CHAPTER

12

Environmental drivers of blue carbon burial and soil carbon stocks in mangrove forests

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OUTLINE

Dynamic Sedimentary Environments of Mangrove Coasts
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1. Introduction

There is growing evidence that the conservation or restoration of blue carbon ecosystems such as mangroves, saltmarshes, or seagrass meadows offers effective nature-based solutions to climate change impacts (Alongi et al., 2015). These highly productive ecosystems can help offset greenhouse gas emissions by sequestering and storing large amounts of atmospheric derived CO_2 in the form of aboveground and belowground carbon (C). Belowground C pools are often stored under waterlogged and anoxic conditions that can inhibit or slow down microbial breakdown of organic matter. As a result, C buried in sediments of blue carbon habitats can remain there for millennia if left undisturbed, making them critical long-term C sinks.

Blue carbon was first introduced in 2009 in response to the increased importance of terrestrial or "green" carbon in climate change adaptation and mitigation. Organisms living in the seas can capture more than half the amount of C captured in forested lands. Blue carbon is therefore equally important for climate change adaptation and mitigation (Nellemann and Corcoran, 2009). Mangroves, saltmarshes, and seagrass beds are the main blue carbon ecosystems, storing up to 70% of all C in ocean sediments despite only covering <0.5% of the ocean floor (Chmura et al., 2003; Duarte et al., 2004; Bouillon et al., 2008; Lo Iacono et al., 2008). Long-term C sequestration per unit area is also much greater in blue carbon ecosystems compared with terrestrial forests despite the global area of the latter being one to two orders of magnitude smaller (Mcleod et al., 2011). A study conducted by Donato et al. in 2011 further supported these arguments. They found that C stocks from Indo-Pacific mangroves were three times greater than any other major forest domain (e.g., boreal, temperate, tropical upland; Fig. 12.1). This was due to the greater belowground C stores measured in mangrove forests and that represented 71%–98% of total mangrove C stocks (Donato et al., 2011). Since then, the role mangrove forests play in climate change and mitigation strategies has significantly grown (Duarte et al., 2013b; Lovelock and Duarte, 2019; Macreadie et al., 2019) as have the number of studies that have documented mangrove C stocks and the impacts of land use change on those stocks (Atwood et al., 2017; Cameron et al., 2019; Kauffman et al., 2020; Sharma et al., 2020).

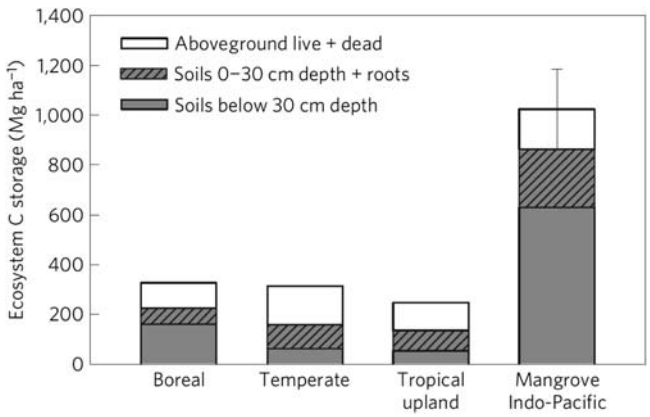

FIGURE 12.1 Comparison of mean Indo-Pacific mangrove C stocks (±95% confidence interval) with that of major global forest domains. *Reprinted from Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. Nat. Geosci. 4, 293–297 with permission.*

Most C stored in mangrove sediments is largely derived from mangrove roots, though this varies across different coastal landforms and stage of peat development (e.g., Ezcurra et al., 2016). Compared with terrestrial forests, mangrove trees allocate more sequestered C to belowground roots to replace sloughed root hairs or fine roots (Alongi, 2014). Thus, the bulk of belowground C is stored in dead roots that represent 75%–95% of root biomass (Alongi et al. 2003, 2004b; Cormier et al., 2015). Other autochthonous C sources include macro- and microalgae growing on or within aboveground roots and sediments, respectively (Alongi, 2014). External sources of C also contribute to mangrove soil C stores, though this can vary within a mangrove. Mangrove areas adjacent to or near riverine or upland systems can receive C inputs from upland forests, while areas adjacent to the mangrove-ocean ecotone can receive inputs from seagrass ecosystems (Saavedra-Hortua et al., 2020; Sasmito et al., 2020). Seagrass beds and coral reefs directly adjacent to mangrove forests can also enhance mangrove soil C stocks by protecting mangroves through reduced wave action (Gillis et al., 2014; Huxham et al., 2018). The combined high inputs of autochthonous and allochthonous C result in C burial rates in mangroves being 20–70x greater than upland forests (Mcleod et al., 2011). High C burial rates also result in 10%–15% of coastal sediment C being stored in mangrove soils and, along with saltmarshes and seagrass systems, account for 50%–70% of annual C burial in oceans despite only representing ~0.5% of global coastal area (Chmura et al., 2003; Duarte et al., 2004; Bouillon et al., 2008; Lo Iacono et al., 2008).

