Chapter 3
Mangrove Forests

Mangrove forests are composed of woody trees and scrubs living along many coasts within low latitudes. These tidal forests attain peak luxuriance in sheltered muddy areas where quiescent conditions foster establishment and growth of propagules, but they do occur on rocky and sandy shores. Growing above mean sea-level, forest establishment involves positive feedback in which the trees trap silt and clay particles brought in by tides and rivers to help consolidate the deposits on which they grow. This feedback continues until the forest elevation lies above the reach of tides, and mangroves give way to terrestrial plants over years and decades (Alongi 2016).

As in salt marshes, the mangrove intertidal zone is highly dynamic in space and time, ever changing and disturbed often enough by storms and cyclones, disease, pests and anthropogenic intrusions that the natural progression from mangrove to land occurs rarely along most coastlines. Mangroves are subjected daily to a harsh environment, experiencing daily tides and seasonal variations in temperature, salinity and anoxic soils, and are thus highly robust and adaptable to ever-changing conditions.

Mangroves develop and persist in relation to the geomorphological evolution of low-latitude coastlines, pioneering newly formed mudflats but also shifting their intertidal position in the face of environmental change.

Mangrove development, like their salt marsh counterparts, can follow a number of patterns in relation to changes in sea-level. First, the mangrove surface may accrete asymptotically until sediment accumulation raises the forest floor above tidal range; this pattern occurs when sea-level is in equilibrium. Second, accretion may keep pace with a constant rise in sea-level. Third, the forest floor accretes at times above tidal range when sea-level rise is irregular. Fourth, the forest floor accretes back to the tidal range with episodic subsidence but with a stable sea-level. Fifth, under conditions of episodic subsidence but rising sea-level, mangrove accretion continues at an irregular pace. And finally, when there is no change in sediment volume with a rise in sea-level, the forest floor is set back (Woodroffe et al. 2016). These responses point to ever-changing conditions in which mangroves

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have been traditionally classified as forests occupying overwash islands, coastal fringes, riverine areas and intertidal basins; scrub forests and other unique settings do occur including forests lying atop carbonate deposits as on coral islands.

Mangroves have evolved many morphological, reproductive and physiological traits for life in waterlogged saline soils including aerial roots, viviparous embryos, sclerophylly, low assimilation rates, high root/shoot ratios and high water-use and nutrient-use efficiencies. Forest structure is relatively simple compared with terrestrial forests, often lacking an understorey and having comparatively low tree diversity. Species richness is greatest in the Indo-West Pacific. Like salt marshes, tidal differences in species are frequently expressed in relation to combinations of tidal gradients in salinity, frequency of tidal inundation, seed predation, competition and other drivers, the complex interplay of which leads to forests that are mosaics of interrupted successional sequences.

There are about 70 true mangrove species in 40 genera in 25 families with 25 species in the families Rhizophoraceae and Avicenniaceae, plus a loosely defined group of mangrove associates that also occur in lowland rainforests, freshwater swamps and salt marshes. Mangrove food webs are dominated by bacteria and sesarmid and grapsid crabs but, like salt marsh food webs, have rich pelagic and benthic components consisting of both terrestrial and marine fauna and flora.

3.1 Capturing and Accumulating Sediment and Carbon

3.1.1 Mechanisms of Capture

Like salt marshes, mangroves actively and indirectly facilitate the capture and storage of sediment particles and associated carbon into soil horizons and capture sunlight to fuel growth and production of above- and below-ground biomass. Unlike salt marshes, above-ground biomass is substantial and can be an important store for carbon if left uncut. Mangroves are highly productive plants, and these forests can rival tropical rainforests in production and carbon storage, but can vary in size and age and thus in rates of primary productivity and carbon balance.

The dynamics of mangrove forests are similar to other forests in that there is an initial period of early rapid growth during colonisation with early establishment followed by a slow decline in growth rate into maturity and senescence. The mature old-growth phase is often prolonged such that an alternate succession state is reached as the climax stage is reset by successive disturbances. The net result of this phenomenon is that mangroves may be a carbon sink for up to a century if left relatively undisturbed.

