

Mud-associated organic matter and its direct and indirect role in marsh organic matter accumulation and vertical accretion

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Abstract

In situ plant production is often assumed to be the major contributor to organic matter (OM) accumulation and vertical accretion in tidal marshes. Here, we evaluate the contribution of mud-associated OM in salt and brackish marshes in Louisiana. Based on 14 soil cores, the OM content of the mud fraction—i.e., any material smaller than 64 μm —was $17\% \pm 7\%$ for the salt marshes and $28\% \pm 14\%$ for the brackish marshes. This remains nearly uniform over the top 35 cm depth, suggesting that this material is deposited contemporaneously with the mud. The dry bulk density of the mud ($300\text{--}450 \text{ kg m}^{-3}$) is also much lower than what was estimated using a previously proposed two-constituent mixing model (1990 kg m^{-3}). To reconcile this discrepancy, we developed a modified mixing model that includes mud OM and differentiates sand as a separate constituent with its high dry bulk density. The model estimates that mud contributes to $\sim 60\%$ of the total marsh vertical accretion in Louisiana, considerably higher than the $\sim 14\%$ estimated with the two-constituent mixing model. The result, which is a direct consequence of the relatively high porosity of mud, highlights that mud deposition is crucial for the accretion of microtidal marshes. Further, the model estimates that the mud OM constitutes $\sim 60\%$ of the total soil OM, emphasizing that in situ plant production is not the only—and, in minerogenic marshes, not the major—contributor to OM accumulation.

Ostensibly, due to the high primary productivity and relatively high lignin and cellulose composition of vascular marsh plants, the assumption that all OM originates from in situ plant production is often implicit in the interpretation of observed marsh soil properties (Morris et al. 2016). Furthermore, it is well established that OM accumulation is a better (empirical) explanatory variable for vertical accretion than inorganic accumulation (Turner et al. 2002; Neubauer 2008). If all OM is assumed to originate from in situ plant production, the logical implication of the observed trend is that plant processes determine how fast the marsh can accrete and that inorganic deposition is a dependent variable.

Numerical models of marsh vulnerability to sea-level rise are often predicated on the assumption that all organic matter (OM) originates from in situ production by marsh plants (e.g., *Spartina*) and that suspended sediments deliver only inorganic particles (French 2013; Morris et al. 2002; Kirwan and Murray 2007). Based on these models, thresholds of inorganic sediment availability have been identified that presumably determine whether marshes will keep pace with an

accelerating sea-level rise or will drown (Kirwan et al. 2010). The increasing use of these models on spatial scales relevant to marsh and watershed management (Stralberg et al. 2011; Schile et al. 2014) heightens the necessity to assess how well current models represent realistic local processes. For example, it is widely recognized that a portion of the OM in marsh soils originates from allochthonous deposition and from photosynthetic algae including microphytobenthos on the marsh surface (Goñi and Thomas 2000; Unger et al. 2016; Van de Broek et al. 2016; Wollenberg et al. 2018; Shields et al. 2019). Indeed, a relatively high percentage of suspended particulate matter in tidal channels can be organic (generally within 10–50%; Settlemyre and Gardner 1977; Van de Broek et al. 2016; Ganju et al. 2019), and material that deposits on marsh surfaces likewise can have high organic concentrations (5–88% on sediment plates; Elsey-Quirk and Adamowicz 2015). Yet, except for a few cases, the effects of different sources of OM other than in situ plant production on marsh accretion have been neglected in both models and interpretation of field data.

The presence of OM associated with mud deposition in absence of in situ plant production is supported by an analogy with mudflats—which can be considered a low elevation marsh without vegetation. Despite the absence of in situ production of marsh grasses, mudflats have a soil OM content of 5–15% (Folger 1972; Austen et al. 1999; Pedersen and

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[Correction added on June 23, 2020 after first online publication: corresponding author mail id updated.]

Bartholdy 2006). Noticeably, OM in mudflats is also present at depth (i.e., it is preserved through time), likely due its inherent recalcitrance and/or to the slow decay rates and physio-chemical protection offered by inorganic particles (Middelburg et al. 1997; Boschker et al. 1999; Dodla et al. 2012). This preservation might be even stronger in marshes than in mudflats: mudflats are subjected to seasonal cycles of erosion and deposition, which can expose organic material to oxygen and thus lower the preservation potential (Blair and Aller 2012), whereas marshes are relatively stable because of the presence of vegetation. Further, the idea of mud-associated OM as a soil aggregate based upon physiochemical associations largely associated with the clay ($<2\ \mu\text{m}$) fraction has been linked to soil OM stability and long-term carbon storage (Mikutta et al. 2006; Kleber et al. 2015).

Accounting for the presence of OM other than that produced in situ by plants may have important consequences for predictions of marsh vulnerability to sea-level rise and subsequent management planning and practices. Based on stable isotopic signatures, organic marshes can have a soil ^{13}C value within the range of the local plant species (i.e., C4 or C3 plants), while minerogenic marshes can have depleted $\delta^{13}\text{C}$ signatures, similar to that of algae, which may be due to the deposition of estuarine phytoplankton and/or microphytobenthos, the preferential preservation of lignin (Benner et al. 1991) and/or greater allochthonous C inputs consisting of organic matter sorbed onto mineral particles (Middelburg et al. 1997). Similarly, a strong phytoplankton signature has been found throughout soil cores collected in minerogenic marshes dominated by *Spartina alterniflora* and *Juncus roemerianus* (Gebrehiwet et al. 2008). However, despite advances in biogeochemical approaches, such as the use of stable and radio carbon isotopes (Van de Broek et al., 2018), differentiating OM provenance in composite marsh soils generally eludes us for a number of reasons including source mixing, decay processes, and erosion and redeposition.

Here, we suggest that some information about the provenance of marsh OM can be obtained by considering only standard soil measurements such as soil dry bulk density and soil OM content of the top ~ 30 cm layer of the marsh. The starting point of this procedure is an ideal mixing model (Morris et al. 2016), which was able to estimate the dry bulk density of the inorganic material alone (i.e., the deposited sediment) and of the organic material alone (i.e., the plant biomass accumulated in situ) by fitting a dataset of paired soil dry bulk density and OM content from 33 marshes in the United States. This analysis yielded a low dry bulk density for the organic material ($85\ \text{kg m}^{-3}$), which is intuitively explained by the fibrous and porous structure of plant roots and rhizomes, but a particularly high dry bulk density for the inorganic ($1990\ \text{kg m}^{-3}$) soil components. This extraordinarily high inorganic sediment density is inconsistent with the densities of recently deposited mud, which rarely has a dry bulk density greater than $1000\ \text{kg m}^{-3}$. Mudflats, for comparison, have soil dry bulk densities between 300 and $800\ \text{kg m}^{-3}$ in the top ~ 30 cm layer (Austen et al. 1999; Whitehouse et al. 2000; Bale

et al. 2007; Wheatcroft et al. 2013), while even extremely dense mudstone rocks generally have a dry bulk density lower than $1700\ \text{kg m}^{-3}$ (Tucker 2009).

We resolved this inconsistency by considering sand as an additional high dry bulk density constituent in the soil. Then, as a byproduct of the mixing model, the organic matter associated with the deposited mud can be estimated. This mud OM includes all of the sources not associated with in situ plant production, such as from the particulate OM (POM) that deposits contemporaneously with the mud including material from the recycling of old eroded marsh, terrestrial sources, or marine/estuarine sources (Shields et al. 2016; Van de Broek et al. 2018), as well as the OM produced in situ by microphytobenthos or edaphic algae, which are ubiquitous in marshes (Sullivan and Currin 2002).

We support our analysis by directly measuring the mud-associated OM of soil profiles in both salt and brackish marshes in Louisiana. Then, we use our modified mixing model to interpret a large dataset of paired soil dry bulk density and OM content (measured through loss on ignition, LOI) in Louisiana. This analysis allows us to draw general conclusions about the contribution of mud and mud-associated OM to marsh vertical accretion and OM accumulation.

Methods

Field measurements

We collected three soil cores (15 cm diameter and 35 cm deep) from eight salt marshes and six brackish marshes in Barataria Bay, Louisiana (Fig. 1). Soil cores were collected 1–5 m from the marsh edge using PVC pipes that were beveled at the bottom to reduce compaction. Each core was sectioned into seven 5 cm depth sections, resulting in a total of 294 samples.

