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MARINE PRODUCTIVITY

Atmospheric nourishment of global ocean ecosystems

T. K. Westberry^{1*}, M. J. Behrenfeld¹, Y. R. Shi^{2,3}, H. Yu³, L. A. Remer^{2,4}, H. Bian^{2,3}

Over the vast open ocean, vital nutrients for phytoplankton growth in the sunlit surface layer are largely provided through physical transport from deep waters, but some nutrients are also provided through atmospheric deposition of desert dust. The extent and magnitude of dust-mediated effects on surface ocean ecosystems have been difficult to estimate globally. In this work, we use global satellite ocean color products to demonstrate widespread responses to atmospheric dust deposition across a diverse continuum of phytoplankton nutritional conditions. The observed responses vary regionally, with some areas exhibiting substantial changes in phytoplankton biomass, whereas in other areas, the response reflects a change in physiological status or health. Climate-driven changes in atmospheric aerosols will alter the relative importance of this nutrient source.

Earth's atmosphere and ocean ecosystems are intimately linked. A complex milieu of dissolved and particulate organic compounds is mediated by surface ocean plankton and, through wave breaking and bubble bursting, can be injected into the atmosphere, where these compounds influence aerosol and cloud properties and, thus, the radiative budget of the planet (1, 2). In turn, terrigenous matter lofted into the atmosphere over land may be carried out to sea for thousands of kilometers before ultimately being deposited on the surface, where it can stimulate photosynthesis and plankton growth (3). To date, documented responses of marine ecosystems to atmospheric nourishment have largely been restricted to anomalously large local events associated with volcanic eruptions (4, 5), wildfires (6, 7), and extreme dust storms (8). Even mesoscale iron fertilization experiments, where dissolved iron is deposited locally into the ocean, use high concentrations of nutrient unlikely to be matched during typical atmospheric deposition. Nevertheless, the far more common lower-concentration atmospheric depositions that occur across the global ocean have long been anticipated to have widespread effects on ocean productivity because, in most open regions, phytoplankton division rates are limited by macro- or micro-nutrient availability (9, 10). Although this global response has previously eluded detection, regional in situ studies have demonstrated long-term variations in ecosystem functioning in response to climate oscillations affecting low deposition rates (11). We use a 14-year global time series of modeled dust deposition coupled with satellite ocean color data to reveal con-

sistent, broad-scale responses of marine plankton communities to atmospheric nourishment. In stable, low-latitude ocean regions, the signature of these responses is predominantly expressed as an improvement in the physiological status, or health, of phytoplankton communities, whereas in the more seasonally varying, high-latitude seas, an enhancement in phytoplankton biomass is also often observed. When integrated globally, we estimate that deposition of dust onto the ocean supports 255 Tg of C per year of primary production, which represents 4.5% of the global annual export production. Regional variation in this contribution can be much higher, approaching 20 to 40% of the annually exported particulate carbon flux from the surface ocean. Global warming is anticipated to alter atmospheric dust burdens and deposition patterns (12, 13), making their contributions to the future nourishment of ocean ecosystems uncertain.

Patterns in dust deposition over the ocean correlate strongly with atmospheric transport paths downwind from dust sources (Fig. 1A and fig. S1) (14, 15). The nutrient complement carried in this dust is highly variable and dependent on source region (16). Furthermore, chemical transformation during atmospheric transport modifies the bioavailability of the different nutrients in the dust (iron, phosphorus, and nitrogen) (17–19). Thus, at the time of wet or dry deposition (20) on the ocean, the stoichiometry of the different nutrients can vary spatially and temporally (11, 18). Global distributions of surface ocean phytoplankton biomass and chlorophyll concentration (Fig. 1B and fig. S1) exhibit little semblance to these dust deposition patterns (Fig. 1A) because the primary source of nutrients supporting marine ecosystems is through vertical transport from depth (21–23). Nevertheless, the atmosphere represents a source of additional nutrients to the ocean, and the stoichiometric composition of dust nutrients is

