The effect of iron on primary productivity and pelagic ecology: A case study of atmospherically deposited Saharan dust.

Brett Pauli (1015636)

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University of Guelph, Ontario, Canada

Abstract

Matter on Earth largely exist in limited quantities and therefore elements must be recycled in an essentially closed loop via various biogeochemical processes. The latter describe the movements of materials between biotic and abiotic components of Earth via geophysical and chemical processes. In high-nutrient-low-chlorophyl areas, iron is thought to be a limited micronutrient for photosynthetic organisms. Here, the movement of iron through atmospheric, hydrologic, geologic and biotic compartments and its effects on marine ecology will be explored. To narrow the focus of this paper, the effects of iron on marine ecology will explored through a case study of atmospheric deposition of dust from the Sahara Desert into offshore marine surface waters. After reviewing relevant literature for source data, a statistically significant positive relationship was found between the availability of iron and primary productivity of lower trophic level photosynthetic organisms.

Background

Atmospheric deposition of dust is an important source of iron

The largest source of atmospherically deposited dust into ocean surface waters is the Sahara Desert (Chen et al., 2018). Each year around 500 tonnes of dust is swept off the large desert (9.2 x 10^6 km^2) and blown into the Atlantic Ocean (National Oceanography Centre, 2008). Strong winds create turbulence near the ground and dislodge dust particles which are then carried high into the troposphere; similar to how a particle is entrained into the flow of a liquid. Dust from the Saharan Desert (centered at 25° North) is then carried west by north-easterly trade winds (15° North; Boulding and Ackerman, 2017, pg. 79). This process depends on the particle's size, the wind velocity, and the shear stress between the wind and the ground. The amount of dust carried by the atmosphere depends on a variety of factors like temperature (Armengol et al., 2020) and agricultural activity (Jickells and Moore, 2015). The dust from the Saharan Desert contains carbon, silica, nitrogen and phosphorus (Duarte, 2006) as well as micronutrients such as iron, nickel, and copper (Jickells, 1999). On a global scale, atmospheric dust is thought to represent the main influx of iron into surface waters (Nishioka et al., 2021).

Iron enters surface waters

In order for marine organisms to be able to utilize iron, it must first be available in solution. The bioavailability of atmospherically derived iron depends on its solubility in seawater (Rudraswami et al., 2021). This in turn depends on a multitude of factors (Marcotte et al., 2020) such as the amount of dissolved organic matter (Bressac and Guieu, 2013). There are still several ambiguities associated with the solubility of iron from dust (Moore et al., 2002) which can make it difficult to understand causal relationships between the spatio-temporal dynamics of iron from dust deposition and local marine ecological processes like primary production. Over time, iron inevitably sinks in the form of detritus and fecal pellets and eventually reaches the seafloor. After being incorporated into marine sediments, it is recycled back into the Earth's core via geological processes.

Iron in marine sediments is recycled via geological processes

Iron that accumulates in seafloor sediments is eventually reincorporated back into Earth's interior via geophysical processes like Wilson Cycles. The time it takes for a given patch of sediment to be subducted is dependent on its location. For example, the mid-Atlantic ridge is a divergent zone where dense oceanic lithosphere (basalt-rich) is formed and pushed outward towards adjacent plates where it is eventually subducted beneath the less dense continental crust (granite-rich). The oceanic-continental boundary off the west coast of Africa represents a passive margin and therefore iron deposited in marine sediments in the East Atlantic is recycled over very long timeframes of about 200 million years (Duarte et al., 2013). In this way, sediments deposited on the ocean floor, like iron, are recycled back into the mantle. Completing the loop, these materials circulate and are eventually resurfaced in geologically active areas like mantle plumes.

Hypothesis and prediction

The change in photosynthetic quantum efficiency (i.e., Fv/Fm ratio, where Fm is the maximum chlorophyll fluorescence yield and Fv is the difference between Fm and the minimum chlorophyll fluorescence yield; Butler, 1978) is widely used to determine the degree to which iron is the limiting nutrient for phytoplankton growth (Yoon et al., 2008). The photosynthetic quantum efficiency (Fv/Fm ratio) ranges from 0.2 to 0.65 where conditions are less iron limited as Fv/Fm approaches 0.65 (Yoon et al., 2008). If the growth of autotrophic organisms in the euphotic zone of marine waters is limited by iron, then primary productivity will increase as iron becomes less scarce. Increases in the photosynthetic quantum efficiency (percent change in Fv/Fm) will lead to increases in primary production (measured as percent change).

