

Chapter 6

Biogeochemical Cycles: Global Approaches and Perspectives

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6.1 Introduction

Mangrove wetlands are intriguing ecosystems because they share biological, geochemical, and ecological properties from both terrestrial and marine environments (Alongi 2009; Mitsch and Gosselink 2015). The mangrove ecosystem is

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characterized by dense growth of highly productive trees and shrubs (Tomlinson 1994; see Chap. 1). They provide most of the primary production, although other autotrophs, including pelagic, benthic, and epiphytic algae may also contribute significantly to the organic input (Kristensen et al. 2008a). The export of autochthonous production and import of allochthonous material are strongly dependent on complex spatio-temporal hydrological patterns regulated by large-scale physical and geomorphological processes. From a biogeochemical perspective, the input of organic and inorganic matter from various sources and their mixing within the mangrove ecotone create highly spatially and temporally heterogeneous sediments with microbial processes that are challenging to understand and evaluate. The available biogeochemical information is yet to be integrated into a generalized ecosystem model due to the wide variety of geomorphic settings and mangrove ecotypes within and among biogeographical regions (Twilley and Rivera-Monroy 2005).

Although the ecological functioning of mangrove environments has been described for a variety of climatic regions (e.g., tropical, subtropical) and ecogeomorphic settings (e.g. deltas, lagoons, estuaries, oceanic islands) (e.g. Bouillon et al. 2007; Adame and Lovelock 2011; Alongi et al. 2012), our understanding of how carbon (C), iron (Fe), sulfur (S), and nutrient (e.g. N and P) cycling are controlled and interact in these locally diverse environments is still developing. The research has come predominantly from Australasia and North America, with less from locations in Oceania, Asia, Africa, and Central and South America. Information from the understudied regions is, therefore, required to achieve a full global overview. Additional knowledge on the spatiotemporal patterns of biogeochemical mechanisms and processes will improve the reliability of mangrove C and nutrient budgets as well as estimates of the impact of human activities on global cycles (Bouillon et al. 2008; Pendleton et al. 2012). Organic matter decomposition in mangrove sediments is mediated by microbial processes utilizing a variety of electron acceptors under a wide range of redox conditions (Kristensen and Alongi 2006; Ferreira et al. 2007a; Kristensen et al. 2011). The fraction of mangrove detritus that escapes degradation and export is a significant source of in situ C sequestration via accretion and storage (Bouillon 2011; Donato et al. 2011; Pendleton et al. 2012). The accumulation and residence time of C stocks, however, depends strongly on the interaction among local environmental and biological variables such as hydrology, plant activity, crab foraging, and bioturbation (Lee 1997; Kristensen 2008; Mitsch and Gosselink 2015). It is, therefore, imperative not only to evaluate mangrove biogeochemical patterns among biogeographical regions but also to examine the spatio-temporal variability within each region with focus on anthropogenic impacts.

The main objective of this chapter is to advance our understanding of the biogeochemistry of mangrove wetlands by comparing differences in element cycling at biogeographical scales. Through a comparative literature review, we identify potential sources of variation when applying different methods and techniques and provide an understanding of the small- and large-scale variability as well as complexity of biogeochemical transformations in these productive wetlands. Our goal is,

therefore, to identify knowledge gaps, and thus research priorities, in biogeochemical cycling of C and other critical macro (N, P) and micro (e.g., Fe, Mn) elements in mangrove environments across biogeographic regions and latitudes.

6.2 Characteristics of Mangrove Substrata

6.2.1 *Terms and Definitions; Sediment or Soil?*

The operational differentiation between sediments and soils in coastal and wetland-dominated environments has been an ongoing discussion since the insertion of the “subaqueous soil” term in the Soil Taxonomy classification (Soil Survey Staff 1999; Ferreira et al. 2007a; Kristensen and Rabenhorst 2015). This discussion has its genesis in the different methodological and conceptual approaches historically followed by soils scientists (pedologists) and marine scientists and reflects on the current understanding of biogeochemical processes in mangrove wetlands. The development of the subaqueous soil concept was based on the original work by Demas and colleagues (Demas et al. 1996; Demas and Rabenhorst 1999) who defined sediment layers as a function of pedogenesis and proposed the presence of subaqueous soil horizons in wetlands. Along the same line, Ferreira et al. (2007a) argued that sedimentary material (the parental material) that is permanently colonized by higher vascular plants interacting with fauna and microbial activity leads to substantial changes in the composition and properties of the original substratum. These changes transform the original sediment to a more complex, geochemically contrasting environment, which should lead to soil formation. However, the development of oxic or suboxic mosaics within anoxic layers due to plant–substratum interactions is not only associated with soil formation, but is also common in subtidal sediments affected by bioturbation and roots of submerged vegetation (Kristensen and Rabenhorst 2015).

Demas and Rabenhorst (1999) argued that pedogenic processes leading to horizon differentiation are required to consider estuarine substrata as soils. The formation of soil horizons through pedogenesis includes four generalized processes: additions, losses, transfers (or translocations), and transformations (Simonson 1959). Conversely, the biogeochemical zonation of aquatic sediments is controlled by sediment diagenesis, which includes the composition of deposited material and the involved physical, chemical, and biological processes (Burdige 2006; Aller 2014). The generalized pedogenic processes are, therefore, a subset of the sediment diagenetic processes. Under this perspective, Kristensen and Rabenhorst (2015) pointed out that pedogenic processes identified by pedologists in shallow water environments cannot be distinguished from the diagenetic processes described for sediments by marine scientists and concluded that the terms “sediment” and “soil” to describe the substrata in coastal environments vegetated by mangrove forests are not mutually exclusive.

Thus, under these perspectives, which term should be used? In this chapter, we compromise and use the term sediment as a more general historic term. It is not our objective to prefer one term over the other, but to underscore the context of the arguments currently still under discussion (see Ferreira et al. 2007a; Kristensen and Rabenhorst 2015). Our own research and interdisciplinary approach in writing this chapter has motivated us into an inclusive approach to advance the understanding of mangrove wetland spatiotemporal biogeochemical processes and functions. Particularly, in trying to fulfill one of the objectives of the chapter where “both scientific communities (i.e., pedologists, and marine scientists) will benefit from comparable studies in the same environments, (recognizing that) their different backgrounds may even promote collaborations with the developments of new ideas and revolutionary concepts” (Kristensen and Rabenhorst 2015).

6.2.2 Litter Fall and Sediment Organic Matter

Organic matter delivered to microbial decomposers in mangrove sediments is of both autochthonous and allochthonous origin. Litter from mangrove trees (i.e., leaves, propagules, twigs, and wood) is usually considered the most important source of organic C and nutrients to mangrove sediments (Alongi et al. 2005a; Sousa and Dangremond 2011; Murdiyarto et al. 2015). A range of other sources may also provide significant inputs; including below-ground mangrove roots, as well as local production by benthic or epiphytic micro- or macroalgae, phytoplankton in tidal creeks or estuarine waters, and materials imported via rivers (e.g. terrestrial tree litter) or tides (e.g., seagrass)(Kristensen et al. 2008a; Alongi 2009; Twilley and Rivera-Monroy 2009; Adame and Lovelock 2011; Leopold et al. 2015). Because of its important functional role, the quantification of litter fall is crucial for assessing productivity of a mangrove ecosystem and thus forest organic matter contribution to benthic food webs in both the mangrove and its adjacent coastal environment (Imgraben and Dittmann 2008).

Annual litter fall, which is the most widely used proxy of mangrove net productivity, differs substantially within and among forests due to a number of factors including tidal and hydrological gradients (Feller et al. 1999), salinity (Day et al. 1996), anthropogenic influence (Silva et al. 1998), mangrove species composition (Coupland et al. 2005), and latitude (Twilley et al. 1992; Saenger and Snedaker 1993). The global average mangrove litter fall, which is in the order of $\sim 460 \text{ g C m}^{-2} \text{ year}^{-1}$ (range: 48–924 $\text{g C m}^{-2} \text{ year}^{-1}$), does not show a clear biogeographical trend (Twilley et al. 1992; Saenger and Snedaker 1993; Jennerjahn and Ittekkot 2002) due in part to major differences in ecotype dominance and spatial distribution within latitude (Twilley et al. 1998). There are apparently some distinct differences in productivity and litter fall among mangrove species, for example, *Rhizophora* spp. shows about 50% higher litter yield than *Avicennia* spp. (Bunt 1995). It must be stressed, however, that most available estimates of mangrove production do not include wood and below-ground components (Middleton and McKee

2001; Castaneda-Moya et al. 2013). Current below-ground biomass estimates indicate that this component contributes a substantial part (10–55%) of the total mangrove biomass (Twilley et al. 1992; Matsui 1998; Alongi and Dixon 2000; Rivera-Monroy et al. 2013) and probably account for a similar part of the total productivity. The ongoing effort to establish a latitudinal-based network of eddy-covariance towers in mangrove coastal regions in the near future might improve net mangrove ecosystem productivity estimates to include both above- and below-ground production (Rivera-Monroy et al. 2013; see Sect. 6.4).

Regardless of differences in organic matter sources and pathways through food webs among mangrove forests, all organic matter not exported by tidal exchange enters the sediment where it is consumed, degraded, or buried. Mangrove sediments are relatively rich in organic C with an estimated global particulate organic carbon (POC) median value of 2.6% (Kristensen et al. 2008a), ranging from 2.2% in the Indo-west-Pacific (IWP: East Africa, Asia, and Australasia) to 3.1% in the Atlantic-East Pacific region (AEP: West Africa and America) (Fig. 6.1), which is higher than generally observed in marine sediments (Seiter et al. 2004) and terrestrial soils (Donato et al. 2011). Current available information indicates that the fraction of organically enriched mangrove sediments having POC content >10% is higher in America (23%) and Asia (19%) than in East Africa (8%) and Australasia (6%) (Fig. 6.1). These differences in POC among regions are difficult to explain and may be confounded by variations within and among mangrove forests depending on hydrological regimes (i.e., hydroperiod) and mangrove species composition as well as other structural and environmental variables (Alongi 2012). The median sediment molar POC/PN ratios also vary among regions, ranging from 18 to 19 in East Africa and Asia to 24 to 25 in America and Australasia (Fig. 6.1). Most mangrove sediments have POC/PN ratios above 10 (100% in America; 96% in East Africa; 98% in Asia; and 92% in Australasia), whereas POC/PN ratios above 30 are more frequent in America (24%) and Australasia (34%) than in East Africa (9%) and Asia (5%). Although the generally high POC/PN ratios indicate that mangrove sediments contain a significant input of mangrove litter, the large differences among regions may indicate higher inputs of N-rich marine organic matter coupled with global differences in rivers and river flows and more extensive eutrophication in East Africa and Asia than in America and Australasia (Lee 2016).

In addition to the substantial deposition of litter from mangrove canopies, vegetation structure has a profound impact on the magnitude of sedimentation by actively capturing mineral and organic particles (Furukawa et al. 1997). Large trees with complex aerial root systems (e.g. tree height >10 m), such as *Rhizophora* species, facilitate the retention and deposition of particles from tidal currents to a much greater extent than smaller trees with simpler architecture, such as *Avicennia* species. Accordingly, sediments under *Rhizophora* stands are often richer in POC than under *Avicennia* stands (Table 6.1). However, this difference is not always evident and may in some cases be reversed due to location-specific and climatic-driven differences in litter fall rates, litter composition, and hydrological patterns. This is evident from Table 6.1 where two *Rhizophora mangle* locations in the Americas support the lowest sediment POC. Variations in mangrove zonation pattern may