Each sediment depth section was subsampled using a cylinder 2 cm in diameter for soil dry bulk density (ρ_{soil}) and OM content (LOI_{soil}), which was measured by combusting the samples for 4 h at 550°C . The remaining portion of the sample was wet sieved to separate three size classes: the mud fraction (everything smaller than $64\ \mu\text{m}$), the fine fraction ($64\ \mu\text{m}$ – $2\ \text{mm}$), and the coarse fraction (everything coarser than $2\ \text{mm}$). Similar to previous studies (Elsey-Quirk and Unger 2018), the fine fraction was mainly comprised of peat and organic muck, whereas the coarse fraction was mainly comprised of distinct roots and rhizomes. Only a small amount of inorganic material was included in the fine and coarse fraction. To quantify this, 64 randomly selected subsamples of the coarse and fine fractions were combusted for 8 h at 460°C . Inorganic material made up an average of $16\% \pm 5\%$ of the coarse fraction and $29\% \pm 7\%$ for the fine fraction. We then multiplied the total dry mass of the fine and coarse fraction by their respective LOI proportions to obtain the fine and coarse plant biomass. The sum of the fine and coarse biomass per unit of soil volume (i.e., the volume of the soil before the biomass and the mud were separated) is

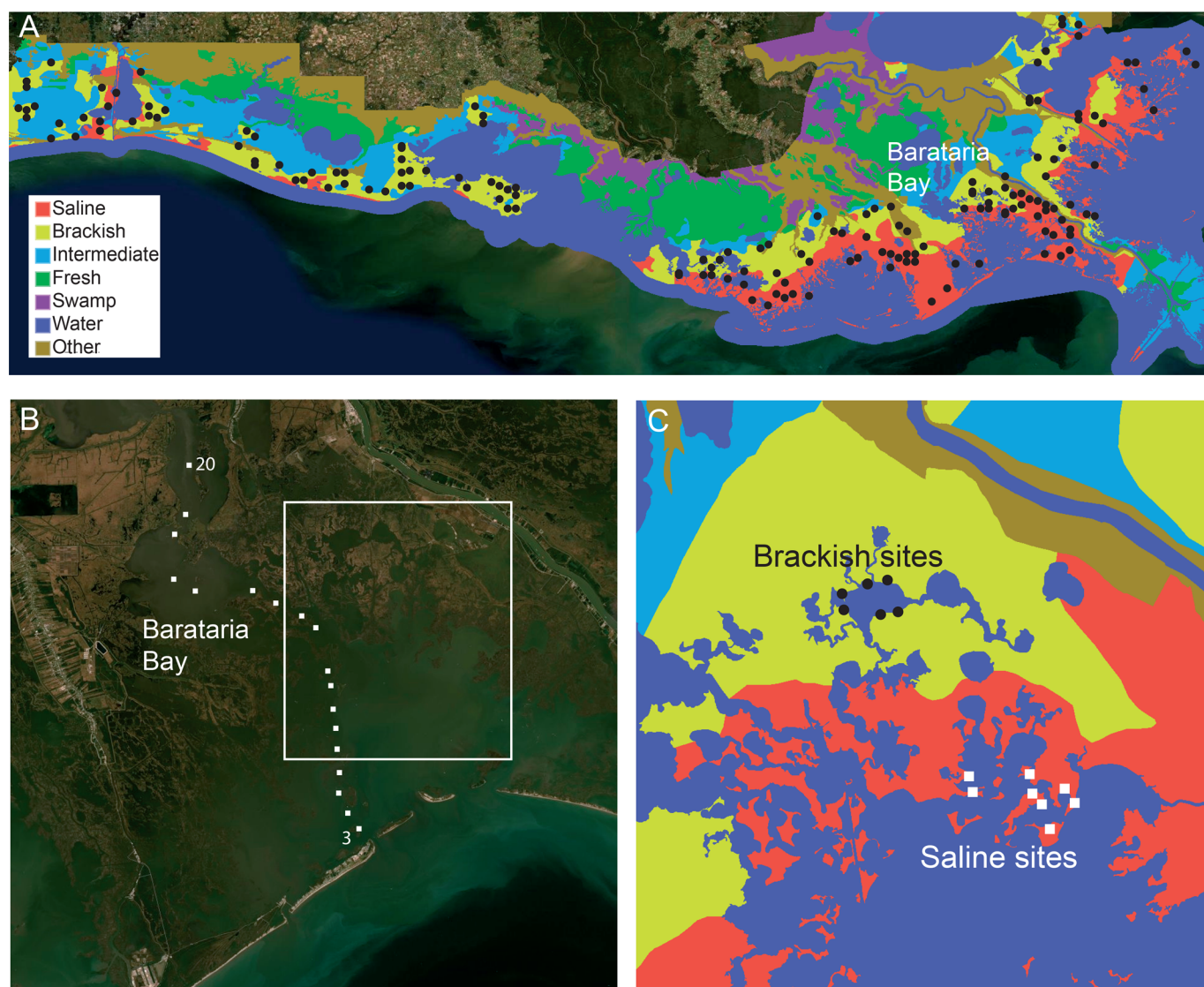


Fig. 1. (A) Map of the study area: the Mississippi Delta and Chenier Plain in coastal Louisiana. (A) The black dots represent sites included in the CRMS dataset (each dot includes three coring locations). The vegetation map was obtained from https://lacoast.gov/crms_viewer/Map/CRMSViewer. (B) Map of Barataria Bay. The white dots represent the sampling stations for the suspended sediments, which are numbered from 3 to 20 (Fig. 8). The image is from NASA and GoogleEarth. (C) Detail of the study area in Barataria Bay. Circles and squares represent the location of soil cores collected for this study (each symbol includes three coring locations).

defined as the biomass-associated volumetric organic content of the soil (OM_{plant}), and is commonly referred to as below-ground biomass. No sand was found in the residue of the combusted fine and coarse fraction, therefore sand was not considered a component of the inorganic material in our samples.

We estimated the mud OM content (LOI_{mud}) using two methodologies. For the first method, we directly measured loss on ignition (by combusting for 4 h at 550°C) of the mud fraction of 18 samples randomly selected samples. For the second method, we used a mass balance approach by calculating the LOI_{mud} using the following formula

$$LOI_{mud} = \frac{\rho_{soil} LOI_{soil} - OM_{plant}}{\rho_{soil} - OM_{plant}}, \quad (1)$$

The strong relationship between these two independent methods of LOI_{mud} estimation shows that the indirect method is reliable (Fig. 2).

The mud dry bulk density was then calculated using the formula

$$\rho_{mud} = \frac{\rho_{soil} - OM_{plant}}{1 - OM_{plant}/\rho_{plant}}, \quad (2)$$

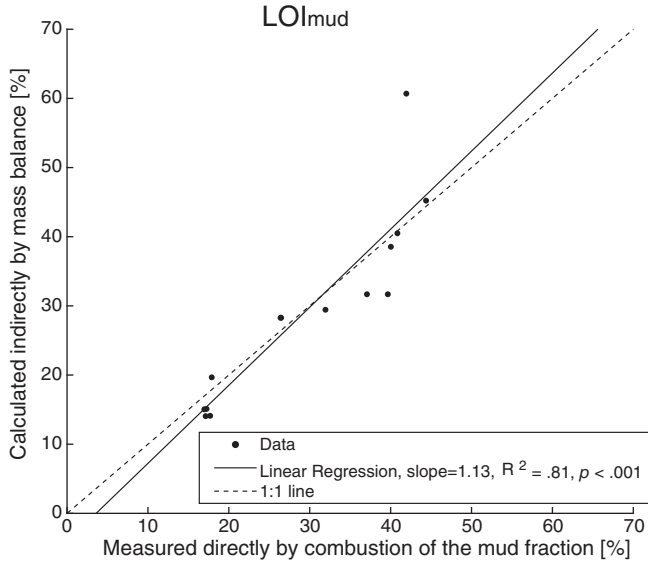


Fig. 2. Comparison of the measured LOI_{mud} from the marshes of Barataria Bay obtained through the direct method and the indirect method (i.e., by measuring the belowground biomass and using Eq. 1).

which requires an estimate of the dry bulk density of the plants (ρ_{plant}), which is the plant biomass per unit of plant biomass volume. Intuitively, ρ_{plant} is the dry bulk density of roots and rhizomes before they are combined in the soil with the mud. Put differently, ρ_{plant} is an intrinsic characteristic of the plants and it is assumed to be nearly constant (at least in the surface layers). On the contrary, OM_{plant} is a derived characteristic of the soil and depends on the mixing between different constituents (e.g., plant biomass and mud). OM_{plant} is always smaller than ρ_{plant} , and only if neither mud nor sand were present in the soil OM_{plant} would be equal to ρ_{plant} . Because ρ_{plant} cannot be measured directly, we consider a range from 55 to 75 kg m⁻³, which is consistent with previous findings (Turner et al. 2002).

