

Atmospheric dust stimulated marine primary productivity during Earth's penultimate icehouse

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ABSTRACT

The importance of dust as a source of iron (Fe) for primary production in modern oceans is well studied but remains poorly explored for deep time. Vast dust deposits are well recognized from the late Paleozoic and provisionally implicated in primary production through Fe fertilization. Here, we document dust impacts on marine primary productivity in Moscovian (Pennsylvanian, ca. 307 Ma) and Asselian (Permian, ca. 295 Ma) carbonate strata from peri-Gondwanan terranes of Iran. Autotrophic contents of samples, detected by both point-count and lipid-biomarker analyses, track concentrations of highly reactive Fe, consistent with the hypothesis that dust stimulated primary productivity, also promoting carbonate precipitation. Additionally, highly reactive Fe tracks the fine-dust fraction. Dust-borne Fe fertilization increased organic and inorganic carbon cycling in low- and mid-latitude regions of Pangaea, maintaining low $p\text{CO}_2$.

INTRODUCTION

Atmospheric dust carries nutrients such as iron and fixed nitrogen that fertilize marine primary producers, impacting carbon cycling (e.g., Martin, 1990; Boyd et al., 2004; Krishnamurthy et al., 2010). Today, eolian delivery of nutrients to iron-limited marine systems controls phytoplankton populations (Guo et al., 2012; Chien et al., 2016) and can intensify carbonate precipitation through stimulation of microbial activity (Bressac et al., 2014; Guieu et al., 2014; Swart et al., 2014; Zhu and Dittrich, 2016).

Despite the importance of eolian dust in supplying marine nutrients, the biotic consequences of dust in Earth's deep-time record remain poorly known. Dust deposits are well documented from the late Paleozoic (Soreghan et al., 2008, 2015), with the possibility of large dust-fertilization effects, but evidence is preliminary and limited to the paleo-equator (Sur et al., 2015).

Establishing a link between atmospheric dust and productivity that extended to mid-latitudes would clarify global biogeochemical responses and carbon cycling during the late Paleozoic ice age (LPIA). These effects also have implications for Earth's climate projections, given the urgent need to achieve negative carbon emissions (e.g., Hauck et al., 2016; IPCC, 2018).

For the first time in the ancient record, we investigated the relationship among concentrations of dust, bioavailable iron, autotroph content, and bacterial biomarkers from shallow-marine carbonate of the Central Persian terrane (present-day Iran) once located in southeastern mid-latitude Pangaea (Fig. 1A) to assess the strength and spatial extent of the iron-fertilization effect in deep time. The findings have potential implications for the influences of atmospheric dust on carbon cycling in Earth's penultimate icehouse and beyond.

