

Review

# Organic Carbon Stabilization Mechanisms in Mangrove Soils: A Review

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**Abstract:** Despite the recognized organic carbon (OC) sequestration potential of mangrove forests, the ongoing climate change and anthropogenic disturbances pose a great threat to these ecosystems. However, we currently lack the ability to mechanically understand and predict the consequences of such impacts, primarily because mechanisms underlying OC stabilization in these ecosystems remain elusive. Research into OC stabilization has focused on terrestrial soils and marine sediments for decades, overlooking the vegetated coastal ecosystems including mangroves. In terrestrial soils and marine sediments, it is widely accepted that OC stabilization is the integrated consequence of OM's inherent recalcitrance, physical protection, and interactions with minerals and metals. However, related discussion is rarely done in mangrove soils, and recalcitrance of roots and high net ecosystem production (high primary production and low heterotrophic respiration) have been considered as a primary OC sequestration mechanism in mangrove peat and mineral soils, respectively. This review presents the available information on the mechanisms underlying OC stabilization in mangrove soils and highlights research questions that warrant further investigation. Primary OC stabilization mechanisms differ between mangrove peat and mineral soils. In mangrove mineral soils, physico-chemical stabilization processes are important, yet grossly understudied OC stabilization mechanisms. In mangrove peat, recalcitrance of mangrove roots and the inhibition of phenoxidase under the anoxic condition may be the primary OC stabilization mechanisms. Salinity-induced OC immobilization likely plays a role in both type of soils. Finally, this review argues that belowground production and allochthonous inputs in mangrove forests are likely underestimated. More studies are needed to constrain C budgets to explain the enigma that mangrove OC keeps accumulating despite much higher decomposition (especially by large lateral exports) than previously considered.

**Keywords:** blue carbon; burial; chemical interaction; decomposition; peat; persistence; physical protection; sequestration; soil organic matter; vegetated coastal ecosystem

## 1. Introduction

Recent research has highlighted the organic matter (OM) sequestration potential of vegetated coastal ecosystems such as seagrass meadows, salt marshes, and mangrove forests. These coastal ecosystems sequester carbon (C) tens of times faster than terrestrial forests [1]. As such, the amounts of C annually sequestered in them are each comparable to those of terrestrial forests, despite covering only a small fraction of the coastal ocean [1,2]. The sequestered C is mainly stored belowground (i.e., in soil) in these ecosystems. Soil C pool constitutes approximately 75% of total ecosystem C storage in mangrove forests and >90% in seagrass meadows and salt marshes, respectively [3]. Therefore, soils are

the largest C reservoir in these coastal ecosystems and a key target of conservation plans. The ongoing climate change and anthropogenic disturbances such as deforestation, reclamation, urbanization, and land-use changes pose a great threat to these ecosystems, yet the magnitude and consequences of these disturbances are just beginning to be examined [4–8]. Although such disturbances can have substantial impacts on C sequestration and existing soil C pool in the coastal ecosystems, we currently lack the ability to mechanically understand and predict such impacts, primarily because mechanisms underlying OM stabilization in these ecosystems are poorly understood [9–12]. Research on C storage in the vegetated coastal ecosystems is on the stage of estimating the global C stocks and cycling [1,3,13,14] and the regional variation of these stocks [15–17]. The specific mechanisms behind soil C stabilization can also be important in explaining these variations yet they have been little studied so far.

The most accepted scenario leading to high C sequestration in mangrove soils has been that high net primary production (NPP) and low decomposition rate (soil respiration rate) because of suboxic conditions favor the sequestration of belowground C. However, recent findings indicate that the decomposition rate as measured by soil respiration has been severely underestimated because of the huge lateral export of dissolved inorganic carbon in groundwater [3,13,18,19]. Moreover, the decomposition rate of mangrove litter and roots varies considerably within and between mangrove forests [11,20,21]. Soils with more saturated conditions can have higher OM decomposition rates compared to drier conditions, for instance by enhanced leaching or through the release of physico-chemically protected OM due to metal reduction [22–26]. As such, the postulated low decomposition rate of mangrove soil C due to the suboxic condition may not be universal to all mangroves. It is therefore of immediate interest to assess other potential mechanisms behind the stabilization of the coastal ecosystem soil C pool.