Despite these capabilities, 75–95% of carbon in mangroves is stored as huge stocks below-ground in dead roots as most above-ground biomass is eventually lost due to clear cutting and human use, decomposition and export to the adjacent coastal zone (Donato et al. 2011; Alongi 2014). Over the long-term and under the right conditions, carbon is stored as peat. The accumulation of peat is a function not only of inputs from litter, roots, fallen tree stems and branches, algae and benthic organisms, such as burrowing crabs (Andreetta et al. 2014), but also slow decomposition rates of refractory material, the magnitude and frequency of tides, micro- and macro-organism activities, tree species and litter composition, moisture and temperature. As a result of a combination of these factors, peat formation and accumulation occur in some mangrove forests but not in others. Despite the fact that microbes and their enzymes are known to play a significant role in decomposition and accumulation of soil organic matter in mangroves, the underlying mechanisms of mangrove peat formation are not fully understood. Peat formation has been described as a 'enzyme latch' mechanism in which the amount of carbon storage is related to the inhibition of a single enzyme, phenol oxidase, under low oxygen conditions (Saraswati et al. 2016). This is in turn reported to result in the accumulation of phenolic materials which inhibits the activity of hydrolase enzymes which suppress the decomposition of organic matter, thus the term 'enzyme latch'. In laboratory experiments with peat from *Rhizophora mangle* forests, Saraswati et al. (2016) found that under aerobic conditions, soil samples have significantly higher phenol oxidase activity compared to anaerobic conditions. Soils supplemented with phenol oxidase show significantly lower phenolic concentration. These findings suggest that the 'enzyme latch' mechanism that operates in peatlands may also operate in mangrove peat soils.

As in salt marshes, carbon accumulation depends on a number of factors such as tidal amplitude, forest elevation, location in relation to the open coast and in relation to a tidal waterway, distance to adjacent aquatic habitats and primary productivity. Mangroves are not just passive importers of fine particulates but actively capture silt, clay and organic particles. Active capture involves maintaining particles in suspension in turbulent wakes created by tree trunks, prop roots and pneumatophores; most small flocs and free particles settle just before slack high tide. Despite the pull of ebb tide, most flocs and particles are retained within the forest as turbulence and water motion necessary for their resuspension is inhibited by the density of tree trunks. Due to the movement of the turbidity maximum zone where incoming bottom flow meets outward river flow within an estuary or waterway, mangrove waters have high suspended loads of mineral and organic particles. Tidal mixing, trapping and pumping within this zone facilitate flocculation and resuspension of particles. As these flocs and particles move into the forest on flood tide, turbulence generated by tidal flow around the trees helps to maintain flocs in suspension. The sticking of microbial mucus on the soil surface and the formation of excreted pellets by invertebrates facilitates rapid settling of particles.

The interrelationships between biotic and abiotic controls on soil accretion and elevation change as the same as those detailed in Sect. 2.1, as are the methods used to measure soil accretion. Woodroffe et al. (2016) reviewed the current status of knowledge of sedimentation and response of mangroves to relative sea-level rise and concluded that (1) accumulation rates of inorganic and organic, allochthonous and autochthonous sediment vary between and with environmental settings; (2) mangroves sequester carbon, but their sediments reveal paleoenvironmental records of adjustments to past sea-level changes; (3) radiometric