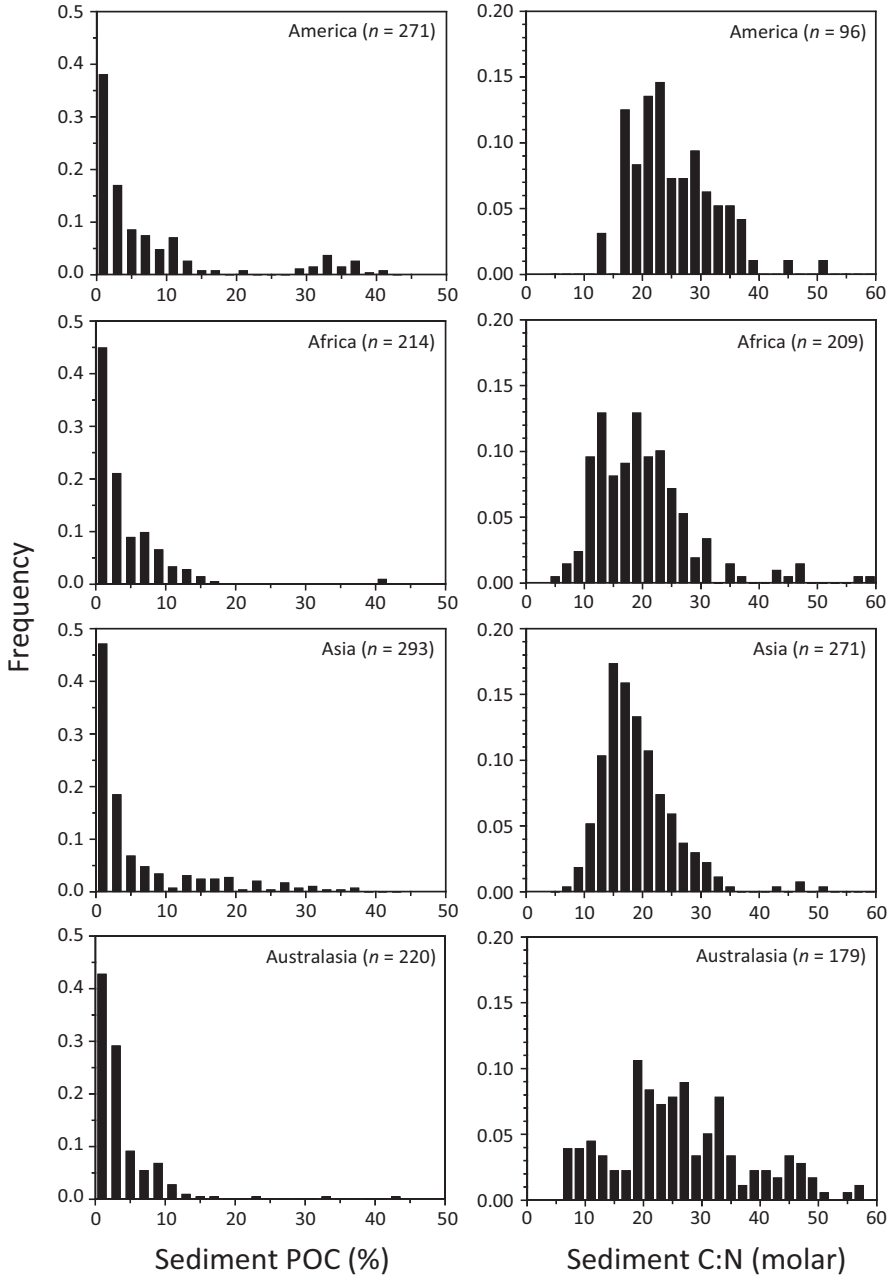


Fig. 6.1 Compilation of (left) bulk POC and (right) bulk POC:T:N ratios of intertidal mangrove sediments from four biogeographical subregions. Data compiled from various sources (Modified from Kristensen et al. 2008a)

Table 6.1 Sediment content of POC and TN in mangrove forests from around the world dominated by *Rhizophora* spp. and *Avicennia* spp. Only data from sediments underlying forests of about the same age (15–30 years) and same intertidal location (mid-intertidal) are included

Location	Tree species	POC (%)	TN (%)	Ref
Pambala, Sri Lanka	<i>Rhizophora apiculata</i>	19.1 ± 2.4	1.04 ± 0.13	1
	<i>Avicennia officinalis</i>	10.4 ± 1.7	0.64 ± 0.05	1
Pichavaram, India	<i>Rhizophora apiculata</i>	10.0 ± 1.9	0.70 ± 0.01	2
	<i>Avicennia marina</i>	7.0 ± 1.0	0.42 ± 0.01	2
Dampier, W. Australia	<i>Rhizophora stylosa</i>	6.5 ± 1.3	0.23 ± 0.03	3
	<i>Avicennia marina</i>	1.4 ± 0.1	0.09 ± 0.01	3
Port Hedland, W. Australia	<i>Rhizophora stylosa</i>	2.3 ± 1.1	0.13 ± 0.02	3
	<i>Avicennia marina</i>	1.7 ± 0.2	0.16 ± 0.02	3
Ras Dege, Tanzania	<i>Rhizophora mucronata</i>	4.3 ± 1.1	0.18 ± 0.07	4
	<i>Avicennia marina</i>	2.9 ± 0.3	0.11 ± 0.02	4
Gazi Bay, Kenya	<i>Rhizophora mucronata</i>	4.4 ± 1.4	0.23 ± 0.06	5
	<i>Avicennia marina</i>	2.2 ± 1.8	0.11 ± 0.05	5
Somone, Senegal	<i>Rhizophora</i> sp.	1.7 – 2.1	–	6
	<i>Avicennia</i> sp.	0.3 – 0.6	–	6
Balandra Bay, Mexico	<i>Rhizophora mangle</i>	3.7 ± 1.8	0.16 ± 0.08	7
	<i>Avicennia germinans</i>	7.9 ± 4.0	0.32 ± 0.17	7
Itacuruca, Brazil	<i>Rhizophora mangle</i>	2.7 ± 0.1	0.17 ± 0.01	8
	<i>Avicennia schaueriana</i>	4.6 ± 1.3	0.26 ± 0.08	8

(1) Bouillon et al. (2003); (2) Alongi et al. (2005b); (3) Alongi et al. (2000a); (4) Kristensen et al. (2011); (5) Andreetta et al. (2014); (6) Sakho et al. (2015); (7) Giani et al. (1996); (8) Lacerda et al. (1995)

partly explain this biogeographic difference in both retention and deposition of POC (Twilley et al. 1992; Chmura et al. 2003). Intertidal position may also affect POC deposition as frequently exposed upper intertidal mangrove areas are often dominated by simple scrub vegetation with limited POC accumulation capacity due to evaporation-driven high porewater salinity (>50) (Adame et al. 2010; Deborde et al. 2015). Conversely, mangrove margins and adjacent intertidal mudflats where tall and dense fringing mangrove stands dominate are often sites of higher POC accumulation (Sanders et al. 2010). However, changes in hydrodynamics, especially turbulent kinetic energy from waves and currents at the edge of the forest, may alter sediment/organic matter deposition and its interaction with different species of mangroves and density of roots (Wolanski et al. 1990; Zhang et al. 2015).

The complex composition of mangrove litter with high content of structural organic polymers and polyphenolic compounds (e.g., cellulose, lignin, and tannins) hampers degradation and promotes long-term preservation of organic C once these organic substrates enter anoxic conditions in waterlogged sediments (Hernes et al. 2001; Marchand et al. 2005; Alongi 2009). Although detrital POC from litter fall is a mixture of more or less refractory biomolecules in various stages of decomposition, it also contains labile components (mainly amino acids, proteins, and sugars). Root exudates are particularly rich in these reactive components and may represent

an important source of labile POC in sediments densely vegetated by mangrove trees (Reddy and DeLaune 2008; Weng et al. 2013). Such subsurface sources of reactive POC may be the principal drivers of fast microbial processes deep in mangrove sediment in contrast to oceanic sediments, where partly degraded POC from the water column is deposited at the surface, and slowly buried through active sedimentation and accretion. The reactivity, rather than the quantity of POC, is, therefore, a key factor driving anaerobic respiration in mangrove sediments (Opsahl and Benner 1999; Tremblay and Benner 2006).

6.2.3 Sediment Geochemical Characteristics

Redox processes involving reactive Fe are important for sediment biogeochemistry in most mangrove areas. The actual role of Fe in any mangrove ecotype depends on the availability and delivery of reactive forms and the concentration is typically high in tropical mangrove regions receiving surface runoff and groundwater from adjacent land and watersheds with Fe-rich soils (Souza-Júnior et al. 2007; Sanders et al. 2012; Gonnee et al. 2014; Noel et al. 2014). Much of the Fe delivered to sediments occur as solid phase Fe(III) oxyhydroxides (Table 6.2). These forms are generally very reactive and can be reduced considerably faster than solid phase crystalline Fe(III), such as silicate-bound Fe. The reactivity of Fe(III) forms to undergo reduction by microorganisms typically follows the sequence: iron phosphate tetrahydrate ($\text{FePO}_4 \cdot 4\text{H}_2\text{O}$) > ferrihydrite ($\text{Fe}_{10}\text{O}_{14}(\text{OH})_2$) > iron hydroxide ($\text{Fe}(\text{OH})_3$) > lepidrocrocite ($\gamma\text{-FeO}(\text{OH})$) > goethite ($\alpha\text{-FeO}(\text{OH})$) (Fischer and Pfanneberg 1984; Roden and Zachara 1996). Once amorphous Fe(III) forms more reactive than goethite has been reduced, sulfate reduction becomes energetically favorable (Canfield et al. 2005). This shift in microbial reactions may be the reason for the presence of goethite in mangrove sediments dominated by sulfate reduction (Otero et al. 2009). Dissolved Fe^{2+} generated by reduction of solid phase Fe(III) oxyhydroxides may either diffuse to oxic layers where it is reoxidized and precipitated as Fe(III) forms,

Table 6.2 Chemical species and characteristics of iron oxides, with information on crystal structure, color, weight-specific area of reactive surfaces, and reactivity (Adapted from Cornel and Schwertmann 1996; Canfield et al. 1992; Poulton et al. 2004)

Mineral name	Crystal structure	Color	Surface area ($\text{m}^2 \text{g}^{-1}$)	Reactivity (yr^{-1})
Ferrihydrite ($\text{Fe}_{10}\text{O}_{14}(\text{OH})_2$)	Trigonal	Reddish-brown	200–400	500–2200
Lepidrocrocite ($\gamma\text{-FeO}(\text{OH})$)	Orthorhombic	Orange	15–260	85–557
Goethite ($\alpha\text{-FeO}(\text{OH})$)	Orthorhombic	Yellowish-brown	30–90	4–22
Haematite ($\alpha\text{-Fe}_2\text{O}_3$)	Trigonal	Bright red	10–36	1–12
Magnetite (Fe_3O_4)	Cubic	Black	20–60	10^{-2} –4

or precipitate in anoxic sediment as carbonate (siderite, FeCO_3), phosphate (vivianite, FePO_4), or sulfide (mackinawite, FeS and pyrite, FeS_2), depending on the sediment geochemical conditions (Fig. 6.2). As a result, Fe speciation changes dramatically with depth in mangrove sediments from dominance of Fe(III) oxyhydroxides near oxic surfaces to primarily pyrite (FeS_2) in reduced layers. Close spatial coupling of iron and sulfate reduction favors rapid precipitation of Fe(II) sulfides as mackinawite (FeS) that may act as a transient phase in pyrite formation (Holmer et al. 1994; Butler and Rickard 2000; Ferreira et al. 2007b). Analyses using scanning electron microscopy and dispersive X-ray spectroscopy have revealed that pyrite framboids are commonly formed along mangrove roots (Noel et al. 2014). However, newly formed pyrite near sediment interfaces can be rapidly reoxidized to amorphous Fe(III) oxyhydroxides by oxygen intrusion through the action of tides, bioturbation, plant roots, and seasonal changes in hydrology (Noel et al. 2014).

The spatial heterogeneity of redox processes is much more complex and variable in intertidal mangrove sediments with high abundance of roots and burrows than in oceanic sediments (Fig. 6.3; Otero et al. 2006; Ferreira et al. 2010). The upper 60–100 cm of the sediment is normally characterized by a substantial redox variation, in some cases without any clear vertical trend. However, redox models consistently show an oxidized surface zone of variable thickness (upper oxidation zone) overlying a zone with more reducing conditions (upper reduced zone; Clark et al.