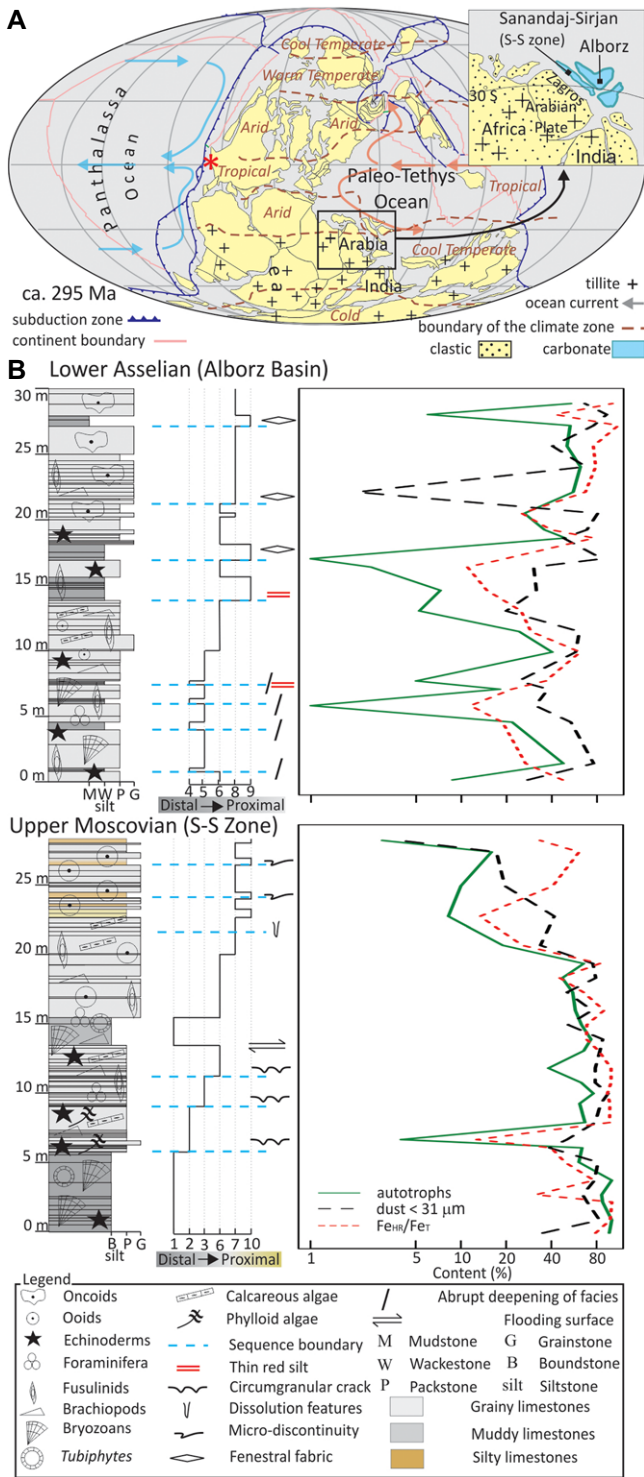
BACKGROUND AND METHODS

Pennsylvanian–Permian carbonate strata of the study area were located at $\sim 30^\circ\text{S}$ at the time of deposition, adjacent to the northeastern Arabian margin of Gondwana, in relative proximity (~ 1000 km) to Gondwanan ice centers (e.g., Arabian shield; Sardar Abadi et al., 2019). The upper Moscovian of the Sanandaj-Sirjan zone and lower Asselian of the Alborz Basin record deposition of warm, shallow-marine carbonate isolated from fluvial-deltaic sediment sources (Sardar Abadi et al., 2019). These strata record multiple glacioeustatic sequences, and high-resolution (20 cm) sampling was conducted through 28 m of the study intervals to capture several sequences. Petrographic and biomarker data indicate a diverse biotic assemblage including speciose cyanobacteria, phylloid algae, other calcareous green and red algae, and heterozoans, as well as abundant abiotic components.

We point-counted (400 points per sample) thin sections from 21 Asselian and 25 Moscovian samples, selected to capture facies variation. Components were categorized into abiotic, autotrophic, heterotrophic, and symbiotic attributes (following Schlager, 2003; Table DR1 in the GSA Data Repository¹). In this terminology, “abiotic” refers to physically precipitated carbonate (e.g., ooids), “autotrophic” components are primary producers (e.g., calcareous green algae), “heterotrophic” components are consumers (e.g., bryozoans), and “symbiotic” components are two cooperating organisms,

¹GSA Data Repository item 2020064, Figures DR1–DR5, Tables DR1 and DR2, and supplemental data set with iron speciation, ICP-MS results, and grain-size analysis, is available online at <http://www.geosociety.org/datarepository/2020/>, or on request from editing@geosociety.org.

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the 2-methyl hopane index (2-MHI) (Summons et al., 1999). All samples ($n = 50$) were analyzed for bulk-rock geochemistry using inductively coupled plasma–mass spectrometry.

Samples were processed for dust extraction by sequential steps to remove carbonate, organic, pyritic, iron-oxide, and authigenic silica components (Sur et al., 2010); subsequently, the extracted dust was analyzed by laser particle-size analysis (Malvern Mastersizer 3000). A standard sequential extraction (Poulton and Canfield, 2005) was used on (unprocessed) sample splits to assess the amount of highly reactive iron (Fe_{HR}) species (cf. Raiswell et al., 2018). Fe_{HR} is generally determined by summing dithionite iron (Fe_D), acetate iron (Fe_{ac}), oxalate iron (Fe_{OX}) and pyrite iron (Fe_{py}). However, we did not include Fe_{py} in our calculation of Fe_{HR} because samples ($n = 5$) with petrographic evidence of pyrite documented very low Fe_{py} (0.01–0.03 wt%). The ratio of Fe_{HR} to total iron (Fe_T) is a proxy for initially bioavailable iron; while this approach does not quantify bioavailable iron, this is the best available proxy for quantifying potential ancient iron bioavailability (Sur et al., 2015). Additionally, iron extraction quantifies the various fractions of Fe corresponding to different iron species that are highly reactive. Importantly, Fe_T does not vary appreciably through the analyzed samples, thus the ratio of Fe_{HR} to Fe_T reflects changes in Fe_{HR} in the sample.

