other environmental conditions, but forest production declines significantly with increasing latitude, and production is lower in the dry tropics than in the humid tropics (Alongi 2009).

How does the NPP of mangroves compare with that of other tropical forests and marine ecosystems? The NPP of mangroves is greater than that of salt marshes ($8.34 \text{Mg C ha}^{-1} \text{y}^{-1}$), seagrasses ($1.04 \text{Mg C ha}^{-1} \text{y}^{-1}$), macroalgae ($3.8 \text{Mg C ha}^{-1} \text{y}^{-1}$), and coastal phytoplankton ($1.7 \text{Mg C ha}^{-1} \text{y}^{-1}$) but roughly equivalent to that of coral reefs ($10 \text{Mg C ha}^{-1} \text{y}^{-1}$) (Duarte & Cebrián 1996, Duarte et al. 2010). Variability within each ecosystem is very large, encompassing many geographical and ecological differences, but mangroves are on average among the most proficient carbon fixers on earth and are certainly the most productive ecosystem in the coastal zone. Terrestrial humid evergreen forests ($10.8 \text{Mg C ha}^{-1} \text{y}^{-1}$) and peat swamp forests ($11.1 \text{Mg C ha}^{-1} \text{y}^{-1}$) are as productive as mangroves (Pregitzer & Euskirchen 2004, Chimner & Ewel 2005, Miyamoto et al. 2007, Malhi et al. 2011, Migeot & Imbert 2012), underscoring basic similarities in ecological and physiological functions among all tropical trees.

Very few studies have measured the growth of a mangrove forest over time, but data suggest that the maturity phase of a mangrove forest may be prolonged when disturbed, resetting or arresting forest development to a stable state. This phenomenon implies that disturbances, including climate change, may facilitate carbon uptake in mangrove forests for decades. Indeed, the photosynthetic production of *Rhizophora apiculata* in Southeast Asia (Alongi 2009) increases rapidly from the seedling stage to approximately 20 years of age, then levels off, without declining, for up to 80 years. Some mangrove forests may thus serve as carbon sinks for nearly a century, but long-term measurements are lacking, and all tropical forests may be experiencing changes in metabolism and carbon balance in the Anthropocene that are not well understood (Malhi 2012).

On an area-specific basis, mangrove forests store more carbon than other ecosystems (Figure 1), especially in soils: Mangroves have a mean whole-ecosystem carbon stock of 956t C ha^{-1} , compared with 241t C ha^{-1} for rain forests, 408t C ha^{-1} for peat swamps, 593t C ha^{-1} for salt marshes, and 142.2t C ha^{-1} for seagrasses. Not all mangrove forests are large, and mangroves in the dry tropics are smaller than those in the wet tropics

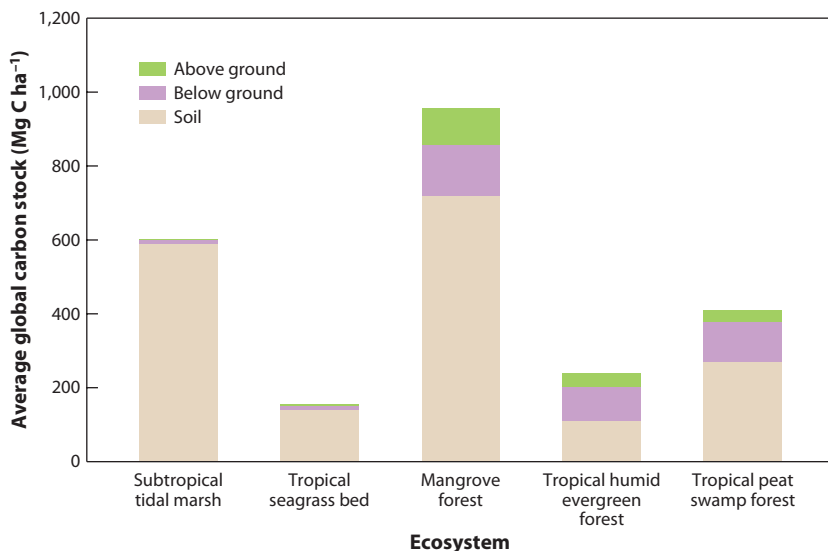


Figure 1

Average global carbon stocks of subtropical tidal marsh, tropical seagrass bed, tropical humid evergreen forest, and tropical peat swamp forest ecosystems compared with those of subtropical and tropical mangrove ecosystems. Tidal marsh data are compiled from Kirby & Gosselink (1976), Linthurst & Reimold (1978), da Cunha Lana et al. (1991), Cartaxana & Catarino (1997), Curcó et al. (2002), Scarton et al. (2002), Neves et al. (2007), and Darby & Turner (2008). Seagrass data are compiled from Ogden & Ogden (1982), Brouns (1985, 1987), Williams (1987), Lindeboom & Sandee (1989), Nienhuis et al. (1989), Moriarty et al. (1990), van Lent et al. (1991), Aoi & Pollard (1993), Coles et al. (1993), Ismail (1993), Vermaat et al. (1993, 1995), McKenzie (1994), Poovachiranon & Chansang (1994), Lee (1997), van Tussenbroek (1998), Rasheed (1999), Udy & Dennison (1997), Holmer et al. (2001), Paynter et al. (2001), Halun et al. (2002), Mellors et al. (2002), Daby (2003), Povidisa et al. (2009), Devereux et al. (2011), and Fourqurean et al. (2012). Humid evergreen and peat swamp data are compiled from Golley et al. (1975), Brown et al. (1993), Schöngart et al. (2008), Laumonier et al. (2010), Lorenz & Lal (2010), Hergoualc'h & Verchot (2011), Page et al. (2011), Saatchi et al. (2011), Vieira et al. (2011), Kronseder et al. (2012), and Meister et al. (2012). Mangrove data are from Alongi (2012).

(Adame et al. 2013). Regardless of forest size, soils constitute the largest carbon pool, with the percentage of the total soil pool varying from 44% for rain forests to 70% for peat swamps, 75% for mangroves, and >90% for marshes and seagrasses; roots are a comparatively small pool, with mangroves and rain forests having the largest relative pools, at approximately 13–15%. Mangroves, tidal marshes, and seagrasses have large amounts of carbon vested belowground owing to their aquatic milieu. Large reservoirs conserve nutrients and help stabilize the vegetation against tides, waves, wind, and storms. For mangroves, it is physiologically advantageous to invest more fixed carbon in growing extensive root systems to maximize water gain.