Mixing model with three constituents: organic mud, plant material, and sand

We formulate a model to estimate LOI_{mud} using only a dataset of paired soil dry bulk density and OM content. We assume that the OM present in the marsh is from one of two sources: the OM from in situ plant productivity and the OM associated with mud. Even though the latter can be composed of a variety of sources, including recycled particulate matter as well as new production from algae and autotrophic bacteria, for simplicity, we group them together into a single term. Hereafter, we use the term “mud” to refer to any material with a size smaller than 64 μ m, which thus includes both the organic and inorganic components of the mud, and we use the term “mud OM” to refer to the organic component of the mud. Accordingly, the dry bulk density of the soil reads

$$\rho_{soil} = \left[\left(\frac{LOI_{soil} - LOI_{mud}}{1 - LOI_{mud}} \frac{1}{\rho_{plant}} \right) + \left(\frac{1 - LOI_{soil}}{1 - LOI_{mud}} \frac{1}{\rho_{mud}} \right) \right]^{-1} \quad LOI_{soil} \geq LOI_{mud}, \quad (3)$$

This model is only valid for LOI_{soil} greater than LOI_{mud} and cannot explain dry bulk densities higher than the dry bulk density of mud. The model is extended to predict higher dry bulk densities by assuming the presence of sand as a third constituent in the soil mixture. For simplicity, we assume that sand is present only for LOI_{soil} lower than LOI_{mud} , and that plant material is not present for LOI_{soil} lower than LOI_{mud} , as mixing models illustrate little to no OM content at bulk densities greater than 1.7 g cm⁻³ (Morris et al. 2016). We thus formulate a mixing model between sand and mud

$$\rho_{soil} = \left[\left(\frac{LOI_{mud} - LOI_{soil}}{LOI_{mud}} \frac{1}{\rho_{sand}} \right) + \left(\frac{LOI_{soil}}{LOI_{mud}} \frac{1}{\rho_{mud}} \right) \right]^{-1} \quad LOI_{soil} < LOI_{mud}, \quad (4)$$

where ρ_{sand} is the dry bulk density of sand.

According to this model, the volumetric organic content can be partitioned into mud and plant components

$$OM_{mud} = \frac{\frac{(1 - LOI_{soil})LOI_{mud}}{\left[\frac{LOI_{soil} - LOI_{mud}}{\rho_{plant}} \right] + \left[\frac{1 - LOI_{soil}}{\rho_{mud}} \right]}}{LOI_{soil}(1 - LOI_{mud})} \quad LOI_{soil} \geq LOI_{mud}, \quad LOI_{soil} < LOI_{mud}, \quad (5)$$

$$OM_{plant} = \frac{\frac{LOI_{soil} - LOI_{mud}}{\left[\frac{LOI_{soil} - LOI_{mud}}{\rho_{plant}} \right] + \left[\frac{1 - LOI_{soil}}{\rho_{mud}} \right]}}{0} \quad LOI_{soil} \geq LOI_{mud}, \quad LOI_{soil} < LOI_{mud}, \quad (6)$$

where OM_{mud} is the mass of the organic fraction of the mud per unit of soil volume, and OM_{plant} is the mass of the OM associated with plants per unit of soil volume. Similarly, the contribution of the mud and plants to the soil volume are $V_{mud} = \frac{OM_{mud}}{LOI_{mud}\rho_{mud}}$ and $V_{plant} = \frac{OM_{plant}}{\rho_{plant}}$.

Following a previous study (Morris et al. 2016), this model can be fit to datasets of paired dry bulk density and LOI_{soil} to estimate the unknown parameters. For simplicity, we fix the dry bulk density of sand to 1990 kg m⁻³ (Morris et al. 2016). Assuming a specific density of 2650 kg m⁻³, this corresponds to a porosity of 20%, which is nearly the minimum achievable

by well-packed sand (Manger 1963). We also fix the dry bulk density of mud as informed by field measurements (Eq. 2).

The remaining variables are LOI_{mud} and ρ_{plant} , which are determined by minimizing the mean square difference between the measured and modeled volumetric OM content (which is equal to the product of dry bulk density and OM content). This analysis is performed using the Coastwide Reference Monitoring System (CRMS) dataset from Louisiana marshes (all of which are within the Mississippi Delta and the Chenier Plain). The dataset includes 76 salt marshes and 91 brackish marshes, spanning an area of $\sim 20,000 \text{ km}^2$ (CPRA 2019) (Fig. 1). At each marsh, three cores were collected and each core was divided into six 4 cm thick sections up to a depth of 24 cm. Thus, the datasets contain 3006 paired values of soil dry bulk density and OM content, all collected and analyzed within the last 10 yr using a consistent procedure.

Predictive model for vertical accretion and organic accumulation

We consider a simple model for marsh accretion that includes both the contribution from in situ plant production (D_{plant}) [L/T] and by mud deposition (D_{mud}) [L/T]. Deposition by in situ plant production is formulated as $D_{\text{plant}} = D_{\text{pmax}} \cdot B$,

where B is the function that describes the variability with marsh elevation, formulated as a parabola set equal to zero at elevations lower than MSL and higher than MHW, and equal to one midway between MSL and MHW (Morris et al. 2002). D_{pmax} [L/T] is the maximum deposition by in situ plant production, here set equal to 6 mm yr^{-1} , which is consistent with previous estimates (Morris et al. 2016) if the maximum below-ground plant production is set equal to $5 \text{ kg m}^{-2} \text{ yr}^{-1}$ as suggested by rates measured in some Mid Atlantic US marshes (Roman and Daiber 1984; Wigand 2008). For the mud accretion, we use $D_{\text{mud}} = hC/(T\rho_{\text{mud}})$, where h is the water depth on the marsh at high tide, C is the suspended sediment concentration (which includes both inorganic and organic sediments), and T is the tidal period. In order to represent typical conditions for coastal Louisiana, the tidal range is assumed equal to 0.7 m, thus including the meteorological tides in addition to the astronomic tide (Mariotti 2016), and the tidal period is set equal to 24 h.

The key assumption made in this model—absent in previous models of marsh evolution (Fagherazzi et al. 2012)—is that the mud that deposits on the marsh surface has a certain amount of OM associated with it (i.e., $\text{LOI}_{\text{mud}} > 0$). The rate of OM accumulation by mud is thus $D_{\text{mud}} \cdot \rho_{\text{mud}} \cdot \text{LOI}_{\text{mud}}$, the rate of OM