We used linear and polynomial regressions to examine relationships between Fe_{HR}/Fe_T and proportions of autotrophic, heterotrophic, symbiotic, and abiotic components. We performed a redundancy analysis (RDA) to examine relationships among Fe_{HR} , dust grain size, and biotic and abiotic components. RDA is an ordination technique that allows hypothesis testing for multiple driver and predictor variables (Legendre and Legendre, 1998). RDA was conducted using the *vegan* package (Oksanen et al., 2018) in the R program version 3.5.3 (R Core Team, 2019). To limit collinearity in our models, we tested for variance inflation factors (VIFs) and included only predictor variables with VIFs <4 (Groß, 2003). Driver variables demonstrated no variance inflation (all VIFs <4).

RESULTS

High-frequency sequences of the study sections generally comprise intervals with high heterotrophic content that, in the Asselian, yield upward to autotroph-dominant, and in the Moscovian, yield to abiotic-dominant facies, with minor evidence for lowstand (incipient exposure) at sequence tops.

Biomarker results of the six samples display a range of 5.5%–12.5% (average 8.0%) for 2-MHI, which indicates the relative proportion of organic matter contributed by cyanobacteria (Summons et al., 1999). These results imply a high influence of cyanobacterial activity for all of our samples.

one providing nutrients and one providing carbohydrates (e.g., fusulinids). Additionally, total lipids were extracted from six samples, selected to represent a range of cyanobacterial content based on point-counting; hopanoid biomarkers

were targeted for measurements on gas chromatography–mass spectrometry under multiple reaction monitoring (MRM) to evaluate the presence of cyanobacteria, indicated by the ratio of 2-methyl hopane to total hopane, also known as

