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Quantification of the lithogenic carbon pump following a dust deposition event

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Abstract

Lithogenic particles, such as desert dust, have been postulated to influence particulate organic carbon (POC) export to the deep ocean by acting as mineral ballasts. However, an accurate understanding and quantification of the POC-dust association that occurs within the upper ocean is required in order to affine the “ballast hypothesis”. In the framework of the DUNE project, two artificial seedings were performed seven days apart within large mesocosms. A suite of optical and biogeochemical measurements were used to quantify surface POC export following simulated dust events within a low-nutrient low-chlorophyll ecosystem. The two successive seedings led to a 2.3–6.7 fold higher POC flux as compared to the POC flux observed in controlled mesocosms. A simple linear regression analysis revealed that the lithogenic fluxes explained more than 85 % of the variance in POC fluxes. At the scale of a dust deposition event, we estimated that 42–50 % of POC fluxes were strictly associated with lithogenic particles through an aggregation process. Lithogenic ballasting also likely impacted the remaining POC fraction which resulted from the fertilization effect. The observations support the “ballast hypothesis” and provide a quantitative estimation of the surface POC export abiotically triggered by dust deposition. In this work, we demonstrate that the strength of such a “lithogenic carbon pump” depends on the biogeochemical conditions of the water column at the time of deposition. Based on these observations, we suggest that this “lithogenic carbon pump” could represent a major component of the biological pump in oceanic areas subjected to intense atmospheric forcing.

1 Introduction

The magnitude of downward particulate organic carbon (POC) export and its subsequent sequestration depends on the flux generated within the euphotic zone, the velocity with which sinking occurs, and the rate at which it decomposes (De La Rocha and Passow, 2007). In the past, strong correlations within the deep ocean between mineral (biogenic calcite, biogenic opal, and lithogenic particles) and POC fluxes have been reported (e.g. Deuser et al., 1981, 1983). To explain this predictive power, a "ballast hypothesis" was proposed, and it has been suggested that the downward POC flux is partly driven by associations with denser mineral particles that increase the overall sinking velocity for aggregates and that provide physical protection against the remineralization of labile organic matter (OM) (Ittekkot, 1993; Armstrong et al., 2002; Francois et al., 2002; Klaas and Archer, 2002). Although little evidence for a direct protective mechanism has emerged from in situ observations (Ingalls et al., 2006; Ploug et al., 2008; Iversen and Ploug, 2010), a recent experiment has demonstrated the potential for minerals to inhibit the destruction of OM by zooplankton grazing (Le Moigne et al., 2013). On the other hand, it has been demonstrated that minerals could increase the sinking velocity of aggregates (e.g. De La Rocha and Passow, 2007; De La Rocha et al., 2008; Thomalla et al., 2008; Engel et al., 2009; Iversen and Ploug, 2010) and drive large POC flux events (e.g. Thunell et al., 2007; Lee et al., 2009; Sanders et al., 2010; Ternon et al., 2010). Such fast sinking POC, negligible within the euphotic zone, is sufficient to explain deep-ocean POC fluxes (Honda and Watanabe, 2010; Riley et al., 2012), emphasizing the importance of the mode by which carbon is transferred downward when considering carbon flux parameterization.

Atmospherically and river-derived lithogenic material could act as an important carrier phase for POC to the deep ocean (Dunne et al., 2007; Salter et al., 2010). Often characterized by extreme events (Mahowald et al., 2003), atmospheric dust deposition could induce a sudden and drastic increase in particle concentration and pronounced differential settling rates within surface waters. Such physical perturbation could profoundly change collision and coagulation rates, and, therefore, act as a catalyst during the aggregation process (Hamm, 2002; Lee et al., 2009). Atmospheric desert dust particles also constitute an important external source of new nutrients in large oceanic areas (Duce et al., 1991; Mahowald et al., 2009) that may alleviate biological limitation (Boyd et al., 2010 and references therein) and enhance export production (e.g. Bishop et al., 2002). Therefore, such a fertilization effect coupled with lithogenic ballasting has major consequences on ocean biogeochemistry and particle flux. However, while these simultaneous POC fluxes are selectively removed with respect to the ballast hypothesis, difficulty remains in rigorously quantifying lithogenic ballasting due to this coupling between biotic and abiotic contributions.

As implicitly suggested by the ballast hypothesis, it has been demonstrated that POC-ballast associations take place within the upper ocean (Lee et al., 2009; Iversen et al., 2010; Sanders et al., 2010; Le Moigne et al., 2012) (i.e. before aggregates reach the mesopelagic where processes are determinant in setting the fraction of OM that reaches the deep ocean, Boyd and Trull, 2007). Although our mechanistic understanding of such an association must be improved, it seems that most lithogenic particles are not directly attached to biogenic particles but form clusters that are likely bound by extracellular organic material (Hamm, 2002). In light of this fact, an alternative explanation has been proposed which states that correlations between POC and mineral fluxes may result from OM, providing “glue” for aggregate minerals that would otherwise not sink (Passow, 2004; Passow and De la Rocha, 2006). Without determining the catalyst for aggregation, Ternon et al. (2010) concluded that the simultaneous presence of OM and lithogenic particles is required for the formation of large and fast sinking particles in the western Mediterranean Sea. Considering the strong spatial and temporal variability of dust deposition events (Jickells et al., 2005; Mahowald et al., 2009), the water column into which atmospheric particles are deposited is characterized by a wide-ranging OM composition and abundance. Therefore, the intensity of the aggregation process and subsequent particulate export could vary, limiting the relevance of a global scale approach for estimating the contribution of lithogenic ballasting to POC export (Ragueneau et al., 2006; Boyd and Trull, 2007; De La Rocha and Passow, 2007).

Since only a few studies have reported the enhancement of export production following dust deposition pulses in low-nutrient low-chlorophyll (LNLC) areas (e.g. Ternon et al., 2010), through this work, we sought to improve our understanding of this mechanism. As a result of the episodic nature of dust deposition, artificial seeding in mesocosms constitutes a suitable approach for following, on an environmentally relevant timescale, the surface POC export associated with dust deposition events. In this study, particulate export was investigated using two complementary approaches, as follows: (1) optical measurements were used to assess the rapid transfer of suspended particulate matter occurring a few hours following seeding, and (2) daily sediment trap samples were used to discriminate organic and lithogenic fractions and to provide a global view of the flux that occurs following seedings. While determining surface fluxes is subject to trapping artefacts (Gardner, 2000; Scholten et al., 2001; Yu et al., 2001), such an experimental approach enabled us to investigate particulate fluxes using vertical coherence and a higher time resolution than that feasible with sediment traps. The purpose of the study was to determine (1) the causality of the relationship between dust deposition and subsequent POC export increase, (2) the respective contribution of biotic (fertilization) and abiotic (lithogenic ballasting) processes to total POC export, and (3) the variability of these processes using different initial biogeochemical conditions.

