

1 **Blue carbon sequestration dynamics within tropical seagrass sediments: long-term**
2 **incubations for changes over climatic scales**

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10 Determination of blue carbon sequestration in seagrass sediments over climatic time scales (>100 years)
11 relies on several assumptions, including no loss of particulate organic carbon (POC) after 1–2 years, tight
12 coupling between POC loss and CO₂ emissions, no dissolution of carbonates, and removal of the recalcitrant
13 black carbon (BC) contribution. We tested these assumptions via 500-day anoxic **decomposition and**
14 **mineralisation** experiment to capture centennial parameter decay dynamics from two sediment horizons
15 robustly dated as 2 and 18 years old. No loss of BC was detected, and decay of POC was best described for
16 both horizons by near-identical reactivity continuum models. The models predicted average losses of 49 and
17 51% after 100 years of burial for the surface and 20–22-cm horizons respectively. However, the loss rate of
18 POC was far greater than the release rate of CO₂, even after accounting for CO₂ from particulate inorganic
19 carbon (PIC) production, possibly as siderite. The deficit could not be attributed to dissolved organic carbon
20 or dark CO₂ fixation. Instead, evidence based on δ¹³CO₂, acidity and lack of sulfate reduction suggested
21 methanogenesis. The results indicated the importance of centennial losses of POC and PIC precipitation and
22 possibly methanogenesis in estimating carbon sequestration rates.

23 **ToC Summary.** Seagrasses remove and bury CO₂ as sedimentary organic matter in sufficient amounts to
24 mitigate global warming. However, a 2-year sediment-incubation study indicated that 50% could be lost over
25 climatic time scales, forming greenhouse gases such as CO₂ and methane. This could lead to underestimated
26 emissions within a carbon cap and trade market, if such losses are not taken into account.

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29 Seagrass sediment decomposition and mineralisation

30 **Additional keywords:** carbonate, diagenesis, methane, pyrogenic carbon, sediment geochemistry,
31 sediment isotope tomography.

32 **Introduction**

33 Seagrasses, along with mangroves, saltmarsh and seaweeds, are increasingly touted as a
34 significant global carbon (C) sink (McLeod *et al.* 2011). For seagrass in particular, this service is

35 based on two separate concepts, namely, sedimentary C stocks and rates of sedimentary C
36 sequestration. The stock- or storage-service concept, in the mitigation of greenhouse-gas
37 emissions, is a scalar concept and conceived at the meadow scale. It has traditionally been
38 estimated by potential C loss to mineralisation should it be disturbed over a climatic timescales
39 (Pendleton *et al.* 2012). Climatic timescales are defined to be close to c. 100 years, over which the
40 full impacts of feedbacks on climatic variability become evident (IPCC,2013). The depth of such
41 disturbances, and the extent of its effect on the C stock, is dependent on the type of disturbance
42 (Siikamäki *et al.* 2013; Gallagher 2017) and is independent of the time it took the C to accumulate.
43 The sediment found within seagrass beds contains a sizable detrital organic component, consisting
44 of a mix of deposited seagrass litter, associated epiphyte and microalgal detritus, and additional
45 inputs from adjacent land activities, fluvial deposition, and saltmarsh and mangroves (Kennedy *et*
46 *al.* 2010). Inputs other than surface deposition have been recognised, such as seagrass root
47 exudates. Exudates feed the rhizosphere anoxic microflora under nitrogen (N)-depleted conditions
48 (Welsh 2000); however, how much this contributes to the sedimentary particulate organic C (POC)
49 is still unclear, and is beyond the scope of the present study. In contrast, the C-sequestration
50 service is a vector concept. Rates of sequestration depend on the balance between detrital
51 production and mineralisation relative to an alternative and likely non-vegetated state (Siikamäki *et*
52 *al.* 2013; Gallagher 2017). Non-vegetated sediments have, in general, shown increased rates of
53 mineralisation (Kristensen *et al.* 1995) and mobilisation of dissolved organic C (DOC) during
54 resuspension (Koelmans and Prevo 2003). Because this is a service in the mitigation of global
55 warming, its extent has been traditionally estimated as the rate at which sedimentary organic mass
56 accumulates over time scales ranging from inter-decadal to centennial (Duarte *et al.* 2013;
57 Gallagher 2015), **subsequently integrated** across the meadow.

58 Notwithstanding uncertainties about the size of past meadow coverage and the amount and fate
59 of exported litter (Gallagher 2014; Duarte and Krause-Jensen 2017), researchers are increasingly
60 recognising that the traditional methods of calculating sedimentary C-accumulation rates may have
61 built-in biases (Gallagher 2015; Johannessen and Macdonald 2016; Chew and Gallagher 2018).
62 For example, previous studies have failed to subtract allochthonous recalcitrant forms of C such as
63 black or pyrogenic C from estimated C stocks. Pyrogenic C is produced by incomplete combustion
64 of biomass and fossil fuels. It is considered sufficiently stable to be outside the climatic C loop
65 (Liang *et al.* 2008; Wang *et al.* 2016), and, thus, its storage and sequestration within seagrass-
66 ecosystem sediments cannot be counted as a greenhouse gas-mitigation service (Chew and
67 Gallagher 2018). **Mass-accumulation** rates of POC per unit time and area, the product of
68 sedimentation rates and POC concentrations, have assumed no significant losses after 1–2 years
69 within their surface sediments (Cebrian 1999). The humification of seagrass, macroalgae and
70 mangrove detritus has been shown to occur over several months after deposition, becoming more

