



A model for microbial phosphorus cycling in bioturbated marine sediments: Significance for phosphorus burial in the early Paleozoic

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Abstract

A diagenetic model is used to simulate the diagenesis and burial of particulate organic carbon (C_{org}) and phosphorus (P) in marine sediments underlying anoxic versus oxic bottom waters. The latter are physically mixed by animals moving through the surface sediment (bioturbation) and ventilated by burrowing, tube-dwelling organisms (bioirrigation). The model is constrained using an empirical database including burial ratios of C_{org} with respect to organic P ($C_{org}:P_{org}$) and total reactive P ($C_{org}:P_{react}$), burial efficiencies of C_{org} and P_{org} , and inorganic carbon-to-phosphorus regeneration ratios. If P_{org} is preferentially mineralized relative to C_{org} during aerobic respiration, as many previous studies suggest, then the simulated P_{org} pool is found to be completely depleted. A modified model that incorporates the redox-dependent microbial synthesis of polyphosphates and P_{org} (termed the microbial P pump) allows preferential mineralization of the bulk P_{org} pool relative to C_{org} during both aerobic and anaerobic respiration and is consistent with the database. Results with this model show that P burial is strongly enhanced in sediments hosting fauna. Animals mix highly labile P_{org} away from the aerobic sediment layers where mineralization rates are highest, thereby mitigating diffusive PO_4^{3-} fluxes to the bottom water. They also expand the redox niche where microbial P uptake occurs. The model was applied to a hypothetical shelf setting in the early Paleozoic; a time of the first radiation of benthic fauna. Results show that even shallow bioturbation at that time may have had a significant impact on P burial. Our model provides support for a recent study that proposed that faunal radiation in ocean sediments led to enhanced P burial and, possibly, a stabilization of atmospheric O_2 levels. The results also help to explain $C_{org}:P_{org}$ ratios in the geological record and the persistence of P_{org} in ancient marine sediments.

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1. INTRODUCTION

Permanent burial of phosphorus (P) in continental margin sediments is a major control on the marine P inventory, primary productivity and possibly interglacial CO_2 concentrations (e.g. Broecker, 1982; Wallmann, 2014). On Myr

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Table 1
Observations of C and P geochemistry in oxic and anoxic margin sediments.

	Oxic	Anoxic
$C_{\text{org}}:P_{\text{org}}$	30–115 ^a	200–700 ^b
$C_{\text{org}}:P_{\text{reac}}$	21 ^c	54–161 ^c
C_{org} burial efficiency (CBE, %)	25 ± 10 ^d	>40 ^e
P_{org} burial efficiency (PBE, %)	20–40 ^f	<2–11 ^g
$(C:P)_{\text{REG}}^h$	118 ± 24 ⁱ	<70 ^j

^a From the data corresponding to ‘oxic sites’ in Fig. 3 of [Slomp and Van Cappellen \(2007\)](#).

^b From the data corresponding to ‘low oxygen and anoxic sites’ in Fig. 3 of [Slomp and Van Cappellen \(2007\)](#), as well as data from the anoxic Arabian Sea oxygen minimum zone from [Kraal et al. \(2012\)](#). Values exceeding 1000 observed in the paleo record are rare in modern sediments.

^c [Slomp et al. \(2004\)](#)

^d Literature data show that CBE depends non-linearly on the sediment mass accumulation rate (e.g. [Burdige, 2007](#)) and, possibly, the availability of dissolved oxygen. A mass accumulation rate of 0.075 g cm⁻² yr⁻¹ can be calculated for a typical upper slope/shelf setting using the formula $\rho(1 - \phi)\omega_{acc}$ where ρ (2.5 g cm⁻³) is the density of sediment particles, and ϕ (0.7) and ω_{acc} (0.1 cm yr⁻¹) are the porosity and sedimentation rate of compacted sediments, respectively. For oxygenated bottom waters (>20 μM O₂), this mass accumulation rate corresponds to a CBE of around 25% ([Dale et al., 2015b](#)).

^e As footnote ^d, for <20 μM O₂.

^f Data on PBE in oxic, bioturbated sediments are scarce and there is high uncertainty in this value. PBE can be estimated using the CBE and $C_{\text{org}}:P_{\text{org}}$ burial ratios for which more data is available: $PBE_{\text{OX}} = \frac{PBE_{\text{AN}} \cdot CBE_{\text{OX}} \cdot (C_{\text{org}}:P_{\text{org}})_{\text{AN}}}{CBE_{\text{AN}} \cdot (C_{\text{org}}:P_{\text{org}})_{\text{OX}}}$, where subscripts ‘OX’ and ‘AN’ denote oxic and anoxic sediments, respectively. Assuming average values for CBE_{AN}, PBE_{AN} and $(C_{\text{org}}:P_{\text{org}})_{\text{AN}}$ of 50%, 7% and 400, respectively, and CBE_{OX} and $(C_{\text{org}}:P_{\text{org}})_{\text{OX}}$ burial ratios of 25% and 50 (respectively), PBE_{OX} is 28 ± 14%, hence the proposed range of 20–40. Notwithstanding the uncertainty arising from the input parameters, PBE in oxic sediments is at least a factor of 2–4 that in anoxic sediments. For comparison, [Jensen et al. \(1995\)](#) calculated a PBE of 29–35% in oxic Aarhus Bay sediments, whereas [Ingall and Jahnke \(1994\)](#) reported lower PBE in oxic sediments ranging from 6% to 23% based on a few observations on the continental slope.