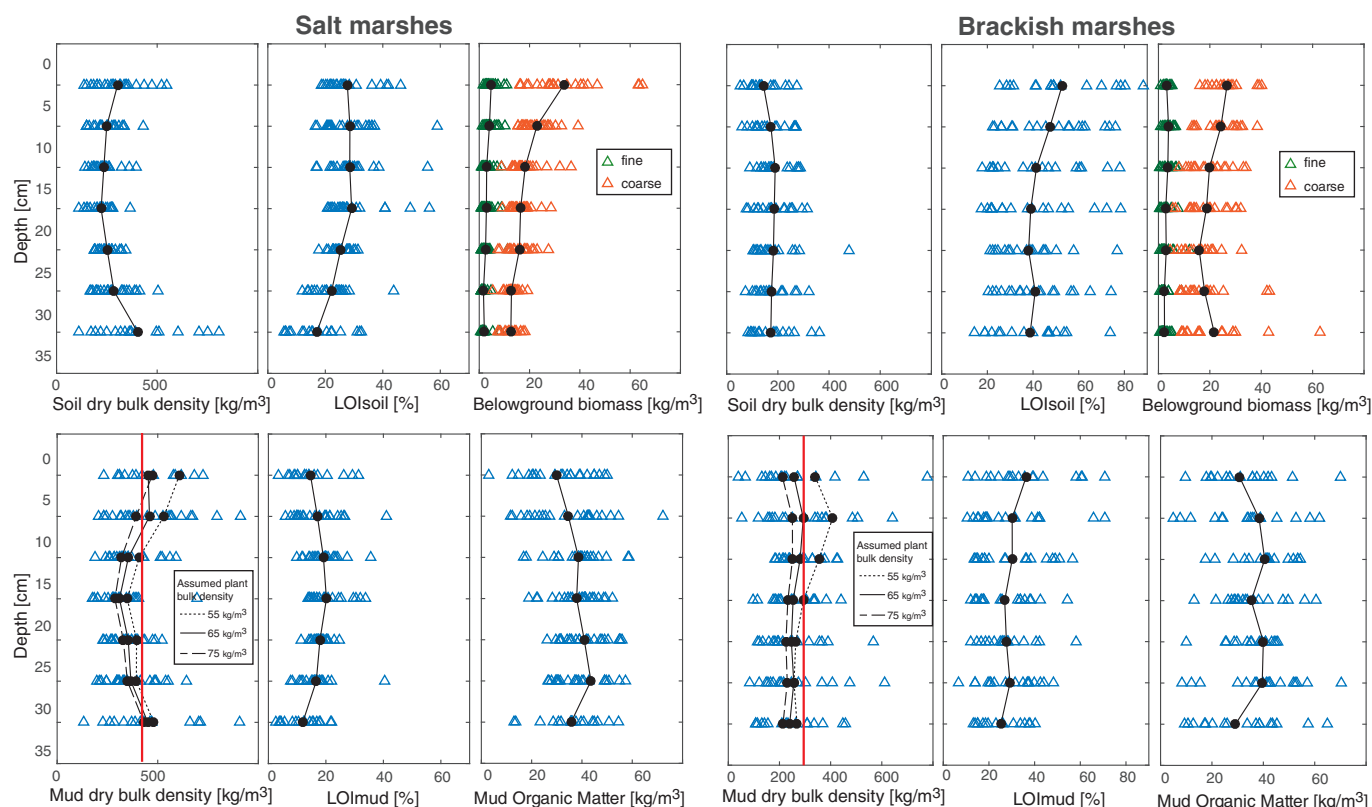


Fig. 3. Field measurements from the salt and brackish marshes in Barataria Bay (Fig. 1C). The top panels are the soil properties (soil dry bulk density, soil OM content, and belowground biomass per unit of soil volume). The bottom panels are properties related to the mud fraction (mud dry bulk density, LOI_{mud} , and mud OM content per unit of soil volume). The triangles are individual measurements, the solid circles indicate the mean value at each depth. The triangles in the mud dry bulk density panel are calculated assuming a plant dry bulk density of 65 kg m^{-3} . The red lines in the mud dry bulk density panels indicate the value assumed for the interpretation of the CRMS dataset (450 kg m^{-3} for the salt marshes and 300 kg m^{-3} for the brackish marshes).

accumulation by in situ plant production is $D_{\text{plant}} \cdot \rho_{\text{plant}}$, and the rate of inorganic accumulation is $D_{\text{mud}} \cdot \rho_{\text{mud}} (1 - \text{LOI}_{\text{mud}})$.

Results

Field data for the marshes in Barataria Bay

Salt marshes in Barataria Bay have a dry bulk density of $270 \pm 110 \text{ kg m}^{-3}$ and a LOI_{soil} of $26\% \pm 8\%$, whereas brackish marshes have dry bulk density of $170 \pm 70 \text{ kg m}^{-3}$ and a LOI_{soil} of $43\% \pm 18\%$ (Fig. 3). Overall, these values are in range of the values from the CRMS dataset, which includes a much larger number of samples over a broader spatial scale (Fig. 4).

For both the salt and brackish marshes, belowground biomass is greater at the surface (equal to $\sim 30 \text{ kg m}^{-3}$) and decreases with depth ($\sim 20 \text{ kg m}^{-3}$). Both salt and brackish marshes have, on average, a similar belowground biomass ($25 \pm 9 \text{ kg m}^{-3}$ for the former and $28 \pm 12 \text{ kg m}^{-3}$ for the latter).

For both the salt and brackish marshes, LOI_{mud} varies little with depth (averaging $17\% \pm 7\%$ in the salt and $28\% \pm 14\%$ in the brackish). Despite the higher LOI_{mud} in brackish marshes, salt marsh soils have an amount of mud OM content per unit of soil volume that is similar that of brackish marsh soils ($37 \pm 15 \text{ kg m}^{-3}$ for the salt and $37 \pm 18 \text{ kg m}^{-3}$ for the brackish). Also, in both marshes the amount of mud OM per

unit of soil volume is relatively constant with depth. Considering all the samples in Barataria Bay, mud contributes to 60% of the total OM in salt marshes and to 57% of the total OM in brackish marshes over the top 35 cm of the soil column.

The estimation of the dry bulk density of the mud fraction requires us to assume the dry bulk density of the plant fraction (ρ_{plant}). The estimated mud dry bulk density increases as the assumed plant dry bulk density decreases, but the variability associated with this uncertainty is comparable to the variability among different samples (Fig. 4). Despite this uncertainty, it is clear that the dry bulk density of the mud for the salt marsh is higher ($\sim 450 \text{ kg m}^{-3}$) than for the brackish marshes ($\sim 300 \text{ kg m}^{-3}$). There is not clear trend with depth (at least over the top 35 cm), and therefore we assume that the dry bulk density is constant over the depth. We thus conduct the analysis considering these fixed values, and we then perform a sensitivity analysis.

Mixing model applied to the CRMS dataset

We fit the mixing model to the CRMS dataset assuming a constant mud dry bulk density (Fig. 5). For the salt marshes, we find ρ_{plant} equal to 66 kg m^{-3} , which is consistent with previous results (Turner et al. 2002; Morris et al. 2016), and LOI_{mud} equal to 14.4% (Table 1). For the brackish marshes, we find ρ_{plant} equal to 58 kg m^{-3} and LOI_{mud} equal to 22.2% (Table 1). As a sensitivity analysis, we repeat the same

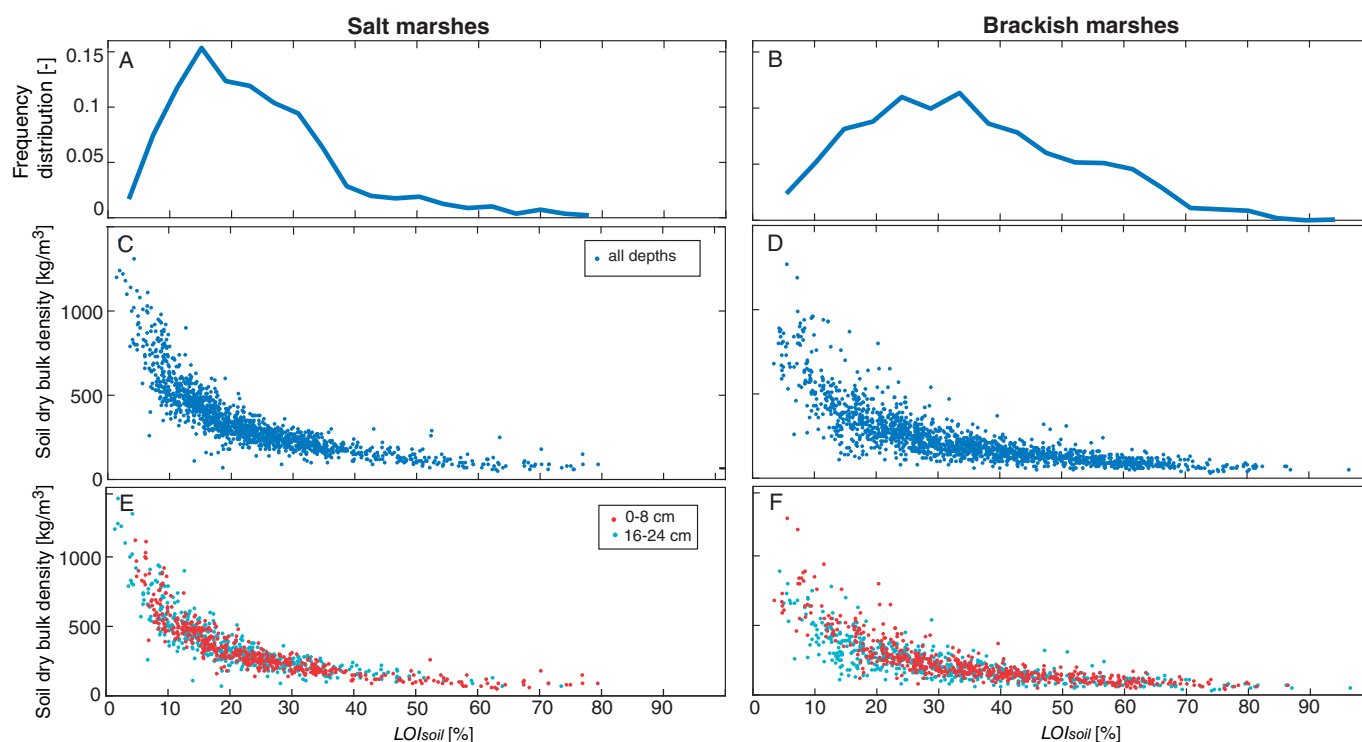


Fig. 4. Soil properties of the salt and brackish marshes from the CRMS dataset (Fig. 1A). (A,B) Frequency distribution of soil OM content. (C,D) Soil dry bulk density as a function of soil OM content. (E,F) Soil dry bulk density as a function of soil OM content separated by depth intervals (only including the upper- and lower-most depth classes to highlight that there is no difference with depth).