The partitioning of fixed carbon in mangrove trees is similar to that in tropical rain forest and peat swamp trees, but data for belowground root production and respiration of woody parts in mangroves are scarce (Romero et al. 2005, Huxham et al. 2010). A preliminary budget for carbon allocation in *Rhizophora apiculata* trees indicates that, of a total net daytime fixed production of 56 t C ha⁻¹ y⁻¹, 22% is respired by foliage overnight, 11% accumulates as aboveground biomass, 8% falls as litter, and 1% accumulates as belowground biomass; 58% is therefore presumably used in root turnover and respired by roots, branches, and stems (Clough et al. 1997). Roughly 65% of assimilated carbon is respired, as in terrestrial trees. These data agree with estimates from other

Table 1 Estimates of allocation of fixed carbon in tropical mangrove, rain forest, and peat swamp ecosystems

Ecosystem	CUE	NPP _{CANOPY}	NPP _{WOOD}	NPP _{ROOT}
Mangrove	0.33	32%	32%	36%
Rain forest	0.35	35%	25%	38%
Peat swamp	0.46	36%	30%	12%

Mangrove data reported by Alongi (2009); rain forest data reported by Malhi et al. (2011) and Malhi (2012); peat swamp CUE data reported by Suzuki et al. (1999); peat swamp NPP data reported by Chimner & Ewel (2005). Abbreviations: CUE, carbon use efficiency; NPP_{CANOPY}, canopy net primary production; NPP_{WOOD}, wood net primary production; NPP_{ROOT}, root net primary production.

mangrove forests (Alongi et al. 2004a, Suwa et al. 2006). Recent estimates of whole-ecosystem forest-atmosphere CO₂ exchange using eddy covariance techniques (Monji 2007, Ganguly et al. 2008, Barr et al. 2010) confirmed that roughly 60–90% of ecosystem GPP is respired.

Although the percentage of GPP that is shunted into NPP varies among mangroves, rain forests, and peat swamps (**Table 1**), rain forest trees allocate carbon nearly equally among wood, canopy, and roots, and the bulk of fixed carbon (70%) is respired back to the atmosphere. Mangrove trees allocate carbon identically into roughly equal amounts for wood, canopy, and roots, although the percentage for mangrove roots is based on sparse data. Indeed, the lack of root data has significant implications for the global carbon budget for mangroves, as discussed below. Twenty-two percent of fixed carbon is unaccounted for, but peat swamp trees appear to allocate carbon to wood and canopy production similarly to the way other tropical trees do. Any differences are probably insignificant or not apparent owing to inherent variability among trees and forests of different species compositions and ages. The similarities among ecosystems suggest common physiological constraints of carbon assimilation and allocation. However, the unique feature of a large pool of dead roots belowground makes evolutionary sense for mangroves as an effective counterbalance to the loss of litter and other carbon via tides and subsurface advection. Tropical terrestrial forests recycle elements by rapid litter decomposition in a relatively thin humus layer, whereas mangroves recycle elements via tight coupling between roots and microbes that coexist several meters into the forest floor, possibly to curtail losses and minimize energetic costs.

Sedimentation

Mangroves capture carbon both passively and actively from river water discharged from upstream and from tidal water laden with fine particles from the adjacent coastal ocean. Not all mangroves accumulate fine sediment particles, but those that inhabit soft sediment deposits do. Many studies have measured sedimentation onto the forest floor, and a number of workers have determined the mechanisms by which sediments and associated carbon accrete. The transport of suspended materials in overlying water is controlled by the tidal prism, tidal pumping and trapping, baroclinic circulation, flocculation, microbial mucus production, and physicochemical processes that disaggregate flocs of cohesive sediment (Wolanski 1995).

The size, shape, and distribution patterns of trees play a defining role in sedimentation (Mazda et al. 1997, 1999). As tides enter the forest, flow around the trees generates turbulent wakes that keep flocs suspended. When the tide turns from flood to ebb and waters become quiescent, a short period of particle settling occurs, facilitated by the particles sticking to mucus on surfaces. Particle flocculation results in larger particles with faster settling velocities, and high tree densities also inhibit water motion.

Methods of measuring soil accretion vary in accuracy, with some being highly inaccurate (a mass balance approach) and others measuring only short-term accumulation rates. The least arguable method is to measure the vertical decline in concentrations of radioactive elements derived from atomic bomb fallout (excess ^{210}Pb and ^{137}Cs), which, coupled with soil organic carbon concentrations, provides a chronology of sedimentation for up to the past century.

The rate of soil accretion in mangroves averages 5 mm y^{-1} , with measurements ranging from 0.1 to 10.0 mm y^{-1} (Alongi 2012). A few forests show net erosion and massive accretion. The frequency of tidal inundation is the main driver controlling sedimentation rate (Adame et al. 2010); as inundation frequency decreases with increasing surface elevation, particles have less chance to accumulate, so forests located farther from the sea experience less soil accretion than forests closer to mean sea level do (Cahoon et al. 2006). Vertical accretion resulting from belowground root growth as well as from surface algal mats and litter accumulation can, in some forests, be greater than particle accretion (McKee 2011). Accretion and surface elevation vary over long timescales as environmental processes such as natural subsidence and changes in sea level come into play (Krauss et al. 2010, Sanders et al. 2010, López-Medellín et al. 2011, Smoak et al. 2013). Mangrove sedimentation is currently keeping pace with local rises in sea level throughout most of the tropics (Alongi 2008). This is not true in parts of the Caribbean and South Atlantic (López-Medellín et al. 2011, McKee 2011) or on islands in the Pacific (Krauss et al. 2010), where sedimentation varies greatly in relation to fluctuations in climate variability. Storms, hurricanes, and other climatic disturbances play a strong role in net sedimentation in mangrove forests (Smith et al. 2009, Whelan et al. 2009, Smoak et al. 2013).

Carbon Storage

The annual burial rate of soil carbon is estimated by the difference between carbon losses (export, consumption, and mineralization) and the annual accumulation rate, as what remains is presumably preserved. Heavily impacted mangroves such as those in southern India and China accumulate soil carbon at a rate of more than $200 \text{ g C m}^{-2} \text{ y}^{-1}$, but carbon sequestration in most forests is much lower (**Figure 2**); the current global mean of $174 \text{ g C m}^{-2} \text{ y}^{-1}$ is very close to earlier estimates by Twilley et al. (1992), Jennerjahn & Ittekkot (2002), Chmura et al. (2003), and Duarte et al. (2005), as well as to the more recent estimates by Bouillon et al. (2008), Alongi (2009), and Breithaupt et al. (2012) of 134, 211, and $163 \text{ g C m}^{-2} \text{ y}^{-1}$, respectively. Assuming that all $138,000 \text{ km}^2$ (Giri et al. 2010) of the world's mangroves sustain carbon burial, the mean global burial rate for soil carbon is 24 Tg C y^{-1} (**Table 2**).

How does carbon sequestration by mangroves compare with that estimated for other coastal ecosystems? On an areal basis, salt marshes have a similarly high sequestration rate of approximately $218 \text{ g C m}^{-2} \text{ y}^{-1}$, but seagrasses, estuaries, and continental shelves have lower rates (**Table 2**). Mangroves occupy only approximately 0.5% of global coastal ocean area, yet they account for approximately 10–15% of total carbon sequestration; salt marshes, seagrasses, and estuaries also sequester more carbon within their relatively small areas than the shelf proper does. The mangrove contribution is very small compared with sequestration in all other tropical forests (422 Gt C y^{-1}), accounting for approximately 3% of total tropical forest carbon sequestration, although mangroves occupy <1% of the total area of the world's tropical forests.