This brief review presents the available information on the mechanisms underlying OM stabilization in mangrove soils, inspired by the advancement of understanding of OM stabilization mechanisms in terrestrial soils and marine sediments in the last two decades. OM stabilization broadly refers to mechanisms that decrease the potential for OM loss by respiration, erosion or leaching, promoting its accumulation and preservation [27]. Due to the lack of empirical studies, the quantitative relevance of some mechanisms in the field currently remains speculative (particularly physico-chemical stabilization). Part review, part perspective, the main intention of this contribution is to highlight research questions in relation to the soil C stabilization in mangrove soils and encourage future studies on this direction.

## 2. Organic Matter Stabilization Mechanisms in Terrestrial Soils and Marine Sediments

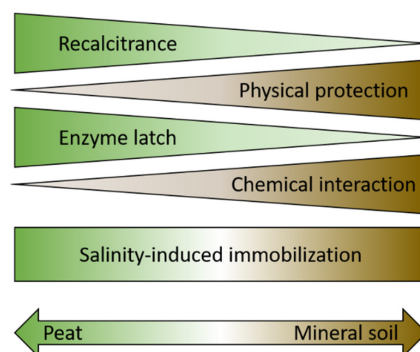
The decomposition rate of soil C generally depends on the environmental condition where the C is placed as well as its composition. The initial decomposition rate of plant residues broadly reflects their bulk chemical composition, while biotic and abiotic environmental conditions may primarily determine the stability of C over residence time of decades to millennia [28]. A recent review that compiled soil C recovery after mangrove regeneration revealed that the decadal time scale is not enough for complete recovery of soil C stock to the levels before disturbances in many mangroves [8]. This emphasizes the importance of long-term (centuries to millennia) soil C stabilization mechanisms in mangrove forests.

Both soil and sediment researchers focused on the stabilization of OM for many years and reached some common mechanisms behind OM stabilization in the respective environments [29,30]. They are categorized into three general types: (i) inherent recalcitrance, which is a molecular-level characteristics of OM; (ii) physical protection (inaccessibility) of OM from soil microorganisms and enzymes; and (iii) chemical interaction with soil minerals or metals [27]. Physical protection of soil C takes place through occlusion of OM within aggregates or small pores. Chemical interactions occur through interaction of OM with mineral surfaces or metals. This physico-chemical stabilization reduces the bioavailability and accessibility of OM for microorganisms and enzymes [31,32]. For instance, in marine sediments, a physical diffusion model has suggested that the encapsulation of OM by clay

materials plays a key role in determining the degradation rate of OM [33]. In soils, these mechanisms have been suggested to be several times more important than the inherent recalcitrance of roots [34]. Consequently, there has been a paradigm shift in how we perceive the reasons behind the long-term persistence of soil C [28,31,35]. Under this new paradigm, intrinsic recalcitrance may play only a secondary role and physico-chemical stabilization primarily determines the long-term persistence of soil C [28,31,35]. Considering mangrove's transitional location between terrestrial and marine environments, the same mechanisms likely take place in mangrove soils as well.

### 3. Mangrove Soils: Mineral or Peaty

Peat formation and accumulation occur in some mangrove forests (e.g., Indonesia, Florida Everglades, and oceanic islands such as Micronesia and the Caribbean) but not in others (e.g., Brazil and most of East Asia). Since environmental conditions where the soil C is stored are expected to vary between peaty and non-peaty (mineral) mangrove soils, primary soil C stabilization mechanisms may differ between these soils. Here, we summarize potential soil C stabilization mechanisms (see Figure 1) and discuss each mechanism below. All of the aforementioned common mechanisms as well as those specific to mangroves are presented. We note that each mechanism is neither mutually exclusive nor strictly applied to only mineral or peaty mangrove soil. For example, recalcitrance of mangrove roots and selective preservation of phenolic materials may also be important in mineral soils [36], and OM–iron (Fe) interactions can happen in peaty environments [37]. However, such recalcitrance of roots is expected to be more important in mangrove peat where physico-chemical stabilization of OM by soil minerals and metals plays a small role.



**Figure 1.** Proposed mechanisms underlying soil C stabilization in mangrove forests. Physical protection of soil C takes place through its occlusion within aggregates and/or small pores, while chemical interaction refers to interactions of organic matter with soil minerals and/or metals. Relative importance of each mechanism along the spectrum of the two types of mangrove soils is depicted schematically by the widths of the diagrams. Each mechanism is neither mutually exclusive nor strictly applied to only mineral or peaty mangrove soil, and overall stabilization of soil C pool is determined by combinations of these mechanisms plus environmental factors.