The amount of belowground C stored in mangrove sediments can significantly vary among countries, regions, and land uses. For example, Jardine and Siikamäki (2014) used a climate-based model to estimate global mangrove soil organic C stocks. They found soil C stocks to 1 m vary nearly threefold (272 ± 49 to 703 ± 38 Mg C/ha), while (Atwood et al., 2017), based on country-level soil C density reference values, found a larger and more than tenfold difference in theirs (80.7–935.67 Mg C/ha). Later, Rovai et al. (2018) found global mangrove soil organic C stocks range from 33 to 465 Mg C/ha and suggested that differences in soil C stocks across these studies are partly explained by the omission of key geophysical drivers (e.g., river/sediment discharge, tidal influence) and partly by the inclusion criteria established by former studies to extrapolate soil C stocks from site to global level. More recently, Kauffman et al. (2020) reported a greater range of 46–2076 Mg C/ha that is due to the inclusion of soil C stocks to 3 m depth.

Soil carbons stocks in mangroves are largely influenced by C burial rates (Kristensen et al., 2008), though evidence suggests this may be an inverse relationship (Breithaupt et al., 2012). Regardless, burial rates, like soil C stocks, exhibit high levels of variability among countries, regions, and land uses. Alongi (2012) reported a global mean (±1 SD) of 174 ± 184 g C/m^2 yr with a range of 10–920 g C/m^2 yr. Breithaupt et al. (2012) argued that a geometric mean of 163 (+40; −31) g OC/m^2 yr (95% CI) may be a more reasonable global mean estimate due to the extreme low and high (5–1129 g C/m^2 yr) values in their review. For this review, we report a new global mean in C burial rates of 239 g C/m^2 yr, with a range of 5–1722 g C/m^2 yr (Fig. 12.2).

While plausible relationships between mangrove soil organic C stocks and climate and geophysical drivers seem to have been reasonably determined (Kristensen et al., 2008; Atwood et al., 2017; Rovai et al., 2018), it is still unclear what abiotic or biotic drivers, either independently or combined, and across different spatial scales, are responsible for the variability observed in C burial rates. However, because soil C stocks represent a "snapshot"

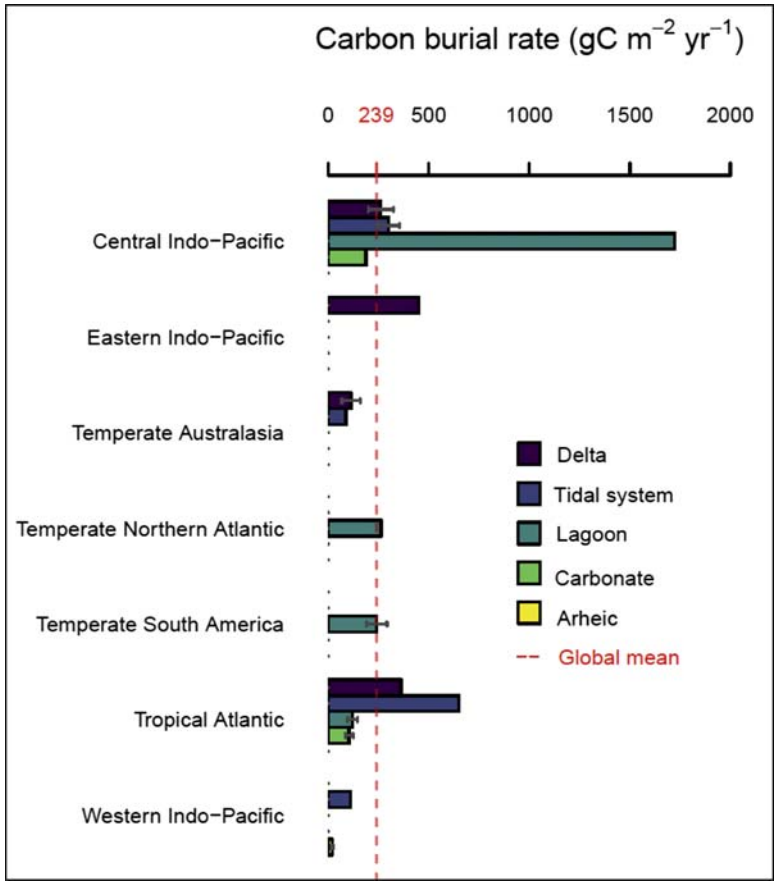

FIGURE 12.2 Average carbon burial rates from regions estimated from various studies (Lynch et al., 1989; Furukawa and Wolanski, 1996; Callaway et al., 1997; Fujimoto et al., 1999; Alongi and Dixon, 2000; Alongi et al. 2001, 2004a, 2005; Brunskill et al. 2002, 2004; Chmura et al., 2003; Duarte et al. 2004, 2013a; Gonneea et al., 2004; Tateda et al., 2005; Sanders et al. 2008, 2010a, 2010b, 2010c; Xiaonan et al., 2008; Alongi 2009, 2011; Cerón-Bretón et al., 2011; Ray et al., 2011; Smoak et al., 2013; Yang et al., 2014; Kusumaningtyas et al., 2019; MacKenzie et al., 2016).

of the process of soil formation, it is reasonable to assume that C burial in these ecosystems is controlled by similar mechanisms that explain soil C stock distributions (e.g., Atwood et al., 2017; Rovai et al., 2018; Twilley et al., 2018). Identifying these factors and understanding the different roles they play in C burial is critical if we wish to implement management efforts to conserve or restore mangrove forests for climate change mitigation and adaptation or to increase the resilience of mangrove forests to climate change impacts, such as sea level rise. This chapter will attempt to identify some of the major abiotic and biotic factors across different spatial scales (e.g., site level to global level) that have been identified in the literature to influence C burial rates and soil C stocks in mangrove forests.

