

Seagrass sediments as a global carbon sink: Isotopic constraints

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[1] Seagrass meadows are highly productive habitats found along many of the world's coastline, providing important services that support the overall functioning of the coastal zone. The organic carbon that accumulates in seagrass meadows is derived not only from seagrass production but from the trapping of other particles, as the seagrass canopies facilitate sedimentation and reduce resuspension. Here we provide a comprehensive synthesis of the available data to obtain a better understanding of the relative contribution of seagrass and other possible sources of organic matter that accumulate in the sediments of seagrass meadows. The data set includes 219 paired analyses of the carbon isotopic composition of seagrass leaves and sediments from 207 seagrass sites at 88 locations worldwide. Using a three source mixing model and literature values for putative sources, we calculate that the average proportional contribution of seagrass to the surface sediment organic carbon pool is ~50%. When using the best available estimates of carbon burial rates in seagrass meadows, our data indicate that between 41 and 66 gC m⁻² yr⁻¹ originates from seagrass production. Using our global average for allochthonous carbon trapped in seagrass sediments together with a recent estimate of global average net community production, we estimate that carbon burial in seagrass meadows is between 48 and 112 Tg yr⁻¹, showing that seagrass meadows are natural hot spots for carbon sequestration.

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1. Introduction

[2] Although seagrass meadows account for only a relatively small area of the coastal ocean (~0.1%), they play an important role in the coastal zone and provide ecosystem goods and services that have been estimated to be of high value compared with other marine and terrestrial habitats [Costanza *et al.*, 1997]. The annual rate of carbon accumulation in seagrass meadows of ~83 gC m⁻² yr⁻¹ [Duarte *et al.*, 2005a] is larger than that in most terrestrial ecosystems [Pidgeon, 2009] and their global carbon burial rates of

27–44 Tg C yr⁻¹ are an important component (10–18%) of the total carbon burial in the ocean. A proportion of the carbon that accumulates in seagrass meadows derives from excess photosynthetic carbon fixation within the meadows, some of which is placed directly into the sediments as roots and rhizomes [Duarte and Cebrián, 1996]. Alongside this direct source of carbon from seagrass tissues, organic matter from other sources accumulates in the sediments due to the seagrass canopies acting as efficient filters, stripping particles from the water column and adding them to the sediment load [Hendriks *et al.*, 2008]. As a result of these processes there is a net transfer of allochthonous carbon to the sediments of seagrass meadows that enhances their capacity for long-term carbon sequestration.

[3] When the major sources of organic matter have distinct isotopic signatures from each other, their individual contribution to the sediment can be successfully resolved through the measurement of the stable isotopic composition ($\delta^{13}\text{C}$) of the sedimentary organic matter ($\delta^{13}\text{C}_{\text{sediment}}$) deposited in seagrass meadows [Fry *et al.*, 1977; Gacia *et al.*, 2002; Kennedy *et al.*, 2004]. For at least half a century [Craig, 1953], the $\delta^{13}\text{C}$ of marine plants, including seagrass, has been known to be isotopically heavy relative to those of other organic matter sources in the coastal zone, such as plankton, seagrass epiphytes, or terrestrial vegetation

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[Moncreiff and Sullivan, 2001]. While carbon sources to specific seagrass meadows in one location, or within a particular region have been reported, as yet there has not been any global synthesis and interpretation of the sources of organic carbon that accumulate in seagrass sediments and their importance in the sequestration of organic carbon. The most comprehensive study thus far [Bouillon and Boschker, 2006] summarized data on seagrass and sediment carbon isotopic composition for 44 seagrass sites from 6 different locations. However, their study was focused on the examination of carbon sources to sediment bacteria and so their data set comprised only a small subset of the currently available data.

[4] Here we examine the $\delta^{13}\text{C}$ of seagrass sediments to elucidate the contribution of seagrass and other putative sources to the sedimentary organic carbon pool, thereby helping to apportion the organic carbon buried in seagrass meadows to different sources. Using a globally distributed data set, analysis of the data is used to obtain a better understanding of the fate of organic matter in seagrass meadows and in elucidating the role of seagrass sediments as carbon sinks of global significance.

2. Methods

[5] We searched the literature for estimates of $\delta^{13}\text{C}_{\text{sediment}}$, organic carbon (C_{org}), and total nitrogen (N_{T}) concentration (as % of dry weight, wt%) for seagrass sediments and adjacent bare sediments. We calculated $\text{C}_{\text{org}}:\text{N}_{\text{T}}$ molar ratios and recorded the dominant species in the seagrass meadow along with the $\delta^{13}\text{C}$ of the aboveground tissues ($\delta^{13}\text{C}_{\text{seagrass}}$). The published reports retrieved, were supplemented by unpublished data derived from the authors' own research. (Data for Cuba provided by C. M. Duarte, data for Florida Keys and Florida Bay provided by J. W. Fourqurean, 2001–2003, data for Ria Formosa provided by H. Kennedy, 2001, and data for Australia (2007–2008) and Spain (2004) provided by M. Holmer.)

[6] In the studies included here sediment samples were usually restricted to the upper 5–10 cm of the sediment column. The sediment had been dried and analyzed either as a bulk sample or sieved to provide different grain size fractions. The largest percentage of samples in the data set are from bulk (83%) analyses, with only 11% of the analyses being made on the fine (<63 micron) fraction. The fine fraction consists of silts and clays and has the highest organic matter content (OM). Analysis of the bulk and fine fraction of five samples from this study showed little difference in isotopic composition ($0.26 \pm 0.9\%$, $n = 5$). In the aboveground biomass of the seagrass, younger leaves with little epiphyte cover were processed without any additional treatment, but older leaves generally had their epiphyte cover removed through scraping with a scalpel blade, or similar tool. The seagrass or sediment was subsequently ground and homogenized, and a subsample acidified to eliminate carbonate material. Fuming or acidification and rinsing, as well as direct acidification in sample cups have all been utilized in the selective removal of calcium carbonate. The fraction of carbon lost by these techniques and any alteration of the isotopic composition of the organic matter during treatment is variable and depends on the

nature and lability of the organic matter being treated [Kennedy et al., 2005]. Hydrochloric acid is mainly used for this purpose and only small artifacts (up to $\sim 0.3\%$) have been reported during method intercomparisons [e.g., Kennedy et al., 2005]. The OM was typically measured from the loss on ignition (at 440–500°C), and sediment C_{org} and N_{T} were measured on acid treated samples using CHN analyzers on their own, or in conjunction with an isotope ratio mass spectrometer. The stable carbon isotopic composition is reported in the δ notation as the ratio of the heavy to the light stable isotope in the sample, R_{sample} , relative to that of a standard, R_{standard} , i.e., $\delta_{\text{sample}} = 1000 [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, with standard = Vienna Pee Dee Bellemnite (VPDB) and $R = {}^{13}\text{C}/{}^{12}\text{C}$. The reproducibility for elemental analysis is generally better than 5% and for stable isotopic analysis usually better than 0.5%. Data sets from each seagrass meadow do not always contain values for each parameter and so the number of data points and the location that the data represent may differ between graphs.