Results

Using data from existing literature, a simple linear regression revealed a statistically significant (α=0.05) positive relationship between the percent change in primary production (mg C m^{-2} day^{-1}) and the percent change in photosynthetic quantum efficiency (Fig. 1; $F_{(1,10)}$=9.649, p<0.05, R^2=0.49) The dependent variable (percent change in primary productivity) was checked for normal distribution prior to conducting the statistical analysis.

Discussion

Liebig's "law of the minimum" argues that growth should be limited by the most deficient nutrient (Martin, 1990; Bristow et al., 2017). The "Iron Hypothesis", a logical derivation of Liebig's Law, argues that marine phytoplankton are unable to take advantage of excess surface nitrate and phosphate because of iron deficiency (Martin, 1990). Allochthonous iron from Saharan dust has important implications for offshore marine ecosystems in low-nutrient low-chlorophyll areas (Ventura et al., 2021) and especially in areas of high-nutrient low-chlorophyll (HNLC; Zeebe, 2005; Boyd et al., 2007). HNLC areas, characterized by excess nutrients and low chlorophyll conditions, make up about 20% of the surface ocean (Zeebe, 2005) and are often caused by upwelling (Cullen, 1991). It has been argued that these areas are often most deficient in iron (Martin et al., 1991; Martin et al., 1994). The "Iron Hypothesis" has previously been used to explain HNLC conditions and limited productivity in the open ocean

(Cullen, 1991; Mahowald et al., 2005). The results here (Fig. 1) support the notion that reducing iron-limitation leads to increased primary productivity in autotrophic organisms which has important implications for pelagic food-web planktonic dynamics (Bonnet et al., 2005) and community structure (Marañén et al., 2010).

The response of the phytoplanktonic community to dust and iron addition is rapid and nonuniform (Ridame et al., 2014). The transient nature of depositional events and short blooms in productivity (weeks) trigger rapid food-web responses (Martin et al., 1994) with initial increases in all plankton groups (Boyd et al., 2007). After the initial bloom, there is a shift in species composition from nanoplankton (<10 mm) to mostly microplankton (>10 mm; de baar et al., 2005) and a general dominance of diatoms (Marañén et al., 2010). Pennate species of plankton like *Pseudo-nitzschia* sp., *Fragilariopsis kerguelensi*, and *Chaetoceros debilis* have been observed to dominate under these conditions (de baar et al., 2005). This unequal effect upon autotrophs, favoring diatoms instead the smaller autotrophs, could enhance the biological pump due to a higher carbon export flux resulted from diatom sedimentation (Boyd et al., 2007; Franchy et al, 2013).

The phenomena described above have been explored with respect to climate change (Zeebe and Archer, 2005; Laurendale et al., 2020). The biogeochemist John Martin is famous for saying “give me half a tanker of iron, and I’ll give you an ice age”. The feasibility of using iron for the downward export of carbon is a fascinating field of research and suggests that changes in Saharan dust deposition have important implications for regulating the Earth’s climate (Zeebe and Archer, 2005). In order to understand the large-scale climatic implications, it is important to understand some general dynamics of the pelagic ecosystem.

Community dynamics are affected by top-down and bottom-up controls. Strong top-down trophic control exerted by grazers on phytoplankton is reflected by relatively constant levels of chlorophyll (Cullen, 1991; Marañén et al., 2010) and has been supported by both experimental (Bonnet et al., 2005) and observational (Herut et al., 2005) dust-addition studies. The spatio-temporal stochasticity in resource availability characteristic of dust depositional events has important implications for bottom-up community dynamics in the spatially expansive pelagic ecosystem. While its true that small autotrophic organisms play a disproportionate role in primary production, higher order large mobile predators can take advantage of pulses in productivity by switching prey species which ultimately imparts stability on the whole system (McCann et al., 2005). This rapid switching top-down response in foraging predators stabilizes community dynamics by dampening strong, and potentially destabilizing, consumer-resource oscillations (McCann et al., 2005).