2. Abiotic factors

2.1 Climatic drivers: temperature and precipitation

Temperature and precipitation are two important drivers that can influence mangrove soil C stocks. Global models have predicted that soil C content varies with air temperature, though the strength of this relationship depends on the model used (Chmura et al., 2003; Jardine and Siikamäki, 2014; Rovai et al., 2018). Sanders et al. (2016) reported that 86% of the observed variability in soil C stocks was associated with annual rainfall, which proved to be an effective predictor of mangrove soil C in Indo-Pacific and Australasia mangroves. Latitude, which incorporates both air temperature and rainfall, proved to be a significant predictor of soil C in Cambodia (Sharma et al., 2020) and across the Asia Pacific region (Bukoski et al., 2017), though Atwood et al. (2017), Twilley et al. (2018), and Kauffman et al. (2020) all found a poor relationship between latitude and soil C stocks. Indeed, the usefulness of absolute degrees of latitude is of very limited value as a predictor of species distribution and ecosystem ecological attributes as it does not capture real geographical gradients (Hawkins and Felizola Diniz-Filho, 2004). Furthermore, water temperature, which can also influence productivity (Ellison, 1994; Lovelock and Ellison, 2007), is not controlled by latitude but by other factors such as currents. The independent and interactive influence of temperature and precipitation on soil C stocks clearly varies with scale (e.g., global, regional, local) (Saavedra-Hortua et al., 2020).

As reviewed earlier in this chapter, soil C stocks in mangroves are formed by allochthonous and autochthonous sources. Temperature and precipitation control both the amount of terrestrial C delivered to mangroves from allochthonous upstream sources (Šímová and Storch, 2017; Cragg et al., 2020) and in situ C accumulation via net primary productivity (NPP) (Pool et al., 1975; Twilley, 1995; Day Jr. et al., 1996; Feher et al., 2017). Overall, temperature affects NPP by influencing rates of growth, photosynthesis, and respiration and thereby C storage (Duke, 1990; Lovelock, 2008). Similarly, rainfall reduces stress caused by soil salinity and increases nutrient input via upland runoff, thus stimulating mangrove NPP (Day Jr. et al., 1996; Twilley et al., 1997; Agraz-Hernández et al., 2015). NPP includes aboveground (litterfall, wood) and belowground (root) production that differs in respect to their relative contribution to C sequestration in mangrove soils. The contribution of mangrove aboveground production (e.g., litterfall and wood) to soil organic matter formation is generally negligible (e.g., less than 10%) (Chen and Twilley, 1999) as nearly 50% of the litterfall is exported by tidal action (Jennerjahn and Ittekkot, 2002; Bouillon et al., 2008), though litter retention rates can be greater in basin mangroves with little tidal export (Twilley et al. 1986, 1997). Litterfall export, however, is influenced by rainfall and temperature, with mangroves in regions with lower rainfall and higher temperatures exporting more litter than mangroves in regions with higher rainfall and lower temperatures (Adame and Lovelock, 2011). The remaining amount of leaf litter is either directly buried in soils or is consumed by crabs, other invertebrates, or microorganisms (Robertson and Daniel, 1989; MacKenzie et al., 2020) that then release C to be incorporated into mangrove sediments (Andreetta et al., 2014) or to be lost as dissolved organic carbon to the water column (Lee, 1995; Kristensen et al., 2008). Belowground (or root) production, on the other hand, can account for more than 80% of carbon sequestered and stored in mangrove soils (Saintilan et al., 2013; Kusumaningtyas et al., 2019). Thus, root production is an

important biotic mechanism to C sequestration in mangrove soils (McKee et al., 2007; Krauss et al., 2014; Woodroffe et al., 2016).

Temperature and precipitation also influence C sequestration and thereby soil C stocks in mangrove soils by controlling the balance between organic matter production and decomposition rates. For example, on a global scale, temperatures that occur above a certain threshold have been suggested to decrease C stocks in mangrove soils due to increased microbial decomposition (Chmura et al., 2003). However, increases in minimum annual temperatures can also increase soil organic C stocks as it stimulates mangrove root production and thereby C flux to the soil (Rovai et al., 2018). While mangrove root decomposition rates can also increase with elevated temperatures, root C inputs appear to exceed mineralization rates (Ouyang et al., 2017), resulting in organic matter accumulation and a positive C flux to mangrove soils (Pregitzer et al., 2000). Precipitation is also believed to influence C sequestration in mangrove soils as demonstrated for other functionally analogous tidal saline wetlands where decomposition was accelerated by increased precipitation and slowed by drought (Charles and Dukes, 2009), though longer periods of soil inundation that results from increased rainfall can also decrease organic matter decomposition in mangroves (Alongi, 2005).