Of immediate concern is how much sequestered carbon may be returned to the atmosphere by the continuing losses of mangroves. Clearing and conversion of mangroves for industrial estates and aquaculture enterprises and losses arising from hydrological alterations have led to dramatic changes in soil chemistry, resulting in rapid CO_2 emission rates ($1,500\text{--}2,900 \text{ Mg C km}^{-2} \text{ y}^{-1}$) (Lovelock et al. 2011). Donato et al. (2011) calculated an annual range of CO_2 emissions of

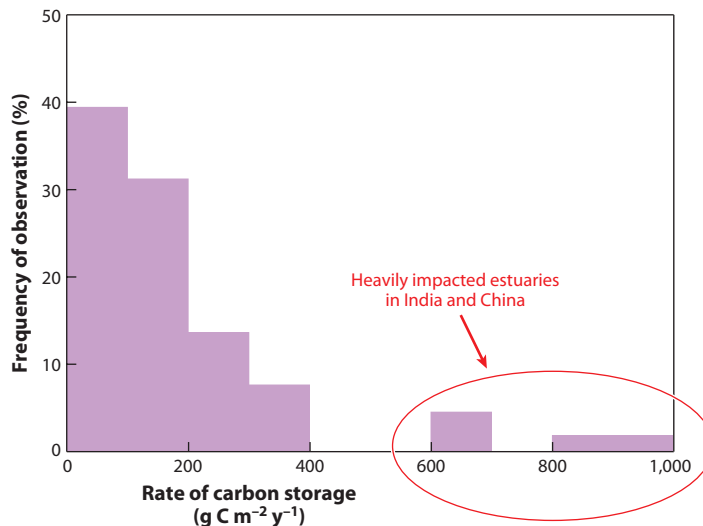


Figure 2

Annual rates of carbon storage in mangrove forest soils ($n = 66$). Data are from references in the figure 3 legend in Alongi (2012).

112–392 Mg C per hectare of forest cleared, giving a potential global emissions range of 0.02–0.12 Pg C y^{-1} . This estimate equates to approximately 2–10% of global deforestation emissions and up to 50% of emissions from tropical peat lands. More detailed estimates by Pendleton et al. (2012) imply even greater emissions from mangroves (**Table 2**), with CO₂ losses from salt marshes and seagrasses on the order of 20–240 and 50–330 Tg C y^{-1} , respectively. These estimates are crude but suggest that greater efforts must be made to conserve preserved carbon.

LOSING CARBON

The principal losses of carbon from mangrove ecosystems are due to respiration and tidal export. There are other losses that all too often may be considerable, such as those caused by the

Table 2 Contributions of mangroves and other coastal habitats to carbon sequestration in the global coastal ocean

Ecosystem	Area (10 ¹² m ²)	Sequestration rate (g C m ⁻² y ⁻¹)	Global sequestration (Tg C y ⁻¹)	Potential global loss (Tg C y ⁻¹)
Mangrove	0.14	174 ± 23	24	90–970
Salt marsh	0.20–0.40	218 ± 24	5–87	20–240
Seagrass	0.17–0.60	138 ± 38	48–112	50–330
Estuary	1.1	45	50	—
Shelf	26	17	44	—

Mangrove area and sequestration data reported in figure 3 of Alongi et al. (2012); salt marsh area and sequestration data reported in table 1 of Mcleod et al. (2011); seagrass area and sequestration data reported by Fourqurean et al. (2012); estuary and shelf area and sequestration data reported by Cai (2011); all potential global loss data reported by Pendleton et al. (2012).

harvesting of wood for human use or clear felling for unsustainable purposes (Sweetman et al. 2010, Kridiborworn et al. 2012). Secondary production and respiratory losses by mangrove macrofauna (such as crabs, shrimp, and fish) also occur, although they are probably small compared with tidal losses and tree respiration. Much faunal production is eventually lost to other consumers (including humans) or to the adjacent coastal zone; this production may also be retained within the forest via positive-feedback loops and eventually remineralized and respired (Scharler 2011, Sousa & Dangremond 2011). For organisms that are small enough, these losses may ordinarily be incorporated into measurements of soil and water respiration. Such losses, though small, are difficult to sum across any forest ecosystem and are likely to be extremely variable (Alongi 2009).

DOC: dissolved organic carbon
POC: particulate organic carbon
DIC: dissolved inorganic carbon

Tidal Export

Export of leaves, bark, branches, twigs, and other plant litter is the most obvious loss of carbon from mangroves and other tidal wetlands, the crux of the outwelling concept first formulated by Odum (1968). The outwelling concept was that tidal export of carbon, nitrogen, and other elements from fertile wetlands provides a subsidy to nourish adjacent nearshore food webs. We know now that the reality is much more complex and that the role of mangrove litter in adjacent coastal food webs is limited (Adame & Lovelock 2011, Adame et al. 2012).

A recent analysis of carbon exchange (Adame & Lovelock 2011) found that litter export from mangroves averages $202 \text{ g C m}^{-2} \text{ y}^{-1}$, or roughly 50% of average mangrove litterfall. Rainfall and temperature are the main drivers of litter export, accounting for 77% of the variation in global litterfall, with mangroves in regions with lower rainfall and higher temperatures exporting more litter than those in regions with higher rainfall and lower temperatures. The mean rate of dissolved organic carbon (DOC) export across all mangroves is $26.6 \text{ g C m}^{-2} \text{ y}^{-1}$, with tidal amplitude being the main driver of export (Adame & Lovelock 2011).

Mangrove particulate organic carbon (POC) export accounts for as much as 10–11% of total terrestrial carbon input to the ocean and 12–15% of total carbon accumulation in shelf margin sediments (Jennerjahn & Ittekkot 2002, Dittmar et al. 2006). Most of the carbon exported from mangroves is refractory to immediate decay and normally restricted to a few kilometers offshore owing to local geomorphology. Such factors militate against extensive outwelling, as coastal boundary layers offshore and tidal trapping or high-salinity plugs within mangrove estuaries efficiently trap litter (Stieglitz & Ridd 2001). The export of dissolved inorganic carbon (DIC) is equally complex, and is discussed below in the context of the forest floor as a virtual pump for transporting respired carbon to adjacent creek and inshore waters.