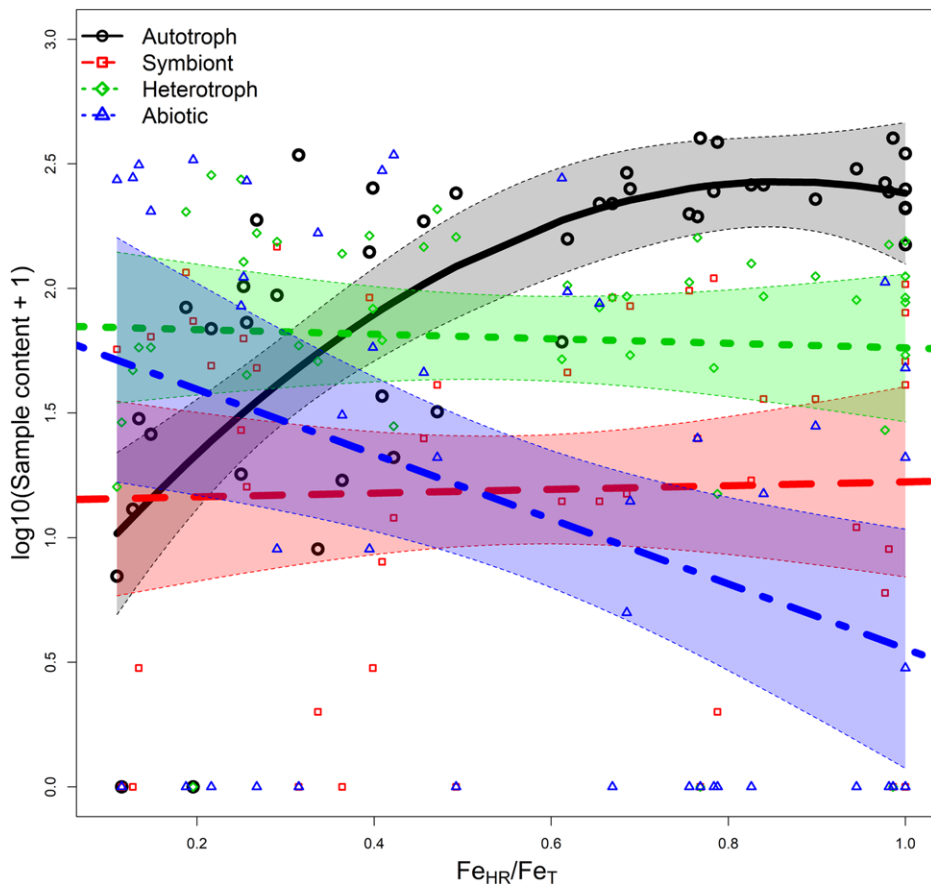


Figure 2. Relationship between proportion of highly reactive Fe over total Fe (Fe_{HR}/Fe_T) and $\log + 1$ -transformed count of the number of points containing autotrophs, symbionts, heterotrophs, and abiotic content in peri-Gondwanan terranes of Iran. Colored bands represent 95% confidence intervals. Fe_{HR}/Fe_T correlates significantly with increased sample autotrophic content ($R^2 = 0.51$; F -test statistic of a linear regression [F] = 46.7, degrees of freedom [df] = (1,44); $P < 0.001$) and decreased abiotic content ($R^2 = 0.20$; $F = 10.7$, df = (1,44); $P = 0.002$), and had no significant effect on symbiont ($R^2 = 0.002$; $F = 0.08$, df = (1,44); $P = 0.78$) or heterotrophic content ($R^2 = 0.003$; $F = 0.1$, df = (1,44); $P = 0.71$). The relationship between community composition and Fe_{HR}/Fe_T of both intervals exhibits the same pattern (Fig. DR2 [see footnote 1]). Abiotic here refers to ooids, peloids, and intraclasts. A detailed explanation is provided in Table DR1.

The Fe_{HR}/Fe_T values range from 0.1 to 1, with an average of ~ 0.7 , similar to those reported from eolian-transported upper Gzhelian mudstone of western equatorial Pangaea (Sur et al., 2015). The Fe_{HR}/Fe_T values reported here significantly exceed values reported from Saharan soil dust (0.33 ± 0.01 standard error [SE]; Poulton and Raiswell, 2002; 0.37 ± 0.03 SE; Raiswell et al., 2016). Our values are more similar to those from modern euxinic settings, such as the Black Sea and the Cariaco Basin (offshore Venezuela) (Raiswell and Canfield, 1996), even though low Fe_{py}/Fe_T indicates mildly reducing conditions in the Central Persian terrane during the late Paleozoic. The Fe_T/Al values range from 0.22 to 6.91 (average 3.8), and importantly, the Fe reactivity decreases with increasing Fe_T/Al ($R^2 = 0.18$; F -test statistic of a linear regression [F] = 10.4, degrees of freedom [df] = (1,48); $P = 0.002$).

Figure 1B illustrates variation in Fe_{HR}/Fe_T , fine-dust and autotroph content across the

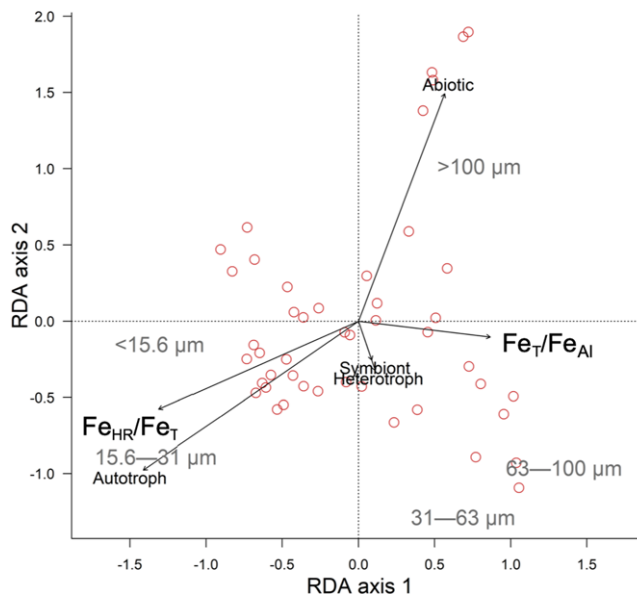


Figure 3. Redundancy analysis (RDA) visualizing the relationships among the proportion of highly reactive Fe (Fe_{HR}) over total Fe (Fe_T), dust grain size (in μm), and proportions of biotic and abiotic components in peri-Gondwanan terranes of Iran. Each point (red circle) indicates an individual sample. Closer proximity to a given predictor or driver variable indicates higher values of that variable for the sample.