71 recalcitrant after burial (Middelburg 1989; Burdige 2007). Further, any such losses are assumed to
72 be tightly coupled with carbon dioxide (CO₂) emissions, ostensibly from aerobic mineralisation or
73 sulfate reduction (Burdige 1991), whereby the release of ammonia can feed further production.
74 Methanogenesis has been known to play a measurable role within highly organic non-vegetated
75 coastal sediments (Boehme *et al.* 1996). However, long-term incubation experiments with marine
76 non-vegetative sediments consisting of predominantly, but not exclusively, phytoplanktonic
77 sources have suggested that POC continues to be lost within deeper and older sediments (Westrich
78 and Berner 1984; Burdige 1991; Arndt *et al.* 2013; Canuel *et al.* 2017), with further losses of the
79 POC fraction being transformed to a mobile DOC pool (Holmer 1996; Hee *et al.* 2001; Burdige *et*
80 *al.* 2016). Furthermore, the CO₂ need not be from organic mineralisation. Sulfate reduction within
81 non-vegetated coastal sediments has been found to result in sufficient alkalisation to produce CO₂
82 from the subsequent precipitation of calcium carbonate (CaCO₃) in the form of particulate
83 inorganic C (PIC; Mucci *et al.* 2000; Rassmann *et al.* 2016). Should this be a phenomenon within
84 anoxic seagrass sediments, then this apparent emission source needs to be balanced with PIC
85 dissolution subsequent to re-alkalisation of the water column after disturbance of the non-vegetated
86 state. This can reduce the partial pressure of carbon dioxide (*p*CO₂) in the water column, which
87 ironically becomes a net CO₂ sink from the atmosphere, the extent of which depends on the
88 residence time of the water body (Howard *et al.* 2018).

89 *Aims*

90 This study aims, for the first time, to use long-term (500 days) ‘open’ anoxic slurry incubations
91 of tropical seagrass-meadow sediments to (1) estimate any centennial losses of POC by capturing
92 the rates and dynamics of POC and possibly otherwise stable black C (BC) mineralisation and
93 decomposition within highly organic sediments, and (2) recognise the suite of chemical and
94 geochemical processes involved. Incubation was followed by a relatively short period of aeration
95 (30 days) to the anoxic incubation as a model for the immediate effects of disturbance on the
96 mineralisation and decomposition of both POC and PIC. Younger (1–2 years old) surface
97 sediments were used to compare the POC and PIC decomposition and mineralisation rates with
98 those of deeper, older horizons. This was undertaken by fitting the time series to the most
99 appropriate diagenetic model (Arndt *et al.* 2013). After sediment deposition, ages were determined
100 with either an evaluated event or ²¹⁰Pb geochronology; the model was used to extrapolate any
101 losses over 100 years for a more considered rate of POC sequestration. The newly measured POC
102 was then further constrained by measurements of additional diagenetic variables, namely CO₂,
103 coloured dissolved organic matter (CDOM) as a proxy for the DOC pool, ammonia as evidence of
104 sulfate reduction and PIC, in the form of carbonate, so as to disentangle changes in CO₂ from
105 inorganic and organic dynamics.

106 **Materials and methods**

107 *Study site*

108 Two similar subtidal *Enhalus* sp. seagrass meadows in separate branches of the Salut–
109 Mengkabong estuary were chosen for the study (Fig. 1). The region can be considered as
110 moderately urban; it is located 20 km north of a city centre (Kota Kinabalu, Sabah, Malaysia) and
111 within the penumbra of the near-annual south-western Borneo and Sumatra haze events. These
112 events ostensibly deposit BC into the estuary from peat fires on the southern part of the island as
113 well as from slash-and-burn land-clearing activities (Gaveau *et al.* 2015; Chew and Gallagher
114 2018). The two bays are both turbid and shallow (1–3 m) and surrounded by mangrove forests with
115 exposed intertidal mud banks. The diurnal spring tides range between 1.4 and 1.7 m and
116 neaps can vary between 0.2 and 0.8 m (Hoque *et al.* 2010). One meadow, within the Salut branch,
117 was used to collect sediments for the slurry incubations, whereas the other meadow, within the
118 Mengkabong branch, was used to constrain the Salut meadow's geochronology. This was
119 necessary for disentangling and identifying the likely and known regional-storm depositional
120 events from unknown local disturbances (Gallagher and Ross 2018).

121 *Sediment collection and incubation*

122 The sediments for the decomposition experiment were taken in 2016 from 22 cores spaced ~30–
123 150 m apart. The cores were transported back to the laboratory under ice (ambient temperature in
124 icebox = 10.2°C), where the surface 2-cm and 20–22-cm horizons were extracted and pooled. The
125 latter horizon was taken a short distance ahead of the start of a transition to a lower, more fibrous
126 brown facies (>26 cm). Samples from each sediment horizon were pooled in the manner of
127 Westrich and Berner (1984) after wet sieving (1 mm) with previously filtered boiled seawater to
128 remove large shells, debris and benthic fauna. This was undertaken to remove the organic-matter
129 contribution of any live fauna from anoxic detrital decay, while maintaining the natural bacterial
130 flora present (Gontikaki *et al.* 2015). After this, the pooled samples were divided into four separate
131 Mason jars under N₂, and filtered boiled seawater was added to make up a 400-cm³ slurry with a
132 final water content of 81.9%. Before the start of the incubation, the slurries were bubbled with N₂
133 for 25 min and the anoxic status was checked (ellow Springs Instruments (YSI) Xylem-Analytcs
134 Ltd, Australia ProDSS probe) before the Mason jar lids were replaced. To ensure that the sulfate
135 supply was not limiting sulfate reduction, additional sulfate was added in a stoichiometric
136 proportion to the measured amount of CO₂ emitted. This was undertaken after the first month and
137 again a further three times over the course of the first 300 days of the experiment. As a further
138 precaution, sulfide and CO₂ traps were placed in the jar headspace to both inhibit and control any
139 build-up of metabolites and to measure net accumulative mineralisation. The sulfide traps were
140 constructed by using epoxy to fasten a 110-mm-diameter Whatman No. 1 filter paper saturated
141 with 1‰ zinc acetate to the underside of each jar lid. These were strategically folded to present a

142 large total surface area and were placed alongside lead acetate paper strips to visibly detect any
143 ongoing emissions of hydrogen sulfide (H₂S). The filter papers were refreshed with fresh solution
144 after every sampling procedure. The CO₂ traps contained 2–3 g of dried high absorbance-capacity
145 soda lime (Dharmakeerthi *et al.* 2015) placed in 15-cm³ polypropylene centrifuge tubes. The tubes
146 were open to the headspace and were replaced after each sampling time for further gravimetric
147 measurements of CO₂ accumulation rates. An additional set of soda lime traps was also placed in
148 four Mason jars filled with filtered boiled seawater (400 cm³), which were added to the incubation
149 cohort as CO₂ procedural blanks (Keith and Wong 2006).