Pelagic Respiration

Respiration in tidal creeks and waterways snaking through mangrove ecosystems is a significant but only recently quantified loss of carbon. Pelagic metabolism averages $846.9 \text{ mg C m}^{-2} \text{ d}^{-1}$ and ranges from 0.1 to $3.5 \text{ g C m}^{-2} \text{ d}^{-1}$. A recent analysis (Alongi 2009) indicated that pelagic respiration correlates only with standing stocks of chlorophyll *a*, which implies close linkage between phytoplankton and microheterotrophs; it also suggests that phytoplankton contribute significantly to water column respiration. Drivers of pelagic respiration are multitudinous: temperature, bacterioplankton growth rates, dissolved and particulate nutrient concentrations, grazing intensity, and availability of organic substrates. Despite high rates of respiration in polluted estuaries, mangrove waters are, on average, net autotrophic, with a mean GPP/R ratio of 1.8 ± 0.3 , substantially higher than the mean ratios of 0.8–1.0 calculated for estuarine waters globally (Gattuso et al. 1998). Organically enriched mangrove estuaries, such as those in many Asian systems, are net heterotrophic or oscillate seasonally between net autotrophy and net heterotrophy (Ram et al. 2003).

High rates of pelagic metabolism result directly in supersaturation of mangrove waters with respect to DIC; CO₂ dissolved in pore water and transported laterally by tidal pumping to adjacent waters also contributes to CO₂ supersaturation. Recent studies of water-air CO₂ fluxes confirmed that mangrove waterways are another significant pathway of carbon loss (Borges et al. 2003, Bouillon et al. 2003, Biswas et al. 2004, Koné & Borges 2008, Ralison et al. 2008, Zablocki et al. 2011). Water-air exchange averages 43 mmol C m⁻² d⁻¹ and ranges from 3 to 114 mmol C m⁻² d⁻¹, varying most closely in response to tidal stage and, to a lesser extent, temperature and precipitation (Alongi 2009). Fluxes are usually minimal during the postmonsoon months and maximal during the premonsoon and early monsoon months (Biswas et al. 2004). CO₂ emissions from mangrove waterways correspond to approximately 5% of total emissions from subtropical and tropical oceans and approximately 15% of total emissions from the global coastal ocean (Koné & Borges 2008). The mangrove contribution of DIC to the coastal ocean is disproportionate to the relatively small areas of waterways and creeks.

Forest Floor Respiration

Forest soils are where most heterotrophic respiration occurs. Metabolism at the surface of the forest floor is relatively easy to measure and until recently was thought to be a good measure of total benthic metabolism. Recent measurements of microbial metabolism in deep (>50 cm) soils and of the chemical constituents of groundwater seepage suggest that belowground fluxes of respired carbon are larger and more complex than previously believed.

Surface fluxes. Most measurements of soil respiration have been made from chambers enclosing a small area of the soil surface, preferably avoiding the numerous burrows, tubes, cracks, fissures, and surface roots that pockmark the forest floor. The assumption of this method is that metabolism throughout the sediment deposits is in steady state and that measurement of gaseous or dissolved O₂ and CO₂ from the soil surface represents total soil metabolism. In reality, such measurements more likely represent metabolism of microbes (including algae) only within a few millimeters of the soil surface, as a number of factors militate against steady-state metabolism (Alongi et al. 2012). A large number of observations ($n > 140$) indicate that rates of O₂ consumption and CO₂ release (mean \pm 1 SE) from the soil surface are significantly greater from exposed soils (O₂: 65 \pm 11 mmol m⁻² d⁻¹; CO₂: 69 \pm 8 mmol m⁻² d⁻¹) than from inundated soils (O₂: 36 \pm 5 mmol m⁻² d⁻¹; CO₂: 49 \pm 6 mmol m⁻² d⁻¹). These differences reflect that gases have a faster molecular diffusion than fluids and that openings are replenished with air during exposure, increasing the available surface area and possibly increasing aerobic respiration and chemical oxidation.

Higher rates of CO₂ and DIC release compared with the rate of O₂ consumption result in respiratory quotients slightly less than 1, implying decomposition of organic matter compositionally close to the Redfield ratio, such as microalgae, phytoplankton, or a mixture of readily decomposable organic matter. Respiration correlates best with temperature, redox potential, grain size, and organic content, but there is no single driver of soil respiration, as different regulatory factors have been found in forests dominated by different mangrove species. Mechanisms responsible for this pattern are unclear, but species-specific factors cannot be excluded.

Microbial methane production accounts for only a small fraction (1–10%) of total carbon mineralization (Kristensen 2007), but methane is an important greenhouse gas, with a global warming potential 7–62 times greater than that of CO₂. Methane production in mangrove soil is low and highly variable, often undetected in some forests. When measurable, emission rates range from 0.1 to 5.1 mmol CH₄ m⁻² d⁻¹. In highly polluted ecosystems, these rates can approach 60 mmol CH₄ m⁻² d⁻¹—highlighting the importance of abundant organic matter in driving methanogenesis (Kristensen 2007). Methanogens also live in tree parts, with emission rates ranging

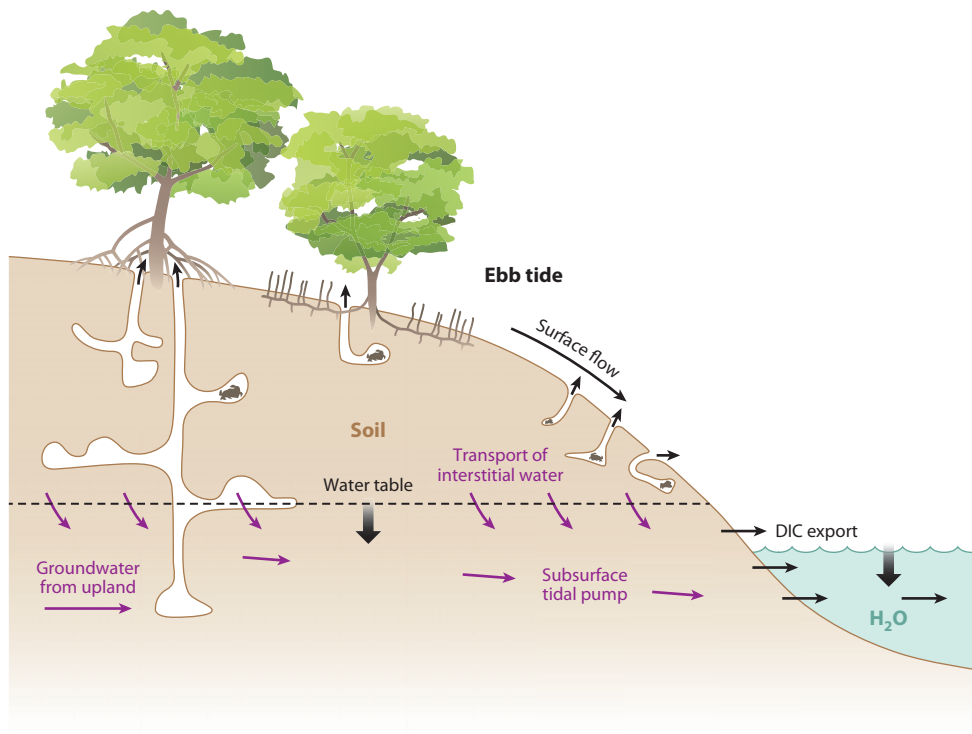


Figure 3

Schematic of the flow of interstitial water containing supersaturated concentrations of dissolved inorganic carbon (DIC) via subsurface pathways in relation to surface runoff as the forest water table lowers during an ebb tide. Water flow reverses on the incoming tide via the same pathways, percolating upward as the forest floods. Vertical and horizontal profiles are not to scale.

from 2 to 5 $\mu\text{mol CH}_4$ per square meter of root surface per day on prop roots and pneumatophores (Kreuzwieser et al. 2003, Purvaja et al. 2004). Mangrove waterways are a further source of methane, with emission rates in unpolluted waters ranging from 3 to 10 $\text{mmol CH}_4 \text{ m}^{-2} \text{ d}^{-1}$; in polluted estuaries, emissions can approach 5,000 $\text{mmol CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ (Ramesh et al. 2007). Some methane is undoubtedly oxidized to CO_2 , but how much is unknown and likely to be highly variable.