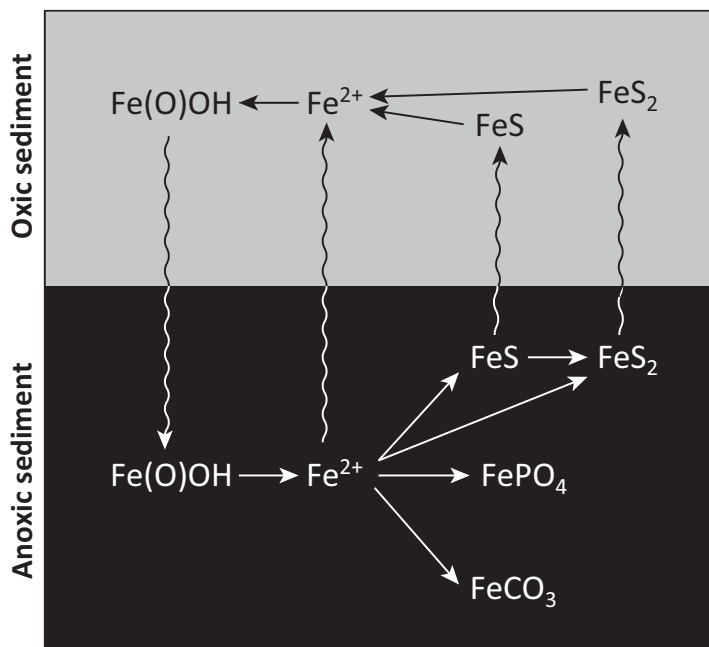


Fig. 6.2 Oxidation and reduction processes involving Fe in mangrove sediment. The zig-zag arrows indicate solid phase (Fe(O)OH , FeS , and FeS_2) and solute (Fe^{2+}) transport between oxic and anoxic sediment. Straight arrows indicate a chemical reaction or process

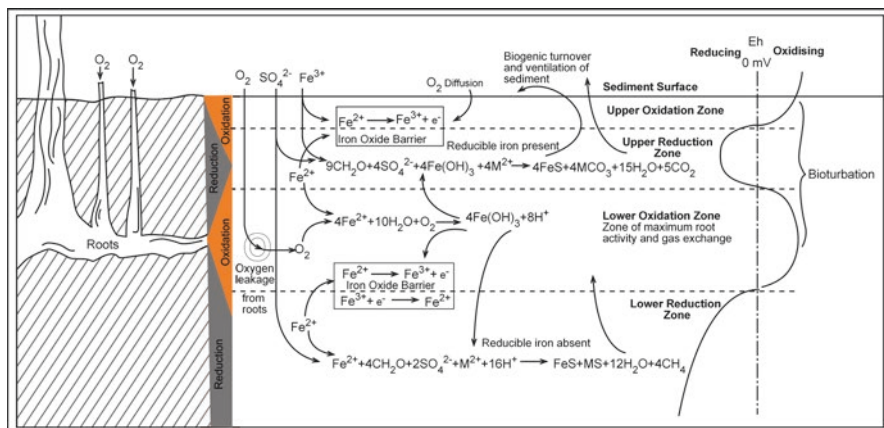


Fig. 6.3 Vertical redox zones in mangrove sediment. The drawing to the left indicates the position of *Avicennia* spp. roots. All redox relevant microbial reactions and transport processes are indicated

1998). The thickness of the upper oxidation zone in mangrove forests typically ranges from <2 cm at the seaward edge to >10 cm near the landward edge (Clark et al. 1998). The upper oxidation zone may vary seasonally and can disappear when intense rain causes prolonged flooding events, or expand after long drought periods. These changes are particularly evident in the high intertidal part of the forest, where tidal inundation normally is infrequent (Marchand et al. 2004, 2006). Below the upper reduction zone, a second oxidizing layer is found (lower oxidation zone) at a depth that can vary between 30 and 60 cm (Clark et al. 1998). The oxidizing effect in this layer is the result of downward translocation of oxygen by bioturbation and via aerenchyma tissue in roots followed by release into the sediment (Fig. 6.3). The lower oxidation zone is actually a mosaic of alternating oxidizing areas near burrows and roots and reduced areas away from biogenic structures (Kristensen and Alongi 2006). The thickness of the lower oxidation zone depends on the forest structure, mangrove species composition, and hydrological regime (Marchand et al. 2006). Thus, this zone is typically less distinct in *Avicennia* spp. than in *Rhizophora* spp. dominated forests due to the restricted root depth of the former (Fiala and Hernandez 1993). Finally, a permanently reduced layer (lower reduced zone) with high pyrite content is found below the root penetration depth (Clark et al. 1998; Marchand et al. 2006; Otero et al. 2009).

The redox depth profiles and spatial distribution also vary among biogeographical regions and types of mangrove forest (basin, fringe, scrub, overwash, and riverine; Lugo and Snedaker 1978). For example, monospecific *Rhizophora mangle* forests in Sao Paulo State (SE Brazil) show redox conditions that vary according to their physiographic position (Ferreira et al. 2007c). Basin forests in this region have strongly reducing conditions throughout the sediment profile, whereas fringe and riverine forests typically have oxidized surface sediments (Table 6.3). Similar to the vegetation zones, the intertidal gradient also affects the redox zonation. The

Table 6.3 Geochemical characteristics of near-surface sediment in various forest types of Sao Paulo State, Brazil (Ferreira et al. 2007b)

Location	Forest type	Depth cm	Sand %	TOC %	Eh mV	Total S %	Total Fe %	Fe oxides %	Pyrite Fe %
Cardoso Island	Basin	0–15	12	8.5	–52	1.85	2.46	0.46	0.57
	Riverine	0–15	86	2.0	102	0.35	0.57	0.15	0.09
Paimatos Island	Fringe	0–15	8	5.2	300	0.80	5.63	0.79	0.22
Baixada Santista	Riverine	0–10	15	23.7	331	2.89	3.23	0.17	0.73

infrequent tidal flooding near the mangrove landward side may result in the formation of numerous mud cracks due to desiccation allowing downward penetration of oxygen causing oxidation of deeper sediment layers (Marchand et al., 2011; Noel et al., 2014; Deborde et al., 2015). Consequently, Fe and S redox cycling intensifies significantly from the landward to seaward section of mangrove forests due to differences in duration and frequency of tidal inundation (Noel et al. 2014). Moreover, the higher tree productivity generally observed toward the seaward front of the forest may lead to strongly reduced sediment conditions because of lower saline stress, higher input of labile POC, and faster microbial activity.

6.3 Factors Affecting Element Cycling in Mangrove Sediments

Rates and pathways of microbial C and nutrient transformation in mangrove sediments are dependent on a number of key factors. The most important are organic matter input, availability of electron acceptors, bioturbation activity, and presence of tree roots, as well as geomorphology and hydrology (Canfield et al. 2005; Kristensen et al. 2008b; Mitsch and Gosselink 2015). The reactivity of organic matter toward microbial degradation using a variety of electron acceptors maintains a delicate redox zonation (Ferreira et al. 2007b). However, this zonation can be interrupted by downward translocation of oxygen via crab burrows and tree roots (Kristensen and Alongi 2006). C oxidation by heterotrophic microbial communities in mangrove environments is also dependent on the interaction between tidal elevation and hydroperiod (frequency, duration, and depth of inundation). Release of CO₂ may in certain cases vary several folds during different tidal conditions with the highest rates observed during low tide promoting degassing through air exposure (Alongi et al. 2004; Kristensen and Alongi 2006). It is not yet fully understood how this CO₂ exchange is controlled, but large biogenic structures (e.g. pneumatophores

and crab burrows) may have an important role as conduits for O₂ intrusion and CO₂ release (Kristensen et al. 2008b).

6.3.1 Carbon Oxidation and Partitioning of Electron Acceptors

Sediment C oxidation can be quantified as CO₂ release in the dark, which represents the sum of all aerobic and anaerobic respiration processes and provides a reliable estimate of the total organic matter decomposition occurring within the sediment (Kristensen et al. 2011). To obtain the actual dark CO₂ fluxes in intertidal mangrove environments, measurements should be performed both during inundation and air exposure. The global average dark CO₂ release from inundated mangrove sediments is 62 mmol m⁻² d⁻¹ (range: 8–224 mmol m⁻² d⁻¹) and 44 mmol m⁻² d⁻¹ (range: 4–156 mmol m⁻² d⁻¹) for air-exposed sediments (Table 6.4). The variability in fluxes among study sites is undoubtedly a valid indication of regional environmental differences. However, the quite inconsistent differences between inundated and air-exposed rates must partly be caused by the applied methodological approach. Most of the reported CO₂ fluxes are probably underestimated, particularly during air exposure because measurements are typically performed on bare sediment away from trees and burrows. Air-exposed pneumatophores and open crab burrows considerably increase CO₂ release by efficient translocation of CO₂ gas from deeper sediments. For example, measurements of CO₂ efflux in a Tanzanian mangrove forest revealed that 100 pneumatophores per m² of the mangrove species *Sonneratia alba* and *Avicennia marina* released about 170 and 60 mmol CO₂ d⁻¹, respectively, whereas 100 crab burrows (*Uca* spp.) per m² released about 90 mmol CO₂ d⁻¹ (Kristensen et al. 2008b). However, the contribution of biogenic structures to CO₂ exchange may vary among mangrove ecotypes and biogeographical regions, depending on mangrove species composition as well as the abundance of both trees and burrowing crabs (see Sect. 6.3.3; Araújo et al. 2012). Future studies on sediment metabolism in mangrove environments, therefore, need to incorporate the role of aerial roots and crab burrows when quantifying sediment CO₂ exchange and estimating reliable whole-forest C budgets (Rivera-Monroy et al. 2013; Troxler et al. 2015).

Microbial electron acceptor utilization in mangrove sediments follows the same energy yield sequence observed in other marine sediments: O₂, Mn⁴⁺, NO₃⁻, Fe³⁺, and SO₄²⁻ (Kristensen et al. 2000; Alongi et al. 2005b). Aerobic microorganisms have the enzymatic capacity for complete oxidation of organic C to CO₂ using oxygen as electron acceptor (Canfield et al. 2005). In contrast, anaerobic heterotrophic processes occur stepwise involving several competitive respiration pathways (Mn respiration, denitrification, Fe respiration, and sulfate reduction) (Canfield et al. 2005). However, the bioavailability of organic macromolecules requires the prior intervention of fermenting microorganisms to generate low molecular organic substrates (e.g. lactate, butyrate, propionate, and acetate) that allow uptake and metabolism by anaerobic respiring microorganisms (Valdemarsen and Kristensen 2010). The specific role of each respiration process depends on the environmental setting

Table 6.4 O₂ and CO₂ exchange by exposed (air) and inundated (water) mangrove sediments in various biogeographical regions. Values in parentheses indicate \pm SE ($n = 3-4$). Locations are within forested areas in the mid- to low-intertidal zone. The forests are older than 10 years since the last clearing. The dominant tree species and the season are indicated. The contribution of sulfate reduction and iron reduction to the daily integrated carbon dioxide efflux is given in percent

Location	Dominant tree	Season	O ₂ air mmol m ⁻² d ⁻¹	O ₂ water	CO ₂ air	CO ₂ water	SRR %	FeR %	Salinity		Temp ^b °C	Ref
IWP: West Pacific												
Hinchinbrook, Australia	<i>R. stylosa</i>	Dry	–	43 (14)	–	21 (13)	79	0 ^a	31		9–24	1
Hinchinbrook, Australia	<i>R. stylosa</i>	Wet	18 (5)	–	12 (6)	12 (9)	100	0 ^a	24		27–36	1
Port Hedland; Australia	<i>R. stylosa</i>	Dry	16 (5)	18 (6)	14 (5)	27 (25)	100	0 ^a	43		21–33	2
Port Hedland; Australia	<i>A. marina</i>	Dry	14 (7)	33 (21)	15 (3)	8 (3)	94	0.1 ^a	51		22–32	2
Dampier, Australia	<i>R. stylosa</i>	Dry	24 (2)	38 (15)	36 (3)	25 (7)	90	0 ^a	50–53		24–29	2
Dampier, Australia	<i>A. marina</i>	Dry	12 (1)	39 (15)	4 (0)	20 (4)	58	0 ^a	44–54		23–30	2
Bay of Rest, Australia	<i>R. stylosa</i>	Dry	18 (5)	17 (8)	25 (12)	44 (7)	100	0.1 ^a	42–50		22–28	2
Mangrove Bay, Australia	<i>A. marina</i>	Dry	14 (5)	12 (5)	26 (7)	30 (11)	56	0 ^a	38–45		20–23	2
Haughton, Australia	<i>A. marina</i>	Dry	49 (7)	14 (2)	36 (5)	47 (5)	44	37	35		25–31	3
IWP: SE Asia												
Ao Nam Bor, Thailand	<i>R. apiculata</i>	Dry	–	45 (2)	–	70 (10)	100	–	34		29	4
Ao Nam Bor, Thailand	<i>R. apiculata</i>	Dry	35 (2)	19 (2)	–	35 (5)	85	–	34		29	5
Bangrong, Thailand	<i>R. mucronata</i>	Dry	46 (8)	21 (2)	–	70 (2)	18	–	35		29	6
Bangrong, Thailand	<i>R. mucronata</i>	Wet	29 (2)	24 (2)	–	96 (27)	20	–	35		29	6
Bangrong, Thailand	<i>R. mucronata</i>	Dry	–	15 (1)	–	43 (4)	19	79	35		29	7
Bangrong, Thailand	<i>R. mucronata</i>	Wet	–	24 (2)	–	49 (8)	19	79	35		29	7
Khlong Sawi, Thailand	<i>R. apiculata</i>	Dry	45 (17)	28 (2)	17 (4)	26 (26)	59	0 ^a	8–10		~30	8
Khlong Sawi, Thailand	<i>R. apiculata</i>	Wet	9 (79)	24 (5)	19 (7)	21 (14)	100	0 ^a	1–2		~30	8
Timor Leste	<i>R. apiculata</i>	Wet	16 (6)	69 (7)	–	81 (13)	85	–	20		~30	9
Timor Leste	<i>R. mucronata</i>	Dry	28 (7)	37 (6)	–	61 (10)	100	–	44		~30	9

(continued)

Table 6.4 (continued)