[7] We test for consistent enrichment of C_{org} and N_{T} in seagrass relative to adjacent bare sediments using Wilcoxon's signed-ranks test. Relationships between variables are described using least squares regression analysis type II on log transformed variables. The significance of differences in seagrass contribution to sediment organic matter pools across species is assessed with ANOVA.

3. Results

[8] The data set contained 219 analyses of $\delta^{13}\text{C}_{\text{sediment}}$, which had been collected at 88 locations around the world (Figure 1) and at these locations a total of 207 seagrass sites had been sampled. The data set was dominated by meadows from the Tropical Western Atlantic, Europe and SE Asia and no data were found for seagrass meadows in South America (Figure 1). The $\delta^{13}\text{C}_{\text{seagrass}}$ in the assembled data set spanned a range of values from -19.6% to -4.8% , with a median value of -10.3% (Figure 2a). A subset of the seagrass data (25 observations) were from samples where epiphytes had not been removed prior to stable isotope analysis (Figure 2a). The $\delta^{13}\text{C}_{\text{seagrass}}$ values of this subset were significantly more enriched in ${}^{13}\text{C}$ than the $\delta^{13}\text{C}_{\text{seagrass}}$ of leaves where epiphytes had been removed prior to analysis (mean $-8.7\% \pm 0.2\%$ and $-10.6\% \pm 0.1\%$, respectively; $t = -4.0$, $p < 0.001$). This comparison appears initially to be at odds with other published data sets as epiphytes are isotopically lighter than seagrass leaves [Moncreiff and Sullivan, 2001]. The samples where the epiphyte had not been removed, had all been acidified prior to analysis and so the presence of carbonate was not the cause of the ${}^{13}\text{C}$ enrichment. The subset did represent only a small fraction (0.12) of the total number of observations and consisted of data from six species of seagrass, but predominantly *Thalassia testudinum*. The $\delta^{13}\text{C}$ value for every seagrass species in the subset was not outside the range observed for the rest of the seagrass leaves without epiphytes. Given these constraints we still retain these observations within our subsequent analysis. The $\delta^{13}\text{C}_{\text{sediment}}$ showed a broad range, from -26.6% to -7.3% , with a median ($\pm\text{SE}$) value of $-16.3\% \pm 0.2\%$ (Figure 2b). The distribution of $\delta^{13}\text{C}_{\text{sediment}}$ was consistently shifted



Figure 1. Distribution of seagrass meadows where $\delta^{13}\text{C}_{\text{sediment}}$ has been reported (see Tables S1 and S2 and Text S1).¹

toward lighter values relative to the $\delta^{13}\text{C}_{\text{seagrass}}$ (Figures 2a and 2b), and the differences in $\delta^{13}\text{C}$ between seagrass leaf tissue and sediment ($\Delta^{13}\text{C}_{\text{seagrass-sediment}}$) ranged from -5.4‰ to $+16.9\text{‰}$, with an average of $+6.3\text{‰} \pm 0.2\text{‰}$ (i.e., isotopically lighter sediment than seagrass tissue; see Figure 2c). The average $\delta^{13}\text{C}_{\text{seagrass}}$ for individual species ranged between -14.5‰ (for *Thalassodendron ciliatum*) and -7.1‰ (for *Syringodium filiforme*), whereas the average $\delta^{13}\text{C}_{\text{sediment}}$ of the corresponding meadows spanned a wider range than that of the seagrass leaves, varying between -26.4‰ (for *Zostera japonica* sediments) to -12.9‰ (for *Thalassia testudinum* sediments; see Table 1). Similarly, differences among species in the $\Delta^{13}\text{C}_{\text{seagrass-sediment}}$ values were statistically significant, accounting for 30.5% of the observed variance (ANOVA, $F = 5.3$, $P < 0.001$; see Table 1). Variation in $\Delta^{13}\text{C}_{\text{seagrass-sediment}}$ between seagrass meadows dominated by a single species ranged from $+4.0\text{‰}$, for meadows of *T. testudinum*, to $+14.2\text{‰}$, for meadows of *Z. japonica*, indicative of variable contributions of the seagrasses to the sediment organic carbon pool. Sediments in seagrass beds displayed a skewed distribution of OM, with a range of 0.6 wt% to 13.2 wt% and a mean of 4.1 ± 0.8 wt% (Figure 2d). Because of the nonnormal distribution, the median OM of 2.8 wt% is a better measure of central tendency. We suspect the bimodal nature of the data represents the difference between relatively low OM sandy sediments compared to more organic-rich silty and muddy sediments.

[9] The $\delta^{13}\text{C}_{\text{sediment}}$ changed as a function of $\delta^{13}\text{C}_{\text{seagrass}}$ (Figure 3) but the slope of the relationship (1.39 ± 0.08) was significantly different from unity. Nearly all the $\delta^{13}\text{C}_{\text{sediment}}$ values were lighter than $\delta^{13}\text{C}_{\text{seagrass}}$, showing that organic matter from sources other than seagrass, were accumulating in the sediment. Other potential sources of organic carbon, like plankton, collected as suspended particulate organic matter, (SPOM, ca. $\delta^{13}\text{C} -20\text{‰}$), epiphytes, microphytobenthos and

macroalgae (all with typical ca. $\delta^{13}\text{C} -17\text{‰}$), and terrestrial organic matter (ca. $\delta^{13}\text{C} -27\text{‰}$) are all isotopically light relative to $\delta^{13}\text{C}_{\text{seagrass}}$ [Moncreiff and Sullivan, 2001].