studied sections. Fe_{HR}/Fe_T and autotroph content exhibit a significant polynomial relationship (Fig. 2). Autotrophic content increases with Fe_{HR}/Fe_T in samples with $Fe_{HR}/Fe_T < 0.5$, whereas autotrophic content remains high and relatively invariant in samples with $Fe_{HR}/Fe_T > 0.5$ (Fig. 2).

The size distribution of the dust varies from a minority (<4%) of short-range-transported coarse particles (15–120 μm) to a majority of long-range-transported fine particles (<15 μm). The coarsest grains (>63 μm) are commonly well rounded, inferred to represent eolian sand that accumulated near shore, and finer grains represent particles potentially sourced from regions $>10^3$ km distant. The samples with a larger proportion of fine dust (<31 μm) have significantly higher Fe_{HR}/Fe_T values, and positively covary with autotroph content (Fig. 3). These samples are also enriched in Fe_{HR} , whereas facies with low or minimal autotroph content exhibit lower Fe_{HR} . Moreover, samples dominated by fine dust (<31 μm) are enriched in Fe_{HR} without a corresponding increase in Fe_T .

DISCUSSION

Autotrophic predominance increases with Fe_{HR} which corresponds with fine (<31 μm) dust in the study region. Considering the sample location, these results highlight dust as the primary input of Fe_{HR} into the carbonate platforms of the Central Persian terrane during the Late Pennsylvanian–early Permian. Furthermore, the high values of 2-MHI indicate a large contribution of cyanobacteria to the organic matter, which can drive fixation of local nitrogen—an important macronutrient. Quantification of the autotrophic content via both the biomarker index (2-MHI) and the point-count results reveals a robust positive relationship between dust-borne Fe_{HR} , autotrophic activity, and carbonate precipitation.

Increasing Fe_{HR} with decreasing Fe_T/Al likely indicates significant influence of non-aluminosilicate (clastic) sources predominated by iron-oxide-rich dust.

Fine dust lingers in suspension, and is subject to more cloud processing and can be transported greater distances compared to coarser particles. Enhanced bioavailability of Fe in finer-grained dust likely reflects both longer residence time in the water column and greater surface area, which increases the potential for biological and/or chemical alterations. The sample location is near a predicted upwelling zone (Golonka et al., 1994) and where a warm western boundary current and a polar front may have met (Sardar Abadi et al., 2019), so mesoscale eddies could have brought non-Fe nutrients into the area (Garçon et al., 2001). However, neither upwelling nor hydrothermal sources for Fe are consistent with either the facies data or the predominance of iron oxide. Additionally, because the local continental margin was isolated from fluvial sources of Fe, greater non-Fe nutrient input from coastal waters would have enhanced Fe limitation (Hogle et al., 2018).

The hypothesis that Fe-rich dust stimulated productivity, enhancing carbon burial and decreasing atmospheric CO_2 , explains a major quandary in understanding pCO_2 during the waning stages of the LPIA: namely, the disconnect between evidence for carbon sequestration on land and trends in atmospheric pCO_2 . Atmospheric pCO_2 reaches a nadir near the Pennsylvanian-Permian boundary, even though the hypothesized drivers of decreasing pCO_2 for this interval—namely, peak coal burial and continental weathering—occurred in the Early to Middle Pennsylvanian (Fig. 4; Montañez et al., 2016; Nelsen et al., 2016; Goddérís et al., 2017; Chen et al., 2018). Chen et al. (2018) inferred a shift in the locus of carbon burial from the terrestrial to the marine biosphere during this interval, consistent with the results of Sur et al. (2015) who posited substantial fertilization of the marine

biosphere by iron-rich dust. Indeed, the onset of aridification during the Late Pennsylvanian is consistent with an increase in atmospheric dustiness during the LPIA (Heavens et al., 2015; Soreghan et al., 2015), which likely stimulated marine productivity, shifting carbon burial from the continental to the marine realm (Sur et al., 2015; Chen et al., 2018).