Is the forest floor a DIC reservoir-pump system? Mangrove trees grow atop sedimentary deposits that can be up to several meters thick. These deposits are heavily populated by a high diversity of microbial types, including sulfate and metal reducers, denitrifying bacteria, and methanogens, as well as higher organisms such as protists, meiofauna, and macroinfauna. Their biological activities and resultant biogenic structures result in the forest floor being thoroughly riddled with burrows, tubes, cracks, mounds, fissures, and, of course, coarse and fine roots and root hairs. In essence, the forest floor acts like a sponge, being alternatively drained and replenished with dissolved gases and fluids by the ebb and flood of tides (Figure 3).

Soil-microbe relations are tightly interwoven into the rhizosphere, where unique, efficient, and highly evolved groups of archaea, bacteria, and fungi modify their microenvironment, transforming plant dissolved organic matter (DOM) into metabolic gases and solutes. Mangroves alter the soil by translocating oxygen to their roots to help oxidize toxic metabolites. All of these

DOM: dissolved organic matter

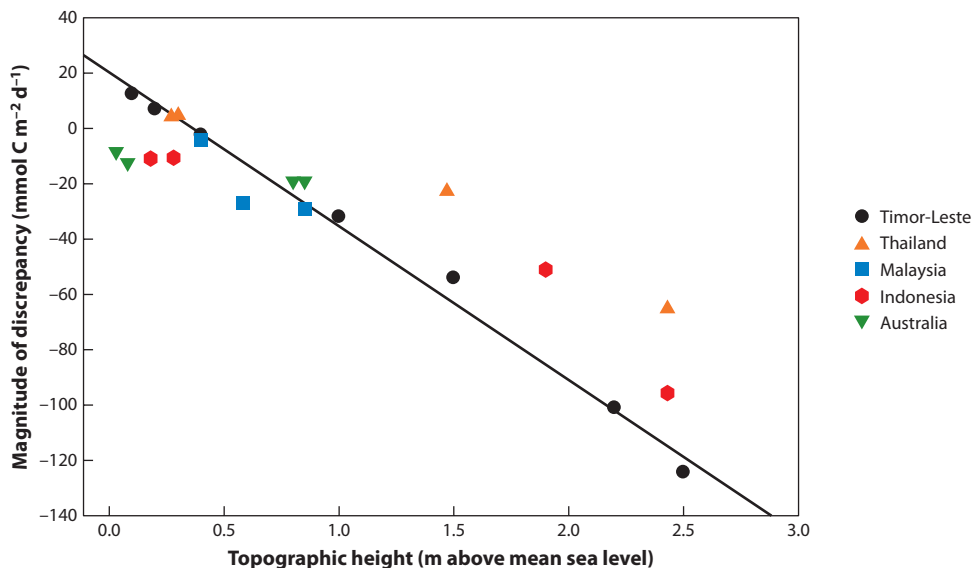


Figure 4

Is there a dissolved inorganic carbon (DIC) reservoir-pump system beneath the forest? The evidence is based on increasing discrepancies between CO₂ fluxes from the soil surface and total rates of carbon respiration with increasing topographic height of the forest. The magnitude of the discrepancy, shown as increasing negative numbers, was calculated by subtracting total carbon respiration from surface-soil CO₂ fluxes measured in each forest. These discrepancies, along with other evidence discussed in the main text, imply that large volumes of interstitial DIC are being lost from mangroves to adjacent coastal waters. Data compiled from Alongi et al. (1999, 2000, 2001, 2004a, 2008, 2012).

biological and physical activities foster substrate development and a shift in the competition for those substrates. Below the oxic soil surface and surfaces lining biogenic structures, suboxic and anoxic decomposition takes place, often to a depth of several meters. Aerobic respiration and sulfate reduction are usually the major pathways in mangrove soils, but recent work suggests that iron and manganese reduction are important processes, providing essential soluble iron and manganese required for tree growth (Kristensen 2007).

The end result is a deep factory with delicate microbial machinery producing metabolites such as ammonium and CO₂. Some CO₂ seeps from the forest floor across the soil surface and from tubes and burrows, but large amounts produced throughout several meters of subsurface deposits are dissolved in interstitial water (Sweetman et al. 2010, Krumins et al. 2013). The production of this subsurface DIC was thought to be in steady state, percolating continuously to the soil surface to be released in dissolved or gaseous form, but recent measurements indicate non-steady-state conditions in which large amounts of DIC are transported laterally via tidal advection and in groundwater (Bouillon et al. 2007, Alongi et al. 2012). The proportion of total soil respiration lost via these subsurface or lateral pathways increases with tidal elevation as the volume of soil susceptible to drainage increases above mean sea level. Thus, the forest floor apparently functions as a DIC reservoir-pump system.

A good illustration of this phenomenon is the clear inverse relationship of increasing discrepancies between surface and subsurface respiration rates with increasing topographic forest height—that is, the greater the tidal elevation of a mangrove forest, the greater the discrepancy is between CO₂ respiration at the soil surface and CO₂ respiration in deep soil deposits (**Figure 4**).

The simplest explanation for this relationship is that the deeper sediments act like a sponge through which interstitial water is pumped by tidal advection or seeps through from beneath the forest floor to adjacent waterways, where it causes supersaturation of DIC and subsequent CO₂ outgassing (Miyajima et al. 2009). Such drainage of interstitial water from tidal marshes has been observed and measured (Howes & Goehringer 1994, Gribsholt & Kristensen 2003).

Groundwater seepage is controlled by several physical forces (Mazda & Ikeda 2006) that result in interstitial water oozing out through the bottom soil, which is most clearly seen at low tide as water moving through seepage channels between the forest and adjacent creek bank. A recent study in mangroves adjacent to the Great Barrier Reef coast (Stieglitz et al. 2013) found that subsurface water flow, facilitated greatly by animal burrows, equates to 30 L m⁻² d⁻¹, which extrapolated to the entire coast is equivalent to 20% of total annual river discharge. An explicit test of the subsurface DIC pump theory (Maher et al. 2013) measured concentrations and δ¹³ values of DIC, DOC, POC, and ²²²Rn (a natural tracer of groundwater discharge) over tidal cycles in a mangrove tidal creek. A coupled radon/carbon model revealed that 93–99% of the DIC and 89–92% of the DOC exported from the creek were driven by groundwater advection, at rates equivalent to the amounts of DIC unaccounted for by measurements of surface metabolism alone, which has great relevance to balancing the mangrove carbon budget.