Location	Dominant tree	Season	O ₂ air mmol m ⁻² d ⁻¹	O ₂ water	CO ₂ air	CO ₂ water	SRR %	FeR %	Temp ^b		Ref
									Salinity	°C	
Timor Leste	<i>S. alba</i>	Dry	19 (10)	15 (39)	–	224 (8)	97	–	35	~30	9
Hurun Bay, Indonesia	<i>R. stylosa</i>	Dry	29 (24)	38 (15)	23 (9)	34 (2)	66	0 ^a	–	~30	10
Hurun Bay, Indonesia	<i>R. stylosa</i>	Wet	203 (19)	39 (3)	26 (6)	45 (6)	77	0 ^a	–	~30	10
Matang, Malaysia	<i>R. apiculata</i>	Dry	15 (4)	–	17 (4)	–	95	–	24	28–31	11
Matang, Malaysia	<i>R. apiculata</i>	Wet	58 (34)	13 (6)	114 (44)	11 (15)	63	11	–	~30	12
Mekong Delta, Vietnam	<i>R. apiculata</i>	Dry	55 (18)	–	53 (25)	–	5	0 ^a	14	29–33	13
Mekong Delta, Vietnam	<i>R. apiculata</i>	Wet	13 (2)	–	80 (16)	28 (8)	48	0 ^a	14	29–33	13
Jiulongjiang, China	<i>K. candell</i>	Dry	83 (13)	–	40 (14)	–	100	0 ^a	17	28	14
IWP: S Asia											
Indus delta, Pakistan	<i>A. marina</i>	Dry	45 (9)	17 (1)	–	50 (10)	64	–	30	30	15
Pichavaram, India	<i>A. marina</i>	Dry	–	80 (16)	–	74 (13)	85	1 ^a	72	32	16
Pichavaram, India	<i>A. marina</i>	Wet	–	59 (4)	–	196 (38)	85	–	63	24	16
Pichavaram, India	<i>R. apiculata</i>	Dry	–	58 (3)	–	165 (11)	65	3 ^a	45	32	16
Pichavaram, India	<i>R. apiculata</i>	Wet	–	66 (5)	–	214 (18)	65	–	39	24	16
IWP: East Africa											
Mtoni, Tanzania	<i>S. alba</i>	Dry	45 (13)	32 (5)	88 (3)	57 (6)	12	77	34	28	5
Ras Dege, Tanzania	<i>R. mucronata</i>	Dry	55 (9)	54 (12)	69 (7)	88 (8)	46	37	37	28	5
AEP: America											
Cananea, Brazil	<i>L. ramososa</i>	Dry	–	30 (5)	156 (17)	15 (6)	–	–	23	28–30	17

(1) Alongi et al. (1999); (2) Alongi et al. (2000a); (3) Kristensen and Alongi (2006); (4) Kristensen et al. (1991); (5) Kristensen et al. (1994); (6) Holmer et al. (1999); (7) Kristensen et al. (2000); (8) Alongi et al. (2001); (9) Alongi et al. (2012); (10) Alongi et al. (2008); (11) Alongi et al. (1998); (12) Alongi et al. (2004); (13) Alongi et al. (2000b); (14) Alongi et al. (2005a); (15) Kristensen et al. (1992); (16) Alongi et al. (2005b); (17) Kristensen et al. (2011); (18) Quintana et al. (unpublished)

^aIron reduction determined from accumulation of dissolved Fe²⁺

^bWater temperature for inundated and sediment temperature for air-exposed measurements

(e.g., salinity, hydroperiod), biota composition (e.g., plant and crab species), and biogeographical factors (e.g., temperature, precipitation) at the local scale. Aerobic degradation of labile materials near the mangrove sediment surface is usually so rapid that O_2 rarely penetrates more than 2 mm into the sediment (Kristensen et al. 1994). Most of the sediment, therefore, remains largely anoxic, except for translocation of oxygen deep into the sediment through a network of roots and infauna burrows (Kristensen and Alongi 2006).

Aerobic respiration and anaerobic sulfate reduction are usually considered the most important C oxidation pathways in mangrove sediments, with a typical share of 30–50% each (e.g. Alongi et al. 2000a; Kristensen et al. 2011). Other metabolic pathways such as denitrification, Mn, and Fe respiration have traditionally been considered unimportant for the C cycling of old-growth forests due to limited availability of the electron acceptors NO_3^- , Mn(IV), and Fe(III) (e.g., Rivera-Monroy and Twilley 1996; Alongi et al. 2000a; Kristensen et al. 2000). Yet, recent evidence suggests that the role of Fe respiration may be comparable to or higher than that of sulfate reduction in Fe-rich mangrove sediments (Fig. 6.4; Kristensen et al. 2000; Kristensen and Alongi 2006; Kristensen et al. 2011). A critical consideration when assessing the relative role of microbial Fe reduction is related to how this process is measured. Most studies use anaerobic sediment incubations to provide reliable measures of solid-phase Fe reduction (Kristensen and Alongi 2006). However, some studies have only included dissolved Fe^{2+} accumulation (e.g. Alongi et al. 2000a), which greatly underestimates actual rates of Fe reduction. The drawback of this approach is that most Fe^{2+} produced from Fe reduction will rapidly precipitate with sulfide, carbonates, and phosphates or be chelated into sheet silicates and organic matrices (Thamdrup 2000). Instead, it is recommended that reactive solid phase Fe(III) and Fe(II) are extracted over time with a sufficiently strong extractant (e.g., 0.5 M HCl, Lovley and Phillips 1987). Using this method, the decrease in extracted Fe(III) and corresponding increase in extracted Fe(II) provide a reliable measure of Fe reduction (e.g., Kristensen and Alongi 2006). This approach to measure Fe reduction has been applied in some mangrove settings (Table 6.4) and other coastal sediments (e.g., saltmarshes, Kostka et al. 2002; Gribsholt et al. 2003).

The rates of microbial C oxidation and partitioning of electron acceptors within mangrove sediments are also dependent on other factors. These include forest age, species diversity, forest density, root physiological activity, extent of water logging and flooding duration, and the intensity of faunal burrowing activities. For example, sulfate reduction accounts for less of the total sediment respiration in young (i.e., 20–30%) than old (i.e., >50%) *Avicennia marina* and *Rhizophora apiculata* forests (Alongi et al. 1998, 2000b). Similarly, aerobic respiration usually dominates in permeable sandy sediments under young *Rhizophora* stands characterized by low plant biomass and high exposure to tidal forcing. Conversely, in older forests where iron reduction and sulfate reduction are the dominant respiration processes, most of the oxygen uptake is driven by oxidation of reduced metabolites (e.g., HS^- and Fe^{2+}) diffusing from deeper sediment layers (Canfield et al. 2005; Kristensen et al. 2011). Furthermore, the impact of water logging is evident in regions with distinct dry and

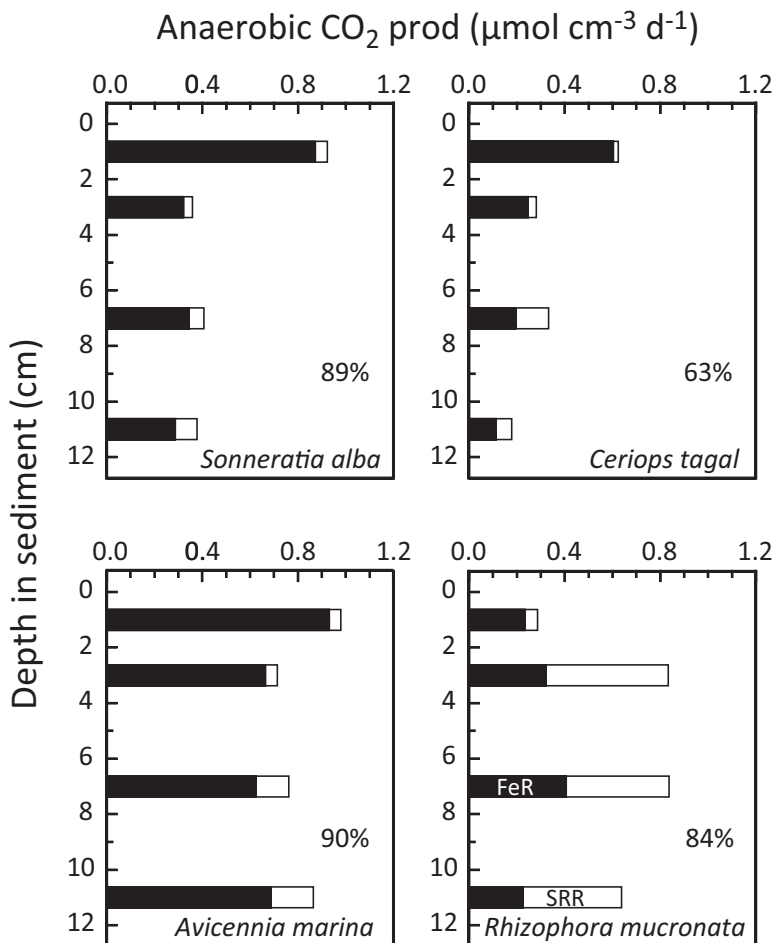


Fig. 6.4 Partitioning of anaerobic CO₂ production into Fe reduction (FeR) and sulfate reduction (SRR) in sediments vegetated by four mangrove species. Results are from two Tanzanian mangrove forests. The percentages given in the figure indicated how much FeR + SRR accounts for of the total C-oxidation in the sediments (Modified from Kristensen et al. 2011)

wet seasons. When the water table is low during the dry season, oxygen penetrates deep into the sediment through gas-filled crab burrows and cracks, which enhances the oxidizing effect and promotes oxidation of organic C via denitrification and Fe reduction. In contrast, prolonged flooding during the rainy season prevents transport of oxygen into the sediment and sulfate reduction becomes the dominant pathway (Clark et al. 1998; Marchand et al. 2004).

The least energy-yielding step in the sedimentary metabolic pathway of all aquatic environments is methanogenesis. This process is controlled by the organic content of the sediment, oxygen concentrations, temperature, rainfall, substrate acidity, and the presence of inhibitors like sulfide (Livesley and Andrusiak 2012;

Dutta et al. 2013; Konnerup et al. 2014). The formation of CH_4 usually occurs deep in sediments where sulfate supplies are exhausted. Methanogenesis has traditionally been considered negligible in mangrove sediments due to the competitive dominance of sulfate reduction (Livesley and Andrusiak 2012; Nóbrega et al. 2016). Yet, recent discoveries of high numbers of active methanogenic archaea in mangrove sediments have challenged this opinion (Lyimo et al. 2002, 2009). For example, Marinho et al. (2012) found four to five times higher methanogenesis in sediment vegetated by *Rhizophora mangle* than in adjacent seagrass beds and unvegetated subtidal marine sediments. In addition, it was demonstrated that otherwise competitive sulfate-reducing and methanogenic bacteria can coexist in mangrove sediments with ample organic matter supplies (Lyimo et al. 2009; Otero et al. 2014; Chauhan et al. 2015). High rates of methanogenesis can also occur in mangrove environments influenced by freshwater (e.g., rivers, groundwater and precipitation) when sulfate reduction is hampered due to sulfate dilution (Lu et al. 1999; Maher et al. 2015).

6.3.2 *The Importance of Nitrogen and Phosphorus Nutrients*

Nitrogen (N) and phosphorus (P) are critical nutrients that regulate the magnitude and spatial distribution of mangrove forest productivity and structural properties (Lovelock et al. 2009; Feller et al. 2010; Reef et al. 2010; Dangremond and Feller 2014). Although N transformations are generally slow in mangrove wetlands, the actual rates vary among mangrove ecotypes and depend strongly on local (e.g., nutrient gradients, salinity), regional (e.g., geomorphology), and anthropogenic impacts (Alongi 2009; Kristensen et al. 2000; Keuskamp et al. 2015). Generation of newly available N by N-fixation ($\text{N}_2 \rightarrow \text{NH}_3$) and loss of available N through denitrification ($\text{NO}_3^- \rightarrow \text{N}_2$) occur, but to a much lower extent than in other estuarine environments (Twilley and Rivera-Monroy 2009). Given the low and almost similar rates of denitrification and N-fixation (Table 6.5), recycling through mineralization is probably the source of most inorganic N for primary producers in mangrove forests (Feller et al. 2003; Alongi 2011), except when there are significant anthropogenic sources. In fact, eutrophication (effluents from, e.g., aquaculture and human developments) has in recent years significantly changed the nutrient balance and thus impacted biogeochemical cycles and productivity of many mangrove environments (Alongi 2009).