Rainfall events and thus runoff from mangroves may also offset C storage in mangrove soils. Monthly exports of total organic C from Florida mangroves increased 2−10x during large rain events that increased runoff by 3−20x (Twilley, 1985). Similarly, concentrations of dissolved organic C exported from Okinawa mangroves in Japan nearly doubled after a large rainfall event that resulted from a category 4 typhoon (Goni). Episodic increases in freshwater from large storms likely enhance leaching of dissolved organic C from mangrove litter as well as from soils where they are otherwise retained by salinity-induced aggregation (Kida et al., 2019). However, in Brazil, only export of particulate organic C, not dissolved organic C, increased with rainfall (Dittmar and Lara, 2001).

While relationships between climate variables and soil C sequestration have been demonstrated for terrestrial ecosystems, results from mangrove forests are not always consistent in the literature (Breithaupt et al., 2012; Feher et al., 2017). The interaction of these multiscalar climatic factors and stochastic events, coupled with scarcity of data on C burial rates, may explain the low correlation ($R^2 = 0.05$) between mean annual temperature and rates of soil C burial and suggests that regional or local factors must be the dominant controls on rates of C burial in mangrove soils (Chmura et al., 2003).

2.2 Storms

Typhoons, hurricanes, and tropical cyclones can also influence productivity and thus soil C stocks. The lack of these disturbance results in less damage to mangroves, higher levels of productivity, and enhanced C storage (Kauffman and Cole, 2010; Twilley et al., 2017; Thorhaug et al., 2019). Storms can also influence soil C stocks through increased precipitation that can promote mangrove growth and/or release trees from salinity stress (see discussion above). Another mechanism is through the deposition of C-rich and nutrient-rich sediments onto the mangrove forest floor contributing to organic carbon accretion and NPP (Castañeda-Moya et al., 2010; Breithaupt et al., 2017; Castañeda-Moya et al., 2020). Carbon burial rates within storm deposits from Hurricane Wilma (260−393 g/m^2 yr) were nearly double the overall burial rates in the mangrove forest sampled (151−168 g/m^2 yr) (Smoak et al., 2013).

2.3 Geomorphology and nutrients

Coastal morphology influenced by rivers, tides, wave power, and climate has been proposed as a potential framework to explain global variations in mangrove C storage and to an extent C burial (Twilley et al., 2018). These forcings influence the rate and source of sediment and nutrient inputs that result in clastic coastal environmental settings that include riverine/deltas, tidal systems, lagoons, carbonate, and arheic environments (Thom, 1982; Dürr et al., 2011). Models in Twilley et al. (2018) and Rovai et al. (2018) predicted that soil C densities were greatest in carbonate and arheic settings and lowest in riverine/deltaic mangroves. A recent global assessment of field data found opposite patterns. Soil C stocks were lowest in an arheic mangrove and in carbonate-dominated mangroves in the Yucatan peninsula, Mexico. Deltaic mangroves, on the other hand, had some of the greatest (Mexico, Indonesia) and lowest (Gabon, Brazil) soil C stocks in their analysis (Kauffman et al., 2020). These differences are likely due to differences in scale as well as geomorphic classifications.

The patterns reported by Twilley et al. (2018) and Rovai et al. (2018) are likely influenced by the conspicuous nitrogen (N) and phosphorous (P) loads and limitations associated with each coastal environmental setting. In riverine/deltaic mangroves, soil C sequestration is primarily driven by burial of riverine delivered allochthonous material (Hayes et al., 2017; Kusumaningtyas et al., 2019) resulting in elevated burial rates (Figs. 12.2 and 12.3) but lower soil C density due to the high proportion of mineral alluvial material relative to organic matter inputs (Rovai and Twilley this book). Lower soil C stocks are also driven by large P loads from upland catchments (Harrison et al., 2005) that release mangrove trees from nutrient limitations in mangrove soils (Rovai et al., 2018). Trees can then allocate more biomass to aboveground structures since optimum nutrient uptake efficiency can be attained with less complex root systems (Chapin III et al., 1986; Castañeda-Moya et al., 2011; Cormier et al., 2015). Tide- (estuaries) and wave-dominated (lagoons) coastlines have intermediate levels

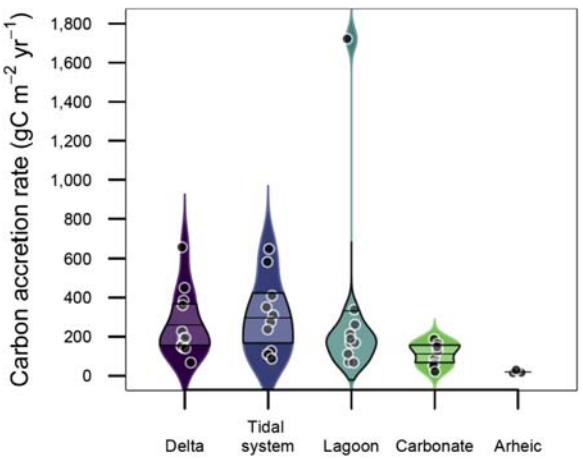

FIGURE 12.3 Average C burial rates across coastal environmental settings as defined by Twilley et al. (2018). See Fig. 12.2 for references used to produce this figure.