2 Materials and methods

2.1 Experimental setup and sampling

In the framework of the DUNE project, a first artificial seeding experiment was performed in 2008 (DUNE-1) and a second in 2010 (DUNE-2). Since no optical measurements were performed during the DUNE-1 experiment, only the results from the DUNE-2 experiment are reported here. The mesocosm's experimental design and the methodology used to produce dust analogues are reported in Guieu et al. (2010). The physicochemical characteristics of produced dust analogues are reported in Desboeufs et al. (2013). Seven large mesocosms (height: 14.7 m, diameter: 2.3 m, surface area: 4.15 m^2, and volume: 52 m^3) were deployed within a coastal area (Corsica; 42.374° N, 8.554° E) during the summer oligotrophic period. Three mesocosms kept without seeding (here, referred to as "control mesocosms") and three seeded mesocosms (here, referred to as "+dust mesocosms") served as the mechanism for monitoring biogeochemical parameters. The seventh mesocosm, also seeded, was utilized for the deployment of optical instruments. The DUNE-2 experiment lasted 14 days, from 26 June to 9 July 2010. Two artificial seedings were successively conducted seven days apart within the same mesocosm and consisted of mimicking realistic wet deposition events with a dust flux of 10 g m^{-2}. Such a flux corresponds to 41.5 g of evapocondensed dust diluted in 2 L of ultrapure water. The mesocosms ended with a sediment trap (a 250 mL HDPE bottle) from which divers collected material every 24 h. Optical measurements were performed for ~2 days following each seeding at high spatial and temporal resolutions during the first ~24 h of each experiment, while biogeochemical parameters were sampled daily during the week. Primary production (PP) measurements were performed every 24 h at a depth of 5 m (Ridame et al., 2013). The data were integrated over the water column (0–12.5 m in depth) by assuming a homogeneous profile.

2.2 Optical measurements

Instruments and measurement corrections are described in detail in Bressac et al. (2012). Briefly, an optical profiling package, including an ECO-BB3 (WetLabs Inc.) backscattering sensor and a LISST-100 (Type B) device (Sequoia Scientific Inc.), was deployed inside and outside the "optical" mesocosm. To minimize perturbation inside the mesocosm when profiling, vertical profiles were performed from 0 to 10 m depth at a speed of 0.1 m s^{-1} at the center of the bag. Vertical profiles, performed every hour using both sensors, consisted of continuous measurements for approximately 20 min between the subsurface and 10 m depth. For the remaining 40 min, measurements were performed continuously at 0.5 m depth. Outside profiles (controls) were performed in the same manner. The particulate backscattering coefficient ($b_{bp}(\lambda)$, m^{-1}) was obtained from the light backscattered at 117° ($\beta(117°)$, m^{-1} sr^{-1}), measured using the ECO-BB3 sensor. Because of a logistic constraint, two different backscattering sensors were employed: a visible (440, 532, and 660 nm) and a near-infrared (720, 770, and 870 nm) ECO-BB3 were deployed during the first and second seeding experiment, respectively.

Only measurements performed at 660 (first seeding) and at 720 nm (second seeding) are reported here and compared to their respective initial values (see Sect. 3.3.2); indeed, the results at other wavelengths were similar. The LISST-100 type B measured the beam attenuation coefficient at 670 nm along a path length of 5 cm. The ratio of the intensity of transmitted light in seawater to the intensity of light transmitted in ultrapure water was used to calculate the attenuation coefficient due to suspended particles, removing the attenuation due to water (Hill et al., 2011). Since light absorption by colored dissolved substances is negligible in the red spectral domain (Bricaud et al., 1981; Boss et al., 2009), the measured attenuation is assumed to be the particulate beam attenuation (c_p, m^{-1}).

2.3 Sediment traps: sample treatment, elemental analyses, and calculations

Samples from sediment traps were analyzed within the seven mesocosms. Means of POC and lithogenic fluxes measured in the "optical" and +dust mesocosms were not significantly different from each other (p values > 0.05). However, since primary production was not measured, data from the "optical" mesocosm are not reported here. Following collection, samples were preserved using a solution of 5 % buffered formaldehyde and stored in the dark at 4 °C until processed. Swimmers were carefully handpicked using a binocular microscope. The remaining sample was desalted using ultrapure water and freeze-dried. Mass flux was determined by weighing the entire freeze-dried sample five times with the accuracy of the weighing being < 1 % over the whole data series.

The total concentration of carbon (TC) was measured in duplicate using a CHN analyzer (Perkin Elmer 2400) on aliquots of desiccated samples (5–10 mg). HNO_3/HF acid-digestion was performed in 7 mL Teflon flasks at 150 °C on aliquots of desiccated samples (~ 20 mg). Following complete evaporation, samples were diluted in 0.1 M HNO_3 and analyzed for their calcium (Ca), aluminium (Al), and sulfur (S) concentrations by ICP-AES using the procedures described by Desboeufs et al. (2013). The detection limit of the apparatus for Ca, Al, and S was well below the lowest concentration of the digested aliquot (Desboeufs et al., 2013). Aliquots of the blanks and the certified reference materials (GBW07313) were digested and analyzed for Al, Ca, and S under the same conditions. In dust analogues Ca is present both as calcium carbonate and calcium sulfate (Guieu et al., 2010; Desboeufs et al., 2013). The part of Ca associated with sulfate ($\%Ca_{CaSO_4}$) was estimated from the particulate S concentration within sediment traps. Therefore, the particulate Ca concentration as carbonate ($\%Ca_{CaCO_3}$) corresponded to the difference between total %Ca and $\%Ca_{CaSO_4}$. Then, the carbonate fraction ($CaCO_3$) was determined from the $\%Ca_{CaCO_3}$, as follows:

$$\%CaCO_3 = 100/40 \times Ca_{CaCO_3} \tag{1}$$

Particulate inorganic carbon (PIC) was deduced from the $CaCO_3$ fraction by assuming that, as follows:

$$\%PIC = 100/12 \times \%CaCO_3 \tag{2}$$

POC was determined by subtracting PIC from TC. The lithogenic fraction was determined from particulate Al concentrations measured in the +dust mesocosms by considering the Al composition of the dust analogue (3.32 %; Desboeufs et al., 2013). The protocol for the elemental analysis, the calculations for the various fractions, and the complete sediment trap data set are fully described in Desboeufs et al. (2013).

3 Results

Calculation and Nomenclature – In this work, POC flux data are presented for all of the mesocosms (Figs. 5 and 6) or as the average of the three +dust and three control values (Figs. 1, 7, and 8). The difference between these averaged POC fluxes is referred to as "net" (Fig. 1). "T_x" represents the sampling time expressed in hours (x) since the first seeding. For samples from the second experiment, time (in hours) since the second seeding (y) is added in parentheses, as follows: "$T_{x(y)}$".