sufficiently distinct from vertically transported nutrients that it can affect the dominant nutrient that limits plankton productivity (11, 24). For example, in low-dust regions with substantial upwelling (e.g., the eastern Equatorial Pacific) or deep mixing (e.g., the Southern Ocean), phytoplankton communities tend to be iron limited, at least seasonally (fig. S2). By contrast, tropical and subtropical regions outside upwelling zones—where the surface mixed layer is permanently stratified above the sunlit photic depth [hereafter referred to as the permanently stratified ocean (PSO)]—are generally viewed as being primarily limited by nitrogen or phosphorus (fig. S2). Yet even in these regions, dust deposition can represent an important source of additional nitrogen and phosphorus and, perhaps equally important, can stimulate nitrogen fixation through its supplementation of iron. PSO waters with high dust inputs (e.g., the North Atlantic subtropical gyre) tend toward phosphorus-limited communities rather than nitrogen-limited phytoplankton (fig. S2).

Detecting a widespread influence of dust deposition on plankton communities is challenging because, across much of the open ocean, mean deposition rates are small (e.g., red line in Fig. 1C). Thus, the responses that they elicit are difficult to decipher from other sources of ecological variability (e.g., changes in mixed-layer growth conditions and stochastic processes in marine food webs). However, a distinct feature of long-term atmospheric deposition records is their frequent punctuation by short-term dust events (black spikes in Fig. 1C). Similarly, temporal records of surface chlorophyll concentration typically exhibit repeated annual cycles (red line in Fig. 1D) interrupted by brief departures from these mean patterns (black spikes in Fig. 1D). These transient dust and chlorophyll features may provide an opportunity to distinguish atmospheric deposition effects from other sources of ecosystem variability. To illustrate the impact of ocean nourishment from the atmosphere, we therefore combined 5°-by-10° gridded 4-day-resolution dust deposition data and satellite-observed ocean color products and evaluated ecosystem responses to the largest 10% of deposition events ($N = 127$) at each grid point between 2003 and 2016 (see materials and methods). These deposition events constitute ~40% of the annual dust mass deposited into the global ocean.

The average mass of dust deposited on the ocean during the top 10% of events varies among our 5°-by-10° bins by nearly five orders of magnitude globally ($\sim 10^{-2}$ to $10^3 \text{ mg m}^{-2} \text{ day}^{-1}$) (Fig. 2A) and exhibits a spatial pattern closely corresponding with that for total annual dust deposition (Fig. 1A). In other words, the largest events in low-dust ocean areas are still far smaller than those in high-dust regions.

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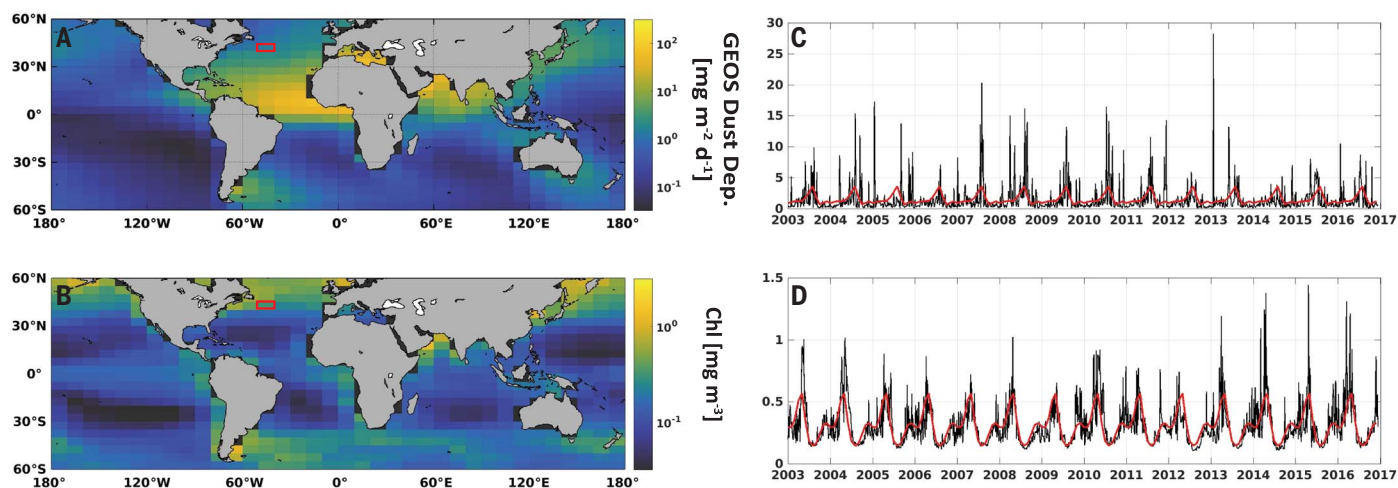