[10] The distributions of observed C_{org} and, particularly, N_{T} in seagrass sediments (Figures 4a and 4b) were skewed in a manner similar to the distribution of OM (Figure 2d), even though the observations of C_{org} , N_{T} , and OM often came from different study sites. The C_{org} ranged from 0.1 wt% to 11.0 wt%, with a mean C_{org} of 1.8 ± 0.3 wt% (Figure 4a). Values above 4 wt% were relatively rare, and the median observed C_{org} was 1.2 wt%. The N_{T} values ranged from 0.01 wt% to 1.01 wt%, with a mean N_{T} of 0.15 ± 0.03 wt% and a median of 0.1 wt% (Figure 4b). The C_{org} and N_{T} in seagrass sediments were closely correlated (linear regression, $\ln(N_{\text{T}}) = -2.3 + 0.79 \ln(C_{\text{org}})$, $R^2 = 0.75$, $p < 0.001$). As a consequence, the $C_{\text{org}}:N_{\text{T}}$ ratios were normally distributed around a mean $C_{\text{org}}:N_{\text{T}}$ of 14.0 ± 2.1 (Figure 4c). Interestingly, the C_{org} in the sediments of seagrass meadows was not correlated with the aboveground biomass of seagrass ($R^2 < 0.001$, $p = 0.77$). In a subset of the studies, C_{org} and N_{T} in sediments both in and outside the seagrass meadows have been measured. The data show that sediment in the meadows had significantly higher C_{org} and, particularly, N_{T} concentrations relative to adjacent bare sediments (median 0.34 wt% versus 0.19 wt% C_{org} , and 0.031 wt% vs 0.024 wt% N_{T} , respectively; Wilcoxon sign ranked test: $P = 0.02$ and 0.007, respectively; $n = 32$). In contrast, the sediments adjacent to and in the seagrass meadows showed no difference in $\delta^{13}\text{C}_{\text{sediment}}$ (t test, $P > 0.05$).

4. Discussion

[11] Compared to earlier assessments, the data set presented here represents a much extended basis to evaluate the importance of sources of organic carbon to seagrass meadow sediments using stable carbon isotopes. The current data set includes approximately five times more observations originating from 82 more locations around the world than those

¹Auxiliary materials are available in the HTML. doi:10.1029/2010GB003848.

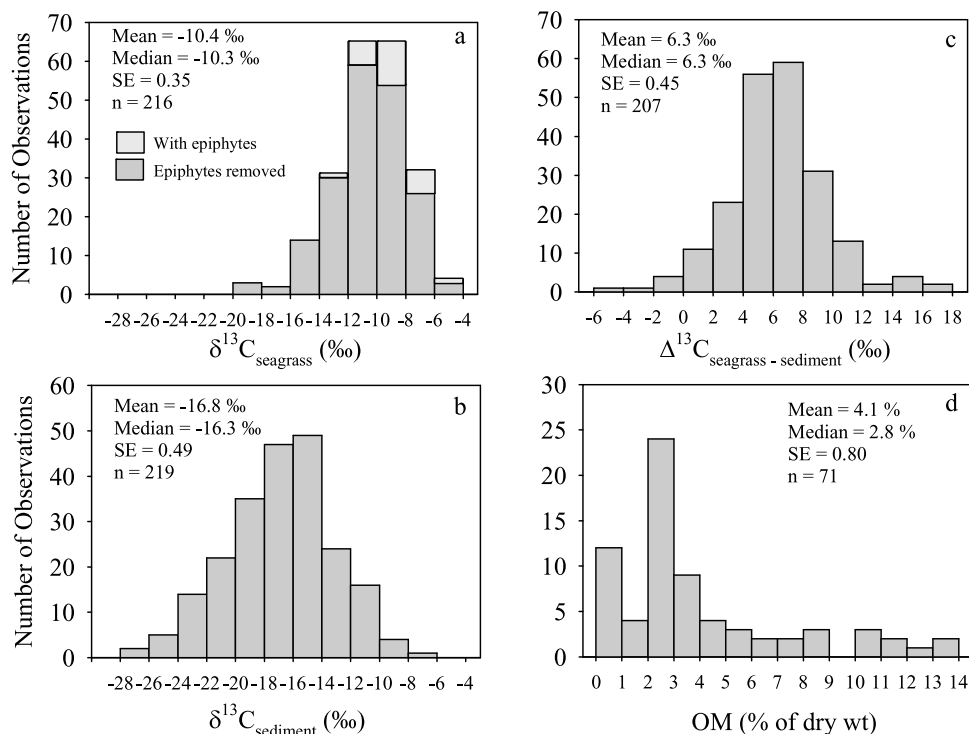


Figure 2. Frequency distribution of (a) $\delta^{13}\text{C}_{\text{seagrass}}$, (b) $\delta^{13}\text{C}_{\text{sediment}}$, (c) the $\Delta^{13}\text{C}_{\text{seagrass-sediment}}$ at each study location, and (d) OM (as % of dry weight) of the sediments of seagrass meadows. In Figure 2a, different colors are used to indicate values of seagrass cleaned of epiphytes (the majority of the data) and decalcified seagrass plus attached epiphyte community (25 observations).

included in the most extensive compilation thus far [Bouillon and Boschker, 2006]. Our results confirm earlier indications that seagrass sediments have significantly higher C_{org} contents than adjacent sediments [Duarte et al., 2005b] and that

more than one primary organic matter source contributes to the carbon stored in the surface sediment of seagrass meadows [Kennedy et al., 2004]. The mean $\Delta^{13}\text{C}_{\text{seagrass-sediment}}$ in our assessment, including the data set of Bouillon and

Table 1. Mean and Standard Error of $\delta^{13}\text{C}$ of Sediment and Seagrass Tissues and the Difference Seagrass $\delta^{13}\text{C}$ and Sediment $\delta^{13}\text{C}$ in Meadows of Different Seagrass Species^a