Unfortunately, the current scientific understanding of iron's effects on ocean ecosystems is limited and does not extend past single-celled organisms (Boyd et al., 2007). Future research should investigate whole food-web responses to dust deposition and should investigate how much iron from atmospheric dust deposition reaches the seafloor and how much is upwelled or recycled by biota in surface waters since these are still unknown (Boyd, 2009). Moreover, understanding how anthropogenic activities are affecting dust composition and quantity (e.g., Ginoux et al., 2012) will be important for predicting how pelagic ecosystems will function in the future. Finally, understanding the connectivity abiotic and biotic systems is paramount for preserving the biogeochemical processes that act as Earth's life support system.

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Figures and Tables

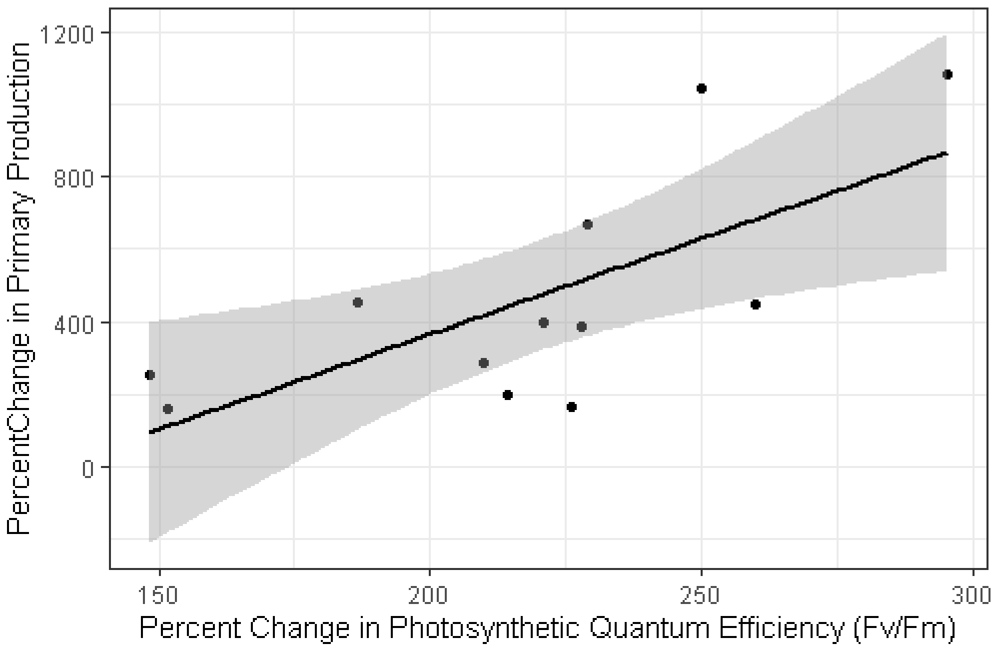

Figure 1. Using data from existing literature, a simple linear regression was conducted using RStudio (Version 1.2.5033) for iron addition experiments in high-nutrient low-chlorophyll (HNLC) regions. Background dissolved iron concentrations in HNLC regions are <0.2nM (Yoon et al., 2018). *Fm* is the maximum chlorophyll fluorescence yield and *Fv* is the difference between *Fm* and the minimum chlorophyll fluorescence yield. A statistically significant (a=0.05) positive relationship between the percent change in primary production (mg C m^{-2} day^{-1}) and the percent change in photosynthetic quantum efficiency ($F_{(1,10)}=9.649$, $p<0.05$, $R^2=0.49$). The dependent variable (percent change in primary productivity) was checked for normal distribution prior to conducting the statistical analysis. The shaded region around the regression line represents the 95% confidence interval around the regression line. Sources are: Martin et al. (1994), Behrenfeld et al. (1996), Boyd et al. (2000, 2005); Tsuda et al. (2007), and Yoon et al., 2018).