ESTIMATING NET CARBON BALANCE: A GLOBAL BUDGET

Large subsurface pools of interstitial DIC and their subsequent transport illustrate that not all carbon can be readily accounted for in mangrove carbon budgets. The two most recent global carbon budgets for mangrove ecosystems (Bouillon et al. 2007 and Alongi 2009) were unable to account for 112 and 160 Tg C y⁻¹ of mangrove carbon, respectively, although both papers pointed to the possibility of subsurface drainage, as discussed in the previous section.

Here, I have constructed a second-order budget that includes new information that updates our understanding of the major pathways of carbon flow throughout the world's mangroves (**Figure 5**). It is still incomplete, as fluxes such as faunal and pelagic production and chemical defenses have not been added, but I have assumed that the missing carbon of the preliminary budgets is mostly subsurface DIC and DOC transported to adjacent coastal waters. My earlier estimate of belowground production has been constrained using a mangrove nitrogen budget that suggests that, at most, 942.8 Gg N may be allocated annually to belowground root production (Alongi 2013). Converting this value to carbon by assuming a mean C:N ratio (g:g) for roots of 78.9 (Alongi et al. 2003, 2004b) gives an average belowground root production figure of 75 Tg C y⁻¹, which is nearly 36% of forest NPP. The remaining 64% of NPP is vested equally in wood (67 Tg C y⁻¹) and litter (68 Tg C y⁻¹) production.

Total carbon burial is 24 Tg C y⁻¹, approximately 15 Tg C y⁻¹ of which is likely derived from litter and dead roots. This estimate is based on the fact that ~58% of soil carbon is mangrove derived, a value that comes from an analysis of stable carbon isotope signatures of mangrove soils worldwide (Kristensen et al. 2008). And because approximately one-third of the total soil carbon pool is composed of dead roots (Alongi et al. 2003, 2004b), I estimate that approximately 5 Tg C y⁻¹ of buried carbon originates from dead roots; by difference, 10 Tg C y⁻¹ is derived from litter. Total carbon burial (24 Tg C y⁻¹) minus mangrove carbon burial (15 Tg C y⁻¹) gives a difference of 9 Tg C y⁻¹ of buried carbon that presumably originates from allochthonous sources upstream, from adjacent seas, or from a mixture of both.

If we assume that 10 Tg C y⁻¹ of litter is buried and that all POC export (28 Tg C y⁻¹) is ultimately derived from litter, then the remaining 30 Tg C y⁻¹ of litter produced must fall to the forest floor, where it enters detritus food webs and is eventually respired by microbes and

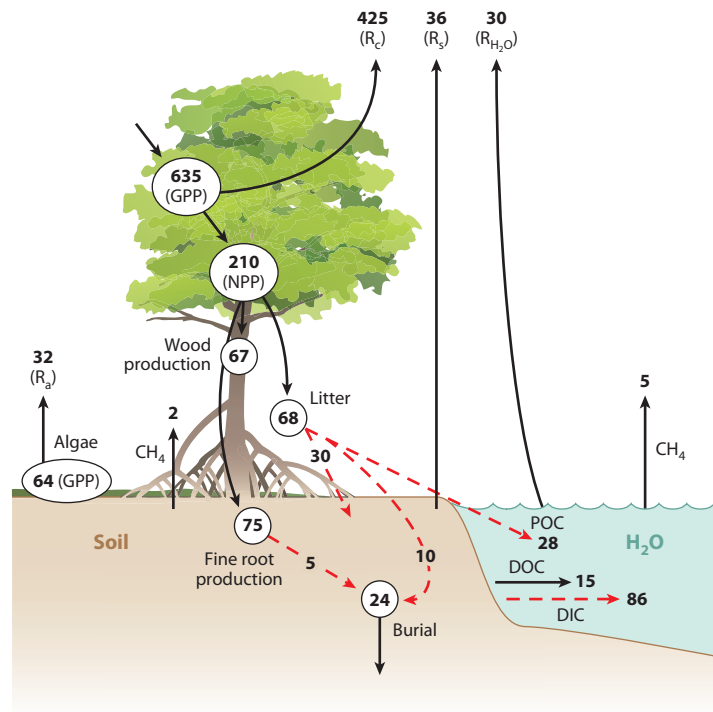


Figure 5

Budget of the major pathways of carbon flow through the world's mangrove ecosystems. Solid black arrows represent mean values based on numerous empirical data. Dashed red arrows represent either mean values estimated indirectly (by difference) or pathways suggested from the most recent literature. All values are in Tg C y⁻¹. The budget assumes a global mangrove area of 138,000 km² (Giri et al. 2010). Abbreviations: DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; GPP, gross primary production; NPP, net primary production; POC, particulate organic carbon; R_a, algal respiration; R_c, canopy respiration; R_s, soil respiration; R_{H₂O}, waterway respiration.

detritus feeders. Wood not remaining as standing biomass must find its way as fallen timber onto the forest floor (assuming that it is not harvested). However, wood decomposition is ordinarily slow (Robertson & Daniel 1989) and is probably a minor flux, so it is not included in the budget.

The global estimates of POC and DOC exported to adjacent waters come from the analyses of Adame & Lovelock (2011) and Dittmar et al. (2006), respectively. By difference, I assume that the remaining mangrove carbon is exported as DIC (86 Tg C y⁻¹) based on the circumstantial evidence presented above that most carbon respired within the forest floor must be exported laterally. It has been estimated that 10 Tg C y⁻¹ of allochthonous carbon is buried in mangrove soils, and this value corresponds closely to the estimate of carbon imported (13 Tg C y⁻¹) from adjacent coastal waters and from upstream (including aquaculture wastes, sewage, etc.) based on data from six mangrove ecosystems (see table 6.4 in Alongi 2009). From these six ecosystems, I also derived an estimate of the GPP of benthic microalgae of 64 Tg C y⁻¹, half of which is probably respired (Alongi 2009). Phytoplankton production averages approximately 0.6 g C m⁻² d⁻¹ (Robertson & Blaber 1992) and is very high in polluted waterways (>2–4 g C m⁻² d⁻¹), but it is not included in the budget. Assuming a global waterway area of 13,800 km² [based on a forest:creek ratio of 10

Table 3 Contribution of mangroves to carbon balance in the global coastal ocean compared with the contributions of other marine ecosystems

Ecosystem	Area (10 ¹² m ²)	R (g C m ⁻² y ⁻¹)	Global R (Tg C y ⁻¹)	GPP (g C m ⁻² y ⁻¹)	Global GPP (Tg C y ⁻¹)	NEP (g C m ⁻² y ⁻¹)	Global NEP (Tg C y ⁻¹)
Mangrove	0.14	4,413 ^a	577 ^a	5,065 ^b	699 ^b	652	90
Salt marsh	0.30 ^c	2,010	603	3,595	1,078	1,585	475
Seagrass	0.40 ^d	692	304	1,903	837	1,211	533
Macroalgae	1.4	2,116	2,962	3,702	5,183	1,587	2,221
Coral reef	0.6	1,572	943	1,720	1,032	148	84
Unvegetated sediments	23.9	83	1,992	68	1,624	-15	-370
Global benthic coastal ocean	26.74	—	7,381	—	10,453	—	3,033
Mangrove contribution	0.5%	—	8%	—	7%	—	3%

Mangrove area and NEP estimates and coral reef data reported by Alongi (2009); seagrass R, GPP, and NPP estimates reported by Duarte et al. (2010); salt marsh, macroalgae, and unvegetated sediment data reported by Duarte et al. (2005). Abbreviations: GPP, gross primary production; NEP, net ecosystem production; NPP, net primary production; R, respiration.