Denitrification in mangrove sediments is primarily controlled by the supply of the electron acceptor nitrate (NO_3^-) and electron donors in the form of labile organic matter, and a number of secondary factors including the presence of macrofauna, macrophytes, benthic microalgae, H_2S , and FeS as mentioned earlier (Sect. 6.3.1). Although the C and N cycles in this way are coupled in mangrove wetlands, NO_3^- removal via denitrification can limit the production of organic matter (Rivera-Monroy et al. 2010). This may under certain conditions be counteracted by dissimilatory nitrate reduction to ammonium (DNRA) that effectively conserves

Table 6.5 Mangrove sediment nitrogen fixation and denitrification at sites from the IWP and the AEP

Region	Site	Mangrove type	Vegetation	N fixation	Denitrification	Ref
				$\mu\text{mol m}^{-2} \text{h}^{-1}$	$\mu\text{mol m}^{-2} \text{h}^{-1}$	
IWP	Makham Bay (Thailand)	Mid-intertidal	<i>Rhizophora apiculata</i>	12	2	1
	Sawi Bay (Thailand)	Managed mid- and high-intertidal	<i>Avicennia alba</i> <i>Ceriops decandra</i> <i>Rhizophora apiculata</i>	0–24	0–160	2
	Mekong Delta (Vietnam)	Managed high-intertidal	<i>Rhizophora apiculata</i>	10–59	0–92	3
	Matang Reserve (Malaysia)	Managed mid-intertidal	<i>Avicennia marina</i> <i>Rhizophora apiculata</i>	0–125	16–458	4
	Jiulongjiang Estuary (China)	Managed low-, mid- and high-intertidal	<i>Kandelia candel</i>	0–2	46–158	5
AEP	Joyuda Lagoon (Puerto Rico)	Fringe	No specified	13–31	1–161	6
	Oyster Bay (Jamaica)	Fringe center, rear	<i>Avicennia germinans</i> <i>Rhizophora mangle</i>	0–100	0–83	7
	Twin Cays (Belize)	Fringe transition, dwarf	<i>Avicennia germinans</i> <i>Laguncularia racemosa</i> <i>Rhizophora mangle</i>	0–17	0–8	8

1) Kristensen et al. (1998); 2) Alongi et al. (2002); 3) Alongi et al. (2000b); 4) Alongi et al. (2004); 5) Alongi et al. (2005a); 6) Morell and Corredor (1993); 7) Nedwell et al. (1994); 8) Lee and Joye (2006)

and recirculates N. Thus, the occurrence of DNRA in mangrove forests has important implications for maintaining N levels and sustaining primary productivity (Fernandes et al. 2012a). However, only few studies have measured DNRA in mangrove wetlands, and it is not yet clear how this pathway contributes to the overall N budgets (Giblin et al. 2013; Molnar et al. 2013). Also, the anaerobic conversion of NO_2^- and NH_4^+ to N_2 (anammox), which in conjunction with denitrification represent a sink of N, requires further study. Estimates of anammox in mangrove

sediments are scarce (Li and Gu 2013; Wang et al. 2013), but two experimental studies have revealed rates that account for <10% of total N_2 production (Meyer et al. 2005; Fernandes et al. 2012b). Work in other coastal ecosystems suggests that denitrification is also much higher than anammox, particularly in sediments receiving a high load of reactive organic matter (Dalsgaard et al. 2005; Fernandes et al. 2012b).

P availability within mangrove wetlands is, in contrast to N, strongly dependent on the dynamic interactions of P with Fe and S cycling (Nóbrega et al. 2014; Deborde et al. 2015). For example, phosphate (PO_4^{3-}) is readily adsorbed and retained by Fe(III) oxyhydroxides in near-surface sediments, around crab burrows and around rhizospheres, thus limiting plant production (Clark et al. 1998). However, the adsorbed PO_4^{3-} can be released back to dissolved form and be available again for primary producers when Fe(III) oxyhydroxides are reduced in anoxic sediment. This oxidation–reduction cycle depends on either transport of particles between oxic and anoxic zones or is due to temporal expansion and contraction of oxic zones. Crabs typically mediate the former mechanism when they rework surface and subsurface sediments, whereas the latter mechanism is primarily due to tidal and seasonal changes in redox conditions.

The use of fertilization experiments under field conditions has advanced our understanding of the complex interaction and relative role of N and P availability for mangrove structural development and productivity (Lovelock et al. 2006; Feller et al. 2007; Simpson et al. 2013). The response of ecological processes to nutrient enrichment depends on site characteristics, species composition and dominance, and the nature of nutrient limitation (Feller et al. 2010; Reef et al. 2010). For example, the resorption of P from senescent tissue by *R. mangle* is under P-limited conditions much higher ($\approx 70\%$) than that for N ($\approx 45\%$). N fertilization does not change this pattern, but P fertilization decreases P resorption (<50%), whereas N resorption ($\approx 70\%$) increases (Feller et al. 1999). Scrub mangrove forests (e.g., *R. mangle* and *A. germinans*) growing in P limited carbonate sediments always respond to P fertilization, while surrounding fringing mangroves (e.g., *R. mangle*) respond mostly to N fertilization, and those exposed to intermediate tidal influence respond to both N and P fertilization (Lovelock et al. 2006) as hydroperiod interacts with nutrient availability (Twilley and Rivera-Monroy 2009). The response of mangrove wetlands to nutrient additions appears to be similar in both the IWP and AEP biogeographical region. Large-scale experimental work on N and P limitation was initially performed in the Caribbean region (Belize), Central America (Panama), and North America (Florida), but has been expanded to areas in Australia and New Zealand, particularly when assessing effects of nutrient availability on C sequestration (Alongi 2011). For example, large-scale comparisons (Caribbean, Australia, New Zealand) revealed that P is less limiting to plant metabolism at higher than lower latitudes (Lovelock et al. 2007). Although this and other large-scale latitudinal comparisons to evaluate differences in N and P responses between the IWP and AEP have been undertaken, there are still large gaps in the overall conceptual framework for mangrove wetlands.

Table 6.6 Burrow and disturbance depths by various invertebrate and vertebrate taxa in mangrove environments from different geographical regions

Geographical region	Taxon (genus)	Burrow/Disturbance		Ref
		Depth (cm)	Density ^a (m ⁻²)	
<i>Indo-west-Pacific</i>				
	Crab			
	<i>Mictyris</i>	~10–30	226	1–2
	<i>Uca</i>	~10–100	~100	3–4
	<i>Ocypode</i>	~16–40	~1	5–6
	<i>Sesarma</i>	~100–120	~12	7
	<i>Helice</i>	~35	36	8
	<i>Neopisesarma</i>	~80	0.2	9–10
	<i>Chiromantes</i>	~10	18	11–12
	Amphipod			
	<i>Victoriopisa</i>	~10	3500	13
	Callinassid, penaeid, alpheid shrimp			
	<i>Trypaea</i>	~120	200	14
	<i>Metapenaeus</i>	~1		15–16
	<i>Alpheus</i>	~50	56	17
	Thalassinid lobster			
	<i>Thalassina</i>	~250	0.5	18
	Sipunculid worm			
	<i>Siphonosoma</i>	~50		19
	Bivalve			
	<i>Geloina</i>	Upper sediment	40 ^b	20
	Teleost fish			
	<i>Periophthalmus</i>	>10		21
	Elasmobranch fish (Ray)			
	<i>Himantura</i>	~5		22
<i>Atlantic-east-Pacific</i>				
	Crab			
	<i>Uca</i>	~40	~70	23 ^c
	<i>Ucides</i>	~200	~3	24
	<i>Ocypode</i>		~0.7	25 42–43
	Penaeid shrimp			
	<i>Penaeus</i>	~5		26
	Thalassinid lobster			
	<i>Thalassina</i>	~250	0.5	27 ^c
	Sipunculid worm			
	<i>Sipunculus</i>	Upper sediment	~240	28
	Bivalve			
	<i>Mytella</i>	Upper sediment	>20 ^b	29

(continued)

Table 6.6 (continued)

Geographical region	Taxon (genus)	Burrow/Disturbance	Density ^a (m ⁻²)	Ref
		Depth (cm)		
	Teleost fish			
	<i>Lutjanus</i>	Upper sediment		30
	Elasmobranch fish (Ray)			
	<i>Dasyatis</i>	~20	~0.6	31

[1] Rossi and Chapman (2003); [2] Shih (1995); [3] Gillikin (2000); [4] Qureshi and Saher (2012); [5] Chan et al. (2006); [6] Dubey et al. (2013); [7] Stieglitz et al. (2000); [8] Mchenga et al. (2007); [9] Thongtham and Kristensen (2005); [10] Kristensen (2008); [11] Gillikin and Kamanu (2005); [12] Xiong et al. (2010); [13] Dunn et al. (2009); [14] Kerr (2001); [15] Joshi et al. (1979); [16] Primavera and Lebata (1995); [17] Dworshak and Pervesler (2002); [18] Kartika and Patria (2012); [19] Zhou and Li (1990); [20] Morton (1976); [21] Clayton and Snowden (2000); [22] O'Shea et al. (2012); [23] Kristensen (2008); [24] Pülmanns et al. (2014); [25] da Silva Castiglioni and Negreiros-Fransozo (2005); [26] Fuss (1964); [27] Dworshak et al. (2012); [28] Rice et al. (1995); [29] Bacon (1975); [30] Vasleta et al. (2012); [31] Cross and Curran (2000)

^aExample density of burrow/disturbance

^bRepresents individuals in lieu of burrow density. Upper sediments represent bioturbation predominantly in shallow surface sediments with no documented depth (cm) from literature

^cIncludes references therein

6.3.3 The Impact of Benthic Fauna

A broad diversity of benthic animals lives or feeds in and on mangrove sediments. Most of these are invertebrates, including crustaceans, polychaetes, sipunculids, and molluscs, whereas teleost fish and rays may be present occasionally (Table 6.6). Brachyuran crabs are particularly dominant because their hard and compact carapace provides good locomotion ability and protection in the harsh mangrove environment, offering evolutionary advantage over other invertebrates (Krobicki and Zatoń 2008). However, the diversity of brachyuran crabs associated with mangroves varies considerably; from over a hundred species in Southeast Asia to only a few dozen species in East African and the Americas (Gillikin and Schubart 2004; Lee 2008). Nevertheless, crabs (especially Grapsoidea and Ocypodoidea) usually dominate both in numbers and biomass in mangrove ecosystems all over the world (Jones 1984).

As expected from their prominent distribution and occurrence, these decapods are key species for regulating and controlling mangrove ecological and biogeochemical functioning. Crabs are known to reduce leaf litter export to adjacent open waters by burial and consumption of leaves (Table 6.7). Litter handled by crabs eventually enters the microbial food chain either in the form of uneaten remains and

Table 6.7 Examples from around the world of removal (litter taken into burrows) and consumption of leaf litter by leaf-eating mangrove crabs

Species	Site	Rate of consumption or removal (% of total litter fall)	Ref
Sesarmid crabs	North Queensland, Australia. High intertidal	Removal: <i>C. tagal</i> forest: 71%, <i>B. exaristata</i> forest: 79%, <i>A. marina</i> forest: 33%	1
<i>Neoepisesarma versicolor</i>	Bangrong, Phuket, Thailand. Mid intertidal	<i>R. apiculata</i> forest: Removal: 87% Consumption: 65%	2
<i>Sesarma meinerti</i>	Mgazana river estuary South Africa. High intertidal	Consumption: <i>A. marina</i> forest: 44%	3
<i>Sesarma meinerti</i>	South Africa. High intertidal	<i>Bruguiera gymnorrhiza</i> forest Removal: 99%; Consumption: 64%	4
<i>Ucides cordatus</i>	Pará, North Brazil. High intertidal	Consumption: <i>R. mangle</i> forest: 81%	5

(1) Robertson and Daniel (1989); (2) Thongtham et al. (2008); (3) Emmerson and McGwynne (1992); (4) Steinke et al. (1993); (5) Nordhaus et al. (2006)

fecal material buried in the sediment or as crab carcasses (Giddins et al. 1986; Robertson 1986; Lee 1997, Twilley et al. 1997) and therefore contributes to nutrient recycling within mangrove forests (Nordhaus et al. 2006). Maceration of plant material during ingestion and contact with digestive enzymes in the gut appears to facilitate microbial attack on insoluble carbohydrates. The rate of microbial decay of recalcitrant leaf litter in sediments is therefore facilitated after passage through crab guts (Kristensen and Pilgaard 2001). In contrast, the intact plant material that escapes crab handling is readily exported by tides and thus lost from the mangrove ecosystem.

A striking performance of bioturbating animals in mangrove ecosystems is the formation of deep and branched burrows and reworking of sediment particles. The animals involved are primarily crabs, but other crustaceans (amphipods, alpheid shrimp, and thalassinid lobsters) and sipunculids also form burrows, whereas mytilid bivalves and fish produce less structured disturbances of surface sediments (Table 6.6). Although the diversity of bioturbating animals in general is greater in IWP than AEP mangrove forests, the functional types of bioturbation are similar, as are the typical densities of burrows (Table 6.6).