150 The Mason jar sediment slurries and blanks were all incubated at 30°C in a constant-temperature
151 room in the dark (covered in aluminium foil as a precaution against disturbance). The slurries were
152 sampled after 7, 21, 42, 63, 105, 140, 175, 210, 308, 365, 400, 420, 470 and 500 days for POC,
153 CDOM, ammonia, pH and CO₂. A Day 0 sample for POC was added after the first year. These
154 were taken from the remaining pooled sediments (stored at –20°C) and replicated with sediments
155 from corresponding horizons within the sediment core used for the meadow's geochronology. At
156 selected times, samples were taken for δ¹³C_{POC}, C:N_{POC} ratios for both horizons and δ¹³CO₂
157 trapped by the soda lime for the surface sediments.

158 After 500 days, additional aerated filtered seawater was added to the jars to bring the volume
159 back to 400 cm³ and the pH was adjusted to 8.5 with sodium hydroxide (NaOH; Analar). The
160 slurries were again kept in the dark at 30°C and aerated for 30 days. To remove any possible
161 organic and BC aerosols that might contaminate the slurry, the air was first passed through high-
162 efficiency particulate arrestance (HEPA) filters. The filters also supported a coarse polyester mat
163 impregnated with charcoal. The pH of the slurry was adjusted every few days to maintain acidity
164 between pH 7 and 8, and distilled water was added to replace any evaporative loss (Westrich and
165 Berner 1984).

166 *Sampling and analysis protocols*

167 The Mason jars were reopened under a N₂ atmosphere and the pH of the slurry water was
168 measured after the sediment had settled (ATC portable PH-107 (PH-009) Shanghai Longway
169 Optical Instruments), and their anoxic status was checked (YSI ProDSS). For sampling of the
170 slurry, a cut-off syringe was used to extract 10 cm³ of slurry after thorough mixing; the subsamples
171 were placed in 15-cm³ polypropylene centrifuge tubes and frozen at –20°C before analysis. The
172 remaining slurry was then bubbled with N₂ for 2 min as a precaution to maintain the anoxic
173 conditions within the jar. The lids of the jars were then resealed under N₂ after the soda lime traps
174 were removed, capped and replaced with identical traps. The traps were immediately oven-dried
175 and reweighed after first softly cleaning the surface of the centrifuge tubes of any accumulated red
176 biofilm, and CO₂ was determined gravimetrically (Keith and Wong 2006). Blanks indicated no

177 significant leakage of air into the Mason jars and typically showed an increase in weight of
178 ~0.0332 g (standard error (s.e.) = 0.014, $n = 4$), a value that is 68% less than the weight increase
179 from the traps in the jars containing slurry samples.

180 After thawing, the slurry samples were centrifuged at **2500g for 20 min at ambient temperature**
181 **(~25°C)** to separate the pore water for measurements of CDOM_{440nm} (**Harvey et al. 2015**),
182 ammonia (**Strickland and Parsons 1968**) and salinity (refractometer). The remaining sediment plug
183 was then dried at 105°C and the amount of water and sediment was noted to calculate the amount
184 remaining in the mason jars for CO₂ accumulation as dry weight of sediment after correcting for
185 salinity (**Lavelle and Massoth 1985**). Particulate organic matter (POM), PIC and black organic
186 matter (BOM) from the dried sediment slug was measured gravimetrically by loss on ignition
187 (LOI_{0.45 g}) in a laboratory furnace (**Carbolite CWF 1.8 L, Carbolite-Gero Ltd (UK); Heiri et al.**
188 **2001; Chew and Gallagher 2018**). Additional inter-batch corrections resulting from possible
189 furnace aging and procedural handling differences were performed using in-house local sediment
190 standards taken from the middle of the cores ($n = 5$) and randomly placed within the furnace.
191 Standards were previously dried (60°C) and stored frozen (-20°C). All POM and BOM values
192 were then converted to C **content** -using a local calibration regression. The regression was
193 constructed previously from sediments taken from Salut–Mengkabong seagrass and mangroves
194 (**Chew and Gallagher 2018**) by using the same furnace and in-house sediment standards. A
195 coefficient of 0.273 used to transform the LOI_{550–950°C} to PIC, by assuming the carbonate species to
196 be calcium salt (**Santisteban et al. 2004**). However, it should be noted that a later analysis of the
197 data suggested that the increase in carbonate may have been from ferrous salt. Until certainty is
198 established, in both the form of thermal decomposition equation during the analysis and identity of
199 the salt, all PIC **contents** are reported as CaCO₃. All measurements are presented, except for
200 CDOM_{440nm}, in molar units for stoichiometric comparisons. CDOM_{440nm} was converted to DOC to
201 give the organic dissolved pool dynamic an order of magnitude significance with other C variables.
202 As far as we are aware, the calibration used for the conversion is the only one available for 440-nm
203 determinations for an estuarine system (**Harvey et al. 2015**). The dataset is provided in the
204 **Table/Fig. Sxx, available as Supplementary material to this paper** should it be necessary for readers
205 to rework the CDOM_{440nm} and PIC **content** in light of new information.