3.1 The physical conditions and the initial chlorophyll *a* concentrations

Throughout the entire experiment, the seawater temperature ranged from 20° to 27.3 °C (Guieu et al., 2013a). The water column was well mixed during the first seeding experiment ($T_0 - T_{166(0)}$). Toward the last day of the first experiment, solar heating within the surface layer led to the onset of stratification. The vertical temperature gradient was rapidly disrupted on the night after the second seeding ($\sim T_{190(24)} - T_{210(44)}$). The water column remained well mixed until the last day of the experiment when a strong thermal stratification appeared. Stratification was higher during the second seeding experiment but interrupted by wind-driven mixing events.

The two artificial seedings were performed within the same water column seven days apart. Considering the biological response to the first seeding (Giovagnetti et al., 2013; Ridame et al., 2013), the biogeochemical status of the water column changed between the experiments. Prior to the first seeding, the chlorophyll *a* concentration (Chla) was characteristic of oligotrophic conditions ($0.07 \pm 0.02\,\mathrm{mg\,m^{-3}}$). Seven days after the first seeding (i.e. prior to the second seeding), Chla was ~ 1.7 times higher ($0.12 \pm 0.04\,\mathrm{mg\,m^{-3}}$). In the control mesocosms Chla remained constant for the entire experiment ($0.06 \pm 0.01\,\mathrm{mg\,m^{-3}}$), indicating that changes in the +dust mesocosms were directly linked to the seeding.

3.2 The POC flux evolution

The temporal evolution of the averaged POC fluxes in the dust seeded ($\mathrm{POC_{dust}}$) and control ($\mathrm{POC_{control}}$) mesocosms, as well as the difference between both fluxes ($\mathrm{POC_{net}}$), are reported in Fig. 1. It should be noted that the organic carbon contained in dust (0.31 %) constituted a very small fraction of the POC flux and is not discussed here since its fate remains unknown (Desboeufs et al., 2013). The first seeding resulted in a 2.3 times higher $\mathrm{POC_{dust}}$ flux ($111\,\mathrm{mg\,m^{-2}}$) as compared to the $\mathrm{POC_{control}}$ flux ($47.4\,\mathrm{mg\,m^{-2}}$). The $\mathrm{POC_{dust}}$ flux remained high during the first 96 h ($> 18.5\,\mathrm{mg\,m^{-2}}$

d^{-1}) and decreased by ~16 mg m^{-2} d^{-1} from T_{96} (Day 5). Until the end of the first experiment (T_{166}), the POC_{dust} flux remained higher than the $POC_{control}$ flux.

The second seeding strongly reactivated the downward POC export, while the $POC_{control}$ flux (on average, ~6.5 times lower) continually decreased, reaching a near zero value at the end of the experiment (~0.8 mg m^{-2} d^{-1}). The increase in POC_{dust} flux was particularly visible during the first 24 h ($T_{166(0)} - T_{190(24)}$) following the second seeding (+22.6 mg m^{-2} d^{-1}), and characterized by a larger variation (45 %) between +dust mesocosms than the variation observed 24 h following the first seeding (20 %).

During the first 24 h following the second seeding, the POC_{net} flux was 1.8 times higher than that 24 h after the first seeding. On Days 2 and 3, POC_{net} fluxes were similar between both experiments (~10–15 mg m^{-2} d^{-1}) but differed widely on Day 4, as follows: 15.4 and 5.5 mg m^{-2} d^{-1} for the first and the second experiments, respectively. The POC_{net} fraction collected over six days was slightly higher following the first seeding (62 mg m^{-2}) than after the second seeding (54 mg m^{-2}). Although these POC_{net} fluxes were similar, export dynamics differed in magnitude and duration. The POC export that stretched over time following the first seeding was intense, but was shorter following the second seeding.

3.3 The evolution of the optical parameters

b_{bp} and c_p measurements are representative of the various fractions of particulate matter stock (e.g. Loisel et al., 2011). b_{bp} is highly sensitive to changes in the small non-living particle abundance, such as dust (Stramski and Kiefer, 1991; Ulloa et al., 1994), while the c_p at 670 nm is dependent on the entire particle assemblage, excluding dissolved matter (Bricaud et al., 1981; Boss et al., 2009).

3.3.1 Depth integration

Thanks to the high-resolution vertical coverage of the water column using optical measurements, the integration of $c_p(670)$ from the surface to 10 m depth (c_p(0–10 m)) provides a record of particulate matter (of both biological and lithogenic origin) accumulation or depletion over time (Fig. 2). At T_0, the c_p(0–10 m) was very low (0.46 m^{-1}) consistent with the oligotrophic status of the water column, and immediately increased by 3.2 m^{-1} following the first seeding, then continually increased reaching 8.7 ± 1.4 m^{-1} ($T_{48} - T_{53}$). At $T_{166(0)}$, the c_p(0–10 m) was ~ 10 times higher (4.93 m^{-1}) than the T_0 value. Immediately following the second seeding the c_p(0–10 m) increased by 4.28 m^{-1} (9.21 m^{-1}), then continually decreased, reaching a lower value (2.62 m^{-1}) than the initial value.

3.3.2 The vertical particle profiles

The different initial values and the opposite evolution of c_p(0–10 m) during the two seeding experiments suggest a difference in behavior for dust and/or biological communities. The calculation of $\Delta c_p(670)$ ($c_p(670) - c_p(670)_{\text{initial}}$; m^{-1}) allowed us to investigate the net effect of seedings over time and depth (Fig. 3). Following the first seeding, the decrease (~ 1 m^{-1}) of $\Delta c_p(670)$ within surface waters was rapidly (T_6) followed by an increase (~ 0.2 m^{-1}) at depth (i.e. by an accumulation of particulate matter in comparison to the initial inventory of the water column). Between T_{30} and T_{48}, high and homogeneous $\Delta c_p(670)$ values were observed over the entire water column. The second seeding induced a higher accumulation of particulate matter within the first two meters of the water column ($\Delta c_p(670)$ up to 2.4 m^{-1} at 0.5 m depth). As demonstrated by the dust profile issued from particulate Al measurements within the water column (Desboeufs et al., in prep.), the accumulation of particulate matter is mainly associated with the addition of dust. Negative $\Delta c_p(670)$ values were rapidly observed ($T_3 - T_8$) at depth, demonstrating the rapid removal of particulate matter present before the second seeding. Between T_8 and T_{30} the decrease of $\Delta c_p(670)$ at the surface was followed by an increase at depth, indicating that an important transfer of matter toward depth occurred. Two days following the second seeding, $\Delta c_p(670)$ was homogeneous but negative along the 0–10 m water column, indicating that most of the particulate export occurred during this period, in agreement with the POC_{dust} flux trend (Fig. 1).