#### 3.1. Mineral Soils

##### 3.1.1. Mineral Soils: Interactions with Soil Minerals or Metals

Interactions with soil minerals or metals (Fe, Al, Ca) are potentially important yet understudied mechanisms behind soil C stabilization in mangrove mineral soils. Although they are well described in soils and sediments [31,32,38], relevant studies in mangrove soils are surprisingly sparse. We could find only one recent study that investigated the role of reactive Fe in mangrove soils [39] (discussed below). The sorptive interactions of OM with mineral surfaces occur through various mechanisms such as ligand exchange, polyvalent cation bridges, ion exchanges, and other weak interactions including van der Waals forces, hydrophobic interactions, and proton binding [32,40]. Many of these are either enhanced or suppressed by the increase in ionic strength (Table 1).

**Table 1.** Mechanisms behind organic matter interactions with mineral surfaces and influence of seawater inorganic ions.

| Mechanism                    | Type of Interaction | Nature   | Influence of Inorganic Ions |   | Reference  |
|------------------------------|---------------------|--|-----------------------------|---|------------|
| Ligand exchange <sup>a</sup> | Inner-sphere        | Covalent to ionic bond                                   | Negative <sup>b</sup>       | Competitive effect by SO <sub>4</sub> <sup>2-</sup>   | [40,41]    |
| Ion exchange                 | Outer-sphere        | Ionic bond   | Negative                    | Competitive effect by inorganic ions  | [40]       |
| Cation bridging              | Inner-sphere        | Ionic bond (Direct cation bridging) <sup>c</sup>         | Negative                    | Partial replacement of Ca <sup>2+</sup> for Na <sup>+</sup> , K <sup>+</sup> , Mg <sup>2+</sup> ; Monovalent cations are not good at bridging, and Mg <sup>2+</sup> does not form inner-sphere bridge | [42,43]    |
|                              | Outer-sphere        | Hydrogen bond (Exchangeable/water bridging) <sup>c</sup> | Negative                    | Partial replacement of Ca <sup>2+</sup> for Na <sup>+</sup> and K <sup>+</sup> ; Monovalent cations are not good at bridging  | [42]       |
| Van der Waals forces         | Outer-sphere        | Dipole–dipole force                                      | Positive                    | The compression of the double-layers of both clays and organic matter at high ionic strength allows closer approach   | [40,44–46] |
| Hydrogen bonding             | Outer-sphere        | Hydrogen bond  | Negative <sup>d</sup>       | Replacement of H with cations   | [47]       |
| Hydrophobic interactions     | Outer-sphere        | Entropy-driven   | Negative <sup>d</sup>       | The presence of hydrated Ca <sup>2+</sup> between OM and mineral surfaces impedes the formation of direct hydrophobic interactions, as opposed to the H <sup>+</sup> -saturated system                | [48]       |

<sup>a</sup> Including chelation [49]. <sup>b</sup> For discussion on inner-sphere complexation of SO<sub>4</sub><sup>2-</sup> to minerals, see [50]. <sup>c</sup> See [40,48,49]. <sup>d</sup> The pH effect is more pronounced for OM with acidic functional groups, because such OM becomes protonated and more hydrophobic at low pH [46,48].

Van der Waals forces are potentially enhanced in saline environments such as mangrove soils and marine sediments (Table 1). Van der Waals forces are due to the permanent polarity of the interacting clay and OM (dipole–dipole force). These forces are short-range associations and become significant only when sorbents and sorbates are in proximity on a molecular level. As such, these forces become progressively more important as the electrical double layer of clays and OM decreases in thickness at high ionic strength [40,44–46]. For instance, Arnarson and Keil estimated that van der Waals forces contributed 60% of OM sorption to montmorillonite in a  $\text{CaCl}_2$  solution, followed by ligand exchange and cation bridging [40]. The enhancement of van der Waals forces with increasing ionic strength overwhelms the competitive suppression of ion exchange due to inorganic ions in OM sorption to montmorillonite [40]. This result is consistent with the findings that van der Waals forces are the dominant interaction mechanism between humic acids and clay minerals at seawater salinity [44–46]. The long-term stabilization of OM interacted with mineral surfaces via van der Waals forces is however unknown. Non-covalently-bonding, outer-sphere interactions such as van der Waals forces, hydrophobic interactions, hydrogen bonding, and outer-sphere cation bridging are reversible and sorbed OM is eventually desorbed once the surrounding environment favors such reactions [44,51]. Desorbed OM is susceptible to microbial degradation and eventually mineralized [38]. As mangrove soils experience daily and seasonal fluctuations in salinity [52], sorption–desorption properties of OM may be critical for its stability and warrant in-situ investigation.