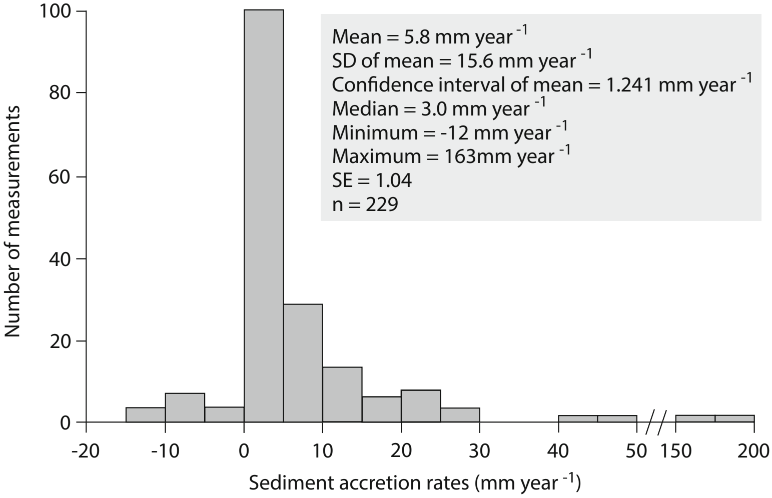

Fig. 3.1 Soil accretion rates measured in various mangrove forests worldwide. Updated from Alongi (2009, 2012) (Sources: Lynch et al. (1989); Furukawa and Wolanski (1996); Cahoon and Lynch (1997); Callaway et al. (1997); Alongi et al. (2004, 2005); Cahoon et al. (2003); Bird et al. (2004); Gonneea et al. (2004); Mahmood et al. (2005); Tateda et al. (2005); Whelan et al. (2005, 2009); Cahoon (2006); Rogers et al. (2006, 2013, 2014); McKee et al. (2007); Howe et al. (2009); Krauss et al. (2010); Alongi (2011); Sanders et al. (2010a, b, 2014); Stokes et al. (2010); Ceron-Breton et al. (2011); Lovelock et al. (2011a, b, 2015b); McKee (2011); Breithaupt et al. (2012); Oliver et al. (2012); Smoak et al. (2013); Lang'at et al. (2014); MacKenzie et al. (2016); Sasmito et al. (2016); Sidik et al. (2016); Ward et al. (2016); Hien et al. (2018); Pérez et al. (2018))

dating indicates long-term sedimentation, whereas RSET measurements indicate shallow subsurface processes of root growth and subsurface auto-compaction; (4) many tropical deltas also experience deep subsidence which augments relative sea-level rise; and (5) the persistence of mangroves implies an ability to cope with moderately high rates of relative sea-level rise. To persist, mangroves must build vertically at a rate equal to the combined rate of eustatic sea-level rise and land subsidence. Thus, mangroves have considerable natural resilience in response to sea-level (Krauss et al. 2013).

3.1.2 Rates of Soil Accretion and Carbon Sequestration

There has been an enormous growth in the literature of soil accretion rates in mangroves to the extent that a revised analysis of Alongi's (2012) figures is necessary. The rate of soil accretion in mangrove forests averages 5.8 mm year^{-1} with most measurements ranging from 0 to 2 mm year^{-1} (Fig. 3.1) The median is 3 mm year^{-1} with one standard error of 1.0 mm year^{-1} based on a sample size of $n = 229$.

A few measurements show either net erosion (Fig. 3.1) or massive accretion in highly impacted estuaries in China and Indonesia (Alongi et al. 2005; Sidik et al. 2016). Soil accretion rate is a function of tidal inundation frequency, as it is in salt marshes, as more frequent inundation of particle-laden water increases the frequency of particle settlement. Mangroves and salt marshes in high intertidal zones experience less soil accretion than wetlands located closer to the sea, so there is an overall pattern of decreasing sedimentation with decreasing tidal inundation frequency.

Below-ground roots and their ability to grow and vertically expand the soil are another driver of soil accretion, and surface growth of microbial mats and algae as well as litter and felled wood also contributes to vertical accretion. In some forests, these biotic forces can contribute more to vertical accretion than accumulation of particles via tides (McKee 2011; Krauss et al. 2013).

Natural subsidence plays a key role in long-term rates of soil accretion, being an important driver in estimating the susceptibility of mangroves to changes in sea-level (Woodroffe et al. 2016). Over long timescales, rates of vertical accretion vary in relation to climatic variability. Most mangroves are accreting sediment and carbon, but on some islands in the Pacific and in the Caribbean, sedimentation rates are slower than rates of sea-level rise. This is despite the fact that accretion rates on some of these islands are higher than eustatic sea-level rise (Sanders et al. 2010b). Throughout the Indo-Pacific, Lovelock et al. (2015c) found that recent trends indicate that at 69 percent of their study sites, the current rate of sea-level rise exceeds the soil accretion rate. They predict that sites with low tidal range and low sediment supply could be submerged as early as 2070. Sasmito et al. (2016) came to a similar conclusion that basin and fringe mangroves can keep pace with sea-level rise up to 2070 and 2055, respectively, on a global basis.