^g For oxygen deficient bottom waters (<20 μM O₂) ([Ingall and Jahnke, 1994](#); [Slomp et al., 2004](#)).

^h Benthic regeneration ratio = DIC flux/PO₄³⁻ flux at sediment surface determined in situ using benthic chambers. It is important to point out that [Colman and Holland \(2000\)](#) caution that benthic phosphate fluxes, and indeed dissolved inorganic carbon fluxes, may exhibit seasonal variability. For the present study, we note these concerns but lay them to one side, and consider that $(C:P)_{\text{REG}}$ ratios are indicative of steady state or seasonally-averaged conditions.

ⁱ Using the empirical transfer function of [Wallmann \(2010\)](#).

^j Values for anoxic bottom waters on the Peruvian margin range from 4 to 68 ([Noffke et al., 2012](#)). The empirical function of [Wallmann \(2010\)](#) based on in situ flux measurements predicts a value of 11 ± 24 for near-anoxic conditions, although the full range of predicted values for anoxic waters is very similar to those measured on the Peruvian margin. [Sannigrahi and Ingall \(2005\)](#) report a value of 39 for an anoxic site in Effingham Inlet.

time scales, P burial exerts a strong, if not dominating, influence on atmospheric O₂ levels ([Van Cappellen and Ingall, 1996](#); [Lenton and Watson, 2000](#); [Boyle et al., 2014](#)). Diagenetic transformations of P and the factors controlling P burial are thus intensively studied (reviewed by [Benitez-Nelson, 2000](#); [Paytan and McLaughlin, 2007](#); [Slomp, 2011](#); [Ruttenberg, 2014](#)).

Particulate organic P (P_{org}) comprises more than 90% of P that rains to the seafloor ([Delaney, 1998](#)). Phosphate (PO₄³⁻) that is solubilized from P_{org} in the sediments can be sequestered into authigenic mineral phases, mainly as carbonate fluorapatite (CFA) and P bound or adsorbed to iron oxyhydroxides (FeP) ([Bernier et al., 1993](#)). These transformations, more generally described as ‘sink switching’, increase the overall benthic retention efficiency of P ([Ruttenberg and Berner, 1993](#); [Anderson et al., 2001](#)). Observations from the North Atlantic suggest that sink-switching is enhanced in sediments that are bioturbated, that is, reworked by infaunal deposit and detritus feeders ([Slomp et al., 1996](#)). The sedimentary retention capacity of P further appears to be sensitive to the ambient redox conditions ([Algeo and Ingall, 2007](#)). For example, FeP content tends to be lower under anoxic bottom waters due to reduced ferrous iron oxidation and co-sequestration of P

([Sundby et al., 1992](#); [Jensen et al., 1995](#); [McManus et al., 1997](#)). CFA content may be higher under these conditions, especially in modern oxygen minimum zones where phosphorites may form ([Papineau, 2010](#)).

The impact of oxygen levels on P_{org} burial is less well understood. Data on P_{org} burial efficiencies (PBE) are scarce, yet point toward lower values under anoxic versus oxic bottom waters, that is, preferential mineralization of P_{org} in anoxic settings (e.g. [Schenau and De Lange, 2001](#); [Jilbert et al., 2011](#)). This trend is opposite to the organic carbon burial efficiency (CBE), which is apparently high under anoxic bottom waters and low under oxic waters (see [Table 1](#) and further discussion by [Burdige, 2007](#)). It thus follows that molar organic carbon to phosphorus ratios ($C_{\text{org}}:P_{\text{org}}$) in laminated anoxic facies commonly exceed the Redfield ratio (106:1), whereas bioturbated sediments have ratios that are around Redfield or lower ([Table 1](#)). This difference is maintained, although less pronounced, for the ratio of C_{org} to reactive phosphorus ($P_{\text{reac}} = P_{\text{org}} + \text{FeP} + \text{CFA}$). Consistent with these findings, the inorganic carbon-to-phosphorus regeneration ratio derived from in situ flux measurements, $(C:P)_{\text{REG}}$, is often above Redfield in oxic settings and below it in sediments underlying intermittently or permanently oxygen-deficient

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