The influence of salinity on cation bridging is less clear than van der Waals forces due to the counteracting effects of polyvalent and monovalent cations (Table 1). Cation bridging allows for the interaction of two negatively charged surfaces such as a phyllosilicate and carboxyl and hydroxyl groups of OM by neutralizing the charges. Mangrove soils are rich in seawater-derived  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  which can form cation bridges between mineral surfaces and OM. Compared to basic soils in terrestrial environments, however, seawater contains high concentrations of  $\text{Na}^+$  (~0.5 M) in addition to  $\text{Ca}^{2+}$  (~0.01 M) and  $\text{Mg}^{2+}$  (~0.05 M). The interference of  $\text{Na}^+$  in the formation of divalent cation bridges is therefore possible. In most cases, mineral particles in mangrove soils are delivered by rivers from upland. Clay surfaces in the riverine environment are mainly occupied by adsorbed  $\text{Ca}^{2+}$  species, but it is mostly (but not fully) exchanged for  $\text{Na}^+$ ,  $\text{Mg}^{2+}$ , and  $\text{K}^+$  in seawater during the estuarine mixing [42]. Analyzing the cation-exchange characteristics of Amazon River suspended sediments, Sayles and Mangelsdorf showed that the exchange sites of sediments in seawater are occupied by on average 38%  $\text{Na}^+$ , 38%  $\text{Mg}^{2+}$ , 15%  $\text{Ca}^{2+}$ , and 9%  $\text{K}^+$  [42]. Therefore, the divalent cations occupy approximately half of the exchange sites, enabling cation bridging. Furthermore, chemical modeling indicates that  $\text{Ca}^{2+}$  could form direct bridges with acidic functional groups of OM, unlike  $\text{Mg}^{2+}$  of which hydration water is more tightly held [43]. This is contrary to the traditional view that  $\text{Ca}^{2+}$  does not make direct (inner-sphere) cation bridges [32]. Accordingly, Ca-mediated stabilization of OM in terrestrial basic soils has been highlighted in a recent extensive review [49]. The role of  $\text{Ca}^{2+}$  (and  $\text{CaCO}_3$ ) in the stabilization of OM in mangrove soils awaits investigation.

Ligand exchange refers to direct (inner-sphere) bond between a carboxylate group of OM and either a Fe(III) or Al(III) metal ion center in minerals possessing inorganic hydroxyl groups. The role of ligand exchange between OM and reactive Fe (nanoparticulate and amorphous phases of ferric oxides) in marine sediments for the OM stabilization has been recently highlighted. Marine scientists have adapted a Fe reduction method previously applied to soils [53,54] and revealed that about 21% of the organic C in global surface marine sediments is directly bound to reactive Fe phases and preserved as a result of its interaction with Fe [55]. A follow-up study revealed that 26–63% of total reactive Fe is directly associated with organic C through inner-sphere complexation via ligand exchange in the coastal sediments [56]. Because inner-sphere complexation is strong and irreversible, this OM–Fe interaction is considered to result in the long-term preservation of OM in marine sediments. Similarly important roles that reactive Fe plays in the stabilization of OM have been reported in estuarine sediments [57,58]. Following these studies, Dicen et al. for the first time investigated the role of reactive Fe in mangrove soils [39]. They found that on average 15% of organic C in the

studied cores is directly bound to reactive Fe, corroborating the findings in estuarine and marine sediments. These results are counter-intuitive because ligand exchange was shown to be suppressed by  $\text{SO}_4^{2-}$  (Table 1) [40,41], which is abundant in seawater (0.03 M), and because Fe can undergo reductive dissolution as Fe(II) in reducing environments, leading to the disruption of the OM–Fe interactions [25,26]. Compared to marine sediments, mangrove soils are a much more redox dynamic environment, thus the interactions of OM and Fe at redox interfaces may be more important than in marine sediments. However, the long-term stability of this OM–Fe interaction in mangrove soils has not been explicitly studied and it requires further investigation. Analysis of  $^{14}\text{C}$ -dated soils or  $^{14}\text{C}$  measurements of the dissolved OM fraction obtained by the inorganic version of the Fe reduction method [53] can shed light on how long OM may persist in mangrove soils through ligand exchange between reactive Fe.