of soil C stocks but high levels of C burial rates (Figs. 12.2 and 12.3). High C burial rates reflect the relative contribution of river-borne organic particles and in situ root production to soil formation. Tides also play a fundamental role in C burial in mangrove soils by promoting nutrient exchange and soil oxygenation and reducing sulfide levels, which altogether regulate root production and organic matter decomposition rates in mangrove soils (Chapman et al., 2019). Tides also carry abundant sediment, promoting trapping of C-rich mud due to reduced water velocity within mangrove forests (Woodroffe et al., 2016). Conversely, the structural development of mangrove forests in carbonate settings (e.g., South Florida and Caribbean region) has been linked to P limitation and hydrologic stress. Phosphorous supply is often limited due to carbonate chemisorption reactions and the sequestering of P into recalcitrant organic pools, which reduces the availability of exchangeable P to plants (Koch et al., 2001). As a result, plants allocate more C to root systems than trunks and branches to increase access to limited P, resulting in well-developed root systems and elevated high soil C stocks (Twilley et al., 2018), but reduced aboveground biomass (Feller et al., 2003; Castañeda-Moya et al., 2013; Adame, 2014). Arheic environments are arid coastlines where mangrove distribution is restricted to tidal range, which regulates soil properties (e.g., salinity, sulfides) and nutrient availability (Castañeda-Moya et al., 2013; Lovelock et al., 2017; Schile et al., 2017). In this coastline type soil C burial is lowest due to negligible freshwater inputs (e.g., rainfall, river discharge) and low NPP rates due to aridity conditions.

2.4 Salinity

Salinity is an important driver of C storage and burial rates, though its impact is not straightforward. Decreased porewater salinities that result from increased precipitation or location (e.g., riverine) can result in increased soil C stocks. Soil C stocks were negatively correlated to porewater salinities in a wall-to-wall C assessment of mangroves across Cambodia (Sharma et al., 2020). Similar results have been reported in Mexico (Adame et al., 2013) and to a degree from West-Central Africa, where correlations between soil C stocks and salinity were much weaker (Kauffman and Bhomia, 2017). Saintilan (1997b) found that root biomass of both *Avicennia marina* and *Aegiceras corniculatum* significantly decreased with salinity in a brackish mangrove in Australia. These relationships between porewater salinities and soil C stocks are likely due to the release of mangrove trees from osmotic stress that increases their productivity and soil C stocks (Sharma et al., 2020).

Alternatively, higher soil C stocks have also been reported under elevated porewater salinities (Ball, 1988; Matsui, 1998). In the Sundarban mangroves of Bangladesh, salinity enhanced soil C stocks relative to aboveground C stocks. Soil C stocks represented only 57.2% of total ecosystem C stocks in freshwater zones and 71.9% of total ecosystem C stocks in higher salinity zones (Rahman et al., 2015). Ball (1988) found that the root:shoot ratios of *A. corniculatum* and *A. marina* increased by 50% and 15%, respectively, when salinity increased from ~1 to 30 ppt. Increased root growth and thus C burial allowed shoots to increase their water demands, though this is more apparent in more salt-tolerant species (e.g., *A. marina*). Higher salinities can also decrease microbial respiration that would also result in increased soil C stocks. Ouyang (2017) found that decay rates declined exponentially with porewater salinity ($R^2 = 0.16$, $P < .001$), similar to other findings (Matsui, 1998).

3. Biotic factors

3.1 Tree diversity

It has been suggested that as mangrove tree species diversity increases, so do the ecosystem services provided by those mangroves (Twilley et al., 1996; Farnsworth, 1998; Field et al., 1998). This would include increased productivity that could potentially increase C burial. Lang'at et al. (2013) found that species mixing boosts root yield in 3–4-year-old planted mangrove saplings, especially when plots included *A. marina*. Belowground production significantly increased within mixed plots of four mangrove species compared with plots of individual species. A global soils analysis found that mangrove stands that had five genera had 70%–90% greater soil C stocks than all other richness levels (Atwood et al., 2017). Similarly, C burial rates increased with each additional species until reaching an average maximum (±1 SD) of 280.5 ± 168.0 gC/m^2 yr at four species, after which C burial decreased (MacKenzie et al., 2016). Belowground root growth and thus soil C stocks and burial rates may be greater in less diverse mangroves forests due to less competition. Increased diversity of an upland forest increased belowground interspecific competition and thus root growth of some species, but not others (Leuschner et al., 2001).