The evolution of $\Delta b_{bp}(\lambda)$ ($b_{bp}(\lambda) - b_{bp}(\lambda)_{\text{initial}}$ in m^{-1}; Fig. 4) was also investigated in order to focus on the fate of the added particles. The wavelength used differed between experiments (see Sect. 2.2); however, we assumed that this calculation allowed us to compare the respective evolution of Δb_{bp}. Differences in the $\Delta b_{bp}(\lambda)$ profiles between experiments were less marked as compared to the $\Delta c_p(670)$ profiles. Decreases in the $\Delta b_{bp}(\lambda)$ within surface waters were not associated with a proportional increase at depth, and could indicate that the "cleaning effect" of the water column highlighted using $\Delta c_p(670)$ profiles could result from the sinking of larger particles such as mixed aggregates that backscatter light less efficiently than small lithogenic particles (Twardowsky et al., 2001), as supported by particulate Al profiles showing a depletion of dust particles in the first 10 meters between T_{24} and T_{48} (Desboeufs et al., 2013). Two days following both seedings, the $\Delta b_{bp}(\lambda)$ profiles were homogeneous along the water column and still positive, indicating that a portion of the lithogenic particle pool was still in suspension as suggested by Bressac et al. (2012).

4 Discussion

4.1 A comparison between primary production, POC and lithogenic fluxes

The isolation of the water mass by the mesocosm could be conceptually compared to the effect of strong stratification within the upper water column that typically occurs during the summer period. Within the sediment traps of control mesocosms, the very high POC to lithogenic ratio, as observed, indicated that lithogenic ballasting was negligible (not shown). In this context, $\text{POC}_{\text{control}}$ export can be considered as representative of the surface POC export that occurs in natural systems during oligotrophic periods without external forcing.

Since optical data was limited to the first 48 h of experiments, sediment trap data and primary production were used to determine the biological and lithogenic contributions in POC export over experiments. Primary production exhibited a significant increase within +dust mesocosms following both seedings, while remaining constant within control mesocosms (Ridame et al., 2013). The continual decrease in $\mathrm{POC}_{\mathrm{control}}$ flux during the experiment (Fig. 1) indicated that the constant primary production observed within control mesocosms was not sufficient for sustaining the longevity of POC export throughout the experiment, in agreement with the critical particle concentration concept which proposed that the (re)activation of the aggregation process and subsequent particulate export requires a particle concentration above a threshold value (Jackson and Lochmann, 1992; Boyd et al., 2005; Burd and Jackson, 2009). Atmospheric deposition could help to reach this threshold via the direct input of lithogenic particles, and indirectly through the supply of new nutrients, leading to an increase in algal biomass.

In the +dust mesocosms, a comparison between integrated primary production data and POC fluxes indicated that no statistically significant relationship existed between these two parameters (p values > 0.05; Fig. 5). Introducing a time lag of 12 or 24 h between production and flux did not improve this relationship. The apparent decoupling between primary production and POC flux indicated that production alone could not be used to accurately predict POC fluxes.

Furthermore, following both seedings, the biomass of siliceous phytoplankton remained very low and a major response was observed for non-siliceous phytoplanktonic organisms (Giovagnetti et al., 2013). Although calcified organisms likely responded to the seedings, the fraction of biogenic $\mathrm{CaCO_3}$ collected in sediment traps of +dust mesocosms remained negligible (3 ± 0.5 % in mass; Desboeufs et al., 2013). Therefore, biomineral ballasting was considered to be negligible and lithogenic particles were considered to be the main carrier phase of POC in +dust mesocosms, as confirmed by the scatter plot of the POC_{dust} flux versus the lithogenic flux that indicated a statistically significant ($p < 0.0001$) correlation (Fig. 6). For these analyses we assumed that the regressions did not pass through the origin (i.e. that an additional POC fraction not directly associated with the lithogenic flux may be a significant component of the fluxes). A simple linear regression analysis revealed that the lithogenic fluxes explained more than 85 % of the variance in POC_{dust} fluxes. The ratios of the POC_{dust} flux to the lithogenic flux (carrying coefficients) ranged from 0.013 (during the second seeding) to 0.016 (during the first seeding). A possible explanation for the decrease in the carrying coefficient following the second seeding is discussed later (see Sect. 4.3.2).

4.2 The dynamics and timing of particulate export

The $c_p(670)$ coefficient, usually associated with the particle concentration ($< 20\,\mu m$) (Chung et al., 1998), is widely used to follow particulate export (e.g. Bishop et al., 2002; Smetacek et al., 2012). As the POC_{dust} fluxes and optical parameters, the phytoplankton community responded differently to both seedings with a distinct magnitude, timing, and composition change (Giovagnetti et al., 2013).

Although optical measurements revealed rapid particulate export following the first seeding (Bressac et al., 2012), $c_p(0\text{–}10\,m)$ continually increased during the $T_0 - T_{53}$ period (Fig. 2). This increase, particularly marked between T_{48} and T_{53}, was consistent with an increase in picophytoplankton biomass ($< 3\,\mu m$) that occurred two days following the first seeding, while larger cell-sized phytoplankton ($> 3\,\mu m$) needed three days to increase in terms of biomass (Giovagnetti et al., 2013). The $c_p(0\text{–}10\ m)$ evolution indicated that biological production exceeded and masked particulate export, explaining the longer duration of POC_{dust} export during the first experiment (Fig. 1). The long time lag between the first seeding and biological response (2–3 days) and immediate POC_{dust} export activation (Fig. 1) highlighted the decoupling between POC export and biological production. On the basis of these observations, we suggest that the immediate twofold increase in POC_{dust} flux resulted from abiotic processes such as lithogenic ballasting, in agreement with the strong correlation observed between the POC and lithogenic fluxes all along the first experiment (Fig. 6).

The opposite evolution of c_p(0–10 m) following the second seeding (Fig. 2) indicated that particulate export exceeded biological production ($T_{166(0)} - T_{214(48)}$). Even if a stronger biological response was observed (a three-fold higher Chla increase), dominated by the nano- and microphytoplankton community (> 3 µm), it only occurred 24–48 h after the second seeding (Giovagnetti et al., 2013). Therefore, the negative Δc_p(670) values rapidly observed ($T_3 - T_8$) at depth following the second seeding suggest that this immediate "cleaning effect" resulted from lithogenic ballasting. On a longer timescale, we can hypothesize that the preferential response of large cells, more prone to be exported, may have increased the budget of exported carbon and changed the "biotic contribution" to POC export.

These observations allowed a suggestion that a sequence of mechanisms controlled particulate export. While the biological response was delayed, particulate export driven by algal aggregation during the first 48 h following both seedings is unlikely (e.g. Prieto et al., 2002). On the other hand, the input of 41.5 g of dust (with a grain size distribution from < 0.1 to ∼ 20 µm) likely catalyzed the aggregation process on a short timescale (e.g. Lee et al., 2009) and activated particulate export. Thus, abiotic processes were likely dominant during the first 24–48 h until the biological contribution became significant and stretched over the time of particulate export. The decline could finally result from the imbalance between production and export, leading to a lower particle concentration within the water column than that required for the aggregation process.