Fig. 1. Model-based dust deposition and satellite-observed chlorophyll concentration over the global ocean. (A) Average GEOS dust deposition rates (milligrams per square meter per day) over the period 2003 to 2016. (B) Average MODIS-Aqua chlorophyll concentration (milligrams per cubic meter) over the period 2003 to 2016. Red boxes outline a single 5°-by-10° grid cell centered on

42.5°N, 45°W, whose time series are shown in subsequent panels. (C) Fourteen-year time series of 4-day average dust deposition (thin black line) over red-outlined region in (A). Also shown is a repeating average annual cycle of dust deposition (solid red line) for the same location. (D) Similar to (C), but for MODIS-Aqua chlorophyll concentration (milligrams per cubic meter).

Fig. 2. High dust deposition and subsequent ocean color response. (A) Average GEOS dust deposition rate to the surface ocean (milligrams per square meter per day) during top 10% of record (2003 to 2016). (B) Median relative change in chlorophyll concentration evaluated between the 4-day period after top 10% of dust events ($N = 127$) and the 4-day period before the events (materials and methods). (C) Median relative change in chlorophyll concentration evaluated similarly to (B), but for the 4-day periods before and after a randomly (bootstrap with replacement, $N = 1000$) sampled 10% of the dust deposition time series at each location. Solid black contour in (B) and (C) shows the 15°C isotherm calculated from the average MODIS Sea Surface Temperature during 2003 to 2016. This boundary is used to demarcate the PSO with annual average sea surface temperature (SST) > 15°C.