Hydrophobic interactions and proton binding are presumably not important in mangrove soils (Table 1). Experimental studies show that other mechanisms such as cation bridging and van der Waals forces are dominant binding mechanisms in OM interactions with clays and Fe in seawater [40,47]. Chemical modeling also shows that these mechanisms are absent from the deprotonated, Ca-saturated OM–montmorillonite system [48]. The presence of hydrated metal cations such as  $\text{Ca}^{2+}$  between OM and mineral surfaces impedes the formation of hydrophobic interactions by preventing close contact between them, as opposed to the  $\text{H}^+$ -saturated system [48]. Hydrophobic interactions and proton binding likely become significant only when OM is strongly protonated, such as in acidic forest soils (Table 1).

### 3.1.2. Mineral Soils: Physical Protection

As far as we know, there is no study to date that investigated the physical protection of OM in mangrove soils, although it may be an important soil C stabilization mechanism in mangrove mineral soils. In addition to physical protection processes generally found in soils such as occlusion of OM within aggregates or small pores [27,31,32], metal concretion on root outer surfaces can be another physical stabilization mechanism specific to vegetated coastal ecosystems including mangroves. Redox state-sensitive metals such as Fe and Mn create localized enrichments of oxides when these metals translocate from reducing to oxidizing zones. In mangrove mineral soils, the outer surface of mangrove roots functions as a hot-spot for such enrichments because of radical oxygen leakage from roots [59,60]. The metal coating of mangrove roots can inhibit bacterial accessibility to such roots, but the long-term stability of this protection needs further investigation [12].

Stabilization of OM can also occur via coprecipitation with metals such as Fe and Al, which is a common process in many kinds of environments due to changes in pH or redox potential. Stabilization of OM by coprecipitation has been suggested to account for the long-term C preservation in both soils and sediments [53,55]. Coprecipitation occurs by complexation of deprotonated acidic functional groups of OM (mainly carboxyl) and the aqueous-phase polyvalent metal ions, or by immediate sorption of OM to freshly formed metal hydroxides [53,61]. Rapid redox changes at redox interfaces between anoxic bottom sediments and surface oxic waters result in oxidation of Fe(II) to Fe(III), inducing precipitation as Fe hydroxides or insoluble OM–Fe(III) complexes [62,63]. Since both Fe and Al exist mostly as (oxy)hydroxides in mangrove soils with neutral pH values, pH is not expected to have as much influence on coprecipitation as in acidic forest soils [63]. Studies that applied the Fe reduction method to sediments often show high molar Fe:OC ratios for the co-extracted species, suggesting that associations between OM and Fe are primarily through coprecipitation in these environments [39,55,57]. Specific mechanisms behind the OM stabilization by coprecipitation remain elusive. Both physical protection by precipitated metal hydroxides [61] or by ternary OM–Fe hydroxides–clay associations [53] and chemical stabilization by inner-sphere complexation [56,64] have been proposed.

### 3.2. Peaty Soils: Inherent Recalcitrance of Roots and “Enzyme Latch” Hypothesis

In some mangrove forests, extensive development of peat can be found. For instance, on a Belizean island, peat deposits accumulate up to 10 m deep, and the bottom peat is about 7500 years old [65]. Although the mechanism of mangrove peat formation and accumulation is not yet fully understood [66], needless to say the reasons mangrove peat can persist for thousands of years. In mangrove peats, where physical protection of OM by soil minerals is minimal, the long-term persistence of mangrove tissues must be associated with the inherent recalcitrance of mangrove tissues or some stabilization mechanisms other than physical protection, or both.

Mangrove peats primarily consist of mangrove roots [65], and roots generally have lower decomposition rates than leaves partly because of the composition relatively rich in recalcitrant material such as suberin and lignin [34,67]. For example, Middleton and McKee showed that in a Belizean mangrove forest roots were highly resistant to biodegradation ( $40 \pm 2\%$  remaining after 584 days) in contrast to leaves ( $27 \pm 5\%$  remaining after 230 days) [68]. Liu et al. reported that in a Chinese mangrove forest 0–41% and 75–88% of leaf litter and fine root, respectively remained after 391 days of decomposition [69]. Due to this relative recalcitrance, total dead root mass sometimes several times exceeds the summed mass of live above- and belowground biomass in mangrove forests [20]. Although past studies suggested that the peat formation has occurred primarily through this slow decomposition rate of mangrove roots under the anaerobic condition, how peats are preserved for millennia remains unexplained. For instance, in the case of the Chinese mangrove forest stated above, the estimated low decomposition rate still requires only 9–55 years for fine roots to reach complete decomposition [69]. This cannot explain the long-term (millennia) stabilization of peats [65]. There should be other mechanisms than recalcitrance that let a fraction of plant residues reside for millennia. The availability of nutrients such as nitrogen and phosphorus to microbial communities can be another important factor that influences the decomposition of OM, but the extent and direction of change in soil respiration after nutrient enrichment in mangrove soils are highly variable [70,71]. Thus, nutrient limitation itself cannot explain the long-term stabilization of mangrove soil C [70].