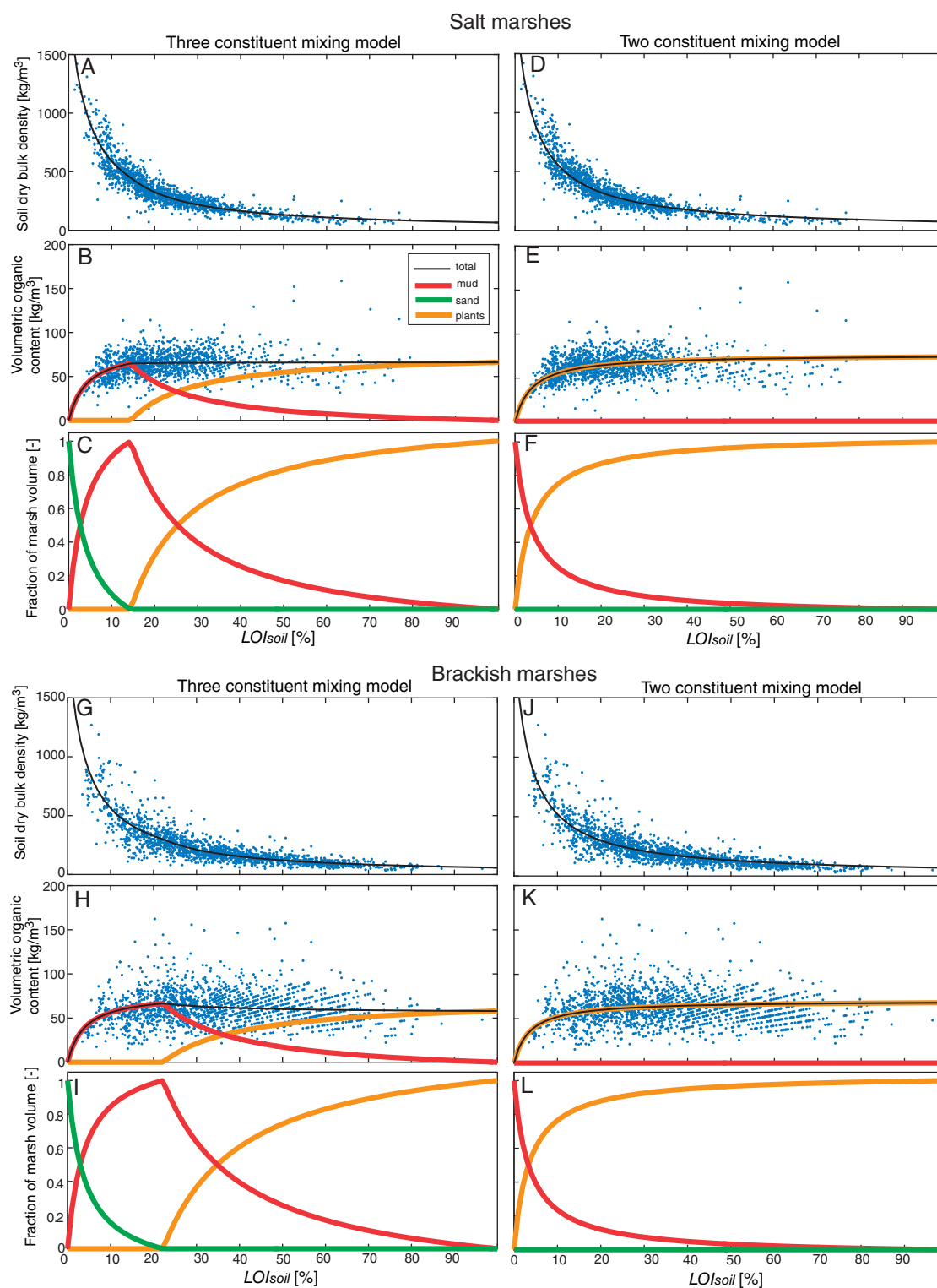


Fig. 5. Interpretation of CRMS dataset (as in Fig. 4) using the two-constituent (A,B,C,G,H,I) and the three-constituent mixing model (D,E,F,J,K,L). The assumed mud dry bulk density is 450 kg m^{-3} for the salt marshes and 300 kg m^{-3} for the brackish marshes. (A,D,G,J) Individual datapoints of bulk density from the CRMS database (as in Fig. 4C,D). (B,E,H,K). Individual datapoints of volumetric organic content (equal to the bulk density multiplied by LOI_{soil}) from the CRMS database. The continuous lines are the predictions from the mixing model. (C,F,I,L) Predicted fraction of marsh volume occupied by the plant, mud, and sand fraction as a function of LOI_{soil} .

Table 1. Estimated plant bulk density and LOI_{mud} for the salt and brackish marsh dataset (CRMS data). The mud bulk density is assumed following the observations in Barataria Bay.

| | Salt marshes (assumed $\rho_{mud}=450\text{ kg m}^{-3}$) | | Brackish marshes (assumed $\rho_{mud}=300\text{ kg m}^{-3}$) | |
|------------|---|-------------------------|---|-------------------------|
| | $\rho_{plant}\text{ (kg m}^{-3}\text{)}$ | $LOI_{mud}\text{ (\%)}$ | $\rho_{plant}\text{ (kg m}^{-3}\text{)}$ | $LOI_{mud}\text{ (\%)}$ |
| All depths | 66 | 14.4 | 58 | 22.2 |
| 0–8 cm | 72 | 13.8 | 60 | 19.5 |
| 8–16 cm | 68 | 14.7 | 58 | 23.4 |
| 16–24 cm | 64 | 14.4 | 58 | 23.4 |

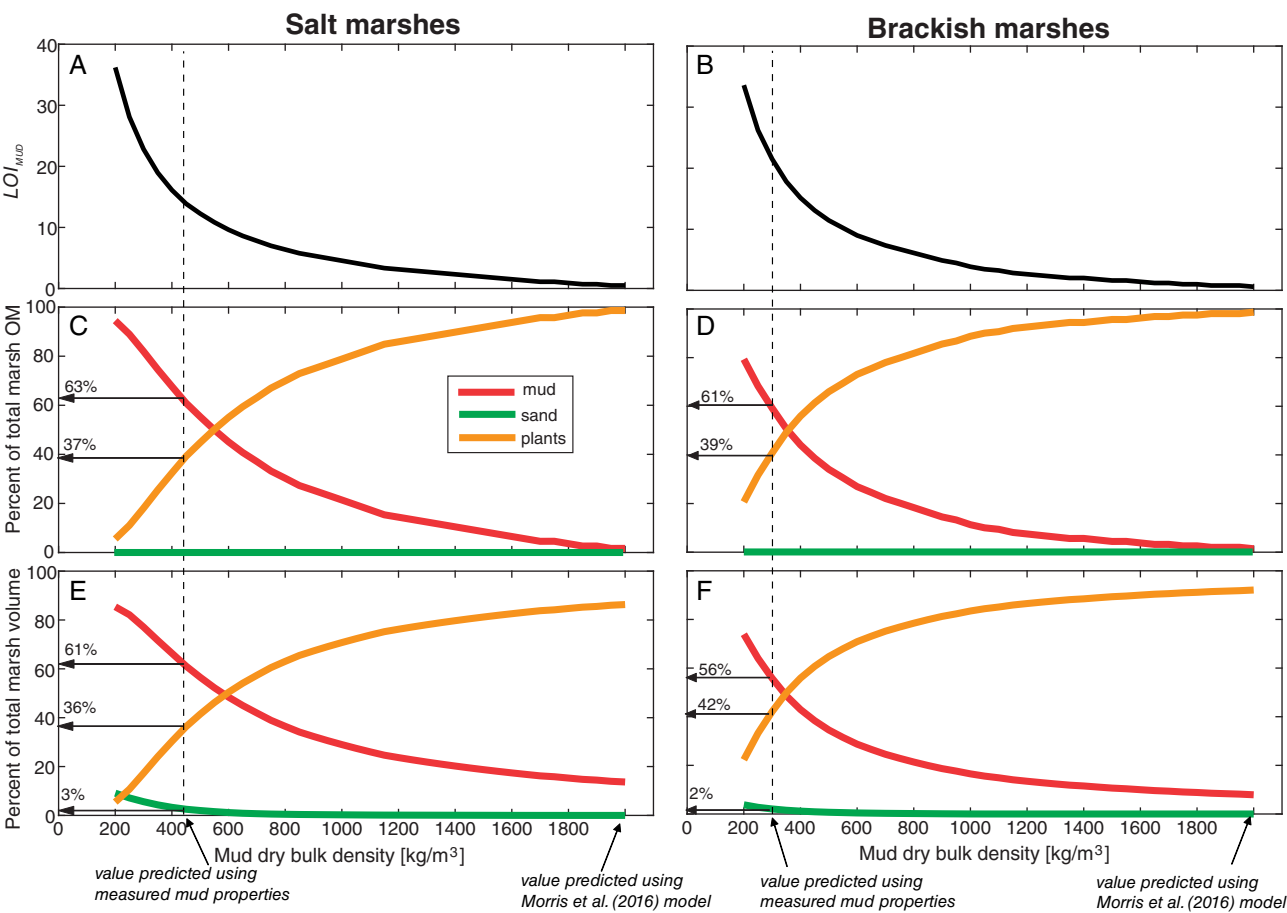


Fig. 6. Estimates for the Louisiana marshes (CRMS dataset) as a function of the assumed mud dry bulk density. The vertical lines indicate the results for a mud dry bulk density of 450 kg m^{-3} for the salt and 300 kg m^{-3} for the brackish marshes (as reported in the text).

data-fitting procedure for estimating LOI_{mud} and ρ_{plant} assuming different mud bulk densities (Fig. 6A,B). In all cases, the estimated plant dry bulk density remains nearly constant (it only increases at most from 66 to 74 kg m^{-3} for the salt marshes and from 58 to 68 kg m^{-3} for the brackish marshes), whereas the estimated LOI_{mud} ranges from 0 to $\sim 30\%$, i.e., it varies by at least an order of magnitude (Fig. 6A,B).