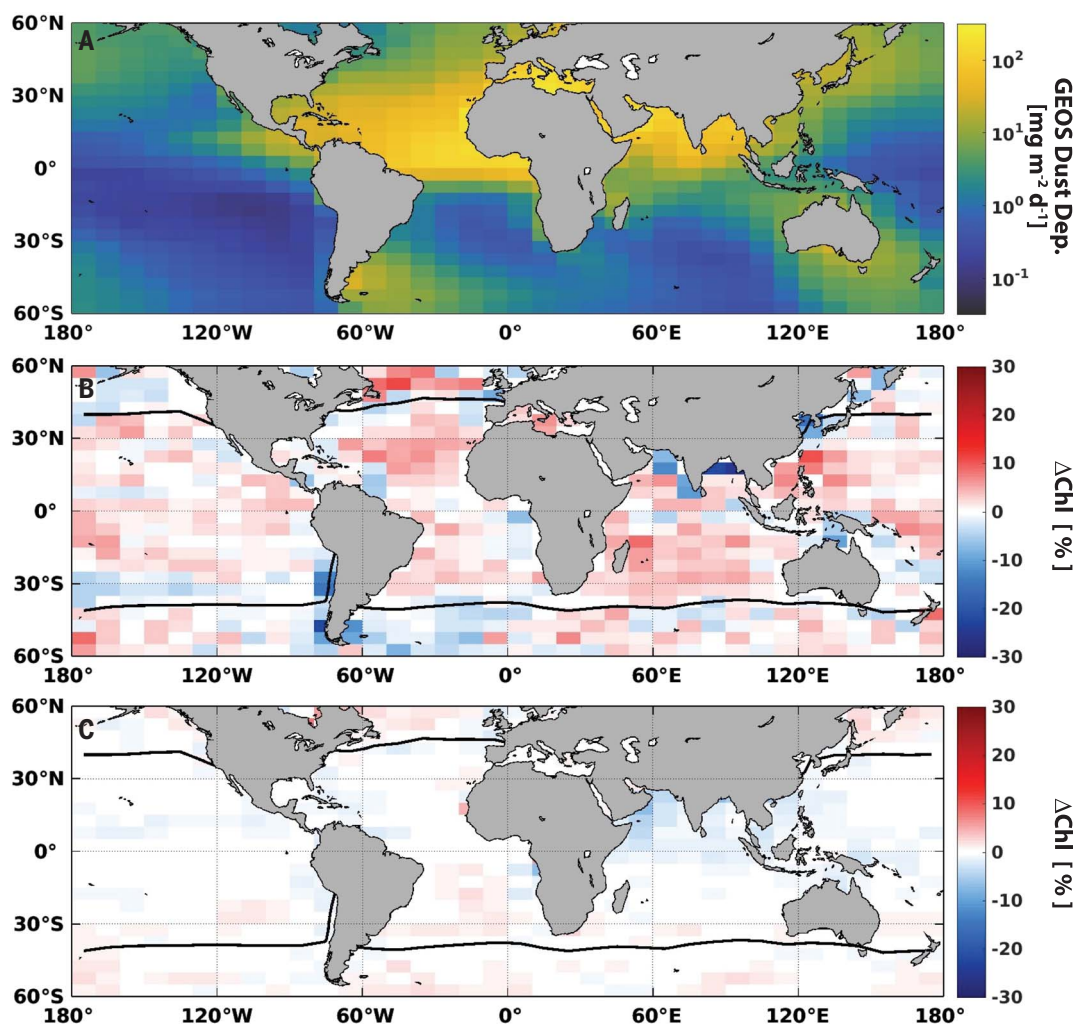
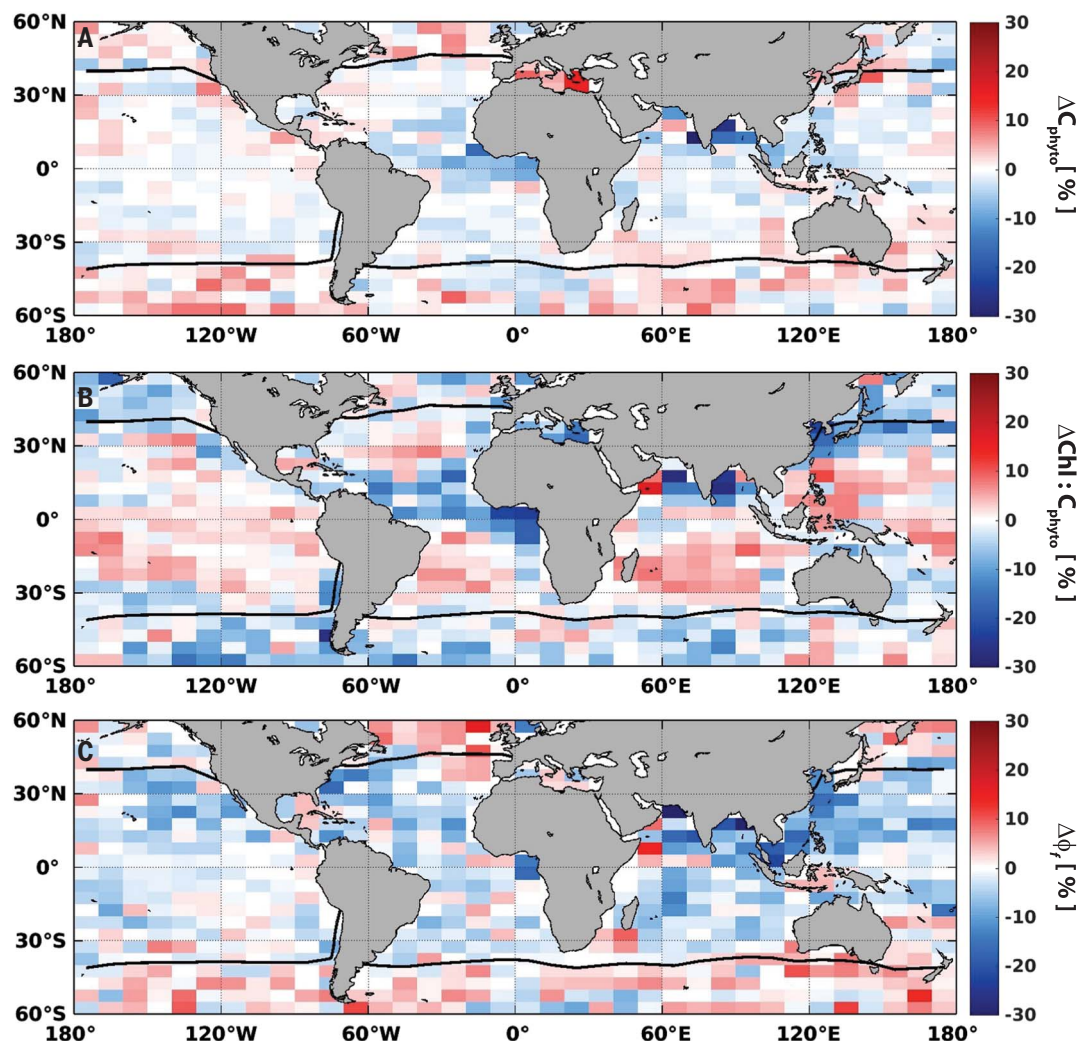