In a recent experimental study, Saraswati et al. proposed that the “enzyme latch” mechanism, which has been proposed as a mechanism of peat stabilization in northern peatlands [72], may also play an important role in the stabilization of mangrove peat [66]. Generally, OM degradation can be considered as two broad steps. The first step is the breakdown of large organic polymers (such as carbohydrates, lignin, and proteins) into small monomers (such as sugars, phenols, and amino acids), and the second step is the mineralization of these monomers to  $\text{CO}_2$  [73]. The degradation of certain compounds in the first step is dependent on the availability of  $\text{O}_2$ . Especially, hydrolysis-resistant (carbon-rich) substrates, such as lignin or some lipids, require  $\text{O}_2$  as an enzymatic co-factor in their initial non-hydrolysis-dominated degradation steps [73]. The enzyme latch mechanism claims that the inhibition of a single enzyme, phenoloxidase, under anaerobic conditions results in the accumulation of phenolic materials, which inhibits the activity of hydrolase enzymes, which suppress the decomposition of peat [72]. Saraswati et al. showed that, using mangrove peat from the Everglades, peat supplemented with lignin-derived phenol solutions had significantly lower (up to  $-82\%$ ) hydrolase activities, peat samples had significantly higher (two-fold) phenol oxidase activity under aerobic conditions (i.e., unlocking of the “latch”), and peat supplemented with phenol oxidase had significantly lower ( $-8.3\%$ ) phenolic concentration [66]. This proposed mechanism seems relevant in the mangrove peat formation and stabilization and awaits its test in the actual field.

### 3.3. Both Type of Soils: Salinity-Induced Immobilization

Mangrove forests are distinguished from terrestrial forests in that they occur in seawater-logged, saline soils, whether its soil is peaty or mineral. Therefore, soil C stabilization mechanisms that are unique to the saline soils may exist. A recent experimental study demonstrated that soil OM was retained in mangrove soils because of the immobilization of OM and/or OM–clay complexes under saline conditions [9]. This proposition was based on the observation that sequential washing with

freshwater (and the corresponding decline in salinity), but not with artificial seawater, caused the enhanced dissolution of OM from the mangrove soil [9]. Here, the term “immobilization” is used instead of “aggregation” because the specific mechanism behind salinity-induced immobilization of OM in soil was not clarified; it can be flocculated OM, aggregated OM–clay colloids, or those sorbed to soil minerals. Immobilization of OM in mangrove soils contributes to its stabilization because OM will be otherwise exposed to oxidation and photodegradation in open coastal water once exported [38,74]. Since every mangrove soil is saline, this proposed mechanism can serve as one of the mechanisms underlying soil C accumulation in the global mangrove soils. In mangrove peat, amorphous, highly degraded OM without visible remains of plant residues should be susceptible to salinity-induced immobilization. In fact, salinity-induced flocculation of terrestrial-derived materials at the estuarine mixing zone has been known for decades (e.g., [75]). It was also documented that saltwater incursion to freshwater wetlands substantially reduced exports of dissolved OM because of the immobilization of OM due to elevated salinity [76]. Investigating a historical C accumulation in a mangrove-fringed coastal lagoon in Java, Indonesia, Hapsari et al. recently revealed a strong positive correlation between soil organic C concentration and a salinity index (chlorine) throughout a 5-m core [77]. Taken together, these findings suggest a universal positive influence of salinity on soil C stabilization in mangroves and warrant further studies.

It should however be noted that higher salinity does not necessarily result in higher soil C accumulation. On the one hand, the flocculation of dissolved OM generally begins at lower salinity than that of seawater [75]. The salinity-induced immobilization of mangrove OM almost reached its upper limit at salinity of around one-tenth of that of seawater [9]. On the other hand, high salinity can be a stress to mangroves and decrease its productivity [52]. Saline soils do not necessarily have favorable conditions for mangroves, although they may have suitable conditions to store OM from a geochemical viewpoint.