206 Analyses of stable POC isotopes of $\delta^{13}\text{C}$ and their C : N ratios were performed on the two
207 horizons across separate mason jars at selected times (Days 0 and 210). Before analysis, the
208 samples were dried and vacuum sealed and sent to the Canadian Rivers Institute, University of
209 New Brunswick Nature Laboratory (SINLAB). Re-drying after acidification (10% HCl, Analar) to
210 remove PIC was performed before analysis at the institute. No isotope or element analysis was
211 undertaken for the local source materials, which would typically be required for an estimation of
212 their relative proportions. Nevertheless, estimations were gauged on the average $^{13}\text{C}_{\text{POC}}$ and N : C

213 endpoint signatures of seagrass, mangrove leaves and suspended particulate matter, using a model
214 constructed for several tropical lagoons (Gonneea *et al.* 2004; Chen *et al.* 2017). In addition, stable
215 isotopes of $\delta^{13}\text{C}$ trapped by the soda lime (Days 7, 210, 308 and 500) were measured from a
216 surface-horizon mason jar replicate. The jar was selected at random, and the analysis at the Central
217 Science laboratory was performed by mixing ground samples and subsamples under an Argon (Ar)
218 atmosphere and placing ~2.5 mg into pre-flushed (Ar) vacutainers. The CO_2 was released after
219 dissolving the powder with pure phosphoric acid before injection. Handling errors were tested on
220 one sample (mean, -19.78 ; s.e. ± 0.98 , $n = 4$). Note that limited resources precluded any additional
221 isotope analysis of either sediments or soda lime.

222 Sediment cores for the geochronology were collected using a sliding hammer Kajak corer
223 (UWITEC, Austria) equipped with a 6-cm internal-diameter polycarbonate core tube; the
224 sediment–water interface was stabilised with a porous polyurethane foam plug. The core was
225 transported vertically under ice to the laboratory for push extraction. Water content, bulk density,
226 porewater salinity and loss on ignition at 550°C and 950°C were measured every 2 cm (Gallagher
227 and Ross 2018). The remaining sediment for each horizon was used to determine particle size
228 (laser diffraction, model: 220 Type B, LISST-Portable XR, Sequoia Scientific (Australia)); after
229 drying (50°C) and storage for 3 months, ^{210}Pb , ^{226}Ra and ^{137}Cs radionuclide analysis was performed
230 using gamma spectroscopy at the Malaysian Institute of Nuclear Technology (Bangi, Selangor).

231 *Decomposition model*

232 The reactivity-continuum (RC) model was chosen to model the POC decomposition time series
233 (Boudreau 1991; Arndt *et al.* 2013; Mostovaya *et al.* 2017). Exploratory analysis indicated that this
234 gave the best fit and was the most parsimonious descriptor of the POC dynamics over single and
235 multi G models (Arndt *et al.* 2013). The model fits a continuous distribution of organic matter
236 decomposition, from labile to increasingly recalcitrant, and was calculated as follows:

$$237 \quad \frac{POC_t}{POC_0} = \left(\frac{a}{a+t} \right)^v \quad (1)$$

238 where a is the apparent age of the organic mixture (years) within the deposit, as a measure of its
239 degradability relative to an apparent age at the time of deposition. The exponent v is the gamma
240 distribution coefficient, which describes the labile–recalcitrant distribution and dominance (1–0
241 respectively) of the organic mix of the sediment horizon. Taken together, the initial first-order
242 decomposition coefficient, k_0 , is defined as v/a , which becomes increasingly recalcitrant with
243 incubation and Burial time t . The parameter solutions were calculated iteratively, using a non-
244 linear least-square parameter estimation within the software platform SigmaPlot™ 12.0. It should
245 be noted that there is a rival continuous diagenetic model. The model, ostensibly constructed
246 within phytoplanktonic and bacteria-dominated sediments, uses a power function to describe how
247 organic matter becomes increasingly recalcitrant over apparent time (Middelburg 1989). Although

248 the two models are equivalent mathematically (Tarutis 1993) when applied within closed systems
249 such as jars (i.e. no sediment accretion), the mix of seagrass litter, microalgae and mangroves in
250 the sediment (see Results), all with very different intrinsic reactivities (Middelburg 1989;
251 Kristensen 1994), would seem more aligned with an RC explanation than a relatively less
252 parsimonious power model as a sum of differing degrees of aging across different organic sources.

253 *Geochronology*

254 Sediment isotope tomography (SIT) was used to model a continuous ^{210}Pb geochronology down
255 the uninterrupted depositional regions of the sediment core (Gallagher and Ross 2018). The model
256 describes how the ^{210}Pb activity of sedimentary horizons can be fitted to a function that includes
257 the changes in the ^{210}Pb flux and sedimentation velocity as the ^{210}Pb decays over time (Carroll *et*
258 *al.* 1999). The algorithm employs a parsimonious inverse solution to best simulate the ^{210}Pb profile
259 by solving for the model parameters for maximum disentanglement of the flux and sedimentation
260 velocity terms (Liu *et al.* 1991). Further constraints and evaluations of solutions can be made by
261 the presence of known events (Carroll *et al.* 1999). Such events are traditionally peaks or horizons
262 of ^{137}Cs from atomic fallout within baseline sediments, and depositional facies characteristic of
263 surrounding material brought in by storms, earthquakes, floods or tsunamis.

264 Supporting data, additional figures cited, and method details can be found in Supplementary
265 material to this paper.

266 **Results**

267 *Sediment-core descriptions*

268 The first 23 cm of the Salut and 25 cm of the Mengkabong meadows were visibly muddy
269 (black), with no evidence of bioturbation. Below the 23-cm and 25-cm horizons, the character of
270 the sediment visibly changed to a coarser mixture of more compact light and dark brown sediments
271 containing a plethora of shell and mangrove wood debris (refer to Fig. S2). No sulfide could be
272 detected by smell or with lead acetate strips left in the sediment for a minute while they were
273 extruded into receiving tubes before separation.