Sur et al. (2015) documented eolian delivery of Fe_{HR} to equatorial western Pangaea during the Late Pennsylvanian (Gzhelian) and speculated on the potential for large repercussions to carbon cycling if this phenomenon were more widespread. The high values of Fe_{HR} in southern mid-latitudes extend Sur et al.'s (2015) results both temporally and spatially. Furthermore, these data represent the first documentation of a positive covariance in marine autotrophs and bioavailable Fe delivered by dust in Earth's deep-time record. Our findings document the ecosystem dependence on dust inputs and demonstrate the viability of the late Paleozoic dust fertilization hypothesis for helping to explain prolonged drawdown of pCO_2 at peak LPIA. Importantly, a shift in the locus (e.g., terrestrial to marine) of organic carbon burial likely has an insignificant effect on the global carbon isotope record, however a small trend toward more positive values (Chen et al., 2018) may suggest an increase in global organic carbon burial, which would correspond with a decrease in pCO_2 . A similar effect has been observed for a Mesozoic event (Jarvis et al., 2011). Additionally, a positive carbon isotope excursion could be dampened by enhanced volcanism and/or increased weathering, both of which have been implicated during this interval (Goddérís et al., 2017; Soreghan et al., 2019); thus, our interpretation is consistent with the known carbon isotope record (Chen et al., 2018).

The remarkably high values of Fe_{HR} documented in both Sur et al.'s (2015) and our data sets imply an enhancement of reactive (and thus bioavailable) Fe for atmospheric aerosols of the LPIA. The mechanism behind this

enhancement has been enigmatic. More recently, however, Soreghan et al. (2019) documented high amounts of explosive volcanism during the LPIA and linked this to increased atmospheric acidity and consequent enhancement of the reactivity of Fe in mineral aerosols. This mechanism would strengthen carbon burial by both stimulating primary producers and—as an auxiliary effect—enhancing microbial carbonate precipitation.

CONCLUSIONS

Atmospheric dust delivered Fe_{HR} to epeiric seas of southern mid-latitude Pangaea during the LPIA, stimulating marine primary (autotrophic) productivity. Fe_{HR} borne by (especially) the finest dust enhanced microbial and cyanobacterial growth, promoting both carbonate precipitation and marine C_{org} burial. Consequently, dust likely stimulated both organic and inorganic carbon cycling, helping to maintain low pCO_2 even as terrestrial repositories for organic carbon (peat and/or coal) and silicate weathering diminished from the Carboniferous into the Permian.

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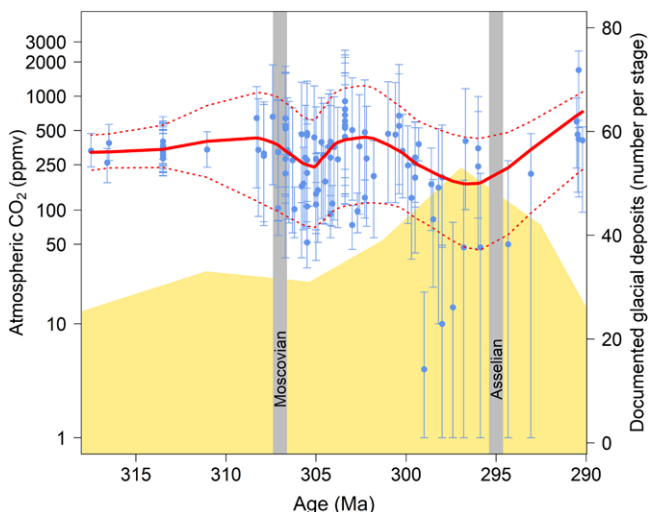


Figure 4. Reconstructed atmospheric pCO_2 between 318 and 290 Ma (Montañez et al., 2007, 2016). Solid red line represents loess fit with 50% smoothing, and dashed red lines represent loess fit of upper and lower confidence-interval values. Documented glacial deposits are illustrated with yellow polygon (Soreghan et al., 2019). Gray bars lines refer to case studies.

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