4.3 The relationship between POC and lithogenic fluxes

The first general assessment for the carrying coefficients of ballast minerals was performed on a global scale (Klaas and Archer, 2002). Others studies that have generally focused on biominerals allowed these coefficients to vary in space (Ragueneau et al., 2006; Wilson et al., 2012), or were assessed from individual sites (Wong et al., 1999;

Conte et al., 2001; Honda and Watanabe, 2010). All of these analyses, performed at an annual timescale, reflect average fluxes during both productive and oligotrophic periods missing important temporal variability within the flux relationships. Therefore, we focused on specific dust deposition events on timescales on the order of a week, representative of the residence time for dust within surface waters estimated from days to month (Buat-Ménard et al., 1989; Bory and Newton, 2000; Croot et al., 2004; Frew et al., 2006). During this artificial seeding experiment in LNLC ecosystems, the lithogenic fluxes were high and the algal biomass was likely too low to drive large POC flux events. Therefore, the low carrying coefficients estimated in this study (0.013–0.016; Fig. 6) did not correspond to a low absolute associated POC flux but rather suggested a low lithogenic normalized POC flux. Despite the strong and statistically robust relationships observed in the +dust mesocosms between POC and lithogenic fluxes (Fig. 6), the mechanistic basis for these OM-lithogenic particle interactions remains uncertain. The correlations could result from (1) the lithogenic ballasting of organic matter (Armstrong et al., 2002; Francois et al., 2002; Klaas and Archer, 2002), (2) the inclusion of lithogenic particles within organic matter (freshly produced) (Passow and De La Rocha, 2006); or (3) the coupling of both processes. To determine the respective contribution of these biotic and abiotic processes to POC export, two comparative approaches were successively employed.

4.3.1 The effect of biogeochemical conditions

As a result of the high variability in physical conditions during the course of this experiment (Sect. 3.1), the direct comparison of POC_dust fluxes between both experiments could bias our interpretation. Therefore, the POC_dust fluxes were compared to the respective $\text{POC}_\text{control}$ fluxes, first highlighting the global effect (the biotic plus abiotic processes) of both seedings (Fig. 7). For the same initial biogeochemical conditions (i.e. the first seeding), the POC_dust flux was, on average, 2.33 (±0.12) times higher than the $\text{POC}_\text{control}$ flux. Under different initial biogeochemical conditions (i.e. the second seeding), the POC_dust flux was, on average, 6.68 (±0.51) times higher than the $\text{POC}_\text{control}$

flux. On the basis of these observations, we conclude that the net effect of a dust deposition event on POC export depends, in part, on the biogeochemical characteristics of the water column (the organic matter pool, the phytoplankton community) at the time of deposition. Among these biogeochemical parameters, the stronger increase in large cell (> 3 µm) biomass (Giovagnetti et al., 2013) could partly explain the larger difference observed during the second experiment. Dissolved organic matter (DOM) and sticky particles such as transparent exopolymer particles (TEP), known for promoting the aggregation process (Chin et al., 1998; Passow, 2002; Engel et al., 2004; Verdugo et al., 2004), could also have indirectly influenced POC export. Indeed, the abundance of such organic material prior to the second seeding was likely higher within the +dust than within the control mesocosms, strengthening the adsorption of DOM onto lithogenic particles and subsequent POC export. During an abiotic experiment, Bressac and Guieu (2013) demonstrated this abiotically driven POC export and its variation as a function of the composition and abundance of DOM. Although lithogenic ballasting cannot be strictly considered as a pump (as surface primary production is required to sustain it), these authors introduced the concept of the "lithogenic carbon pump" in order to highlight the fact that the fertilization effect, which is non-universal (e.g. Marañón et al., 2010), does not constitute a prerequisite for the occurrence of a dust-induced POC export event.

4.3.2 Biotic and abiotic contributions to POC export

With the objective of determining the strength of this "lithogenic carbon pump", the second comparative approach consisted of a deconvolution of the "ballasted" and "unballasted" POC fluxes. For this purpose, the POC_{dust} flux could be partitioned into two pools, a fraction associated with lithogenic particles (POC_{lith}) and a "freshly" produced one induced by the input of new nutrients (POC_{ferti}), as follows: $POC_{dust} = POC_{lith} + POC_{ferti}$. Also known as the particle export efficiency (e.g. Lutz et al., 2002; Henson et al., 2012), POC_{lith} was estimated by normalizing the POC_{dust} fluxes to the respective integrated primary production value (Fig. 8). As biomineral ballasting was negligible during this experiment (Sect. 4.1), the difference in this parameter between control and +dust mesocosms was assumed to result from lithogenic ballasting. Independent biological POC export was 1.17 (±0.19) (during the first seeding) and 2.84 (±0.19) (during the second seeding) times higher than the control's $\mathrm{POC_{lith}}$. According to the relationships obtained using both comparative approaches (Figs. 7 and 8), $\mathrm{POC_{lith}}$ represented 50 ± 8 and 42 ± 3 % of the $\mathrm{POC_{dust}}$ fluxes after the first and the second seeding, respectively; consistent with a higher biological contribution to POC export following the second seeding (Sect. 4.2). A possible explanation of the relative decrease in the $\mathrm{POC_{lith}}$ after the second seeding is the scavenging of most of the biogenic particles from the water column following the first seeding. Such a decrease was observed by Lee et al. (2009) following successive dust deposition events and suggests that $\mathrm{POC_{lith}}$ following the second seeding was allowed by the OM production induced by the first pulse of new nutrients, reflecting a highly dynamic system. A second key finding is that $\mathrm{POC_{ferti}}$ largely exceeded the variance in POC fluxes unexplained by lithogenic fluxes (∼ 15 %; Fig. 6), demonstrating that the carrying coefficient should be carefully interpreted. Such a finding calls into question whether or not a simple fertilization mechanism exists or whether the lithogenic ballasting of $\mathrm{POC_{ferti}}$ could occur and favor its downward export.

4.4 One dust deposition event, several particle settling populations

Both the coupling (e.g. Jickells et al., 1998; Migon et al., 2002; Ternon et al., 2010; Brust et al., 2011) and decoupling (e.g. Buat-Ménard et al., 1989; Migon et al., 2002; Ternon et al., 2010) of dust deposition and particulate export have been reported. During our experiment, only ∼ 52 and 30 % (by mass) of the lithogenic particles initially added were recovered in the sediment traps six days after the first and second seedings, respectively (Desboeufs et al., 2013). Neuer et al. (2004) collected samples at ∼ 500 m depth with between 13 and 20 % of lithogenic material deposited and concluded that a large fraction of lithogenic matter was not removed by particle sedimentation. Based on Stokes law, we estimated that approximately half (in mass) of the dust population was large enough (> 5 µm) to settle without being included in aggregates and reached the sediment traps of mesocosms before the end of the experiment. The smaller lithogenic particles (< 5 µm) that were numerically dominant likely remained in suspension, in agreement with $\Delta b_{\text{bp}}(660)$, still positive at $T_{166(0)}$ (not shown). The result could have been favored by ephemeral dust-induced phytoplankton blooms, which did not supply a sufficient amount of OM "glue", and by the rapid scavenging of most of the biogenic particles following both seedings.