274 *Sediment-horizon organic composition*

275 The $^{13}\text{C}_{\text{POC}}$ and their N:C ratios taken through the incubation did not appear to change and the
276 two horizons exhibited near identical signatures (Table 1). These signatures converged even further
277 when the effects of diagenetic transformations were considered (Gälman *et al.* 2008; Gälman *et al.*
278 2009). Interestingly, it was found that seagrass litter was likely to be a minor component (~5%).
279 The remaining components of surface-suspended matter, ostensibly microalgae, and mangrove
280 sources made up the remaining 25% and 70% respectively (refer to Supplementary material), in
281 agreement with other ecosystems in the region (Chen *et al.* 2017).

282 *Geochronology*

283 Although the depths of the storm facies were similar, it was clear from the ^{210}Pb -activity profiles
284 that the sedimentation dynamics within the baseline sediments were very different. The Salut
285 meadow, an embayment isolated at the head of the branch and fed by a rivulet, supported peaks in
286 activity at ~10 cm (Fig. 2), in contrast to a general decay in ^{210}Pb activity from the surface of the
287 Mengkabong meadow (Fig. 2), an embayment isolated from the main branch. The difference in
288 dynamics was also highlighted in the inability to detect any ^{137}Cs activity from atomic fallout
289 events within Salut sediments, which were evident as significant ^{137}Cs activity between 5 cm and
290 13 cm, peaking at 5 cm down the Mengkabong meadow core. This relatively shallow signal is
291 consistent with blow back of fallout from the 2011 Fukushima Daiichi nuclear accident
292 (Kaeriyama 2017).

293 When the SIT solution for the Mengkabong system was constrained by the timing of the
294 Fukushima fallout, the age of the depositional event was estimated as ~mid-1990s. The only recent
295 weather event of note was from the passage of tropical storm Greg (December 1996). The storm is
296 regarded as a once-in-400-years occurrence for this region, which is commonly known as ‘the land
297 below the wind’ because of its location south of the influence of the typhoon belt. The 1996, storm
298 triggered floods that severely affected the western coast of the state (Abdullah and Tussin 2014),
299 and a local resident shared his experience as a witness to a coastal surge of ~4 m within the
300 adjacent mangrove forests (Mohammad Asri bin Mohammad Suari, pers. comm.). With the
301 confirmation that the depositional event was likely to be tropical storm Greg, the SIT model now
302 adds constraints for the Salut meadow baseline sediments of age no older than 1996. On the basis
303 of these solutions, the origin of the very different ^{210}Pb dynamics becomes apparent. In Salut, both
304 the flux of the excess ^{210}Pb activity and the sedimentation rates of the meadow fell over time. In
305 Mengkabong, rates of sedimentation and ^{210}Pb activities remained relatively constant (220 g m^{-2}
306 per year, Fig. 2) and were interrupted only by an increase in excess ^{210}Pb activity consistent with
307 shoreline development during a peak in annual rainfall (~2005, unpubl. data Swee Theng Chew).
308 These show relatively high sequestration rates near the top of the range, even before any correction
309 for loss over time (Fig. 2).

310 *Incubation experiment*

311 Throughout the incubation experiment, the pH of both surface sediments and sediments taken
312 from 20–22 cm became increasingly acidic over time (Fig. 3). The older sediments taken from 20–
313 22 cm were more acidic and remained invariant and acidic. Surface-sediment slurries, in contrast,
314 were initially less acidic; however, their acidity increased over time, reaching an asymptote after
315 300 days equal to that of the older sediment slurry. The experiment failed to detect the presence of
316 H_2S within the jar headspace (no blackening of the lead acetate strips) that would infer ongoing
317 sulfate reduction.

318 Even though the initial BC represented a modest fraction of the POC (0.079 and 0.067 mol per
319 100 g or 11–13%), its influence on the POC dynamics was not apparent because there was no
320 significant decay in the BC content over the 500 days, and RC solutions with the time series failed
321 to converge. The anoxic decay of POC for the surface- and older 20–22 cm-horizon sediments
322 fitted the RC model well, and the separation of the terms was within acceptable limits (Fig. 4).
323 Surface-sediment POC content was greater than that of sediments taken from 20–22 cm. However,
324 we found no significant difference in their RC decay and apparent age parameters for the
325 decomposable fraction (Fig. 5), despite different interdecadal depositional ages (18 years).
326 Projections suggested that both horizons would have lost close to 30% of their POC content within
327 the first several years (6–7). Nevertheless, the overarching dynamics were such that both horizons
328 converged to losses of ~49 and 51% after 100 years of burial.

329 In contrast to POC, the dynamics of PIC, DOC and ammonia (NH₃) were not continuous. After
330 ~300 days, the carbonate content started to increase for both sediment horizons and appeared to
331 move towards an asymptote. This was accompanied by an increase in NH₃ and a decrease in DOC
332 content (Fig. 3) after the NH₃ content had first fallen and the DOC content increased (Fig. 3). Pools
333 of DOC and NH₃ were notably an order of magnitude smaller than that of POC. Only the
334 cumulative CO₂, after correction for PIC generation after the 300 days, showed steady-state
335 dynamics that slowed towards an asymptote (Fig. 6). However, there appeared to be a notable
336 deficit in the amount of CO₂ emitted for the amount of POC decomposed, in particular, for the
337 deeper, older sediment horizon. Furthermore, the $\delta^{13}\text{C}_{\text{POC}}$ isotopic signatures were not coupled to
338 each other. The $\delta^{13}\text{CO}_2$ values extracted from the soda lime were both relatively constant and very
339 much heavier than those extracted from the POC mixture. The $\delta^{13}\text{CO}_2$ was measured as $-19.78 \pm$
340 1.95 ($n = 4$) at Day 7, -17.74 ($n = 1$) at Day 189, -19.30 ($n = 1$) at Day 308 and -18.56 ($n = 1$) at
341 Day 500, the end of the incubation experiment. Meanwhile, at the same time, the NH₃, DOC and
342 PIC contents in the sediment slurry remained relatively constant up until about Day 365, when a
343 change in trend was observed (Fig. 3). From Day 365 until the end of the incubation experiment,
344 both PIC and NH₃ concentrations in the surface-sediment slurry increased, with an increase of
345 46.48% (s.e. = 3.91, $n = 4$) in PIC and 60.86% (s.e. = 1.57, $n = 4$) in NH₃ concentrations, whereas
346 DOC concentrations dropped by as much as 73.77% (s.e. = 8.75, $n = 4$) over the same period of
347 time. Meanwhile, for the sediment slurry taken from 20–22 cm, PIC and NH₃ concentrations
348 increased by 50.57% (s.e. = 1.44, $n = 4$) and 73.19% (s.e. = 2.17, $n = 4$) respectively, whereas
349 DOC concentrations dropped by 28.44% (s.e. = 4.89, $n = 4$).