Community	N	Sediment $\delta^{13}\text{C}$ (‰)		Seagrass $\delta^{13}\text{C}$ (‰)		$\Delta^{13}\text{C}_{\text{seagrass-sediment}}$	
		Mean	SE	Mean	SE	Mean	SE
<i>Amphibolis australis</i>	2	-18.1	0.1	-10.4	0.5	7.7	0.6
<i>Amphibolis griffithii</i> *	1	-7.3		-12.7		-5.4	
<i>Cymodocea nodosa</i>	26	-17.5	0.8	-9.4	0.4	8.3	0.8
<i>Cymodocea rotundata</i>	1	-22.2		-12.4		9.8	
<i>Enhalus acoroides</i>	6	-19.9	1.8	-9.8	0.9	10.2	1.4
<i>Halodule uninervis</i>	2	-19.5	0.1	-13.6	1.5	5.9	1.3
<i>Halodule wrightii</i>	7	-15.5	0.3	-9.9	0.0	5.6	0.3
<i>Halophila ovalis</i>	2	-19.5	0.1	-13.1	2.4	6.4	2.2
<i>Heterozostera nigraulis</i>	2	-18.1	2.4	-10.7	0.1	7.4	2.3
<i>Posidonia oceanica</i>	42	-18.5	0.4	-12.2	0.3	5.8	0.5
<i>Posidonia sinuosa</i>	3	-16.1	3.8	-10.8	0.3	5.3	4.1
<i>Ruppia megacarpa</i>	1	-19.6		-14.0		5.6	
<i>Syringodium filiforme</i>	3	-17.5	0.1	-7.1	1.3	10.4	1.3
<i>Thalassia hemprichii</i>	2	-19.3	3.0	-11.8		10.4	
<i>Thalassia testudinum</i>	44	-12.9	0.3	-8.9	0.3	4.0	0.4
<i>Thalassodendron ciliatum</i>	17	-20.4	0.8	-14.5	0.8	5.8	0.6
<i>Zostera japonica</i>	1	-26.4		-12.2		14.2	
<i>Zostera marina</i>	17	-18.4	0.5	-10.9	0.6	7.8	0.6
<i>Zostera noltii</i>	13	-18.2	0.5	-10.3	0.3	7.9	0.5
Mixed community	36	-15.2	0.3	-8.6	0.2	6.4	0.3

^aIt is unknown if *Amphibolis griffithii* (*) sediments were acidified prior stable carbon isotope composition analysis.

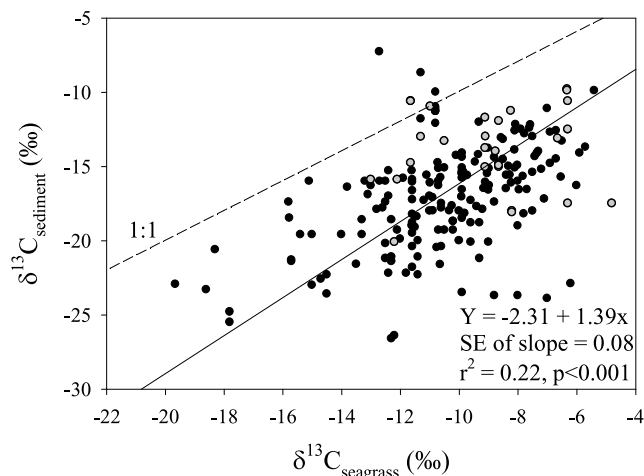


Figure 3. The relationship between $\delta^{13}\text{C}_{\text{sediment}}$ and $\delta^{13}\text{C}_{\text{seagrass}}$. The solid line shows the fitted model II regression analysis, while the dashed line indicates the 1:1 relationship. A different shading is used to indicate values of seagrass cleaned of epiphytes (the majority of the data) and decalcified seagrasses plus attached epiphyte community (25 observations).

Boschker [2006] is $+6.4 \pm 3.4\%$ and excluding their data set is $+6.7 \pm 3.4\%$, neither value is different from the estimate of $+6.5 \pm 3/6\%$ estimated from the data of *Bouillon and Boschker* [2006] alone, indicating that, on average, $\Delta^{13}\text{C}_{\text{seagrass-sediment}}$ is remarkably consistent both spatially and temporally. Given that the other potential sources of organic carbon to the sediment have a more negative $\delta^{13}\text{C}$ than seagrass, the almost exclusive positive values for $\Delta^{13}\text{C}_{\text{seagrass-sediment}}$ also supports previous observations that nonseagrass organic matter makes a strong contribution to the carbon that accumulates in seagrass sediments.

[12] To estimate the likely proportion of seagrass-derived organic matter sources to total sediment organic carbon, the IsoSource software package was used [*Phillips and Gregg*, 2003]. We calculated the proportional contribution to the sediment of three potential organic matter sources, seagrass, phytoplankton, and mangroves/terrestrial organic matter. From the data compiled in the current study, the median and 25th and 75th percentiles of $\delta^{13}\text{C}_{\text{seagrass}}$ (-10.3 , -8.5 and -11.6%) and $\delta^{13}\text{C}_{\text{sediment}}$ (-16.8 , -14.4 and -19.3%) were used as the respective source terms. We additionally used representative values of $\delta^{13}\text{C}$ for the phytoplankton and mangroves from the literature. Values of phytoplankton, collected as suspended particulate matter (SPOM) in the open ocean were used in preference to coastal seston, as the use of the latter can be limited by the presence of organic matter sources in addition to the phytoplankton. *Goericke and Fry* [1994] reported $\delta^{13}\text{C}$ values of SPOM between -18% and -22% between -40°S and 40°N , and these end values, as well as the mean, -20% , were used for the phytoplankton source term. For the mangrove source term, the median (-28%), 25th and 75th percentile (-27% and -29.4% , respectively) of data reported by *Bouillon et al.* [2008] were used. Potential inputs of terrestrial organic

matter have similar isotopic composition (mean $\delta^{13}\text{C}$ of $-28.46 \pm 2.52\%$ [*Diefendorf et al.*, 2010]) as that of mangroves and were thus implicitly included in our assessment. All combinations of these source terms were used to solve for their likely contribution to the sediments at 1% increment and 0.1‰ resolution.