In the open ocean, this pool of small lithogenic particles remains stored within surface layers during the stratification period until the onset of vertical convection during winter (e.g. Migon et al., 2002), their inclusion into faecal pellets (e.g. Buat-Ménard et al., 1989), or into larger aggregates (e.g. Burd and Jackson, 2009). For this last case, POC fluxes could scavenge these slow settling lithogenic particles from the water column and determine their flux (Passow and De La Rocha, 2006). The particle population could also act as a nucleation point for aggregate formation, and, therefore, contribute to a second POC export event (e.g. Ternon et al., 2010). Actually, a decoupling between the deposition and export of this particle population will occur, preventing a direct temporal comparison. Finally, the long residence time within surface waters for such highly refractive submicron lithogenic particles has been advanced in order to explain the color anomaly of the ultra-oligotrophic waters of the Mediterranean Sea (Claustre et al., 2002; Loisel et al., 2011). Our observations demonstrated the possible lasting impact of atmospheric lithogenic particles on seawater optical properties.

5 Conclusions

By combining the use of sediment traps and high-resolution vertical optical profiles inside large mesocosms deployed within a LNLC system, we report surface particulate export following two successive dust deposition events. Although the mechanism driving the relationship between POC and ballast material remains uncertain (De La Rocha and Passow, 2007), in this study we have demonstrated that (1) dust deposition catalyzes particle-sinking events (e.g. Lee et al., 2009; Ternon et al., 2010), and (2) the intensity of POC-lithogenic particle association depends on the biogeochemical conditions of surface seawater at the time of deposition. The results could be used to parameterize surface POC export in oligotrophic systems receiving high rates of dust deposition (e.g. the Mediterranean Sea) and to better predict the effects of future changes in atmospheric dust fluxes (Mahowald et al., 2009).

The lack of a significant relationship between POC flux and primary production combined with the high degree of covariance between POC and lithogenic fluxes adds further support to the ballast hypothesis. The probable composition of sinking aggregates (the high content of lithogenic material and the low amount of relatively buoyant OM), as well as their sinking velocity ($\sim$24–86 m day^{-1}; Bressac et al., 2012) suggest low specific carbon remineralization (Riley et al., 2012). Furthermore, the inherent sporadic character of the lithogenic carbon pump may play a fundamental role in carbon sequestration (Ragueneau et al., 2006) since episodic events may lead to the rapid sinking of particles that will not be fully exploited by the deep sea bacterial community (Hansell and Ducklow, 2003; Nagata et al., 2000, 2010). As a result, the major fraction of the deep sea POC flux following dust deposition events likely corresponds to the remnants of surface ballasted POC stocks (e.g. Thunell et al., 2007; Honda and Watanabe, 2010).

Impacts on heterotrophic activity must be taken into account in order to achieve connections between dust deposition and ocean carbon cycling (Pulido-Villena et al., 2008). Both seedings maintained the net heterotrophic character of the ecosystem (Pulido-Villena et al., 2013), leading to the remineralization of a fraction of fixed algal carbon, and therefore, to a decrease in the amount of exported organic carbon (Guieu et al., 2013b). While dust deposition generally induces the production of labile OM, the adsorption of DOM onto lithogenic particles and subsequent lithogenic ballasting could constitute a pathway by which DOM could escape from being remineralized within the upper ocean. In this sense, the lithogenic carbon pump could be considered as a pathway by which DOM could reenter the biological pump.

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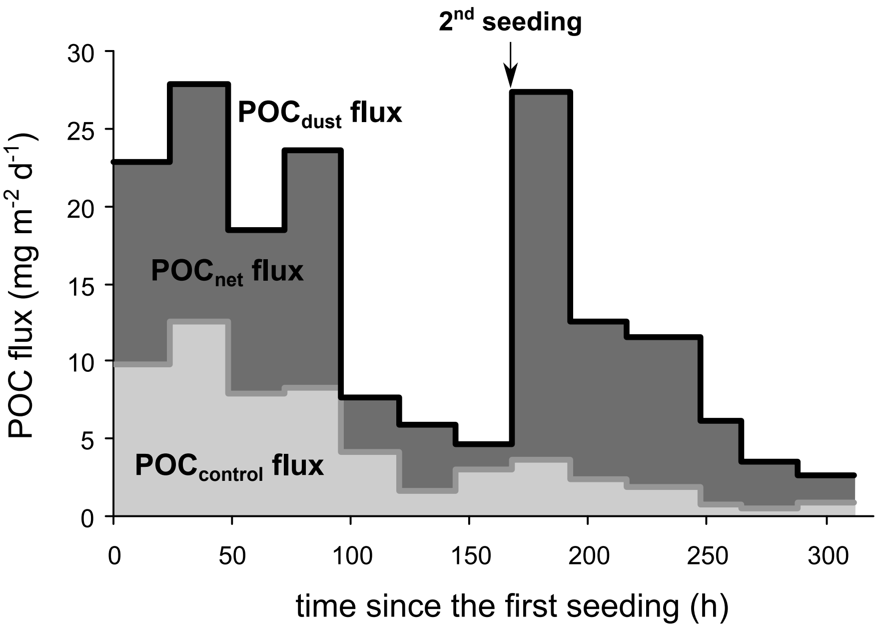

Fig. 1. Temporal evolution of the POC$_{dust}$ flux (the black line), the POC$_{control}$ flux (the light-gray portion), and the POC$_{net}$ flux (the dark-gray portion).

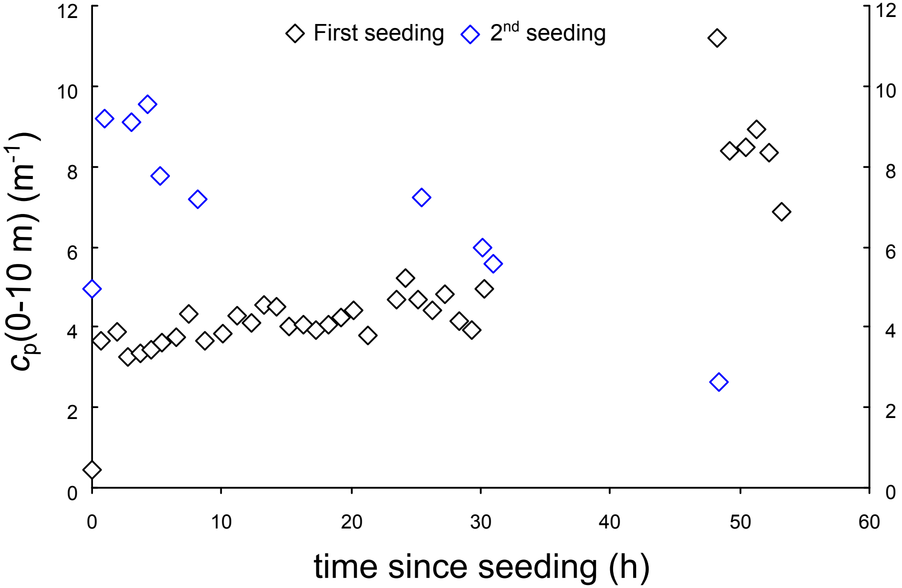

Fig. 2. Temporal evolution of the vertically integrated (0-10 m) particle attenuation coefficient (c_p(0–10 m)) during both seeding experiments.