^aAssumes 50% of algal GPP is R.

^bForest and algal GPP.

^cMedian area reported by Mcleod et al. (2011).

^dMedian area reported by Fourqurean et al. (2012).

(Wolanski et al. 1992)], the maximum global contribution of phytoplankton NPP is approximately 3 Tg C y⁻¹—very small compared with canopy and benthic algal production.

Net ecosystem production (NEP) of the world's mangroves, derived by subtracting all respiratory losses from all mangrove and algal GPP, is approximately 90 Tg C y⁻¹ (**Table 3**). Despite large losses, mangroves are important storage sites of carbon in soils and, to a lesser extent, in standing biomass.

Such a global mass balance has obvious drawbacks, but it does illustrate some characteristics of mangrove carbon flow: (a) Mangrove ecosystems are net autotrophic, with an average NEP of 90 Tg C y⁻¹ and a GPP/R ratio of 1.15; (b) tidal export of dissolved and particulate carbon to the coastal ocean equates to approximately 60% of mangrove NPP; (c) respiration equates to a minimum of 62% of GPP (although respiration from stems and some organisms is not included); (d) mangrove production (635 Tg C y⁻¹) dominates total carbon input, with comparatively little carbon derived from benthic algae (64 Tg C y⁻¹) or imported from other ecosystems (13 Tg C y⁻¹); (e) heterotrophic respiration (152 Tg C y⁻¹) is a moderate loss compared with canopy and algal respiration (457 Tg C y⁻¹); and (f) carbon burial in soils accounts for approximately 10% of net carbon inputs (mangrove and algal NPP plus imports).

Physiological constraints and environmental conditions control mangrove growth and production, but tides are a major driver of NEP. Alongi (2009) found a significant positive correlation ($R^2 = 0.923$) between tidal range and mangrove NEP, supporting Odum's (1968) tidal subsidy idea that maximum power is achieved when biological pulses are in synchrony with external pulses. External energy assists in producing more vigorous mixing of tides and associated carbon and nutrients, which maximizes the transport of wastes, helps to oxygenate what would otherwise be a waterlogged forest, and maintains an intermediate level of environmental disturbance that helps to break down physical, chemical, and biological gradients within ecosystems.

Net ecosystem production (NEP): the rate at which an ecosystem stores net chemical energy (the difference between ecosystem inputs and losses)

Table 4 Comparison of the carbon fluxes of tropical mangrove forests and tropical humid forests

Flux	Mangrove forests (g C m ⁻² y ⁻¹)	Humid forests (g C m ⁻² y ⁻¹)
GPP	4,601 ^a	3,551
NPP	1,522 ^a	1,228
NPP _{CANOPY}	493	452
NPP _{WOOD}	487	307
NPP _{ROOT}	542	469
NEP (GPP – R _e)	420	351
R _a	3,079	2,323
R _h	1,101	877
R _e	4,180	3,200
R _e /GPP	0.91	0.90
CUE	0.33	0.35

Mangrove forest data from **Figure 3** and **Table 1**; humid forest data reported by Luysaert et al. (2007) and Malhi (2012). Abbreviations: CUE, carbon use efficiency; GPP, gross primary production; NEP, net ecosystem production; NPP, net primary production; NPP_{CANOPY}, canopy net primary production; NPP_{WOOD}, wood net primary production; NPP_{ROOT}, root net primary production; R_a, canopy respiration; R_h, heterotrophic respiration; R_e, ecosystem respiration (R_a + R_h).
^aAlgal production not included.

CONTRIBUTING TO THE GLOBAL COASTAL OCEAN

Mangroves compare favorably with other coastal ecosystems with respect to rates of primary production and carbon sequestration, but how do they compare with respect to carbon balance? Although mangroves occupy only approximately 0.5% of total global ocean area, they account for 8%, 7%, and 3% of global coastal respiration, GPP, and NEP, respectively (**Table 3**). On an areal basis, mangroves respire proportionally more carbon than the other coastal marine ecosystems; because they have higher respiration rates, they also have higher GPP rates. Future measurements of algal production may show that the mangrove contribution is even higher; currently, approximately 35% of mangrove NEP is thought to be contributed by algal production.

In contrast, macroalgae produce approximately 70% of the global coastal ocean's NEP, approximately 25 times more than mangroves (**Table 3**). This is not surprising, given their global ubiquity. The contribution of tropical seagrasses is difficult to parse owing to lack of data on carbon production and areal coverage; however, assuming conservatively that half of the world's seagrasses are tropical, their NEP would still surpass mangrove NEP. Coral reefs, often touted as among the most productive ecosystems in the sea (Smith & Gattuso 2009), are on average less productive in terms of organic carbon than their seagrass counterparts but are on par with mangroves.

How do mangroves compare with their distant terrestrial relatives? Despite large differences in the sizes of the respective databases and inherent differences between aquatic and terrestrial ecosystems, a comparison of mangrove and humid evergreen forests (**Table 4**) shows striking similarities in GPP rates, NEP rates, and how fixed carbon is allocated among tree components. This similarity is also reflected in both carbon use efficiency and the ratios of ecosystem respiration to GPP. Both mangrove and terrestrial evergreen trees are subject to similar physiological and thermodynamic constraints that drive carbon production and allocation, as has also been demonstrated by remarkably similar rates of nutrient resorption from leaves and nutrient use efficiency (Ball 1996, Krauss & Ball 2013). These rain forests of the sea are, from a carbon perspective, true descendants of terrestrial rain forests.