Mangrove soils are different from marine sediments in that there is a daily and seasonal fluctuation in salinity and that OM is mainly derived from vascular plants (both mangroves and catchment plants). Vascular-plant derived aromatic materials (lignin, tannins) are known to be more susceptible to salinity-induced flocculation than microbial-derived aliphatic materials [75,78]. Hence, the role that salinity plays on C stabilization may be more important and spatiotemporally dynamic in vegetated coastal ecosystems including mangroves than in marine sediments. Although information on the spatiotemporal variation in salinity in mangrove soils is scarce, Komiyama et al. recently observed that soil water salinity (up to 1 m depth) showed remarkable seasonal variation with salinity similar to that of seawater during the dry season and to that of freshwater during the rainy season in Trat mangrove forest, Thailand [52]. This fluctuation in salinity should affect soil C stabilization, for instance through dissolution and loss of OM under low salinity [79]. Enhanced exports of dissolved OM from mangroves during episodic freshwater inputs can also be partly interpreted as enhanced dissolution of soil OM upon reduction in salinity [79,80].

Finally, conceptually fractionating the soil C pool based on its existing forms aids our understanding of the influence of salinity. We can consider that dead OM in mangrove soils is composed of a fraction of OM that is immobilized under high salinity (immobilized fraction, IF), which undergoes dissolution upon reduction in salinity, and the rest of soil OM. In mineral soils, the rest of soil OM can be divided into three fractions according to the density-separation approach frequently used in both soils and sediments: free low-density fraction (f-LF), mineral-associated low-density fraction (m-LF), and high-density fraction (HF) [81]. The f-LF consists of free plant detritus (mainly dead mangrove roots), the m-LF consists of partly decomposed plant detritus occluded in or attached to soil particles, and the HF consists of highly decomposed, microbially-modified, amorphous OM strongly associated with soil particles [81]. For instance, in the Fukido mangrove forest, Okinawa, the proportions of HF, m-LF, and f-LF were 49–59%, 27–31%, and 14–20% on a C basis, and 62–76%, 17–25%, and 7–13% on an N basis, respectively (Kida, unpublished data, estimated as in [81]). These preliminary data show that HF is quantitatively the most important fraction in terms of the C and N pool in this mangrove



forest and HF is relatively enriched in N due to microbial processing. If intentionally omitting the difference in microbial community and activity in fresh and saline conditions, salinity is unlikely to influence the stability of f-LF and m-LF because these relatively fresh plant detritus does not change their micro-scale conformation by changes in salinity. Thus, it is reasonable to assume that HF is the fraction that is the most influenced by salinity changes. A sizeable fraction of OM in HF may be stabilized by salinity-enhanced interactions with mineral surfaces [40]. Therefore, salinity may positively influence not only IF but also HF in terms of mangrove C stabilization. The combination of density fractionation followed by metal oxides dissolution methods will enable the quantification of the OM tightly associated with soil minerals [53].

#### 4. Slow Decomposition or Higher Inputs?

As stated above, there are a number of cases that question the postulated low decomposition rate of mangrove soil C because of suboxic conditions [3,13,18,19,22,23]. This suggests that other factors must exist that support the large soil C pool of mangroves, such as higher net primary production (NPP) than current estimates. Indeed global estimates of mangrove NPP (210–218 Tg C year<sup>-1</sup>) [3,13,82] are conservative because there are several components that are not included in the estimates, such as coarse root production, litter herbivory, and root exudates [13]. The contributions from these components to NPP are as yet unknown because of the scarcity of data. In addition, recent findings suggest that fine root production and allochthonous inputs may be much higher than the previous estimates [20,69,83–86].