[13] The isotope mixing calculations revealed that seagrass-derived organic matter contributed 51% (25th and 75th percentiles are equivalent to 33% and 62% contribution, respectively) of the carbon in the surface sedimentary organic matter pool. This estimate takes into account the full range of uncertainty in our data and that reported for other organic matter sources, i.e., low to midlatitude phytoplankton and mangroves/terrestrial organic matter. The 50% contribution based on carbon isotopes is also consistent with

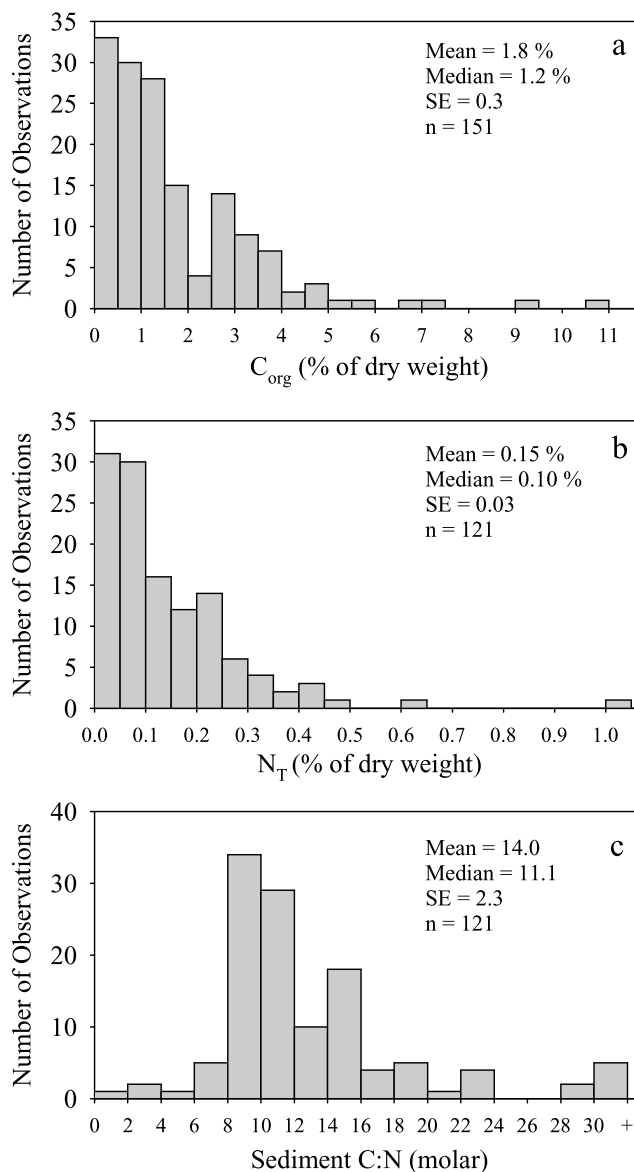


Figure 4. Frequency distributions of the (a) C_{org} as a percentage of the dry weight, (b) N_{T} as a percentage of the dry weight, and (c) $\text{C}_{\text{org}}:\text{N}_{\text{T}}$ molar ratios of seagrass sediment.

sediment $C_{org}:N_T$ ratios, which were intermediate between seagrass and other organic matter sources.

[14] In our calculations, we have assumed that leaf material is a representative tracer of seagrass-derived carbon, although different tissues within seagrass species can have different $\delta^{13}C$ values. Rhizomes of *Thalassia testudinum* have been shown to be enriched by 1.5‰ compared to leaves [Fourqurean and Schrlau, 2003], while in other species, such as *Posidonia oceanica*, the differences can be less marked, between 0.1 and 0.9‰ [Papadimitriou et al., 2005a]. Given that seagrass leaf production is ca. 5 times the rhizome production [Bittaker and Iverson, 1976; Kenworthy and Thayer, 1984] and using losses of leaf biomass due to export and herbivory of 24% and 19%, respectively [Duarte and Cebrián, 1996], about half the leaf production is delivered to the local sediments. This is still equivalent to ~2 times the rhizome production and will reduce any bias in our data through the use of leaf $\delta^{13}C$ alone. Our calculations also assume that there is little or no alteration of $\delta^{13}C$ of seagrass tissues during postdepositional decomposition. Fourqurean and Schrlau [2003] report seagrass detritus becoming more depleted in ^{13}C by ca. 2‰ during the first year of diagenesis, while Zieman et al. [1984] found little or no change in $\delta^{13}C$ during decomposition. Due to lack of data thus far, there is little consensus on how $\delta^{13}C$ changes during decomposition. It cannot be assumed that $\delta^{13}C$ is constant temporally and if the variability in $\delta^{13}C$ of a single source is high, this can limit the utility of the mixing model. The intra-annual variation in $\delta^{13}C_{seagrass}$ has been reported to be up to 3.6‰ for *Thalassia testudinum* and 4.1‰ for *Zostera noltii*, with sometimes even larger annual ranges being observed for seagrass meadows in nutrient impacted environments [Fourqurean et al., 2005; Papadimitriou et al., 2005b, Papadimitriou et al., 2006]. However, these sources of variance, due to within-plant differences, and seasonal and postdepositional change are generally within the end-member values explored in our isotope mixing calculations and thus do not affect the overall outcome. A final limitation of this approach is that in systems that display isotopically depleted values of $\delta^{13}C_{seagrass}$, the calculation of the relative contribution of seagrass organic matter to the sedimentary organic carbon pool becomes more difficult to discern isotopically as there is little separation from the $\delta^{13}C$ of other potential carbon sources.

[15] In our analysis, the mean $\Delta^{13}C_{seagrass-sediment}$ of $+6.4 \pm 3.4\%$ was consistent with other studies but additionally provides evidence for important variability in the $\Delta^{13}C_{seagrass-sediment}$ among seagrass meadows dominated by different species (Table 1). This variability can occur due to differences in 1] the relative supply rates of particular organic matter sources and/or 2] the characteristics of a seagrass species that affects its ability to trap allochthonous organic matter.