350 *Aeration incubation*

351 The short aeration pulse over 30 days after the completion of the 500-day anoxic incubation
352 showed a large decrease in POC (18.86%, s.e. = 4.09, $n = 4$ for surface sediments; 16.99%, s.e. =
353 5.04, $n = 4$ for sediments from 20–22 cm), outside that of the parameters of the anoxic

354 mineralisation models (Fig. 4). This increase in decomposition was also in line with a
355 disproportionate increase in DOC over the anoxic mineralisation, confirming that, for both
356 horizons, organic aging had little effect on the recalcitrance of the buried POC.

357 **Discussion**

358 *Decomposition*

359 Assuming the incubation was sufficiently long to capture interdecadal decay parameters, it
360 appears that POC deposited, on average within 1–2 years of deposition may suffer significant
361 losses over climatic scales (49–51%). However, we must suggest caution in applying the surface-
362 horizon extrapolations as a generalisation to seagrass beds in other locales, as such sediments will
363 inevitably change their redox status from an aerobic- to an anaerobic-dominated form of
364 mineralisation. Aerobic mineralisation is clearly the more rapid of the two, the result of greater
365 efficiency in the mineralisation of the recalcitrant fractions (Kristensen *et al.* 1995). As well as
366 changing redox conditions, the nature of the organic mixture will likely affect the decay parameters
367 of the RC model. Clearly, the remaining half of the organic C, a seemingly recalcitrant fraction, is
368 more than can be accounted for by the <10% contribution of the BC alone. It is also unlikely, in
369 this case, that any presence of phytolith-occluded C was responsible, given that the BC
370 methodology may have inadvertently included this form (Chew and Gallagher 2018). What
371 remains is up to speculation; it may consist of bacterial necromass (Burdige 2007) and, an
372 increasingly important vector, especially within Southeast Asian coastal ecosystems, namely
373 microplastics (Nor and Obbard 2014; Li *et al.* 2019). Although microplastics have turnover times
374 of over 1000 years (Gewert *et al.* 2015), their amounts as C within soils and sediments remain
375 largely unknown. Some values have been estimated for terrestrial soils (Rillig 2018), ranging from
376 0.1–5% of POC for pristine environs to as much as 6.7% by soil weight.

377 Whatever value the overall decay parameters may take over space or time, it remains puzzling
378 that we found little difference in the POC decomposition-model parameters between the surface
379 and the deeper sediment horizons. This was not apparent in coastal non-vegetative sediments,
380 which are dominated by more labile phytoplanktonic organic sources (Burdige 1991; Zimmerman
381 and Canuel 2002). This can be explained by the following two possible theories: either the
382 sediments in these types of meadows were well mixed, which is unlikely given the presence of
383 ¹³⁷Cs peaks and ²¹⁰Pb decay series, or the stable-isotope signatures and recalcitrance are not
384 covariant down the sediment columns. For the latter to be consistent, mangrove sources would
385 need to balance an increase in recalcitrance between or within other organic sources because they
386 are buried over time. In essence, a mix of the reactivity continuum and power models would best
387 describe this. However, it cannot be discounted that changes in physical protection and benthic
388 consumption parameters may also play some role (Arndt *et al.* 2013). Indeed, it is this sedimentary

389 protection component that will likely reduce the generality of the result across meadows. In the
390 more exposed and turbulent meadows, seagrass sediments are composed of larger, sandier particles
391 (Gallagher *et al.* 2019). Such particles lack the necessary cohesiveness, surface area, and fine pore
392 structures required to exclude bacterial influence (Burdige 2007). Furthermore, no account of the
393 role of fauna reworking between surface oxic and surface anoxic sediments was found within the
394 sediments collected. We found no standout evidence of burrows from our multiple core collections,
395 and such reworking can only enhance mineralisation (Burdige 2007). Nevertheless, if prevalent,
396 this would lead to an even larger bias in sediment sequestration assumption than what the present
397 study suggests.

398 *Diagenesis and the coupling between CO₂ and decomposition*

399 The mineralisation and decomposition series have several notable features. These are seemingly
400 punctuated dynamics of carbonate, NH₃ and DOC, the CO₂ deficits with POC decomposition, and
401 the notably heavier ¹³CO₂ signature over that of ¹³C_{POC}. These dynamics suggest that the incubation
402 experiment was not at a steady-state because different diagenetic processes switched on and off.
403 How this affects the decomposition-model parameters is uncertain, but it is unlikely that the result
404 is an underestimate, given that the observed diagenetic switches are likely to reflect a resource
405 limitation that the incubation failed to supply. Nevertheless, this limitation is common to any
406 natural perturbation experiment attempting to discover what is possible under a different set of
407 conditions than that which may be encountered in other systems.