3.2 Carbon Sequestration Rates

The data ($n = 143$) for rates of carbon sequestration (CAR) in mangroves indicates an average (±1 standard error) rate of 171 ± 17.1 g C_{org} m^{-2} $year^{-1}$ with values ranging from 1 to 1053 g C_{org} m^{-2} $year^{-1}$ with a median of 103 g C_{org} m^{-2} $year^{-1}$ (Fig. 3.2). Assuming a global area of 137,760 km^2 (Giri et al. 2011) and using the median value, carbon sequestration in mangroves equates to 14.2 Tg C_{org} $year^{-1}$. This value is lower than the 23–25 Tg C_{org} $year^{-1}$ calculated by Twilley et al. (1992), Jennerjahn and Ittekot (2002) and Duarte et al. (2005). Like the accretion data, the standard deviation (204 g C_{org} m^{-2} $year^{-1}$) is greater than the mean of 171 g C_{org} m^{-2} $year^{-1}$ reflecting the high level of variability in carbon sequestration among mangroves of different ages and locations.

There is no clear relationship with differences in latitude as it is likely that these rates are a function of a number of interrelated factors such as forest age, tidal inundation frequency, tidal elevation, mangrove geomorphology, species composition, soil grain size, catchment and river input, ocean input and degree of human impact. Most values were in the range of 1–100 g C_{org} m^{-2} $year^{-1}$ (half of all

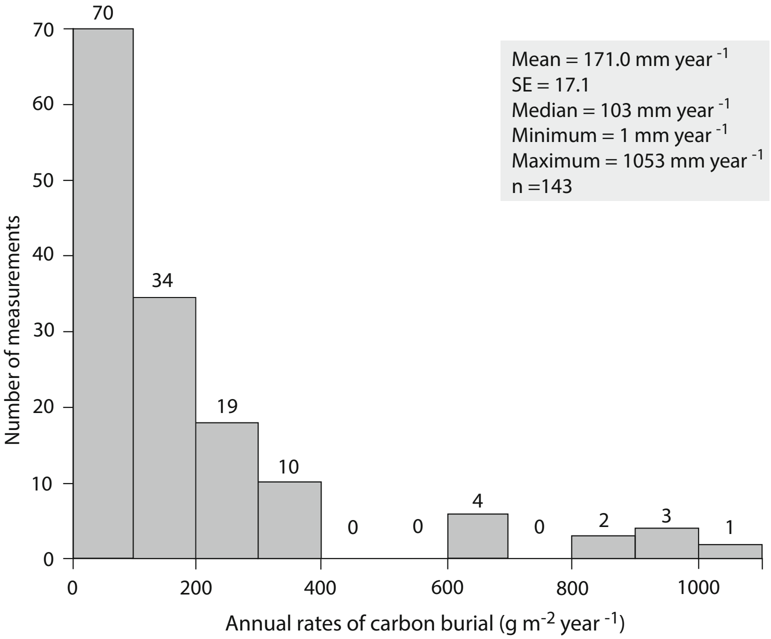

Fig. 3.2 Annual rates of carbon sequestration in various mangrove forests worldwide. Updated from Alongi (2012). (Sources: Lynch et al. (1989); Furakawa and Wolanski (1996); Callaway et al. (1997); Fujimoto et al. (1999); Alongi et al. (2004, 2005); Gonneea et al. (2004); Duarte et al. (2005); Mahmood et al. (2005); Tateda et al. (2005); Xiaonin et al. (2008); Alongi (2009, 2011); Ren et al. (2010); Sanders et al. (2010a, b, c, 2014); Ceron-Breton et al. (2011); Donato et al. (2011); Kauffman et al. (2011); McKee (2011); Ray et al. (2011, 2013); Mitra et al. (2011); Breithaupt et al. (2012); Matsui et al. (2012); Bianchi et al. (2013); Kathiresan et al. (2013); Smoak et al. (2013); Lunstrum and Chen (2014); Lovelock et al. (2015a); Zarate-Barrera and Maldonado (2015); Doughty et al. (2016); Ezcurra et al. (2016); MacKenzie et al. (2016); Marchio et al. (2016))

observations) with the highest values being from mature forests, those in close proximity to river deltas and forests in highly impacted catchments.