As an extreme case, if we assume that mud has a dry bulk density of 1990 kg m^{-3} (i.e., equal to the dry bulk density of sand), the estimated LOI_{mud} is zero, and the three-constituent

model becomes identical to the two-constituent model (Morris et al. 2016). If we assume that, the mud dry bulk density is 20% higher than the value obtained from the field measurements (i.e., assuming 540 kg m^{-3} for the salt marsh and 360 kg m^{-3} for the brackish marsh), the estimated LOI_{mud} is 10% for the salt marshes and 18% for the brackish marshes.

We repeat the same procedure dividing the CRMS dataset into three depth categories ($0\text{--}8$, $8\text{--}16$, and $16\text{--}24\text{ cm}$) assuming the same mud dry bulk density for all depths (Table 1). For the salt marshes, plant dry bulk density decreased with depth

(from 72 to 62 kg m⁻³) whereas LOI_{mud} remained remarkably constant (varies between 15.9% and 16.8%). For the brackish marshes, both the plant dry bulk density and the LOI_{mud} are relatively constant with depth.

The low values for the mud dry bulk density (300–500 kg m⁻³) are motivated by the fact that we are considering recently deposited sediments (i.e., the top ~ 30 cm layer). It is well known that the dry bulk density of both mud and plant material would increase with time (and with depth) as the soil compacts (Zoccarato et al. 2018), and could reach dry bulk densities up to 1600 kg m⁻³ (Bomer et al. 2019). Yet, this increase in dry bulk density with depth does not affect how samples from the surface layers are interpreted. The increase in dry bulk density with depth is instead included as a shallow subsidence effect, which results in a large RSRL rate (on the order of 10 mm yr⁻¹).

Comparison between the two-constituent and three-constituent mixing models

The ability of the our three-constituent mixing model to explain the measured dry bulk density is virtually identical to that of the two-constituent mixing model (Morris et al. 2016) (Fig. 5). However, by partitioning the OM into two sources—one associated with *in-situ* plant productivity and the other broadly associated with suspended sediment mud deposition (which is often referred to as “inorganic deposition”)—our interpretation of the measured data is substantially different.

According to our three-constituent model, mud OM is highest for marshes with intermediate LOI_{soil} (Fig. 5B,H); in marshes with high LOI_{soil} the accumulation is mostly due to plant production, whereas in marshes with very low LOI_{soil} the deposition of sand limits the available space for mud.

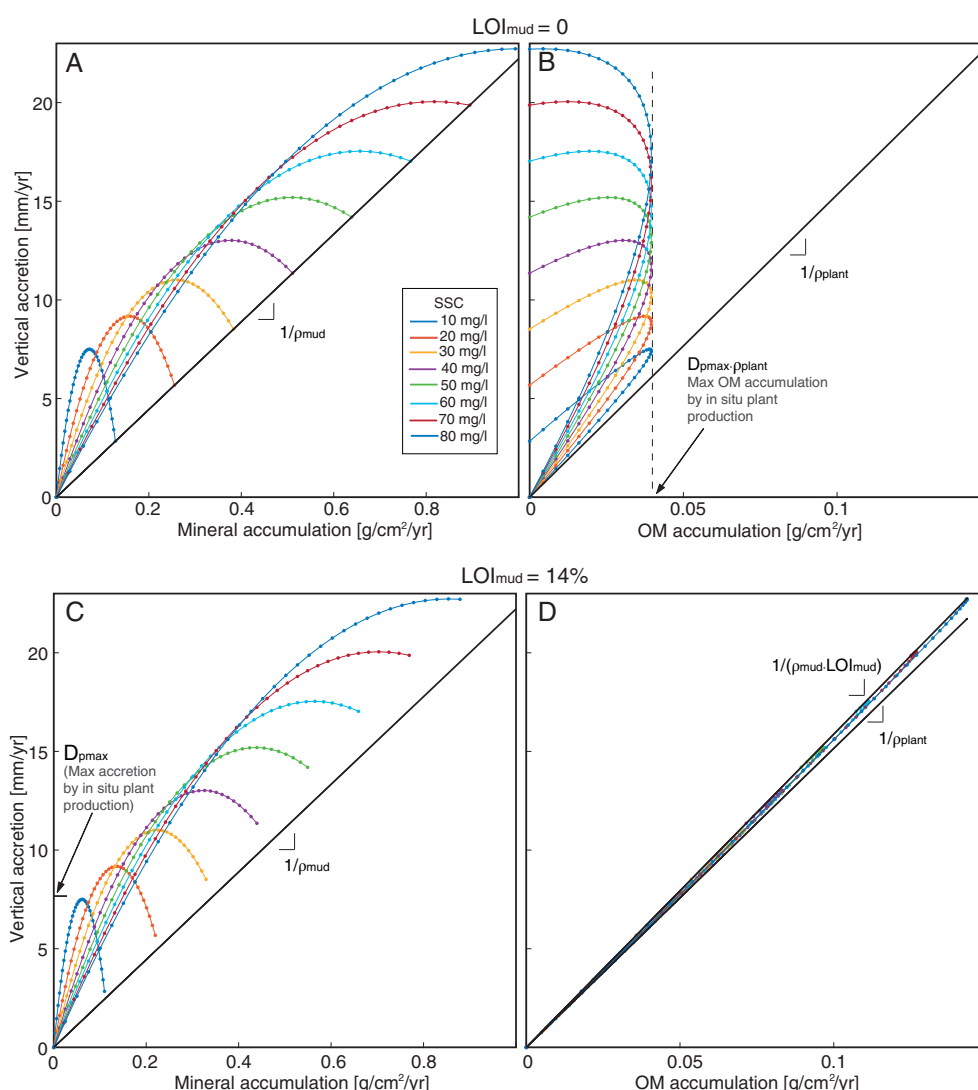


Fig. 7. Model predictions assuming plant dry bulk density of 66 kg m⁻³ and mud dry bulk density of 450 kg m⁻³. Each colored line represents a different sediment supply; each dot along the same colored line indicates a different marsh elevation between MSL and MHW. **(A,B)** Predictions assuming LOI_{mud} equal to zero (i.e., mud accumulation only adds inorganic material). **(C,D)** Model prediction assuming LOI_{mud} equal to 14%. Note that all the curves in panel **(D)** collapse together, i.e., OM accumulation is a good predictor for vertical accretion.

According to the two-constituent model (Fig. 5F,L), plant-derived OM is the major contributor to accretion for any marsh with a LOI_{soil} greater than 4%; our model shows instead that plants are the major contributor to accretion only in marshes with LOI_{soil} greater than 25% for salt marshes and 35% for brackish marshes (Fig. 5C,I).

To put this interpretation into perspective, most marshes in the CRMS dataset tend to have an LOI_{soil} between 10 and 40% (Fig. 4A,B). We calculate the average contribution of the mud OM by weighting the estimated volumetric organic content (Fig. 5C,D) by the frequency distribution of the LOI_{soil} (Fig. 4A,B). Based on this frequency distribution, 63% of the total OM is due to the mud in the salt marshes and 61% of the total OM is due to the mud in the brackish marshes. A similar weighting is performed to estimate the contribution of mud to vertical accretion. For the salt marshes, we estimate that 61% of the total accretion is due to the mud, 36% is due to plants, and 3% is due to sand. For the brackish marshes, we estimate that 56% of the total accretion is due to the mud, 42% is due to plants, and 2% is due to sand.

We repeat this weighted estimate by considering different values for the mud dry bulk density (which is the most uncertain parameter) and for the corresponding LOI_{mud} as estimated by the mixing model (Fig. 6A,B). We find that the mud contribution to OM and vertical accretion decreases as the assumed mud dry bulk density increases (Fig. 6C,D,E,F). Noticeably, if we assume that the mud has a dry bulk density of 1990 kg m^{-3} , the model predicts no contribution from mud to OM accumulation, which is the implicit result of the two-constituent model (Morris et al. 2016). If we assume that the

dry bulk density of the mud is 20% higher than that estimated from our measurements (i.e., assuming 540 kg m^{-3} for the salt marsh and 360 kg m^{-3} for the brackish marsh), mud still contributes to $\sim 50\%$ of the total OM accumulation and to $\sim 50\%$ of the total vertical accretion.