As mentioned in Sect. 6.3.3., bioturbation by crabs has a profound effect on mangrove sediments by constantly disrupting the vertical redox zonation and increasing the complexity of the sediment system (Kristensen 2008). Functionally, bioturbation regulates and controls biogeochemical processes such as organic C oxidation and benthic nutrient fluxes (Table 6.8). Sesarmid and ocypodid crabs are the most prominent taxa affecting biogeochemical transformations in mangrove

Table 6.8 Effects of bioturbating crabs on biogeochemical parameters relevant to mangrove sediments (↑ represents increase and ↓ represents decrease of analyte concentration/process)

Geographical region ^a	Bioturbator	Analyte concentration					Process					Ref
		<i>Chl-a</i>	<i>Org C</i> ^b	NH_4^+	S^{2-}	<i>Eh</i>	<i>Salinity</i>	SO_4^{2-} red	CO_2 efflux	<i>Prod</i>	<i>Resp</i>	
Indo-West Pacific	<i>Micetyris longicarpus</i>	↓		↓					↑	↓	↓	1
	<i>Uca vocans</i>	↓	↓	↓					↓	↓	↓	2
	<i>Sesarma messa</i>						↓					3
	<i>Sesarma messa</i>		↑									4
	<i>Sesarma messa</i> <i>Sesarma semperi</i> <i>longicristatum</i>			↓								5
Indo-Malesia	<i>Helice formosensis</i>					↑						6
	<i>Helice formosensis</i>			↑↑								7
	<i>Uca</i> spp.										↑	8
	<i>Neopisesarma versicolor</i>						↓					9
	<i>Uca</i> spp., <i>Chiromantes</i> spp., <i>Perisesarma</i> spp. <i>Neosarmatium africanum</i>		↑									10
	<i>Uca annulipes</i> , <i>Uca inversa</i>								↑			11
Atlantic East Pacific												
East America	<i>Uca marcoani</i> , <i>Ucides cordatus</i>					↑						12
	<i>Uca</i> spp.						↓					13

(continued)

Table 6.8 (continued)

Geographical region ^a	Bioturbator	Analyte concentration					Process					Ref	
		<i>Chl-a</i>	<i>Org C^b</i>	<i>NH₄⁺</i>	<i>S²⁻</i>	<i>Eh</i>	<i>Salinity</i>	<i>SO₄²⁻ red</i>	<i>CO₂ efflux</i>	<i>Prod</i>	<i>Resp</i>		
	<i>Uca uruguayensis</i> ,		↓										14
	<i>Uca rapax</i>												
	<i>Ucides cordatus</i>		↑										15

[1] Webb and Eyre (2004); [2] Kristensen and Alongi (2006); [3] Stieglitz et al. (2000); [4] Robertson (1986); [5] Smith et al. (1991); [6] Mchenga et al. (2007); [7] Mchenga and Tsuchiya (2008); [8] Nielsen et al. (2003); [9] Thongtham and Kristensen (2003); [10] Andreetta et al. (2014); [11] Penha-Lopes et al. (2010); [12] Araújo et al. (2012); [13] Ferreira et al. (2007a); [14] Sayão-Aguiar et al. (2012); [15] Nordhaus et al. (2006)

^aGeographical regions zoned according to Duke et al. (1998)

^bReported as loss-on-ignition or total organic carbon

ecosystems. Regardless of the species involved and its behavior, bioturbation considerably enhances the transport of O_2 and other electron acceptors to deeper sediment layers and promotes the upward translocation of metabolites (e.g. CO_2) and reduced compounds (i.e. iron sulfides)(Fig. 6.5). Several studies have demonstrated effects of bioturbation on various sediment parameters, including microphytobenthic chlorophyll, C turnover, nutrient (N, P) cycling, and S distribution (Kristensen and Alongi 2006; Bartoli et al. 2009). Some biogeochemical processes are consistently increased or decreased among animal taxa, whereas the impact of others are more genus or species specific, i.e., by shifting the dominance of sulfate reduction to other respiration pathways or vice versa (Alongi et al. 2001; Kristensen 2008). The capacity to promote such biogeochemical shifts depends on crab behavior, such as burrowing and refuge strategies, as well as feeding and mating behavior (Kristensen 2008).

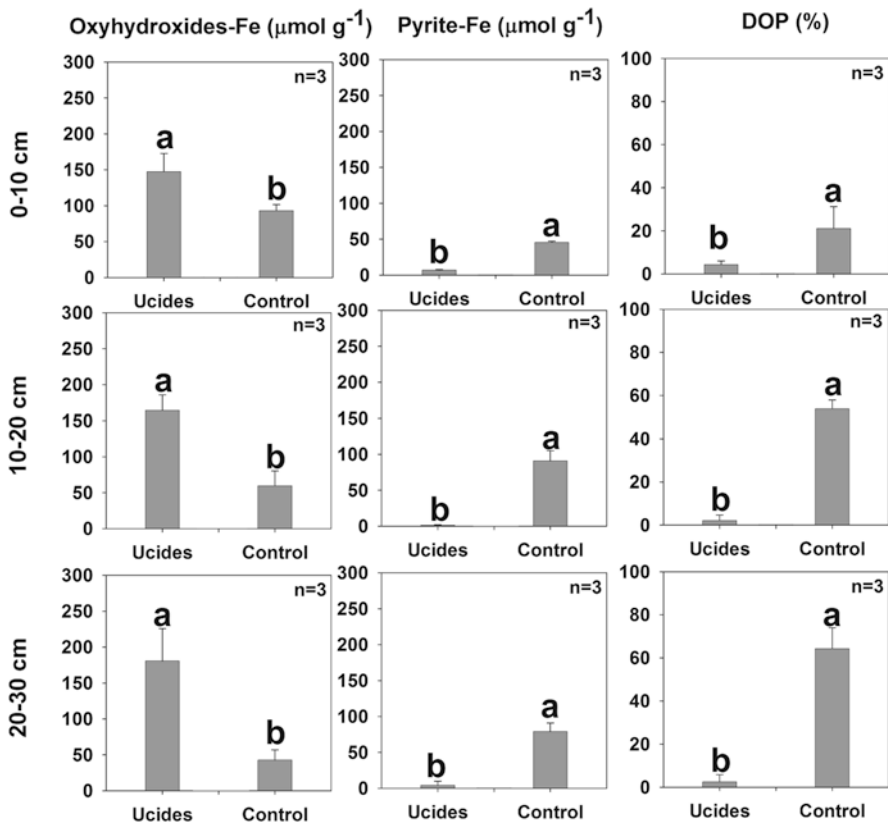


Fig. 6.5 Field exclusion experiment in mangrove forests of NE Brazil. The contribution of oxidized Fe, pyrite Fe, and the degree of iron pyritization (DOP) in different depth layers (mean \pm SD) of sediment taken from plots with and without *Ucides cordatus* is shown. Bars with different letters indicate significant differences at $p < 0.05$ (Modified from Araújo et al. 2012)

Because C accumulation is a key process (and an important Ecosystem Service) in mangrove wetlands, O₂ translocation into deeper layers of the sediment by bioturbation can enhance organic C degradation processes and consequently increase CO₂ emissions to the atmosphere (see Sect. 6.4). Thus, crabs are not only capable of retaining C within mangrove ecosystems through burrowing and mixing of sediment particles, but are also important actors in the opposite process of exporting C by favoring more efficient decomposition pathways and thus boosting CO₂ emissions (Pülmans et al. 2014). This is evident in Tanzanian mangrove forests where crab burrows are responsible for 36–62% of the total CO₂ emission from the sediments (Kristensen et al. 2008b).

6.3.4 *The Importance of Hydroperiod and Hydrology*

Hydrology is recognized by the hydroperiod, which is defined as the depth, duration, and frequency of inundation (Fig. 6.6) (Reddy and Delaune 2008; Twilley and Rivera-Monroy 2009). Mangrove wetland hydroperiod encompasses all aspects of water budgets (rainfall, evaporation, as well as subsurface and surface flow) regardless of the water source (Mazda and Wolanski 2009). In combination with resources (e.g., N, P, light, space) (Tilman 1982) and regulators (e.g., salinity, sulfide, pH, Eh), gradients in hydroperiod control mangrove structural and functional properties (Ellison and Farnsworth 1997; Twilley 1997; Twilley and Rivera-Monroy 2005; Berger et al. 2008). One of the major causes of mangrove mortality and loss at the global scale is the direct and indirect impact of human activities on hydrology, which is perhaps “[...] the single most important determinant of the establishment and maintenance of specific types of wetlands and wetlands processes” (Mitsch and Gosselink 2015). As hydroperiod controls plant growth, it also has a significant role for the availability and concentration of essential elements in mangrove sediments (Twilley and Day 2013; Mitsch and Gosselink 2015). Indeed, studies assessing the impact of hydroperiod include how mangrove species zonation (e.g., Crase et al. 2013), development of sediment physicochemical gradients (i.e., sediment and water quality) (Alongi 2009), and physiological traits of mangrove species (e.g., growth rate, photosynthesis performance, nutrient use efficiency, biomass allocation) and regulator gradients (i.e., salinity) respond to changes in flooding frequency and duration.

As mentioned earlier, there is uncertainty in the magnitude and spatio-temporal variability of biogeochemical transformations in mangrove forests, which in certain cases can be associated with the lack of data on hydrologic parameters (Mazda and Wolanski 2009). For example, mangrove studies assessing the impact of flooding on biogeochemical transformations use water level recorders positioned along tidal creeks at some distance (km) from the study site, whereas other studies rely on data from hydrographic stations installed in nearby ports and coastal cities. Hydrographs or tide tables based on astronomical calculations are then combined with elevation measurements in single points or along transects to produce inundation frequencies (e.g., Mendoza et al. 2012). Few studies have actually deployed water level

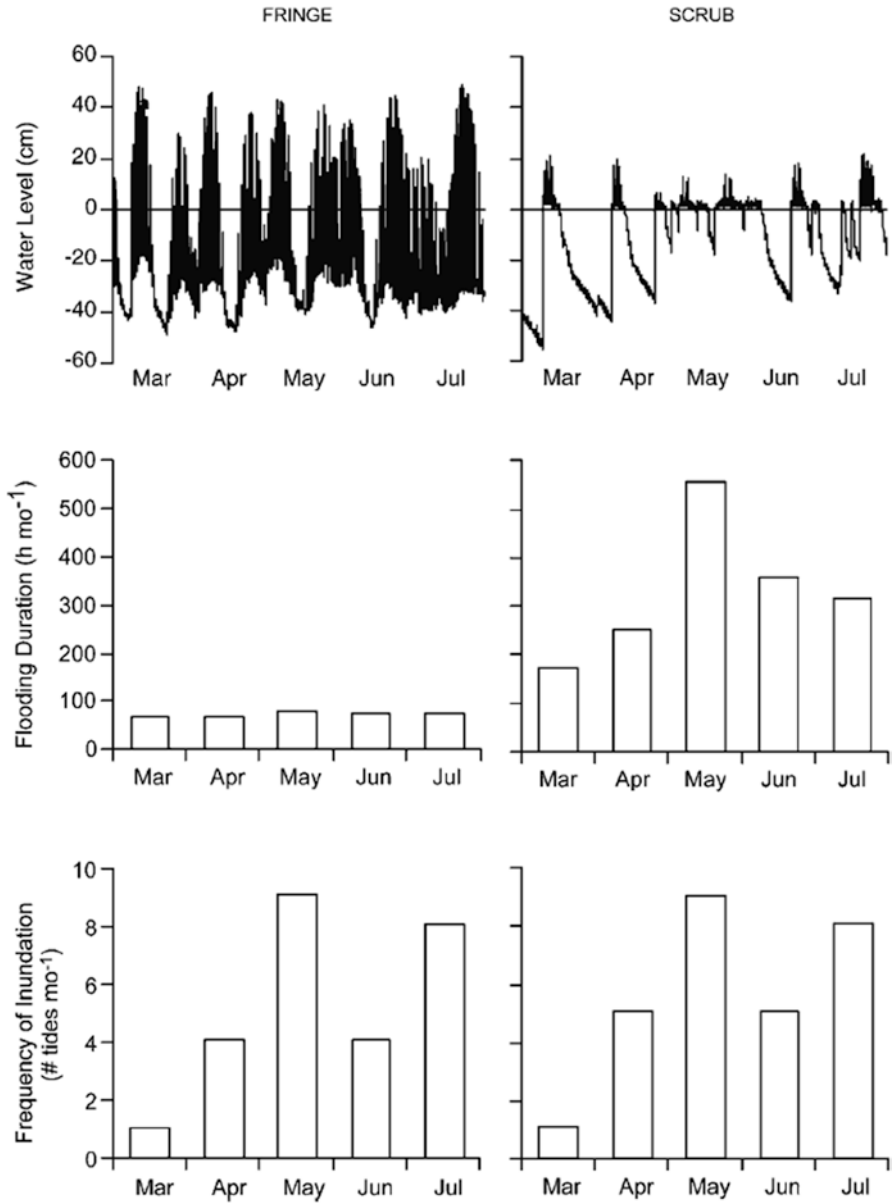


Fig. 6.6 Water level, flooding duration, and frequency of inundation in fringe and scrub mangrove zones of the San Bernardo Estuary, Gulf of Fonseca, Honduras. The zero mark in the upper panel is relative to the ground surface in this site (Modified from Castañeda-Moya et al. 2006)

recorders inside the forest to register long-term flooding frequency and depth of inundation. In fact, modeling of hydrological patterns in estuaries and inside mangrove areas shows distinct differences in tidal patterns and symmetry due to creek geomorphology, local weather, and forest structure (riverine, basin, fringe) (see Chap. 11) (Lugo and Snedaker 1978; Mazda et al. 1995), reinforcing the need to directly measured spatial and temporal variation of hydroperiod parameters at both local and regional scales.