Fine root production and turnover in mangroves remain poorly understood because of the logistical difficulties involved [13,84]. Global synthesis of root production based on limited data shows that average belowground root production is 75–82 Tg C year<sup>-1</sup> [13,87], which corresponds to unit-area root production of 513–544 g C m<sup>-2</sup> year<sup>-1</sup> [21]. Average root turnover is 0.222 (0.048–0.51) year<sup>-1</sup> [21]. However, rapid growth and turnover rates of mangrove fine roots have been suggested in a number of recent studies [20,69,83–86]. For instance, fine roots were reported to be the dominant (up to 98%) contributor to soil OM accumulation in mangroves [69]. Regional studies in Chinese and Malaysian mangrove forests reported much higher root turnover of 0.81–5.96 year<sup>-1</sup> [84,85]. The especially high fine root turnover (5.96 year<sup>-1</sup>) was estimated using a sequential coring method, which was based on the seasonal variations of biomass and necromass of fine roots [85]. Lower estimates from old studies are partly due to methodology [13]. Most of the studies used an in-growth core method that can only measure fine roots that happen to penetrate into the in-growth core during a given time period. Disturbance of soils and root systems during the installation of in-growth cores can lead to underestimation of root production [85]. For instance, root production rates (g m<sup>-2</sup> day<sup>-1</sup>) measured over one year were 2–26 times higher than those measured over six months after the core installation, suggesting a delay in the root recovery [88]. Fine root biomass distribution decreases with increasing distance to the individual tree and prop root, thus the root production will be underestimated if the core is installed in open areas with few aboveground root systems [89]. Although direct comparison is difficult due to the difference in methodology, comparative studies using multiple methods are encouraged for accurate estimates of mangrove fine root production, turnover rate, and ultimately NPP.

Allochthonous (i.e., marine- and terrestrial-derived) inputs to mangroves represent another major but poorly constrained source of soil C in mangrove forests. Allochthonous inputs occur through trapping of suspended solids in upstream and tidal water onto the forest floor. Complex root systems of mangroves are highly efficient in trapping fine particles in water [90,91]. These fine sediment particles are loaded with OM and therefore contribute to OM sequestration in mangrove forests. The contribution from these allochthonous inputs to mangrove soil C pool is highly variable, from mangrove-dominant to allochthonous-dominant [92–94]. Mineral mangrove soils tend to receive higher contributions from allochthonous materials compared to mangrove peat, which is predominantly composed of dead mangrove roots. Recent findings point out that the contributions from allochthonous inputs may be much more important than the current estimates. For instance, Li et al. estimated the C

budgets in Taiwan mangrove forests and found that the summation of the lateral C exports and soil heterotrophic respiration well exceeded the amount of litter decomposition. Although they did not consider belowground production, sediment-stable isotope analyses suggest that the trapping of allochthonous OM contributed more to the mangrove C pool than the primary production by mangroves [10]. Ray et al. also reached a similar conclusion after re-assessing the C budget in Indian Sundarbans mangrove forests [95]. The sum of total C sinks is higher than C sources by 7.3 Tg C year<sup>-1</sup>, which must be accounted for by extra inputs such as benthic primary production and allochthonous inputs [95].

Overall, these recent findings suggest that the soil C turnover rate in mangrove forests may be much higher than the current estimates. In other words, mangrove soil C may keep accumulating despite high decomposition (especially by large lateral exports [3,13,18,19]) owing to higher production and inputs (especially fine root production, benthic primary production, and allochthonous inputs [10,84,85,95]). More empirical studies are clearly needed to better understand C cycling and storage in global mangrove forests.

## 5. Conclusions

We review and propose potential soil C stabilization mechanisms in mangrove forests. Primary soil C stabilization mechanisms differ between mangrove mineral soils and peat. Physico-chemical stabilization by soil minerals and metals is important in mineral soils, while recalcitrance and “enzyme latch” hypothesis could play an important role in organic C stabilization in mangrove peat. While we focus on mangroves, all proposed mechanisms may also play similarly important roles in other vegetated coastal ecosystems considering the similarity in the environmental conditions. A fraction of C that escapes leaching and degradation on the forest floor is buried in soils and ultimately stored for centuries to millennia, likely by a combination of the proposed mechanisms (Figure 1). However, the contribution from each mechanism is currently unknown and awaits further studies. Besides, improved estimates of C cycling in mangrove forests are needed to better constrain the balance of C inputs and outputs in mangrove forests. Quantifying belowground production and allochthonous inputs is future key tasks that need more empirical studies.

Mangrove forests provide a wide range of ecosystem services to human beings and natural habitats, and its high soil C preservation capacity is particularly highlighted in the last decade. Although the global deforestation rate of mangrove forests is now less alarming than previously suggested [96], mangroves are still threatened by a wide range of deforestation and degradation impacts. Many conservation plans are attempting to restore lost and degraded mangroves and expand mangrove coverages. Future research will help to provide a mechanistic understanding of soil C stabilization by focusing on the specific mechanisms of how the vegetated coastal soil C is preserved for over centuries.

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