SUMMARY POINTS

1. Mangroves are among the most productive plants in the sea. Net primary production averages $11.1 \text{ Mg C ha}^{-1} \text{ y}^{-1}$, with nearly equal allocation to foliage, wood, and root production. Ecosystem-scale carbon stock averages 956 t C ha^{-1} . Mangrove productivity and carbon allocation are equivalent to those in tropical humid evergreen forests, but mangrove carbon stocks, sequestered mostly in soils, are greater.
2. Mangroves actively and passively capture fine sediment particles from incoming tidal waters, and the trees are an important driver of net sedimentation. On average, 58% of soil carbon is derived from mangroves, with the balance derived from a combination of oceanic inputs and upland discharge. The rate of soil accretion averages 5 mm y^{-1} , and carbon sequestration averages $174 \text{ g C m}^{-2} \text{ y}^{-1}$. The mean global burial rate for mangrove soil carbon is 24 Tg C y^{-1} .
3. Mangroves inhabit approximately 0.5% of total global coastal area but account for approximately 10–15% of total carbon sequestration in the coastal ocean. Mangroves, salt marshes, seagrasses, and estuaries all contribute disproportionately to coastal carbon storage compared with the shelf proper.
4. Deforestation of mangroves is of immediate ecological and socioeconomic concern, and removal of mangroves at current rates may be returning large amounts of carbon to the atmosphere; the most recent estimate suggests $90\text{--}970 \text{ Tg C y}^{-1}$.
5. Roughly 50% of mangrove litterfall is exported to the adjacent coastal zone, with particulate organic carbon export accounting for approximately 10–11% of total terrestrial carbon input to the ocean. Dissolved organic carbon export averages 15 Tg C y^{-1} . Variations in export rates are directly linked to precipitation and tidal amplitude.
6. Carbon gas and solute fluxes across the soil surface greatly underestimate total carbon mineralization from forest soils. Correlative and experimental evidence suggests that the extensive sediment deposits beneath the forest are a large respiratory reservoir, with tidal advection and groundwater flow transporting $\sim 70\%$ of total soil respiration (86 Tg C y^{-1}) to adjacent waters in the form of dissolved inorganic carbon.
7. The sum of canopy respiration (425 Tg C y^{-1}), surface (36 Tg C y^{-1}) and subsurface (86 Tg C y^{-1}) soil respiration, and respiration in mangrove waterways (30 Tg C y^{-1}) equates to $>90\%$ of mangrove gross primary production. The remaining carbon (net ecosystem production of 90 Tg C y^{-1}), including that fixed by benthic algae, is stored in vegetation and soil and, to a much lesser extent, is lost to fisheries harvesting, migratory birds, fishes, and other organisms, including humans.

FUTURE ISSUES

1. As indicated in the global carbon budget, there are several pathways that are only now being understood more clearly as well as several key pathways whose values constitute best-guess estimates. These include rates of gross canopy production; canopy respiration; gross and net production of other autotrophs, especially benthic microalgae and algae adhering to aboveground tree surfaces; and subsurface and groundwater fluxes.

2. Mangroves inhabit estuaries and other coastal regions that are subjected to numerous human insults, and these need to be considered in terms of how they impact carbon processes. In Southeast Asia and some other locations, there are likely to be significant inputs of black carbon that may add carbon but whose deposition onto leaf surfaces may reduce primary production.
3. The origin of particulate and dissolved organic and inorganic carbon needs to be better understood, especially for carbon buried in soils. The fate of sequestered carbon and its involvement in peat formation needs to be investigated further.
4. As a direct result of disturbance, including deforestation, carbon losses can be severe, but there are few data for gas fluxes from drained mangrove peats or from postdisturbance forests.
5. Microbial processes in deep (>50 cm) soils are poorly understood, especially methane formation and oxidation and metal reduction. These pathways need to be linked much more clearly to groundwater and lateral transport of reduced solutes.
6. Blue carbon is being presented by numerous organizations as a major initiative for conserving, restoring, and creating mangroves. The challenge will be to increase awareness of the need to reconcile realistic time frames for mangrove forest development with short-term funding and project time frames. Increased understanding of the ecological constraints of long-term carbon sequestration is a key priority for blue carbon schemes to be successful.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Contents

Shedding Light on the Sea: André Morel's Legacy to Optical Oceanography <i>David Antoine, Marcel Babin, Jean-François Berthon, Annick Bricaud, Bernard Gentili, Hubert Loisel, Stéphane Maritorena, and Dariusz Stramski</i>	1
Benthic Exchange and Biogeochemical Cycling in Permeable Sediments <i>Markus Huettel, Peter Berg, and Joel E. Kostka</i>	23
Contemporary Sediment-Transport Processes in Submarine Canyons <i>Pere Puig, Albert Palanques, and Jacobo Martín</i>	53
El Niño Physics and El Niño Predictability <i>Allan J. Clarke</i>	79
Turbulence in the Upper-Ocean Mixed Layer <i>Eric A. D'Asaro</i>	101
Sounds in the Ocean at 1–100 Hz <i>William S.D. Wilcock, Kathleen M. Stafford, Rex K. Andrew, and Robert I. Odom</i> ..	117
The Physics of Broadcast Spawning in Benthic Invertebrates <i>John P. Crimaldi and Richard K. Zimmer</i>	141
Resurrecting the Ecological Underpinnings of Ocean Plankton Blooms <i>Michael J. Behrenfeld and Emmanuel S. Boss</i>	167
Carbon Cycling and Storage in Mangrove Forests <i>Daniel M. Alongi</i>	195
Ocean Acidification in the Coastal Zone from an Organism's Perspective: Multiple System Parameters, Frequency Domains, and Habitats <i>George G. Waldbusser and Joseph E. Salisbury</i>	221
Climate Change Influences on Marine Infectious Diseases: Implications for Management and Society <i>Colleen A. Burge, C. Mark Eakin, Carolyn S. Friedman, Brett Froelich, Paul K. Hershberger, Eileen E. Hofmann, Laura E. Petes, Katherine C. Prager, Ernesto Weil, Bette L. Willis, Susan E. Ford, and C. Drew Harvell</i>	249

Microbially Mediated Transformations of Phosphorus in the Sea: New Views of an Old Cycle <i>David M. Karl</i>	279
The Role of B Vitamins in Marine Biogeochemistry <i>Sergio A. Sañudo-Wilhelmy, Laura Gómez-Consarnau, Christopher Suffridge, and Eric A. Webb</i>	339
Hide and Seek in the Open Sea: Pelagic Camouflage and Visual Countermeasures <i>Sönke Johnsen</i>	369
Antagonistic Coevolution of Marine Planktonic Viruses and Their Hosts <i>Jennifer B.H. Martiny, Lasse Riemann, Marcia F. Marston, and Mathias Middelboe</i>	393
Tropical Marginal Seas: Priority Regions for Managing Marine Biodiversity and Ecosystem Function <i>A. David McKinnon, Alan Williams, Jock Young, Daniela Ceccarelli, Piers Dunstan, Robert J.W. Brewin, Reg Watson, Richard Brinkman, Mike Cappo, Samantha Duggan, Russell Kelley, Ken Ridgway, Dbugal Lindsay, Daniel Gledhill, Trevor Hutton, and Anthony J. Richardson</i>	415
Sea Ice Ecosystems <i>Kevin R. Arrigo</i>	439
The Oceanography and Ecology of the Ross Sea <i>Walker O. Smith Jr., David G. Ainley, Kevin R. Arrigo, and Michael S. Dinniman</i>	469

Errata

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