[16] Relative differences in the supply rate of particular organic matter sources often relate to enhanced terrestrial supply, such as found in seagrass meadows located in enclosed bays or close to mangroves, or in areas associated with high deforestation rates. For instance, the $\delta^{13}C_{sediment}$ in the SE Asian seagrass meadows included in this compilation

were found to be much lighter than the corresponding $\delta^{13}C_{seagrass}$ of all species [Kennedy et al., 2004]. The isotope mixing calculations suggest that 70% (median) of the organic carbon trapped in the sediments of these SE Asian meadows derive from allochthonous sources, and that as much as 95% (median) of the organic carbon in the *Zostera japonica* meadow from the Western Pacific in the data set (Table 1) may be derived from terrestrial sources. Features of seagrass leaves also influence the effectiveness of seagrass meadows to act as filters for particles suspended in the water column. The size and shape of the leaves can differentially affect the flow and turbulence of water within the canopy and prevent, through the buffering effect of the canopy, particle re-suspension [Terrados and Duarte, 2000; Gacia and Duarte, 2001; Koch et al., 2006]. In a detailed experimental study of these processes, Hendriks et al. [2008] found that loss of suspended particles from the water column within seagrass canopies is much higher than can be explained by flow reduction alone. Hendriks et al. [2008] calculated that a particle traversing a *Posidonia oceanica* meadow would have a 2% to 3% probability of being lost from the flow by impact with leaves. The results highlight the role that loss of momentum during particle collisions with leaves has, with about 27% of the momentum of a suspended particle being lost upon each collision. Thus leaf characteristics that enhance direct particle collisions and the trapping ability of seagrass canopies [Agawin and Duarte, 2002] will lead to differential retention of SPOM in the sediment. One or both of these effects may account for some of the differences between $\delta^{13}C_{seagrass}$ and $\delta^{13}C_{sediment}$ among species.

[17] The mechanisms above, explain the enhanced accumulation of organic carbon in seagrass sediments, but the role of seagrass sediments as reservoirs of organic carbon requires highly efficient preservation capacity. The high input of organic matter to seagrass sediments stimulates microbial activity, which is generally higher compared to adjacent bare sediments [Duarte et al., 2005b]. However, due to the high proportion of refractory organic matter in seagrass detritus, in particular in rhizomes and roots, the rate of decomposition of this pool is slow resulting in accumulation of refractory organic matter [Kennedy and Björk, 2009]. Additionally, the low oxygen availability in seagrass sediments contributes to low decomposition rates, limiting the aerobic degradation of complex organic molecules [Zonneveld et al., 2010] and potentially increasing burial. The capacity for preservation will vary, with seagrass tissue, seagrass species and environmental setting, but evidence of low remineralization rates have been reported from decomposition experiments, using different seagrass tissues buried at the surface and 20cm sediment depth [Fourqurean and Schrlau, 2003], and from sediment incubations in a *P. oceanica* meadow [Gacia et al., 2002], with the latter study reporting remineralization rates approximately equivalent 7% of the primary flux.

[18] The accumulation and preservation of organic matter in seagrass sediments over the millennia results in faster accumulation rates than adjacent sedimentary environments leading to a local raising of the seafloor. For instance, paleorecords showed that *Posidonia oceanica* meadows in the Mediterranean have led to the seafloor being raised by

as much as 3 m over 2000 years [Lo Iacono et al., 2008], and sediments in the seagrass meadows of Shark Bay (W. Australia) have been steadily accumulating at a rate of 0.5 mm of sediment annually [Walker and Woelkerling, 1988]. Further, seagrass-stabilized mudbanks have trapped 2 m of sediments since Florida Bay flooded in response to rising sea level 5000 years ago [Wanless and Tagett, 1989], while the relatively constant C_{org} of the accumulated sediments [Orem et al., 1999] indicates that the carbon buried in seagrass meadows can be preserved for thousands of years.

[19] The results presented here show that seagrass meadows are important repositories of organic carbon produced in the seagrass meadows and elsewhere (e.g., plankton and terrestrial sources). Using different (either top down or bottom up) approaches, it has been calculated that seagrass meadows bury, on average, 83 to 133 g C m⁻² yr⁻¹ [Duarte et al., 2005a]. Assuming, as indicated by our analysis, that only half of the organic C buried in seagrass sediments derives from the seagrass tissue, this amounts to an accumulation of seagrass organic matter of between 41 and 66 g C m⁻² yr⁻¹, with a similar contribution from allochthonous organic carbon. A recent synthesis of the net community production of seagrass meadows indicated that the mean net community production is about 120 g C m⁻² yr⁻¹ [Duarte et al., 2010]. This suggests that only 30 to 50% of the net community production of seagrass meadows is buried in situ. The rest of the material is either consumed and/or exported elsewhere, such as to the sediments adjacent to seagrass meadows. Evidence for export of the organic matter that was originally produced within the seagrass meadows, is provided by the similarity of the $\delta^{13}C_{sediment}$ between the seagrass meadows and the bare sediments adjacent to the meadows. Assuming the same sources of primary producers (phytoplankton, terrestrial plants and seagrasses) to the area surrounding the seagrass meadows these sources must be delivered in similar proportions as within the meadow itself, consistent with a net export of seagrass organic matter from the meadow. On the wider scale, significant, but as yet unquantified, amounts of seagrass organic matter can be exported to adjacent beaches, or even the deep sea (cf. review by Heck et al. [2008]). Hence, the total organic carbon sink by seagrass meadows may be better approximated by the sum of their net community production and the allochthonous carbon trapped in their sediments, leading to a value of between 160 to 186 g C m⁻² yr⁻¹, rendering seagrass meadows hot spots for carbon sequestration that are of relevance at the biosphere scale [Smith, 1981; Duarte et al., 2005a]. The global extent of seagrass meadows is poorly constrained because large areas of the coastal zone, especially in Asia, Africa and South America, have little or no data on the presence or extent of seagrass meadows. Therefore there is a large uncertainty in the upscaling of the carbon sink capacity of seagrass meadows. We use an upper global estimate for seagrass areal extent of 600,000 km² [Charpy-Roubaud and Sournia, 1990], which is still likely an underestimate. The lower global estimate of 300,000 km² [Duarte et al., 2005a] is a revised value assuming a 50% reduction in seagrass cover since Charpy-Roubaud and Sournia. (1990) Using these upper and lower values with our estimates of the total organic carbon sink, we estimate global seagrass carbon

sinks of 96 to 112 Tg yr⁻¹ (assuming maximal extent) and 48 to 55.8 Tg yr⁻¹ (assuming minimum areal extent).