Duration of inundation is critical because it directly controls sediment redox conditions, and thus microbial transformations and exchange processes within the sediment, whereas inundation depth determines the net material exchange (e.g. organic matter and nutrients) between mangrove forests and adjacent coastal waters (Twilley and Rivera-Monroy 2005; Adame and Lovelock 2011). The direct effect of hydroperiod on O₂ diffusion into mangrove substrata is well documented (e.g., Kristensen 2008; Twilley and Rivera-Monroy 2009), but there is still a lack of knowledge directly linking frequency and duration of inundation to biogeochemical transformations such as denitrification, iron reduction, sulfate reduction, and methanogenesis, or even CO₂ and CH₄ fluxes at sediment–air and sediment–water interfaces. These measurements are necessary to evaluate the uncertainty and applicability of fluxes using sediment under laboratory conditions to extrapolate values to larger scales (see Chap. 11).

Among the variables directly measured along with hydroperiod under experimental and field conditions is salinity of overlying water and sediment porewater. Salinity is an excellent proxy of physicochemical status because it integrates a number of factors controlling hydrology and biogeochemistry in coastal regions; from tidal inundation, evapotranspiration, and river discharge to partitioning between iron reduction, sulfate reduction, and methanogenesis in sediments. Salinity is an easy parameter to measure in hydrological studies as reflected by the number of studies relating hydroperiod and salinity patterns in mangrove zonation studies. For example, Crase et al. (2013) showed that the spatial partition of three mangrove species (*Sonneratia alba*, *Rhizophora stylosa*, *Ceriops tagal*) in northern Australia is significantly associated to hydroperiod and porewater salinity. Similarly, Castaneda-Moya et al. (2006) found clear distinctions in the spatial distribution of mangrove ecotypes (fringe vs scrub forests) and species (*Rhizophora mangle* and *Avicennia germinans*) as a result of the interaction between hydroperiod and salinity (Fig. 6.7). In general, porewater salinity is lower in the fringe zone dominated by *Rhizophora* spp. (<40) than in transition (60) and particularly scrub (>70) mangrove zones dominated by *Avicennia* spp. (Castaneda-Moya et al. 2006).

Although analysis of mangrove hydrology has improved (Mazda and Wolanski 2009), there is still a need to identify the mechanisms by which hydroperiod controls sediment biogeochemistry within different mangrove ecotypes (e.g., riverine, fringe, basin) (Lugo and Snedaker 1978; Woodroffe 1992, 2002). In situ and experimental work is needed to assess how horizontal and vertical hydrodynamics, modified by forest tree density or root structure (Mazda et al. 1995, 2005), enhances or limits the relative role of mangroves wetlands as sinks, sources, and/or transformers of biologically important elements (C, N, P, S) in coastal regions with different eogeomorphic characteristics (Woodroffe 2002).

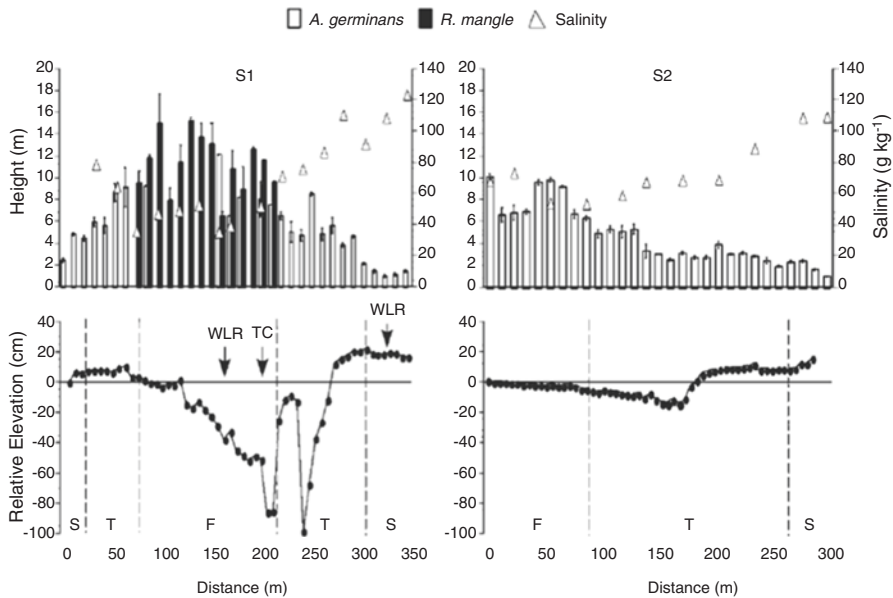


Fig. 6.7 The impact of sediment porewater salinity and relative elevation on the spatial distribution of *Avicennia germinans* and *Rhizophora mangle* at two locations (S1 and S2) in the Gulf of Fonseca, Honduras, Central America. *Upper panel*: tree height and sediment porewater salinity. *Lower panel*: the relative elevation. *Dashed lines* indicate the extent of mangrove zones/ecotypes: (F) fringe, (T) transition, and (S) scrub. *TC* indicates the location of the tidal creek. *WLR* indicates location of water level recorders (Modified from Castañeda-Moya et al. 2006)

6.4 Greenhouse Gas (GHG) Balance of Mangrove Ecosystems

Mangrove wetlands have a potentially high impact on the global C budget because of their high net productivity ($218 \pm 72 \text{ Tg C y}^{-1}$, Bouillon et al. 2008) and C storage capacity ($18\text{--}29 \text{ Tg C y}^{-1}$, Alongi 2012), despite their simple forest structure, low biodiversity, and limited areal cover (less than 150,000 km² worldwide) (Polidoro et al. 2010; Giri et al. 2011). This means that an equivalent of as much as ~10% of the organic C produced in mangrove wetlands escapes export to coastal waters by tidal flushing and pumping, or release to the atmosphere in the form of CO₂. The waterlogged and anoxic mangrove sediments with slow decomposition, therefore, allow a substantial long-term organic C accumulation (Fig. 6.8), and thus function as sinks for atmospheric CO₂ (Donato et al. 2011; Murdiyarso et al. 2015). Accordingly, CO₂ releases at the sediment–air interface in mangrove wetlands are lower than those measured in both temperate and tropical terrestrial environments (Leopold et al. 2015). This is not only true for CO₂ emissions, but also for other GHG such as methane (CH₄) and nitrous oxide (N₂O). However, recent studies report a high variability of GHG emission from mangrove areas depending on their productivity, position in the tidal range, anthropogenic impact and seasons (Livesley

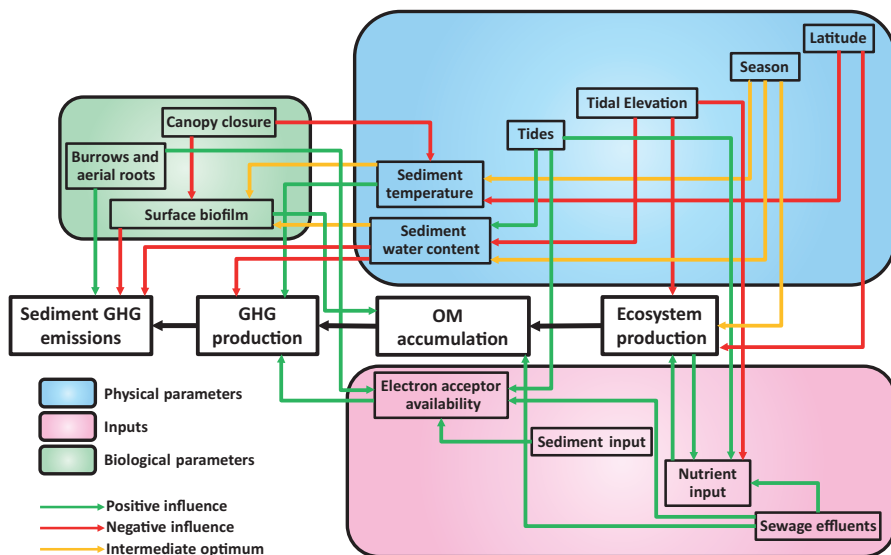


Fig. 6.8 Flow diagram of carbon from fixation of CO_2 by ecosystem production to organic carbon (OC) accumulation, greenhouse gas (GHG) production, and sediment GHG emission. Important controlling factors are indicated, and marked with *green arrows* if they have a positive effect on processes, *red arrows* if they have a negative effect, and *yellow arrows* if they have an intermediate optimum

and Andrusiak 2012; Leopold et al. 2013; Chen et al. 2014; Nóbrega et al. 2016). Thus, it seems, from the studies to date, that particularly mangrove eutrophication caused by discharge of untreated wastewater can substantially enhance GHG production (Fig. 6.8) (Konnerup et al. 2014).

Bouillon et al. (2008) pointed out that the current uncertainty of published mangrove C budgets at the global scale were largely due to lack of reliable sediment-air and water-air CO_2 flux measurements. Several studies have subsequently provided new information about key drivers influencing CO_2 emission at the sediment-air interface (Kristensen et al. 2008b; Chen et al. 2014; Lovelock et al. 2014; Leopold et al. 2015). These studies clearly demonstrate the importance of features such as C stocks, sediment water content, temperature, and crab burrows/pneumatophores density as regulators of CO_2 emission from mangrove sediments (Fig. 6.8). Thus, Lovelock et al. (2014) observed a direct relationship between sediment respiration and aboveground net primary production (a proxy of C accumulation). The role of sediment water content for CO_2 emission is related to the impact of water on transport processes and decomposition efficiency within the sediment. Molecular diffusion is faster in gas than water, and CO_2 fluxes may increase when sediments become partly dry during air exposure (see Sect. 6.3.1), while organic matter mineralization is slow in waterlogged sediment due to the dominance of anaerobic processes (Kristensen et al. 2008a). Consequently, sediment-air CO_2 emissions may decrease under low redox, as observed by the wet conditions during the monsoon season in

India (Chanda et al. 2013). Conversely, CO₂ emission also changes with temperature due to thermal sensitivity of microbial processes. Studies assessing the temperature dependence of CO₂ emission from mangrove sediments reported Q₁₀ values between 2 and 3, which are comparable to other forested ecosystems (Lovelock 2008; Leopold et al. 2015) and marine sediments (Thamdrup et al. 1998). In addition, Leopold et al. (2015) showed that temperature was the main driving factor for seasonal variations of sediment-air CO₂ emissions in *Rhizophora* and *Avicennia* dominated stands in a semi-arid climate. They also suggest that the surface biofilm at sediment surfaces may limit CO₂ efflux towards the atmosphere by forming a protective barrier consisting of extracellular polymeric substances (EPS) and due to microbial assimilation (Fig. 6.8). As mentioned earlier, crab burrows and aerial roots (e.g., pneumatophores) act as efficient conduits that allow the ascent of excess deep CO₂ to the atmosphere (Kristensen et al. 2008b; Troxler et al. 2015). However, due to lack of comparable studies and data on how sediment-air CO₂ fluxes are controlled in various mangrove forest ecotypes, it is presently not possible to perform a thorough analysis of CO₂ emissions among biogeographical regions.

CO₂ release measured across the sediment-water/air interfaces does not represent the total mineralization of organic matter derived from mangrove forests. Part of their net production (e.g. litter) is exported into tidal creeks and the adjacent estuarine and coastal waters through tidal-driven export of particulate materials (Jennerjahn and Ittekkot 2002; Alongi 2014) and dissolved organic C from porewater seepage (Fig. 6.9) (Bouillon et al. 2007; Kristensen et al. 2008a, Maher et al. 2013; Stieglitz et al. 2013). These organic materials may be quickly mineralized in the water column and the generated CO₂ emitted to the atmosphere (Bouillon et al. 2003). As a result, waters surrounding mangrove forests are usually oversaturated in CO₂ (Kone and Borges 2008). This source of CO₂ in tidal creek and estuarine open waters must be considered when assessing C budgets in mangrove ecosystems. Further work is urgently needed to directly measure CO₂ emissions from mangrove waters to the atmosphere, including their seasonal variability from the upper watersheds to the coastal zone (Fig. 6.9).