Predictions from the marsh evolution model

The theoretical marsh evolution model is run using the values of ρ_{plant} and ρ_{mud} found for the salt marshes (66 kg m^{-3} and 450 kg m^{-3}), and by considering a range of marsh elevations (from MSL to MHW) and suspended sediment concentration (from 5 to 80 mg L^{-1}). Considering different elevations and suspended sediment concentrations effectively allows us to reproduce a wide range of mud deposition (D_{mud}) and in situ plant production (D_{plant}) rates, which together give a range of vertical accretion rates between 0 and 25 mm yr^{-1} , which matches the $12.7 \pm 10.0 \text{ mm yr}^{-1}$ measured in salt and brackish marshes in coastal Louisiana (Jankowski et al. 2017).

If LOI_{mud} is set equal to zero—the implicit assumption of previous marsh models (Morris et al. 2002; Fagherazzi et al. 2012)—neither inorganic nor organic accumulation are reliable predictors for vertical accretion across all environmental settings (Fig. 7A,B). On the other hand, if LOI_{mud} is set equal to 14%, inorganic accumulation still does not predict vertical accretion, whereas organic accumulation predicts it well, i.e., it has a linear correlation with a small scatter (Fig. 7C,D).

Discussion

Can mud OM originate from in situ plant production?

The decay of roots and rhizomes produced by plants in situ could contribute to a portion of the OM pool associated with mud. The majority of this decay occurs within the top 20–30 cm where aerobic conditions are more prevalent (Howes et al. 1985; Hemminga et al. 1988). Our measurements, which only separate OM based on size, do not allow for a clear source determination. Nevertheless, we present four lines of evidence suggesting that the mud-associated OM does not only originate from the decay of in situ plant material.

First, the mud OM content is relatively constant with depth and varies little from that on the marsh surface. This contrasts with our expectations under the assumption that mud OM originates from in situ produced plant material, in that the surface mud would be expected to have very low OM, which would increase with depth as new smaller plant particles would be added to the mud OM pool through fragmentation.

Second, despite a decrease in coarse plant biomass with depth—likely due to decomposition—neither fine-sized biomass ($64 \mu\text{m}$ to 2 mm) nor mud OM density shows a complementary increase with depth. Thus, if the mud OM was derived from degradation of coarse belowground material, this process should directly transform coarse size material into fine or mud sized material. The decline in coarse OM without a

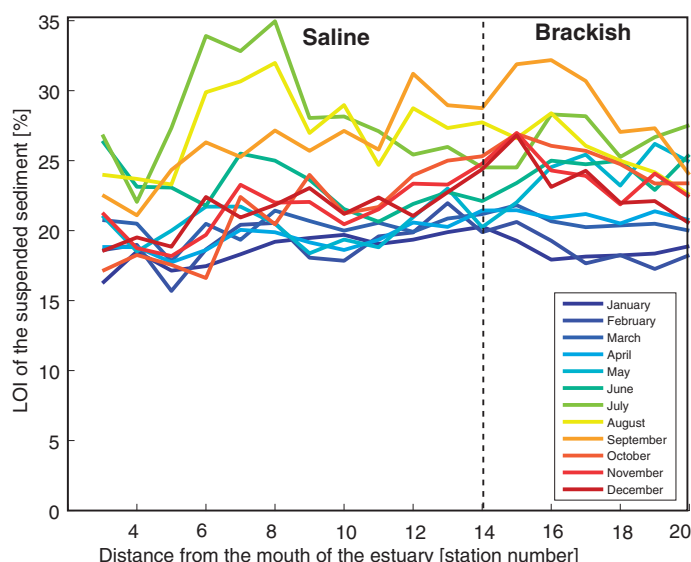


Fig. 8. Measured OM content of the suspended sediment at different stations along Barataria Bay (Fig. 1B). Measurements were collected at each station once a month over a 22 yr period (1994–2015). For each station and each month, the median value over the 22 yr is reported (Turner et al. 2019).

significant increase in fine OM pools at depth suggests that fixed carbon associated with coarse biomass is lost through oxidation just below the marsh surface.

Third, independent observations support the hypothesis that the mud OM was deposited contemporaneously with the mud. In a survey of monthly measurements of water quality in Barataria Bay for over 22 yr, the OM content of the suspended sediment averaged $20\% \pm 5\%$ throughout the year (Fig. 1B) (Turner et al. 2019) (Fig. 8), which matches the OM content of the deposited mud. Given the high accretion rates in Louisiana marshes (Jankowski et al. 2017), this OM could deposit on the marsh surface and be buried in a relatively short time.

Fourth, previous field measurements indicate that the LOI_{soil} of recently deposited sediment (i.e., the top 1 cm) in a brackish marsh in Terrebonne Bay was $20\% \pm 3\%$ (Cahoon and Reed 1995). They also found that the accretion of OM was strongly correlated to the deposition of suspended sediment, and thus concluded that this OM was derived from deposition of allochthonous material and not from in situ plant production.

Even if some of the mud OM originates from the degradation of plant OM produced in situ, there is strong evidence to conclude that the majority of the mud OM in the top 30 cm of the marsh column originates from mud deposition.

Consequences for marsh vertical accretion

The extraordinary ability of mud to contribute to marsh accretion can be explained by its porosity. It is well known that most of the volume in salt marshes (70–90%) is comprised of porespace, which is generally saturated with water (Nyman et al. 1990). This porespace has been assumed to be mainly associated with plant material, given that most of the volume ($\sim 95\%$) occupied by roots and rhizomes is made up of porespace. On the other hand, inorganic material is often assumed to have a very small porosity. This assumption might hold for sand (which has a porosity of 20–40%), but it does not hold for mud. According to our measurements, the porosity of mud is 85–90%. Thus, similar to plant tissues, most of the volume occupied by mud is comprised of porespace. The relatively high porosity of mud (compared to sand) combined with its large abundance in the soil (compared to plants) indicates that it plays a significant role in influencing soil volume.

The extent to which mud contributes to the total soil volume varies depending on the amount of plant material in the soil. Our results illustrate that plants contribute to most of the volume (i.e. 80–100% of the total volume) in marshes with very high LOI_{soil} (i.e., $LOI_{soil} > 60\%$) (Fig. 5). These represent the paradigmatic peat-dominated marshes in which the loss of roots and rhizomes through decomposition causes a rapid elevation loss, also known as “peat collapse” (DeLaune et al. 1994). On the other hand, mud is predicted to be the main contributor to the volume in marshes with low LOI_{soil} (i.e., $LOI_{soil} < 30\%$). Put differently, some marshes might

accrete mainly by “vegetative growth” (Nyman et al. 2006), but this is not necessarily the case for all marshes.

Marshes exhibit high spatial variability; some have a very large LOI_{soil} (and thus their volume is mostly associated with plants) and some have a low LOI_{soil} (and thus their volume is mostly associated with mud). Considering the frequency distribution of LOI_{soil} among the 71 salt marshes and the 91 brackish marshes from the CRMS dataset, we show that mud contributes to an average of $\sim 60\%$ of the soil volume. This value is much higher than the $\sim 14\%$ estimated by using the two-constituent mixing model (Morris et al. 2016), in which sand and inorganic mud components are lumped together into a single constituent.

Our finding that mud has a low dry bulk density should not be surprising. Even without the results from the field measurements, a dry bulk density of $\sim 450 \text{ kg m}^{-3}$ could have been justified by considering the analogy with mudflats (Austen et al. 1999; Whitehouse et al. 2000; Bale et al. 2007; Wheatcroft et al. 2013), and by considering that marshes have a relatively low overburden (given that some of the volume is occupied by low density plant material), and thus mud should not compress greatly. As such, we conclude that the three-constituent mixing model can be applied to other marshes upon a reasonable assumption of the value of mud dry bulk density (possibly higher than 450 kg m^{-3} but definitely much smaller than 1990 kg m^{-3}).

We emphasize that our argument focuses on the relative contribution of mud and plants to vertical accretion in the top $\sim 30 \text{ cm}$ of the soil. As already pointed out, mud would compact with time, i.e., it would attain a higher dry bulk density than $300\text{--}500 \text{ kg m}^{-3}$. Yet, plant biomass is also subjected to compaction, and might compact even more than mud (Brain et al. 2012). Thus, if longer time scales are considered (i.e., deeper soils), we expect that the relative contribution of mud would be even larger than that estimated using the surface layers. In other words, if we could partition the shallow subsidence into an equivalent reduction of the vertical accretion by mud and plants estimated from the surface layers, the reduction for the plant component would be larger than for the mud component.