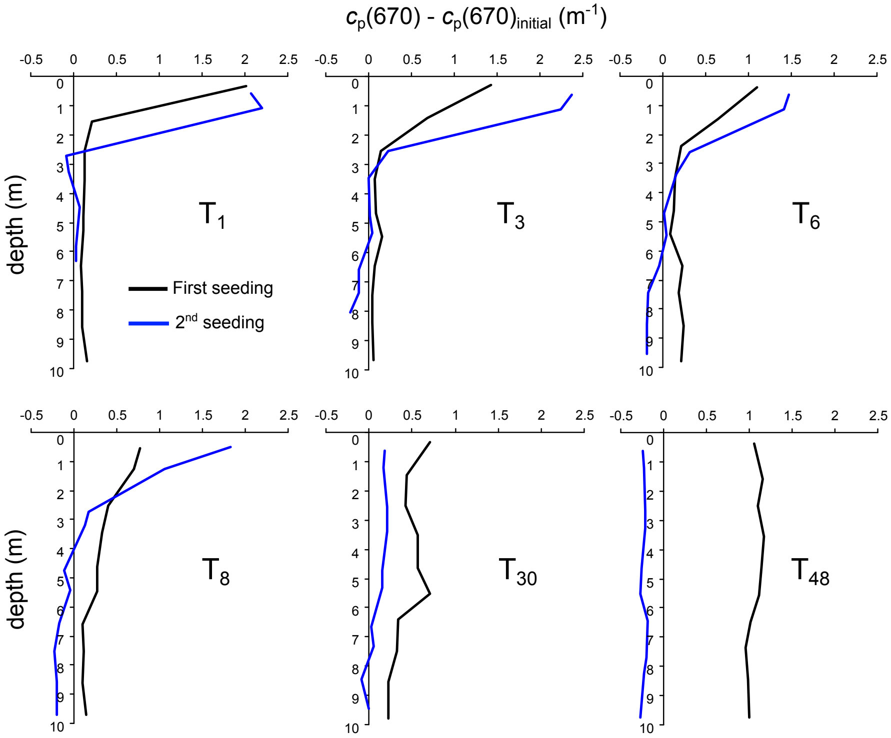

Fig. 3. The vertical profiles of $\Delta c_p(670)(c_p(670)-c_p(670)_{\text{initial}}$ in m^{-1}) for different times following both seedings. As compared to the respective initial $c_p(670)$, negative values correspond to a decrease.

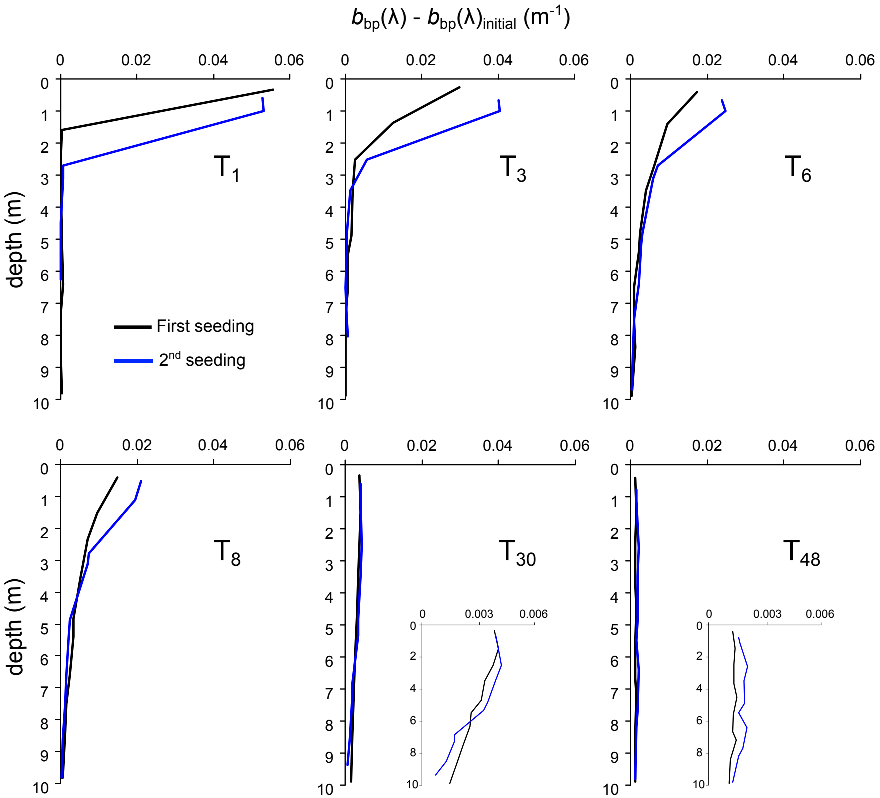

Fig. 4. Vertical profiles of $\Delta b_{bp}(\lambda)$ ($b_{bp}(\lambda) - b_{bp}(\lambda)_{initial}$ in m^{-1}) at different times following both seedings. The wavelength used for this calculation differed between experiments (see Sect. 2.2). The insets (the T_{30} and T_{48} panels) show a zoom of 0–0.006 m^{-1} values.

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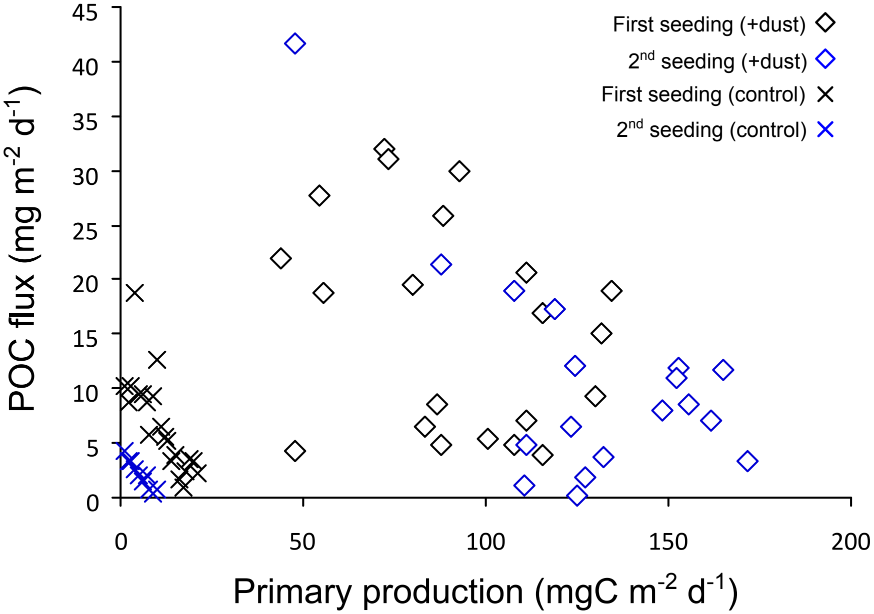

Fig. 5. POC flux for all of the mesocosms versus integrated primary production (PP). No significant correlation existed between PP and the POC flux in the +dust mesocosms (Fisher test, *p* values > 0.05).