[20] Beyond the requirement for a more accurate knowledge of global seagrass cover, better estimates of the total carbon sink capacity of seagrass meadows can be achieved through a more extensive investigation of carbon burial rates and a clearer resolution of the footprint of seagrass carbon burial. For example, the data sets used to derive the average long-term carbon burial rates mainly come from the Mediterranean and thus represent meadows of mostly one seagrass species, *Posidonia oceanica*. In terms of the net export of seagrass organic matter, largely qualitative data currently exist and there is a need for a better understanding of lateral carbon fluxes as well as determining the areal extent of effective burial of exported carbon.

[21] The loss of a substantial fraction of the seagrass area over the past decades [Orth et al., 2006; Waycott et al., 2009] has considerably weakened this important carbon sink in the coastal zone. Bringing these losses to a halt requires actions to abate eutrophication and prevent mechanical and physical damage on seagrass meadows, which may eventually set the scene for the recovery of the lost sink capacity. Seagrass recovery is often a slow process [Olesen et al., 2004] but can be assisted by deliberate transplants and seeding activities that, combined with the exponential clonal growth capacity of seagrass [cf. Sintes et al., 2006], may catalyze and, hence, accelerate the recovery of the seagrass carbon sink.

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References

- Agawin, N. S. R., and C. M. Duarte (2002), Evidence of direct particle trapping by a tropical seagrass meadow, *Estuaries*, 25, 1205–1209, doi:10.1007/BF02692217.
- Bittaker, H. F., and R. L. Iverson (1976), *Thalassia testudinum* productivity: A field comparison of measurement methods, *Mar. Biol. Berlin*, 37, 39–46, doi:10.1007/BF00386777.
- Bouillon, S., and H. T. S. Boschker (2006), Bacterial carbon sources in coastal sediments: A cross-system analysis based on stable isotope data of biomarkers, *Biogeosciences*, 3, 175–185, doi:10.5194/bg-3-175-2006.
- Bouillon, S., R. M. Connolly, and S. Y. Lee (2008), Organic matter exchange and cycling in mangrove ecosystems: Recent insights from stable isotope studies, *J. Sea Res.*, 59, 44–58, doi:10.1016/j.seares.2007.05.001.
- Charpy-Roubaud, C., and A. Sournia (1990), The comparative estimation of phytoplankton microphytobenthic production in the oceans, *Mar. Microb. Food Webs*, 4, 31–57.
- Costanza, R., et al. (1997), The value of the world's ecosystem services and natural capital, *Nature*, 387, 253–260, doi:10.1038/387253a0.
- Craig, H. (1953), The geochemistry of the stable carbon isotopes, *Geochim. Cosmochim. Acta*, 3, 53–92, doi:10.1016/0016-7037(53)90001-5.
- Diefendorf, A. F., K. E. Mueller, S. L. Wing, P. L. Koch, and K. H. Freeman (2010), Global patterns in leaf ¹³C discrimination and implications for studies of past and future climate, *Proc. Natl. Acad. Sci. U. S. A.*, 107(13), 5738–5743, doi:10.1073/pnas.0910513107.