We also emphasize that the high porosity of mud is not necessarily caused by the presence of OM in the mud fraction, but rather by the structure of the clay particles. Clay particles such as smectite, which is the dominant clay type in Louisiana marshes (Stewart 1990), create a very porous lattice. As such, even a purely inorganic mud (i.e., $LOI_{mud} = 0$) could have a very high porosity. Thus, the OM associated with the mud directly contributes to a relatively small amount of vertical accretion. Nevertheless, mud-associated OM plays an indirect role in predicting marsh dynamics because it allows the mixing model to reconcile a low mud dry bulk density with the observed relationship between LOI_{soil} and ρ_{soil} . Put differently, the presence of mud-associated OM is a necessary ingredient to provide a theoretically consistent alternative to the

two-constituent mixing model (Morris et al. 2016) and to refute the paradigm that all inorganic material has a high dry bulk density and thus marginally contributes to marsh vertical accretion.

Consequences for marsh OM accumulation

Our analysis does not affect previous data-driven estimates of the total OM stock and accumulation rates in marshes (Boyd et al. 2017; Callaway et al. 2012; DeLaune and White, 2012; Neubauer 2008). On the other hand, our analysis challenges the interpretation of the OM accumulation being due solely to in situ plant productivity and the use of models that rely upon in situ plant productivity alone for organic matter inputs. Instead, we estimate that in the salt and brackish marshes of Louisiana (as sampled through the CRMS dataset), ~ 60% of the OM is associated with mud deposition. This value, estimated using the mixing model, squarely matches the value obtained by direct measurements from the 14 marsh sites in Barataria Bay (~ 60%), thus reinforcing the validity of our methods.

The key to understanding how mud can contribute to such a large amount of OM is to consider its volumetric OM content. The mud OM content ($LOI_{mud} = 14\text{--}22\%$) is much smaller than the plant OM content. Yet, mud is about six times denser than plants ($300\text{--}450\text{ kg m}^{-3}$ compared to $58\text{--}66\text{ kg m}^{-3}$), and thus more mass is packed into the same volume.

The model predicts that if LOI_{mud} is greater than the value ρ_{plant}/ρ_{mud} , mud is able to store more organic per unit of soil volume than plant-derived OM. This condition is present in the brackish marshes, where $LOI_{mud} = 22.2\%$ and $\rho_{plant}/\rho_{mud} = 19.3\%$. As predicted by the model, we observe in the CRMS dataset that marshes with a higher LOI_{soil} (i.e., a larger amount of plant material) have a slightly smaller volumetric OM content than marshes with a low LOI_{soil} (Fig. 5). Noticeably, this trend cannot be captured by the two-constituent model, which predicts a monotonic increase in volumetric OM content with increasing LOI_{soil} (Fig. 5).

Causal link between OM accumulation and vertical accretion

It is well established that vertical accretion is more highly correlated with OM accumulation than with inorganic accumulation. This trend was found both in salt (Turner et al. 2002) and fresh marshes (Neubauer 2008), as well as in mangroves (Breithaupt et al. 2017). This correlation often leads to the conclusion that in situ plant production (i.e., vegetative growth) controls marsh vertical accretion and that inorganic sedimentation is nearly irrelevant for the fate of marshes.

Our model offers an alternative interpretation. Despite vertical accretion occurring through the independent processes of in situ plant production and mud deposition (i.e., different marshes might accrete by a different proportion of the two mechanisms), we predict a strong correlation between organic

accumulation and vertical accretion (Fig. 7D). The explanation is clear considering that, if $LOI_{mud} = \rho_{plant}/\rho_{mud}$, the volumetric organic content is independent of whether the marsh accretes by in situ plant production or by mud deposition. In this case, the model predicts a perfect correlation between OM accumulation and vertical accretion, with a slope equal to $1/\rho_{plant}$ or equivalently to $1/(\rho_{mud} \cdot LOI_{mud})$. Our measurements confirm that this condition is nearly met in the marshes of Louisiana: $LOI_{mud} = 14\%$ and $\rho_{plant}/\rho_{mud} = 14.7\%$ for the salt marshes, and $LOI_{mud} = 22.2\%$ and $\rho_{plant}/\rho_{mud} = 19.3\%$ for the brackish marshes.

Put differently, OM accumulation predicts vertical accretion because both plant-rich and sediment-rich marshes have nearly identical volumetric OM content. For the former, the OM would be mostly associated with in situ plant production, while for the latter, the OM would be mostly associated with mud. Yet, both types of OM are amalgamated when considering the total OM accumulation. As such, despite the variability of marsh types (plant-rich vs sediment-rich), vertical accretion and OM accumulation would always be tightly correlated. This nearly perfect correlation is indeed reproduced in our model despite having considered a wide range of marsh elevation and suspended sediment concentration (Fig. 7D).

Contrary to the volumetric OM content, the volumetric inorganic content is not constant among marshes: plant-rich marshes have a much lower volumetric inorganic content than sediment-rich marshes. As such, inorganic accumulation and OM accumulation do not always have a tight correlation (Turner et al. 2002), as reproduced in our model while considering a wide range of marsh elevation and suspended sediment concentration (Fig. 7C). Considering an extreme case of marshes that only accrete by in situ plant production (and where this rate could vary because of different plant productivity associated with different marsh elevation), inorganic accumulation would not predict vertical accretion at all. Conversely, for marshes that only accrete by mud deposition, e.g., mudflats, there would be a perfect correlation between vertical accretion and inorganic accumulation.

We emphasize that the assumption about the OM associated with mud is the only aspect of the model that is essential to support our conclusion. Any other formulation for in situ plant production, i.e., a linear increase or a linear decrease with elevation as opposed to a parabolic relationship, as well as any other formulation for the inorganic accretion as a function of elevation would still give the same correlation between vertical accretion and OM accumulation (Fig. 7D).

Origin of mud OM and its implications for blue carbon policy

Our analysis illustrates that the mud OM in Louisiana marshes does not totally originate from in situ plant production, although the source of the mud OM is not discerned. Two sources are likely candidates: recycled marsh material (allochthonous) or new algal production (autochthonous).

This distinction could be important for considerations about blue carbon crediting (Wollenberg et al. 2018).

Eroded and redeposited allochthonous mud OM would not count as new carbon fixation, and thus would not be considered as carbon sequestration. A counterargument is that the OM lost by marsh erosion is generally considered a carbon loss. For example, a recent study in Barataria Bay estimated that marsh edge erosion releases annually 141 kg of OM per meter of marsh shoreline, and then calculated the equivalent CO₂ emission assuming that all the OM was oxidized (Sapkota and White 2019). Following this assumption, the portion of this eroded OM that would eventually deposit on the marsh should be considered as new carbon sequestration. Only if the eroded marsh was assumed to be recycled (i.e., was not removed from the OM budget), then the OM accumulation by mud deposition should not be considered as new carbon sequestration.

The other potential source of mud OM is photosynthetic algae. First, planktonic algae could deposit on the marsh surface. Second, microphytobenthos could grow on the marsh surface and be slowly buried by sediment deposition. Microphytobenthos has been shown to be extremely important in the food webs of Louisiana, and thus it is at least possible that some of it might also contribute to OM accumulation in salt marshes.

Our measurements and our model are unable to differentiate this contribution, and other biogeochemical techniques might be needed. Future studies that include a combination of ¹⁴C dating to determine the age of the mud-associated OM along with compound specific fatty acid analysis may shed light on the provenance and cycling of organic matter in these systems.

Conclusions

Based on field data in salt and brackish marshes of Louisiana, we found that the dry bulk density of mud is much lower than commonly assumed in numerical models. Due to its high porosity and significant contribution to soil mass, mud was the major contributor to marsh vertical accretion. This result challenges the paradigm that marshes in microtidal settings such as coastal Louisiana accrete mainly by vegetative growth. The low mud dry bulk density is confirmed by simple arguments about clay properties and thus should hold also for marshes outside of Louisiana.

Our measurements indicate that mud is the major contributor to OM accumulation in both salt and brackish marshes. Various lines of evidence suggest that this OM is not produced by the degradation of in situ plant production, but it is instead associated with mud deposition on the marsh surface. This result is able to explain the widespread observation that vertical accretion correlates with OM accumulation, and thus is also likely to hold also for marshes outside of Louisiana.

Our three-constituent mixing model is a simple tool that can estimate the OM content of the mud fraction only using datasets of paired soil dry bulk density and OM content. As such, we suggest that this model could be applied to marshes

elsewhere to examine the relative contribution of plant versus mud OM. The remaining challenge is to systematically quantify the various components of the mud OM (Van de Broek et al. 2018), e.g., from recycled eroded marsh and from autotrophic bacteria, and to separately include them in data-driven estimates and process-based models (Fagherazzi et al. 2012).

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Conflict of Interest

None declared.

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