Individual tree species may also influence root production, soil C stocks, and C burial rates. However, it is not clear if this is simply due to the abiotic factors discussed above or if it's a true biotic response. For example, does one species produce more root biomass than another or are there differences in interspecific responses to abiotic factors? McKee (1995) found that *Laguncularia racemosa* produced more roots (1.10 ± 0.11 g) than either *Rhizophora mangle* (0.9 ± 0.08 g) or *Avicennia germinans* (0.84 ± 0.12 g) in a Belize mangrove (0.84 ± 0.12 g). Different monotypic stands of low salinity mangroves along the upper portion of Mary River in Australia exhibited stark differences in total root biomass. Total root biomass from stands of *A. marina* (72.6 Mg/ha) was greater than stands of *A. corniculatum* (13.2 Mg/ha), *Excoecaria agallocha* (45.0 Mg/ha), or *Ceriops tagal* (32.4 Mg/ha). Monotypic stands of mangroves that experienced higher salinities at the mouth of Mary River also exhibited stark differences in total root biomass. Total biomass from stands of *Rhizophora stylosa* (102.0 Mg/ha) were greater than *A. marina* (74.4 Mg/ha), *A. corniculatum* (50.4 Mg/ha), or *E. agallocha* (14.4 Mg/ha) (Saintilan, 1997a). Similarly in Mexico, *A. germinans* and *R. mangle* dominated mangroves had higher root biomass (11.5–30.5 Mg/ha) and root production (1.0–1.9 g/m^2 d) than a forest dominated by *L. racemosa* (9.6 Mg/ha and 0.5 g/m^2 d, respectively) (Adame, 2014). In Kenya, *Sonneratia alba* had greater root biomass (48.4–53.4 Mg/ha) than *A. marina* (39.1–43.7 Mg/ha^{-1}) or *Rhizophora mucronata* (7.5–35.8 Mg/ha) (Tamooh et al., 2008), though values for *A. marina* and *R. mucronata* were similar to those for *Avicennia* spp. and *Rhizophora* spp. from Australia and Mexico (Tamooh et al., 2008). In Micronesia, root ingrowth rates of *S. alba* were also nearly 10x greater than *Bruguiera gymnorrhiza* or *Rhizophora* sp. (Gleason and Ewel, 2002). When data were analyzed at a global scale, soil C stocks ranged fourfold across monotypic stands of different genera. *Laguncularia* sp. (424 ± 262 MgC/ha) and *Rhizophora* sp. (388 ± 227 MgC/ha) had the highest averaged soil C stocks (±1 SE) than any other genera (Atwood et al., 2017). Kauffman et al. (2020) reported no significant differences in soil C stocks among genera (779.1 ± 112.7 to 976.2 ± 92.0 Mg/ha) with the exception of significantly lower soil C stocks for *Avicennia* spp. (361.6 ± 57.2 Mg/ha).

This was attributed to higher porewater salinity. The mean porewater salinity across mangrove forest stands dominated by *Avicennia* spp. was 44 ± 4 ppt, while the mean porewater salinity of mangrove forests dominated by *Rhizophora* spp. was 28 ± 1 ppt ($P \geq .05$) and that of all other stands was <21 ppt.

Increased genera diversity could also result in increased structural complexity on the mangrove forest floor from different aerial root structures (e.g., prop roots vs. pneumatophores). This could affect C burial as different root structures can potentially be more effective at trapping sediments than others. For example, sedimentation can be greater in mangroves with complex trunk and root structures (e.g., *Rhizophora* spp. prop roots) compared to simpler forms, such as single trunked species (e.g., *Ceriops* sp.) or species with pneumatophores (e.g., *S. alba*) or knee roots (e.g., *Bruguiera gymnorrhiza*) as the more complex roots are more effective at slowing the flow of water and allowing C-rich suspended sediments or organic matter to settle out onto the mangrove forest floor (Furukawa and Wolanski, 1996; Furukawa et al., 1997). Average vertical accretion rates (±1 SE) via sediment deposition were enhanced in areas with *Rhizophora* spp. prop roots (11.0 ± 2.9 mm/yr) compared with *S. alba* pneumatophores (7.2 ± 1.1 mm/yr), *B. gymnorrhiza* knee roots (9.3 ± 1.2 mm/yr), and bare soil controls (9.4 ± 2.6 mm/yr) (Krauss et al., 2003). Aside from tertiary structure, the density of aerial roots, stems, and trunks can also increase vertical accretion. This has been demonstrated using natural *A. marina* roots as well as artificial structures (Spenceley, 1977; Bird, 1986; Young and Harvey, 1996) and mangrove seedlings (Huxham et al., 2010; Kumara et al., 2010). In addition to root complexity and density, the influence of pneumatophores of *A. marina* and *S. alba* on sediment deposition may be due to their ability to bind and retain of sediments (Spenceley, 1977). Mangrove species also differ in terms of their specific gravity of wood (e.g., g/cm^3) (see review by Rovai et al., 2016) and thereby C content in belowground woody biomass (Rodrigues et al., 2015; Gillerot et al., 2018). In addition, mangrove species differ as to the quality of the litter which ultimately influence organic matter turnover and C remineralization (Twilley et al., 1986).

3.2 Forest age

Forest age can also influence soil C stocks. Several studies using restored mangroves as chronosequences have found that soil C stocks increase with age. In Florida, C stocks in the upper 10 cm of soils from mangroves that had been naturally restored with *R. mangle*, *L. racemosa*, and *A. germinans* increased linearly over a 20-year period at a rate of 218 g C/m^2 yr. Restored mangroves reached soil C stock levels (52.5 ± 24.4 MgC/ha) similar to reference sites (28.1−50.7 MgC/ha) after 20 years (Osland et al., 2012). In Indonesia, naturally recolonized tidal mangroves in highly productive areas had soil C values that were within 80% of reference values after only 10 years. In contrast, similar aged naturally recolonized mangrove stands in low productive areas on a coral atoll had lower soil C values that were only 20% of reference values (Cameron et al., 2019). Similar results have been seen in planted sites. In Thailand, root biomass of *Rhizophora apiculata* replanted mangrove forests significantly increased from 3 to 25 years until reaching a maximum value of 35.6 Mg/ha (Alongi and Dixon, 2000) and in Brisbane, Australia, 25-year-old replanted stands of *A. marina* (118 Mg/ha) had similar amounts of root biomass as natural stands (121 Mg/ha) (Mackey, 1993). In China, Chen et al. (2018)