- Duarte, C. M., and J. Cebrián (1996), The fate of marine autotrophic production, *Limnol. Oceanogr.*, *41*(8), 1758–1766, doi:10.4319/lo.1996.41.8.1758.
- Duarte, C. M., J. J. Middelburg, and N. Caraco (2005a), Major role of marine vegetation on the oceanic carbon cycle, *Biogeosciences*, *2*(1), 1–8, doi:10.5194/bg-2-1-2005.
- Duarte, C. M., M. Holmer, and N. Marbà (2005b), Plant-microbe interactions in sea grass meadows, in *Interactions Between Macro- and Microorganisms in Marine Sediments, J. Coastal Estuar. Stud.*, 60, edited by E. Kristensen, R. R. Haese, and J. E. Kostka, pp. 31–60, AGU, Washington, D. C.
- Duarte, C. M., N. Marbà, E. Gacia, J. W. Fourqurean, J. Beggins, C. Barron, and E. T. Apostolaki (2010), Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows, *Global Biogeochem. Cycles*, doi:10.1029/2010GB003793, in press.
- Fourqurean, J. W., and J. E. Schrlau (2003), Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA, *Chem. Ecol.*, *19*, 373–390, doi:10.1080/02757540310001609370.
- Fourqurean, J. W., S. P. Escorcia, W. T. Anderson, and J. C. Ziemann (2005), Spatial and seasonal variability in elemental content, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ of *Thalassia testudinum* from South Florida and its implications for ecosystem studies, *Estuaries*, *28*, 447–461, doi:10.1007/BF02693926.
- Fry, B., R. S. Scalan, and P. L. Parker (1977), Stable carbon isotope evidence for two sources of organic matter in coastal sediments: Seagrass and plankton, *Geochim. Cosmochim. Acta*, *41*, 1875–1877, doi:10.1016/0016-7037(77)90218-6.
- Gacia, E., and C. M. Duarte (2001), Elucidating sediment retention by seagrasses: Sediment deposition and resuspension in a Mediterranean (*Posidonia oceanica*) meadow, *Estuarine Coastal Shelf Sci.*, *52*, 505–514, doi:10.1006/ecss.2000.0753.
- Gacia, E., C. M. Duarte, and J. J. Middelburg (2002), Carbon and nutrient deposition in the Mediterranean seagrass (*Posidonia oceanica*), *Limnol. Oceanogr.*, *47*, 23–32, doi:10.4319/lo.2002.47.1.0023.
- Goericke, R., and B. Fry (1994), Variations of marine plankton $\delta^{13}\text{C}$ with latitude, temperature and dissolved CO_2 in the world ocean, *Global Biogeochem. Cycles*, *8*(1), 85–90, doi:10.1029/93GB03272.
- Heck, K. L., Jr., T. J. B. Carruthers, C. M. Duarte, A. R. Hughes, G. Kendrick, R. J. Orth and S. W. Williams (2008), Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers, *Ecosystems*, *11*, 1198–1210, doi:10.1007/s10021-008-9155-y.
- Hendriks, I. E., T. Sintes, T. J. Bouma, and C. M. Duarte (2008), Experimental assessment and modeling evaluation of the effects of seagrass (*P. oceanica*) on flow and particle trapping, *Mar. Ecol. Prog. Ser.*, *356*, 163–173, doi:10.3354/meps07316.
- Kennedy, H., and M. Björk (2009), Seagrasses, in *The Management of Natural Coastal Carbon Sinks in Coastal Ecosystems: Investigating and Realising the Potential*, edited by D. d'A Laffoley and G. Grimsditch, pp. 23–30, IUCN, Gland, Switzerland.
- Kennedy, H., E. Gacia, D. P. Kennedy, S. Papadimitriou, and C. M. Duarte (2004), Organic carbon sources to SE Asian coastal sediments, *Estuarine Coastal Shelf Sci.*, *60*(1), 59–68, doi:10.1016/j.ecss.2003.11.019.
- Kennedy, P., H. Kennedy, and S. Papadimitriou (2005), The effect of acidification on the determination of organic carbon, total nitrogen and their stable isotopic composition in algae and marine sediment, *Rapid Commun. Mass Spectrom.*, *19*(8), 1063–1068, doi:10.1002/rcm.1889.
- Kenworthy, W. J., and G. W. Thayer (1984), Production and decomposition of the roots and rhizomes of seagrasses, *Zostera marina* and *Thalassia testudinum*, in temperate and subtropical marine ecosystems, *Bull. Mar. Sci.*, *35*, 364–379.
- Koch, E. W., J. D. Ackerman, J. Verduin, and M. van Keulen (2006), Fluid dynamics in seagrass ecology: From molecules to ecosystems, in *Seagrasses: Biology, Ecology and Conservation*, edited by A. W. D. Larkum, R. J. Orth, and C. M. Duarte, pp. 193–225, Springer, Dordrecht, Netherlands.
- Lo Iacono, C., M. A. Mateo, E. Gracia, L. Guasch, R. Carbonell, L. Serrano, O. Serrano, and J. Danobeitia (2008), Very high-resolution seismic-acoustic imaging of seagrass meadows (Mediterranean Sea): Implications for carbon sink estimates, *Geophys. Res. Lett.*, *35*, L18601, doi:10.1029/2008GL034773.
- Moncreiff, C. A., and M. J. Sullivan (2001), Trophic importance of epiphytic algae in subtropical seagrass beds: Evidence from multiple stable isotope analyses, *Mar. Ecol. Prog. Ser.*, *215*, 93–106, doi:10.3354/meps215093.
- Olesen, B., N. Marbà, C. M. Duarte, R. S. Savelle, and M. D. Fortes (2004), Recolonization dynamics in a mixed seagrass meadow: The role of clonal versus sexual processes, *Estuaries*, *27*, 770–780.
- Orem, W. H., C. W. Holmes, C. Kendal, H. E. Lerch, A. L. Bates, S. R. Silva, A. Boylan, M. Corum, M. Marot, and C. Hedgeman (1999), Geochemistry of Florida Bay sediments: Nutrient history at five sites in eastern and central Florida Bay, *J. Coastal Res.*, *15*, 1055–1071.
- Orth, R. J., et al. (2006), A global crisis for seagrass ecosystems, *BioScience*, *56*, 987–996, doi:10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2.
- Papadimitriou, S., H. Kennedy, D. P. Kennedy, C. M. Duarte, and N. Marbà (2005a), Sources of organic matter to seagrass-colonized sediments: A stable isotope study in the silt and clay fraction from *Posidonia oceanica* meadows in the western Mediterranean, *Org. Geochem.*, *36*, 949–961, doi:10.1016/j.orggeochem.2004.12.002.
- Papadimitriou, S., H. Kennedy, D. P. Kennedy, and J. Borum (2005b), Seasonal and spatial variation in the organic carbon and nitrogen concentration and their stable isotopic composition in seagrass meadows of *Zostera marina* (Denmark), *Limnol. Oceanogr.*, *50*, 1084–1095, doi:10.4319/lo.2005.50.4.1084.
- Papadimitriou, S., H. Kennedy, R. Rodrigues, D. P. Kennedy, and T. H. E. Heaton (2006), Using variation in the chemical and stable isotopic composition of *Zostera noltii* to assess nutrient dynamics in a temperate seagrass meadow, *Org. Geochem.*, *37*, 1343–1358, doi:10.1016/j.orggeochem.2006.01.007.
- Phillips, D. L., and J. W. Gregg (2003), Source partitioning using stable isotopes: Coping with too many sources, *Oecologia*, *136*(2) 261–269.
- Pidgeon, E. (2009), Carbon sequestration by coastal marine habitats: Missing sinks, in *The Management of Natural Coastal Carbon Sinks* edited by D. d'A Laffoley and G. Grimsditch, pp. 47–51, IUCN, Gland, Switzerland.
- Sintes, T., N. Marbà, and C. M. Duarte (2006), Modeling non-linear seagrass clonal growth: Assessing the efficiency of space occupation across the seagrass flora, *Estuaries Coasts*, *29*, 72–80.
- Smith, S. V. (1981), Marine macrophytes as a global carbon sink, *Science*, *211*, 838–840, doi:10.1126/science.211.4484.838.
- Terrados, J., and C. M. Duarte (2000), Experimental evidence of reduced particle resuspension within a seagrass (*Posidonia oceanica* L) meadow, *J. Exp. Mar. Biol. Ecol.*, *243*, 45–53, doi:10.1016/S0022-0981(99)00110-0.
- Walker, D. I., and W. J. Woelkerling (1988), Quantitative study of sediment contribution by epiphytic coralline red algae in seagrass meadows in Shark Bay, Western Australia, *Mar. Ecol. Prog. Ser.*, *43*, 71–77, doi:10.3354/meps043071.
- Wanless, H. R., and M. G. Tagett (1989), Origin, growth and evolution of carbonate mudbanks in Florida Bay, *Bull. Mar. Sci.*, *44*, 454–489.
- Waycott, M., et al. (2009), Accelerating loss of seagrasses across the globe threatens coastal ecosystems, *Proc. Natl. Acad. Sci. U. S. A.*, *106*, 12,377–12,381, doi:10.1073/pnas.0905620106.
- Ziemann, J. C., S. A. Macko, and A. L. Mills (1984), Role of seagrasses and mangroves in estuarine food webs: Temporal and spatial changes in stable isotope composition and amino acid content during decomposition, *Bull. Mar. Sci.*, *35*, 380–392.
- Zonneveld, K. A. F., et al. (2010), Selective preservation of organic matter in marine environments; processes and impact on the sedimentary record, *Biogeosciences*, *7*, 483–511, doi:10.5194/bg-7-483-2010.

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