3.3 Carbon Stocks

Mangrove carbon stocks ($n = 168$) have been measured in 24 countries spanning the globe from the Americas to Africa to Asia (Table 3.1). Carbon stock for a mangrove forest averages 761.4 ± 45.5 Mg C_{org} ha^{-1} (± 1 SE) with a range of 37 to 2477 Mg C_{org} ha^{-1} and a median of 723.4 Mg C_{org} ha^{-1}. Using the median value and assuming a global mangrove area of 137,760 km^2, we derive a global carbon stock estimate for mangroves of 10 Pg. Jardine and Siilamäki (2014) estimated a global carbon stock of 5 Pg based on a predictive model using soil carbon concentrations against a high-resolution grid. They found that this stock is highly variable over space with considerable within-country variation.

At the forest level, the smallest carbon stocks are small stands that are primarily young plantations, while the largest stocks are mature stands. Because of the various ages and sizes of forest, there is no clear relationship with latitude; some equatorial forests are young stands, while some of the mature forests are at higher latitudes. Thus, older more mature forests store more carbon than young or scrub forests. The median value is close to the value of 703 Mg C ha^{-1} predicted by Jardine and Siilamäki (2014).

On average, 91.8% of the total ecosystem C_{org} stocks is vested below-ground (below-ground biomass + soil) with a mean above-ground to below-ground ratio of 11.2; the median value is 5.6 with a minimum value of 0.32 and a maximum of 83.2. The wide span of values reflects the wide range of ages and types of mangrove forest, from very young monocultures to mature forests. As with salt marshes, the average of 92% of carbon vested below-ground is a minimum estimate as many forests contain soil C_{org} stocks to depths greater than 1 m (Table 3.1).

3.4 Potential Losses

The carbon sequestration and carbon stock data suggest the potential for significant GHG emissions if the high per area carbon stocks of mangroves are disturbed. Losses of mangroves by clearing, conversion to industrial estates and aquaculture and changes in drainage patterns lead to dramatic changes in soil chemistry resulting in rapid emission rates of GHGs, especially CO_2. Lovelock et al. (2011a, b), for instance, measured the flux of CO_2 from mangrove peats that had been cleared for up to 20 years on the islands of Twin Cays in Belize and also measured gas effluxes after disturbing these cleared peats. They found that gas efflux declines from the time of first clearing from 10,600 tonnes km^{-2} $year^{-1}$ in the first year to 3000 tonnes km^{-2} $year^{-1}$ after 20 years since clearing; disturbing peats led to short-term increases in CO_2 efflux, but this returned to baseline levels within 2 days.

Using a stock-change approach, Kauffman et al. (2014) calculated that the potential emissions from the conversion of mangroves to shrimp ponds ranged from 2244 to 3799 Mg CO_2 equivalents ha^{-1} with all of the Dominican Republic's losses of mangroves estimated to have returned 3.8 Gg CO_2 equivalents or about 21% of the country's mangrove carbon stocks to conversion to the atmosphere, an amount that is among the largest measured carbon emissions from land use in the tropics. Kauffman et al. (2017) found that mangrove conversion to shrimp ponds results in GHG emissions ranging between 1067 and 3003 Mg CO_2 equivalents ha^{-1}, while conversion to cattle pastures results in losses estimated at 1464 Mg CO_2 equivalents ha^{-1} (Kauffman et al. 2016). Similarly, Murdiyarso et al. (2015) and Alongi et al. (2016) estimated that losses of Indonesian mangroves, marshes and seagrasses to conversion may equate to losses of roughly 29,040 Gg CO_2 equivalents to the atmosphere. In the world's largest continuous area of mangrove, the