reported that average soil C stocks (±1 SE) in the top meter of soil increased from 130 ± 5 to 151 ± 7 to 170 ± 9 MgC/m^2 in 12-, 24-, and 48-year-old planted mangrove forests, respectively. Similar results were reported for *R. mucronata* planted forests in Kenya, where dry root biomass significantly increased from 7.5 ± 0.4 to 24.9 ± 1.6 to 35.8 ± 1.1 Mg/ha in 6-year, 12-year, and natural mangrove forests. However, while dry root biomass also increased with age in *S. alba* and *A. marina* planted forests in Kenya, dry root biomass was highest in the 12-year-old stands (75.5 ± 2.0 and 43.7 ± 1.7 Mg/ha, respectively) compared with natural stands (48.4 ± 0.7 and 39.1 ± 0.7 Mg/ha, respectively) (Tamooh et al., 2008).

In natural mangroves of French Guiana, Marchand (2017) also found that mangrove forest soil C stocks increased linearly from 4 to 107 Mg OC/ha with forest age (Fig. 12.4). However, while C burial rates also increased with forest age, they peaked after ~10 years at 480 gC/m^2 yr, after which they decreased to 135 gC/m^2 yr in 40-year-old forests and then increased again to 486 gC/m^2 yr in ~50-year-old forests. The increase in the older forest was attributed to these sites being isolated from the sea and developing a community of mangrove associates (fern, epiphytes, etc.) that would have contributed to the NPP of the ecosystem. MacKenzie (unpublished data) also found that C burial increased with stand age until reaching a maximum of (±1 SD) 384.3 ± 176.0 gC/m^2 yr at 10 years, after which C burial decreased. In restored sites in Malaysia, C burial rates were greatest in the first 5 years of recovery (290−610 gC/m^2 yr), which were 2x greater than burial rates in mature forests (>50 years; ~120 gC/m^2 yr) (Adame et al., 2018). Alongi et al. (2004a) reported that while sedimentation rates decreased from 5 to 18 to 85-year-old mangrove forests, average C burial rates increased from 274.4 to 296.2 to 352.2 g/m^2 yr with forest age. However, the greatest C burial observed was from a 5-year-old site (403.7 g/m^2 yr).

It is not entirely clear why the above patterns in C stocks and burial rates were observed. Greater C stocks and C burial rates in younger stands were attributed to greater root growth and thus greater belowground production rates of younger trees compared with older trees (Osland et al., 2012; Krauss et al., 2017; Sharma et al., 2020). However, Alongi et al. (2004a)

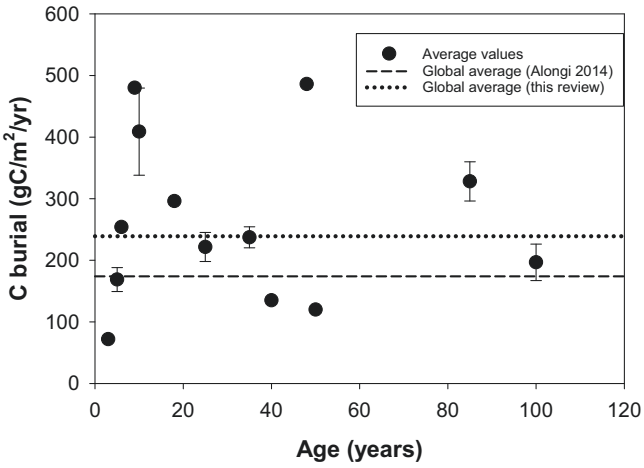

FIGURE 12.4 Average C burial rates (±1 SE) versus stand age (Alongi et al., 2004a; Marchand, 2017; MacKenzie et al., unpublished data; Adame et al., 2018). *Dotted line* represents the global average (Alongi, 2014).

argues the opposite, that the increase in C burial rates observed in Malaysia were due to increase rates of primary production with age. While aboveground NPP did increase with age across the Malaysian sites studied, it is unclear if belowground production also increased. Additional studies are needed to confirm this especially as countries, agencies, and nongovernmental organizations continue to invest in mangrove restoration to offset greenhouse gas emissions or to participate in voluntary C markets.

The lower soil C stocks and burial rates observed in mangroves less than 10 years old likely reflect initial lower values reported from degraded sites or bare landscapes (Kauffman et al., 2017; Sasmito et al., 2020) prior to reforestation or afforestation, respectively. The lower organic matter content from these sites could also result in oxic–suboxic sediment conditions that would allow organic matter decomposition to initially occur until a threshold is reached where sediments become anoxic and decomposition is reduced (Marchand, 2017).