The largest CO₂ exchange between mangrove forests and the atmosphere is through canopy uptake and release. This exchange has traditionally been derived by extrapolating leaf metabolism measurements and leaf-area index (LAI) data (Alongi 2009). However, the recent implementation of the eddy-covariance (EC) technique in mangrove forests has improved our understanding of the gas exchange between forest canopies and the atmosphere (Fig. 6.9) (Barr et al. 2010, Rivera-Monroy et al. 2013). For example, Barr et al. (2010) used the EC technique in a subtropical region of the AEP to evaluate the seasonality in riverine mangrove forest CO₂ assimilation. They showed that assimilation was highest during the winter dry season due to an increase in diffuse solar irradiance to the forest canopy. Furthermore, net ecosystem exchange (NEE) decreased during low tide under both night and daylight conditions. More recently, Troxler et al. (2015) integrated all components of CO₂ fluxes at the same location to the whole forest scale, and found a larger than expected contribution of the below-canopy respiration components to total forest ecosystem respiration (ER). This underscores the need to improve our understanding of

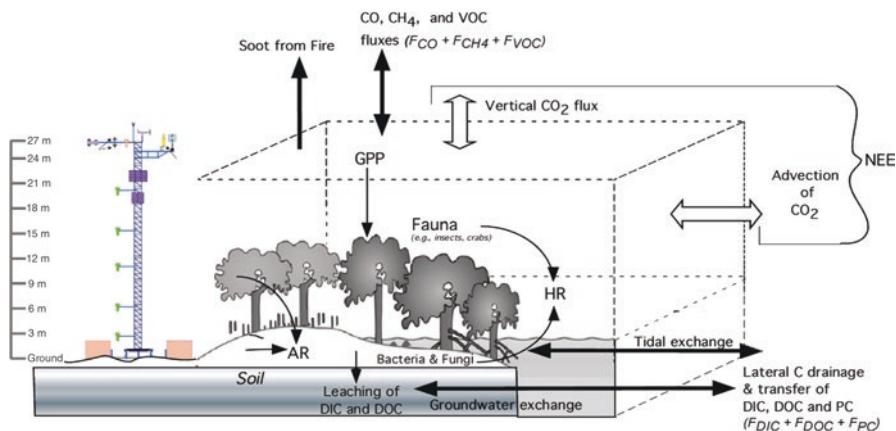


Fig. 6.9 Carbon fluxes identified as the main drivers for net ecosystem C balance (NECB) (solid black arrows) and net ecosystem CO_2 exchange (NEE) obtained with the eddy covariance method (open arrows). The dotted box represents the mangrove forest exchanging C with coastal waters and the atmosphere. The processes contributing to NECB are diffusive and advective exchange of CO_2 (i.e., NEE), CH_4 , CO , volatile organic C (VOC) with the atmosphere (including soot emission during fires), lateral leaching and tidal exchange of dissolved organic C (DOC), dissolved inorganic C (DIC), and particulate C (PC) in mangrove waters. The biological processes regulating net ecosystem production are gross primary production (GPP), autotroph respiration (AR), and heterotroph respiration (HR) (Modified from Chapin et al. 2006; Rivera-Monroy et al. 2013)

below-canopy CO_2 fluxes to elucidate how mangrove C cycling respond to various disturbance events (e.g., hurricanes) and long-term changes (e.g., climate change and sea-level rise). Thus, global mangrove forest C budgets must include both canopy and below-canopy ER at larger geographical scales to fully clarify the role of these forests in mitigating climate change (Rivera-Monroy et al. 2013; Giri et al. 2011).

Methane (CH_4) emissions from mangrove sediments are usually undetectable (Alongi et al. 2000a; Kreuzwieser et al. 2003) or very low (<1% of the total CO_2 emissions; Kristensen et al. 2008b; Nóbrega et al. 2016), mainly because it is oxidized by methanotrophs before reaching the sediment surface (Canfield et al. 2005). Actual methanogenesis within mangrove sediments can be orders of magnitude higher than fluxes measured at the sediment surface (Sotomayor et al. 1994; Giani et al. 1996; Lyimo et al. 2002). Significant CH_4 emissions from mangrove sediments will therefore only occur when environmental conditions (e.g., sediment exposure during low tide) allow rapid transport to the atmosphere. As mentioned earlier in the case of CO_2 flux, crab burrows and aerial roots (e.g. pneumatophores) can also act as efficient conduits for CH_4 emissions. Furthermore, porewater seepage from creek banks during low tide generate a discharge of porewater supersaturated in CH_4 , potentially becoming a source to the atmosphere (Call et al. 2015). Eutrophication can also enhance CH_4 emission as result of large labile OM inputs that increase sediment metabolic activity, leading to near-surface depletion of sulfate and a shift to methanogenesis (Sotomayor et al. 1994; Purvaja and Ramesh 2001).

Nitrous oxide (N_2O) is a potent GHG with a high radiant forcing potential (Lashof and Ahuja 1990). This gas can be produced either by denitrification under anoxic conditions or by nitrification under oxic conditions (Canfield et al. 2005). Mangrove sediments are generally characterized by low levels of porewater NH_4^+ and NO_3^- (Alongi et al. 1998; Deborde et al. 2015), and are considered small N_2O sources to the atmosphere (Chen et al. 2011; Livesley and Andrusiak 2012). N_2O fluxes measured at the sediment-air interface in mangrove environments are closely controlled by oxygen availability, organic C content, tidal exchange, Fe and SO_4^{2-} concentrations, and N availability. However, mangrove forests are areas of intense dissolved inorganic nitrogen (DIN) consumption since NH_4^+ and NO_3^- are assimilated by plants as soon as they are produced (Alongi et al. 2002). Consequently, plant uptake strongly limits N_2O emissions to the atmosphere, and high rates from mangrove sediments have only been reported under excessive anthropogenic DIN input (Konnerup et al. 2014; Chauhan et al. 2015).

6.5 Ecosystem Services: Local and Global Perspectives

Mangrove wetlands provide a number of ecosystem services (ES) through their biogeochemical functions. Using the Millennium Ecosystem Assessment classification (Carpenter et al. 2006, 2009), these services include climate change mitigation, flood regulation and water purification (see Chap. 8). A monetary value has been proposed for other mangrove ES (e.g., raw material and food, coastal protection, erosion control, maintenance of fisheries, tourism/recreation), but there are no comprehensive economic estimates for functions linked to biogeochemical transformations (Barbier et al. 2011). A possible exception is the role of C sequestration for climate change mitigation as recent studies have provided C storage estimates in some IWP and AEP locations. A major reason for the lack of economic information is the nonmarket benefits and social values of these biogeochemical functions in contrast to the more straightforward estimates for services like fish and fish habitats (Alongi 2011; Barbier et al. 2011). Another key service provided by mangroves is the export of organic material and nutrients that drives foodwebs in adjacent habitats such as coral reefs and seagrass meadows and support fisheries (Bouillon and Connolly 2009). The monetary values of this service have not been rated, but quantification (e.g. Davis et al. 2014) and incorporation into more comprehensive assessments of the ecological value of mangrove export has been initiated (Sheaves et al. 2015).

Furthermore, there is a need to assign the potential role of mangrove forests and their biogeochemical functions as sinks, sources, and transformers of C, nutrients, and heavy metals correctly in relation to the nature and location of the original inputs. Because different mangrove types (fringe, basin, riverine) provide different ES (Ewel et al. 1998), it is critical to determine the precise functional role and ES capacity of each mangrove type. Yet, given the diverse range of mangrove ecogeomorphic settings, further information is needed about, for example, the range of nutrient loadings and removal efficiencies along complex hydrological gradients

(Rivera-Monroy et al. 1999). Currently, this information is lacking for a wide range of coastal environments, including mangrove forests in both IWP and AEP regions (Barbier et al. 2011).

Discussions about the optimal use of mangrove wetlands for wastewater treatment have emerged regularly since the 1980s (Clough et al. 1983). However, there is lack of reliable field data to support the implementation of this management strategy at appropriate spatial scales (i.e., hectares) (Robertson and Phillips 1995; Rivera-Monroy et al. 1999), particularly in areas strongly impacted by aquaculture and agriculture practices and urban development (Lee et al. 2014). A potential opportunity to advance mangrove biogeochemical studies at local and regional scales is through climate-related and inspired restoration and rehabilitation projects coupled with C sequestration studies (Manez et al. 2014). Although the economic valuation of C sequestration in mangrove areas is still under discussion (Alongi 2012; Hemati et al. 2015; Huxham et al. 2015), the local incentive for such efforts can be stimulated by including nutrient removal and sewage treatments in the long-term estimates of the economic and social value of these presently nonmarket ES.

6.6 Conclusions and Research Directions

Mangrove forests are ecotones between marine and terrestrial environments. These productive wetlands possess attributes of both environments, but also have intrinsic ecological mechanisms and processes that clearly differentiate them from their immediate surroundings, defined by distinct hydrological and elevation gradients. Because of their transitional position in coastal regions, mangrove forests around the world are increasingly vulnerable to anthropogenic impacts (i.e. deforestation and urban settlement), and associated environmental alterations (e.g. erosion and fluvial contamination and alteration of marine currents). Biogeochemistry research has focused on C, N, P, and mineral cycling in mangrove ecosystems, but most surveys have been short-term (months or less) and lacking a comprehensive regional coverage to evaluate processes and transformations at the landscape level. Our current understanding of the complex interactions between multiple factors and processes that characterize mangrove biogeochemical transformations is limited and prevents extrapolation of information from one biogeographical region to another. More detailed studies must be performed at larger temporal (decadal) and spatial (watershed, regional) scales to characterize and compare environmental processes controlled by both natural and human disturbances.

Mangrove forests are particularly sensitive to rising sea level because of their direct hydrological interactions with coastal waters (Lovelock et al. 2015). The Intergovernmental Panel on Climate Change predicts that the sea level rise for the years 2081–2100 relative to 1986–2005 will range from 40 to 60 cm (IPCC 2013). Detailed studies of the response of mangrove environments to changes in sea level are, therefore, urgently required. Research initiatives should include an international network of permanent plots for long-term monitoring of biogeochemical pro-

cesses, biodiversity, and plant structure among selected mangrove locations where mangrove distribution is rich and extensive in both the IWP and AEP regions. These proposed studies should include the establishment of eddy-covariance stations along biogeographical and anthropogenic gradients to improve our assessment of factors controlling mangrove net ecosystem productivity and GHG dynamics. Such EC systems will also facilitate our understanding of how recurrent natural disturbance (cyclones, tsunamis) and climate change, causing seasonal and interannual variability in precipitation, temperature, river discharge, will affect mangrove spatial distribution, productivity, and CO₂ exchange.

The interaction between mangrove forests and neighboring ecosystems with respect to exchange of materials and energy is another important aspect for consideration in future studies. For example, inland zones at higher relative elevation adjacent to mangrove forests (e.g. hypersaline sandy flats) are considered potential refuges for mangrove expansion as response to sea level rise. Although mangrove ecosystems are legally protected against deforestation or land use conversions in many countries, those inland areas are not included in conservation plans and are consistently developed for human use. Given the increasing demand for space as human populations expand into the coastal zone at an increasing rate, sometimes triggered by a high demand of mangrove ES (e.g., fisheries, recreation), there is an urgent need to develop conservation alternatives tailored to local and regional needs. Managers and decision makers must acknowledge this problem now to avoid further mangrove “squeeze” effects in the future that may cause a dramatic loss of mangrove area.

A clear example of the need to understand how mangrove biogeochemical cycles interact with pressing management priorities is the use of mangrove wetlands as tertiary treatment of waste water (e.g., aquaculture, urban). To evaluate the consequences of such disturbance, more knowledge is urgently needed about cascading effects of hydroperiod on sediment redox conditions and how this may alter, e.g., C, N, P or S cycling. The current lack of understanding could result in destructive effects on both forest productivity and survival and even conversion of mangrove forests from functional C sinks to sources of GHG. The main issue is not if this type of management (tertiary treatment) is feasible and effective because this approach has been used in other temperate wetlands, but rather to ensure correct implementation of water and nutrient management practices (aquaculture, agriculture, urban) at adequate spatial scales in combination with an understanding of the critical biogeochemical transformations.

We have undoubtedly advanced our understanding of the most critical biogeochemical transformations controlling mangrove productivity during the last 35 years, but the disproportion in the scope and quantity of mangrove biogeochemical studies across and within the IWP and AEP regions is troublesome. We advocate for collaboration and expansion of biogeochemical studies around the world. This is urgent because of the increasing rate of mangrove fragmentation and area loss at continental scales. The scientific community should soon translate current data and information about the complexity of mangrove biogeochemistry (i.e., supporting ES) into robust and applicable performance measures in management programs. It is our hope that such action may advance the conservation and protection of one of the most productive coastal ecosystems in the world.

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