Table 3.1 Estimates of organic carbon stocks (Mg C_{org} ha^{-1}) in mangrove biomass and soils to a depth of 1 m

Location [Sources]	Number of Observations	Range	Mean
Indonesia[a]	42	415–2202	1048
Vietnam[b]	18	979–1904	945
Honduras[c]	18	570–1060	921
United Arab Emirates[d]	18	77–515	218
India[e]	13	159–360	219
China[f]	11	114–619	321
Dominican Republic[g]	9	743–1142	922
Mexico[h]	8	381–1358	822
Ecuador[i]	6	425–580	485
Mozambique[j]	6	219–621	478
Ivory Coast[k]	4	51–176	128
Philippines[l]	4	241–660	438
Singapore[m]	4	37–227	133
Australia[e]	3	662–2139	1221
Malaysia[e]	3	995–1432	1267
Micronesia[n]	3	479–1218	1064
Palau[n]	3	625–840	720
Thailand[e]	3	579–808	662
Madagascar[o]	3	367–593	499
Bangladesh[p]	2	343–604	566
Cameroon[q]	2	2102–2477	2289
Japan[r]	1		107
Myanmar[s]	1		274
Colombia[t]	1		196
USA[u]	1		122
Senegal[v]	1		674
Liberia[v]	1		949
Gabon[v]	1		801

[a] Sources: Donato et al. (2011) and Murdiyarso et al. (2015)
[b] Sources: Alongi (2012) and Nam et al. (2016)
[c] Source: Bhomia et al. (2016a)
[d] Source: Schiele et al. (2017)
[e] Source: Rahman et al. (2015) and Bhomia et al. (2016b)
[f] Sources: Alongi (2012), Alongi (unpublished data), Lu et al. (2014), and Lunstrum and Chen (2014)
[g] Source: Kauffman et al. (2014)
[h] Source: Adame et al. (2013, 2015a, b) and Kauffman et al. (2016)
[i] Source: DelVecchia et al. (2014)
[j] Sources: Sitoe et al. (2014) and Stringer et al. (2015)
[k] Source: Osemwegie et al. (2016)
[l] Sources: Thompson et al. (2014) and Bigsang et al. (2016)
[m] Source: Friess et al. (2016)
[n] Source: Kauffman et al. (2011) and Donato et al. (2012)
[o] Source: Jones et al. (2014, 2015)
[p] Source: Donato et al. (2011)
[q] Source: Ndema et al. (2016)
[r] Source: Khan et al. (2007)
[s] Source: Thant et al. (2012)
[t] Source: Zarate-Barrera and Maldonado (2015)
[u] Source: Doughty et al. (2016)
[v] Source: Kauffman et al. (2017)

Sundarbans of India, Akhand et al. (2016) estimated that between 1975 and 2013, potential carbon dioxide emission due to the degradation of just the above-ground biomass of mangroves was about 1570 Gg. Globally, Pendleton et al. (2012) estimated that total loss of mangroves may account for about 0.09 to 0.45 Pg CO_2 equivalents year^{-1}.

Using the known area of mangroves (137,760 km^2; Giri et al. 2011) and the median carbon stock (723.4 Mg C_{org} ha^{-1}) and assuming a destruction rate of 1–2% per year, we can estimate a loss of between 0.27 and 0.59 Pg CO_2 equivalents year^{-1} which is within the wide range estimated by Pendleton et al. (2012) and is an order of magnitude greater than the estimate of Atwood et al. (2017). The annual losses of mangroves add another 5–11% to the recent estimate (Hansen et al. 2013) of global deforestation (4.6 Pg CO_2 year^{-1}) or offset 23–49% of the carbon sink in the global ocean's continental margins (Chen and Borges 2009). These are only rough estimates, but the range of values underscores the global significance of continuing mangrove losses. If all of the world's mangrove forests were destroyed and assuming that 95% of all mangrove carbon was oxidised to CO_2 (Kennedy et al. 2014), the loss would be 30.2 Pg CO_2 equivalents which is equal to 6.5 years of carbon emissions from global forest loss.

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