3.3 Algae

Primary production from seagrass litter, macroalgae (e.g., *Ulva pertusa*, *Enteromorpha intestinalis*), filamentous algae, microphytobenthic algae, or diatoms growing on aerial roots or on/within sediments can also be a source of allochthonous or autochthonous C to mangrove sediments (Kristensen 2007, 2008; Alongi, 2014; Sasmito et al., 2020; MacKenzie et al., 2020). A recent review found that gross primary production of microphytobenthic algae can be comparable to the amount of C delivered as litterfall from trees, though standing stocks may be less due to consumption by crabs (Kristensen, 2008; MacKenzie et al., 2020). Contributions of algae to sediment C likely varies with season (Mfilinge et al., 2005) as well as forest age. Marchand et al. (2003) reported that algae growing on the surface of sediments in younger stands of *A. germinans* in French Guiana significantly contributed to organic C content in the upper portions of the sediment. However, he concluded algal contribution to soil C stocks/burial rates likely decreased over time as older stands developed closed canopies (Marchand, 2017). Turnover of algae is also likely to be much greater than leaf litter as algae can decompose quite rapidly before being buried in the sedimentary column. Algae may also contribute to soil C stocks and burial by helping trap and retain C-rich sediments and detritus (McKee, 2011).

3.4 Crabs

Bioturbating sesarmid and ocypodid crabs are important ecological engineers that may also influence C dynamics in mangrove sediments, though this depends on various environmental condition such as soil, vegetation (Wang et al., 2010), and hydrological conditions (Sharma et al., 2014). One of the few studies recently conducted in Kenya found higher soil C stocks in forests with greater abundances of sesarmid crabs (Andreetta et al., 2014). While this might not necessarily imply causation, soil C stocks can be affected via the complex burrow networks created by crabs. Sesarmid tree crabs typically create burrows that can be meters deeper than ocypodid fiddler crabs (Robertson and Daniel, 1989; Smith III et al., 1991), though ocypodid burrows typically occur at much greater densities sesarmids (Cannicci et al., 2008). Burrows can increase the amount of sediment surface area that is exposed to the atmosphere at low tide. Increased surface area is greater in sesarmid burrows

(150%−380%) than ocypodid burrows (~1%), though the greater densities of ocypodids result in comparable surface area increase for both types of crabs. As a result, oxygen can diffuse into anaerobic sediments at low tides when sediments are exposed, which oxidizes elements toxic to plants (i.e., iron and sulfur) (Mitsch and Gosselink, 1993), and can increase tree productivity (Smith III et al., 1991; Kristensen and Alongi, 2006) and potentially belowground production and C burial. During high tides, many crabs plug their holes and thus provide an effective barrier at shielding organic matter from flushing at high tides (Kristensen, 2008).

Crabs also likely influence soil C stocks and burial through feeding. Mechanical fragmentation of decayed and fresh leaves by sesarmid feeding coupled with enzymatic activity within their guts reduces leaf litter particle size (Mouton and Felder, 1996; Botto and Iribarne, 2000; Werry and Lee, 2005) and increases the surface area available for microbial colonization litter (Lee 1997, 2005). Fragmentation, enzymatic activity, and increased surface area all increase leaf litter decomposition and release of C that is either incorporated into mangrove sediments (Andreetta et al., 2014) or lost through outwelling to nearshore waters (Lee, 1995). Crabs also directly transfer C to sediments through the direct transport of leaf litter, propagules, algae, feces, and exuviae into their burrows (Lee, 1997; Alongi, 2002; Huang et al., 2007). The importance of vertical transport into sediments by crabs was demonstrated via radiocarbon dating of sediment cores from a Kenyan mangrove. Modern C was found as deep as 115 cm, confirming that sesarmids are supplying fresh organic matter to deeper sediments (Andreetta et al., 2014). The relationship between macrofauna (e.g., burrowing crabs, polychaete worms, etc.) and soil C stocks and burial rates deserved increased attention in the future. It appears that these macrofaunal diversity could be a key driver of C dynamics in these systems and these organisms are currently threatened by human activities such as pollution, eutrophication, and sea level rise (Andreetta et al., 2014).

4. Conclusion

Many studies have attempted to identify key parameters to develop models that can be used to predict soil C stocks and burial rates as this is where the majority of C is stored in mangrove systems. While we have attempted to present these factors, what is clear is that there are a range of values that differ at the local, regional, and global scale. Some factors that are important at one scale may not be as important at another scale (e.g., porewater salinity). While global or regional models are valuable and play an important role in predicting soil C dynamics, site-level assessments, upon which the quality of these larger-scale efforts rely on, are still scarce, thus preventing the development of robust extrapolation of C burial rates across spatial scales. Complications also arise in comparing results of different studies or in creating global models, as methods used to collect soil C data often vary, which can significantly influence reporting of soil C stocks or burial rates, particularly timescale measurement bias (Breithaupt et al., 2018). It is also clear that, while the number of studies that report soil C burial has significantly increased, gaps remain and additional studies are needed at different scales to increase our understanding of various abiotic and biotic factors. For example, there appear to be several studies that have focused on abiotic factors (e.g., temperature, precipitation, salinity), but fewer studies have examined biotic influence,

specifically the role of burrowing crabs or other macrofauna. This information can be used to guide more successful conservation and restoration efforts globally.

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