408 Within the limits of our monitored variables, the results imply that the initial fall in NH₃ content
409 under dark anoxic conditions is synonymous with coupled dissimilatory nitrate reduction (DNRA)
410 and denitrification by anammox autotrophic CO₂ fixation (Ni and Zhang 2013). Indeed, recent
411 work has also shown an unexpectedly high degree of anammox and DNRA in the upper muddy
412 seagrass sediments of a subtropical lagoon (Salk *et al.* 2017). Nevertheless, the relatively small
413 changes in NH₃ indicate that any dark CO₂ fixation would not have affected the overall CO₂
414 dynamics, even after considering a stoichiometry of C:NH₃ of 15:1 (Koeve and Kähler 2010).
415 However, it could be argued that the production of archaeal necromass may have contributed to an
416 increasingly recalcitrant pool of POC over time (Burdige 2007); the extent to which this would
417 contribute to the decomposition dynamics would depend, in part, on the supply of nitrate for
418 coupled DNRA. A reduction in the supply of nitrates may perhaps be responsible for a change to
419 another mineralisation process responsible for the increase in both NH₃ and PIC after 300 days.

420 Anoxic PIC and NH₃ production within marine coastal sediment, although consistent with
421 sulfate reduction (Burdige 1991; Mucci *et al.* 2000), is also inconsistent with several sedimentary
422 parameters and observations. First, we could not detect any H₂S produced within the Mason jar
423 headspace throughout the incubation period. Second, molar NH₃:CO₂ ratios were clearly an order

424 of 10^3 larger than those found for marine sediments dominated by sulfate reduction (Burdige
425 1991). What is not clear are the reasons for the increase in PIC, of sufficient amounts to affect the
426 CO_2 dynamics. Nevertheless, the lack of evidence for significant levels of sulfate reduction and
427 alkalisation points to another type of mineralisation, one that can support a suitable acidic
428 microenvironment. Recently, it has been demonstrated that an iron-reducing bacterium can
429 precipitate siderite (FeCO_3) within acidic sediments at ambient temperatures (30°C). It was
430 suggested that alkalisation at the cell walls was induced mainly by its production of NH_3 . Indeed,
431 the dynamics of the parameters measured herein fall within the scientific justification of inference
432 to the best explanation (Lipton 2000). The sediments were acidic and there was a parallel rise in
433 NH_3 production with PIC outside the stoichiometry of sulfate reduction. Furthermore, additional
434 analysis of selected remaining sediment samples retained throughout the incubation experiment
435 indicated that the total iron content was sufficient to support siderite formation ($0.051 \text{ mol } 100 \text{ g}^{-1}$,
436 s.d. = 0.0064, $n = 60$; see Table/Fig. Sxxxx), but only to levels to which the carbonate appears to
437 be reaching an asymptote ($\sim 0.15 \text{ mol } 100 \text{ g}^{-1}$, Fig. 3).

438 However, what is clear is that the overall CO_2 dynamics observed fall well short of accounting
439 for the continued loss of POC, irrespective of PIC and DOC. By itself, this implies that there must
440 be another mineralisation product. As far as we are aware, methane (CH_4) formed from
441 methanogenesis is the remaining alternative. Methanogenesis would result in the release of both
442 CO_2 and CH_4 , within its own sedimentary niche, where any iron reducers cannot directly compete
443 (Bray *et al.* 2017). Although we did not measure CH_4 during this incubation, the supposition is
444 supported by the relatively constant $^{13}\text{C}_{\text{POC}}$ values and considerably heavier $^{13}\text{CO}_2$ ratios of it
445 mineralised gas, trapped on the soda lime, over the incubation (Table 1). Such patterns have also
446 been found for highly organic coastal marine sediments where a considerably lighter $^{13}\text{CH}_4$
447 ($\sim 58.9\%$) balances out the heavier $^{13}\text{CO}_2$ ($\sim 19.2\%$) fraction, to maintain a constant heavy source
448 of $^{13}\text{C}_{\text{POC}}$ over time (Boehme *et al.* 1996). Why methanogens should dominate mineralisation over
449 sulfate reduction is not clear. Perhaps it is due to the high acidity of sediments seemingly supplied
450 from the adjacent mangrove mudflats (Marchand *et al.* 2004) and iron-reducing bacteria
451 (Koschorreck 2008).

452 Conclusions

453 The incubation experiment appears to capture the long-term decomposition parameters for POC.
454 The RC model seems to indicate that current estimates of C sequestration may be significantly
455 overestimated, in this case, by $\sim 50\%$, unless corrections can be made for loss over centennial time
456 scales. More information is needed across different sedimentary environs covariant with tropical
457 species and sources of organic C (Gallagher *et al.* 2019). Furthermore, much remains to be
458 investigated on the coupling of POC losses to greenhouse-gas emissions that have different
459 atmospheric warming effects and the roles of processes post-disposition, such as dark CO_2 fixation

460 and carbonate formation on net CO₂ emissions. Without certainty in both the estimates and the
461 conceptual model, there will not be sufficient certainty in the estimates of C storage and
462 sequestration services rendered by seagrass ecosystems for use in cap-and-trade C markets to
463 embrace these ecosystems as part of a solution to climate change.

464 **Author contributions**

465 CHC and JBG assisted in fieldwork and design of equipment and analysis of the iron **content**.
466 CHC conducted the incubation experiment and the **remaining variables**, created the figures and
467 tables, compiled the supplementary material and the statistical analyses within the tables, and
468 contributed to the modelling. JBG was responsible for the concept, the final modelling solution and
469 led the writing of the manuscript. STC collected cores and performed the SIT ²¹⁰Pb event
470 geochronology under supervision from JBG. NMZ provided the statement on recalcitrant carbon in
471 the form of microplastics found in the discussion. All authors approved the final version of the
472 manuscript and agree to be accountable for all aspects of the manuscript.