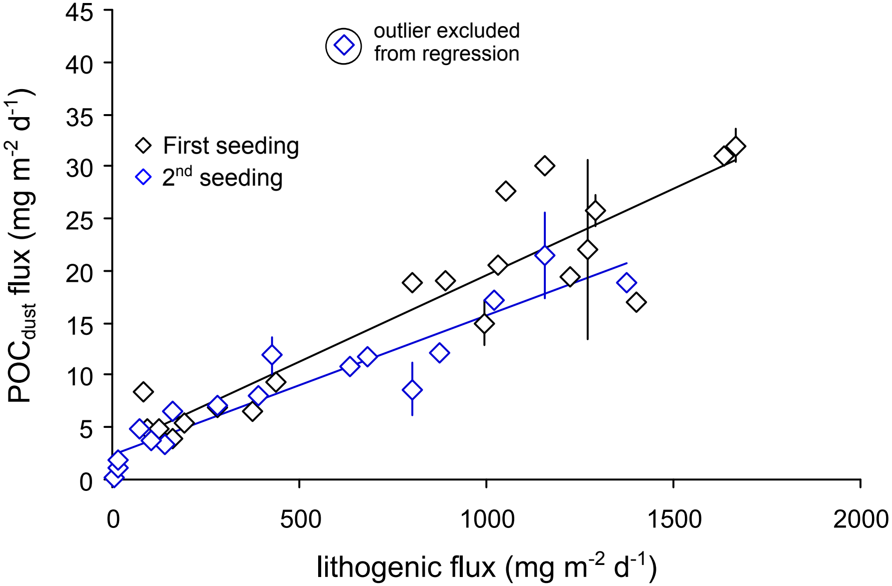

Fig. 6. POC$_{dust}$ versus lithogenic fluxes. Solid lines represent linear regressions with the following slopes, intercepts, determination coefficients, and probabilities (Fisher test): first seeding: $N = 21$, slope $= 0.016 \pm 0.002$, intercept $= 3.11 \pm 1.48$, $R^2 = 0.85$, $p < 0.0001$; and Second seeding: $N = 17$, slope $= 0.013 \pm 0.001$, intercept $= 2.41 \pm 0.80$, $R^2 = 0.88$, $p < 0.0001$. The highlighted outlier was excluded from the linear regression for second seeding data. The uncertainties correspond to the standard deviation of a same sample measured two times.

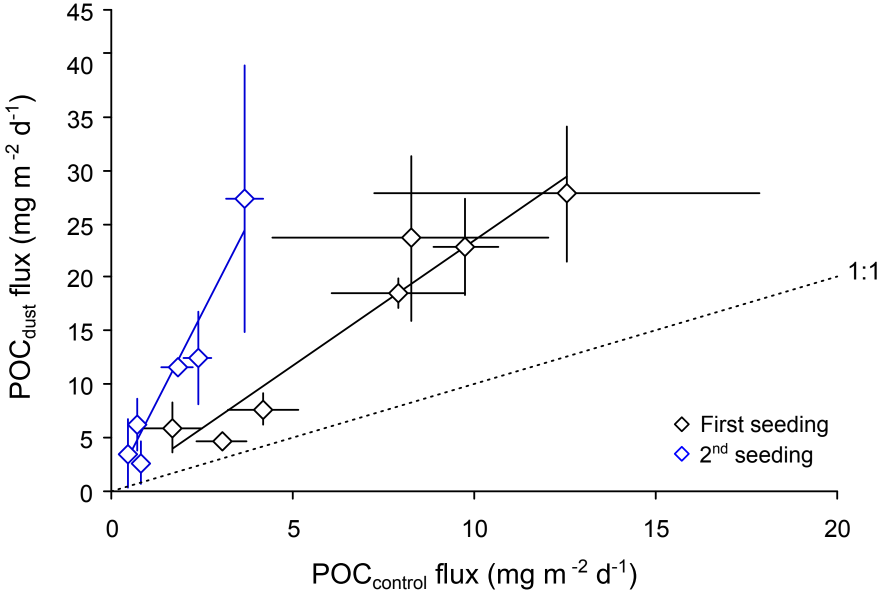

Fig. 7. POC_{dust} versus $POC_{control}$ fluxes (mean fluxes and standard deviations of the mesocosm triplicates). The best linear regressions and the 1:1 lines are shown. First seeding: $N = 7$, slope = 2.33 ± 0.12, $R^2 = 0.94$, $p < 0.0001$ (Fisher test); and Second seeding: $N = 6$, slope = 6.68 ± 0.51, $R^2 = 0.93$, $p < 0.0001$ (Fisher test).

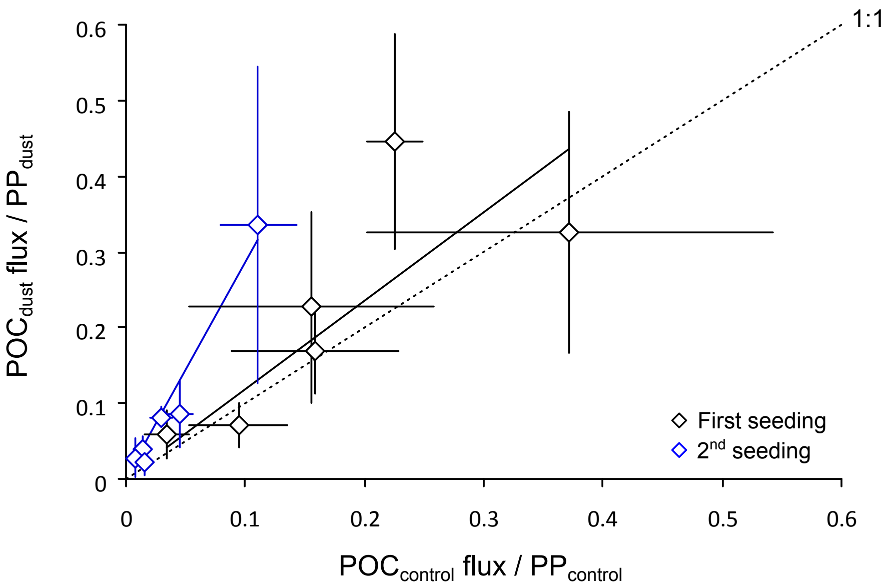

Fig. 8. POC_{dust} versus $POC_{control}$ fluxes, both normalized with respect to integrated primary production values (PP). The best linear regressions and the 1 : 1 lines are shown. First seeding: $N = 6$, slope = 1.17 ± 0.19, $R^2 = 0.56$, $p < 0.0001$ (Fisher test); and Second seeding: $N = 6$, slope = 2.84 ± 0.19, $R^2 = 0.96$, $p < 0.0001$ (Fisher test).