473 **Conflicts of interest**

474 The authors declare that they have no conflicts of interest.

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680 **Fig. 1.** The Salut–Mengkabong estuary site used in the study. Salut is the southern arm of the estuary,
681 whereas Mengkabong is the lagoon situated to the North. The sites at which the seagrass sediments were
682 obtained for the incubation experiment (▲) and the sample cores used for SIT data (○) are indicated. The
683 seagrass distribution information is based on collective indigenous knowledge, whereas the mangrove
684 distribution is obtained from the World Atlas of Mangroves Version 3 (Spalding *et al.* 2018) and from
685 Google Earth. (Map data: Google 2019; Landsat/Copernicus, Digital Globe, Bornean Biodiversity and
686 Ecosystems Conservation (BBEC) Sabah and WWF Malaysia 2017.) The line map was produced with QGIS
687 v3.6.0 and Adobe Illustrator CS6.

688 **Fig. 2.** Radiogeochronological profiles down the upper seagrass sediments of Salut estuary–Mengkabong
689 lagoon. The shaded area represents the mangrove deposition event. (a) The ^{137}Cs activity (►) down the
690 Mengkabong meadow sediments; no activity could be detected down the Salut meadow sediments. (b, c) The
691 respective supporting ^{226}Ra (●) and total $^{210}\text{Pb}_{\text{total}}$ activity (○). (d, e) The resultant mean excess or
692 unsupported $^{210}\text{Pb}_{\text{excess}}$ activity, corrected for ^{226}Ra , outside the deposition event (●) superimposed on their
693 respective stable sediment isotope tomography (SIT) simulations (○), together with (f) their resultant
694 particulate organic carbon (POC) sequestration rates for Mengkabong (○) and Salut meadows (●). (g, h)
695 Changes over time in the sedimentation and $^{210}\text{Pb}_{\text{excess}}$ parameters as simulated by SIT in the Mengkabong
696 and Salut sediment columns, with the actual recorded $^{210}\text{Pb}_{\text{excess}}$ activity (●) and $^{210}\text{Pb}_{\text{excess}}$ activity (○) being
697 indicated as modelled by SIT. Error bars denote the standard deviations of the counts of the radioactive
698 decay for each horizon.

699 **Fig. 3.** Values of pH, particulate inorganic carbon (PIC), dissolved organic carbon (DOC) and ammonia
700 measured in the sediments throughout the incubation experiment. (a) The pH of the sediment slurries from
701 Day 105 until the end of the anoxic incubation period. (b, c) The PIC content of the sediment. (d, e) The
702 DOC content of the porewater of the sediment slurry. (f, g) The ammonia concentrations of the porewater of
703 the sediment slurry. Values are given for (b, d, f) sediment collected from the surface 2-cm horizon and (c, e,

704 g) sediment collected from the 20–22 cm horizon. The last point in each series (*) shows the final values of
705 the sediments after a 30-day re-oxygenation period. Error bars indicate standard errors ($n = 4$).

706 **Fig. 4.** Particulate organic matter (POC) content and loss of POC fraction of the sediments used over the
707 anoxic incubation and subsequent re-oxygenation. The mean POC content corresponds to (a) the surface 2
708 cm and (b) the sediment collected from the 20–22-cm horizon. Error bars indicate the standard errors ($n = 4$).
709 The loss of the POC fraction over time in (c) the surface 2 cm and (d) the sediment collected from the 20–22-
710 cm horizon, using the reactivity continuum model. Broken lines indicate the 95% confidence limit, as do the
711 errors on the final point. The last point in each series (*, for a and b; ■, for c and d) shows the final value of
712 the sediments after a 30-day re-oxygenation period.

713 **Fig. 5.** Extrapolations of the fraction of remaining particulate organic carbon (POC) within the sediments
714 over 100 years following deposition. The broken line corresponds to the sediments collected from the 20–22-
715 cm horizon, which were dated to deposition c. 1996, whereas the solid line corresponds to the sediments
716 collected from the surface 2 cm, deposited in 2016.

717 **Fig. 6.** Cumulative CO₂ absorbed by soda lime and net loss of the particulate organic carbon (POC)
718 fraction of the sediments used over the anoxic incubation. (a) The sediment was collected from the surface 2
719 cm and (b) the sediment was collected from the 20–22-cm horizon. Error bars indicate the standard errors (n
720 = 4). The series indicated by circles (●) is the cumulative CO₂ absorbed over the course of the incubation,
721 whereas the series indicated by triangles (solid triangle) is the cumulative loss of POC over the same period.

722 **Table 1. Dry mass of particulate sedimentary carbon (C) and stable nitrogen (N) isotopes**
723 **and their molar ratios from the incubation jars**

724 S and B refer to the surface (0–2 cm) and bottom (20–22 cm) horizons, followed by the day
725 number during the incubation on which the sediments were extracted. All $\delta^{13}\text{C}$ values have been
726 normalised to preindustrial times (Suess effect), using their modelled depositional age. S0 and B0
727 are from single samples, whereas S210 and B210 are the means of four subsamples with their
728 respective standard errors

Sample	$\delta^{13}\text{C}$ (‰)	C (%)	N (%)	N : C ratio
S0	-24.61	7.83	0.61	0.066
S210	-24.71 ± 0.04	7.64 ± 0.13	0.58 ± 0.004	0.065 ± 0.0007
B0	-24.06	7.47	0.62	0.071
B210	-24.22 ± 0.03	7.61 ± 0.11	0.63 ± 0.004	0.070 ± 0.0007

729 ¹The 30% was calculated as the time of symmetry of the second derivative of the decay series, as percentage
730 lost over percentage of time over a span of 100 years ($\Delta\text{lost}/\Delta t = 1$). Although it is a continuous
731 function, because both scales are of the same magnitude, it, thus, marks the threshold time of a significant
732 slowdown in decomposition.