Fig. 3. Biological response to dust deposition in various satellite ocean color–based properties. (A) Median relative change in phytoplankton carbon biomass (C_{phyto}) evaluated between the 4-day period after top 10% of dust events ($N = 127$) and the 4-day period before the events. (B) Median relative change in phytoplankton chlorophyll to carbon ratio ($\text{Chl}:C_{\text{phyto}}$) evaluated between the 4-day period after top 10% of dust events and the 4-day period before the events. (C) Median relative change in chlorophyll fluorescence quantum yield (Φ_F) evaluated between the 4-day period after top 10% of dust events and the 4-day period before the events.



For each of these events, we first quantified an ocean ecosystem response as the relative change (in percent) in surface chlorophyll (ΔChl) 4 days after the event relative to 4 days before the event (materials and methods). This analysis revealed widespread mean enhancements in ΔChl (65% of total bins) across the global ocean resulting from the dust events (red pixels in Fig. 2B). These responses are of modest magnitude (generally $\leq 20\%$) and are comparable (as a percentage) between the PSO and higher-latitude seasonal seas [delineated by annual mean sea surface temperature $\geq 15^\circ\text{C}$ (25); black lines in Fig. 2B]. Ocean regions deviating from the predominant positive ΔChl values are generally restricted to continental shelf waters and a limited region of the Southern Ocean east of Argentina (Fig. 2B, blue pixels). Chlorophyll anomalies in our 14-year record calculated for randomly sampled time points not associated with high dust deposition events consistently exhibit mean ΔChl values close to zero (Fig. 2C). This result thus supports the direct connection between the top 10% of

dust events and surface chlorophyll changes (Fig. 2B).

Traditionally, dust deposition has been envisioned as primarily relevant to iron-limited, high-nutrient low-chlorophyll (HNLC) ocean regions (26). This is because dust is generally high in iron content, phytoplankton have low cellular iron requirements (i.e., it is a micronutrient), and HNLC waters have ample macronutrients to support significant biomass increases when amended with iron (27, 28). Our results (Fig. 2B) instead suggest a far broader stimulatory effect of atmospheric depositions. This finding could reflect a variety of factors, including (as noted above) stimulation of diazotroph nitrogen fixation by dust iron and input of macronutrients during deposition events. In addition, iron-stressed phytoplankton assemblages are now recognized as commonplace outside of HNLC regions, including in central ocean gyres (11, 29, 30), coastal upwelling areas (31, 32), and classical bloom-forming areas (33–35). Finally, variations in limiting nutrient for different phytoplankton groups can occur within a given

community (9, 36) such that stimulation of specific groups by dust deposition contributes to broadly observed bulk ΔChl enhancements (Fig. 2B).

Notably, chlorophyll concentrations change in the surface ocean as a result of both variations in phytoplankton biomass and physiological status. With respect to the latter, phytoplankton increase cellular chlorophyll concentrations as nutrient stress (or light availability) decreases. Accordingly, a broadly consistent increase in ΔChl after dust deposition events (Fig. 2B) does not necessarily imply an equally consistent underlying basis. Fortunately, additional satellite ocean color products are available to disentangle observed changes in chlorophyll and have now been used to illustrate the pervasive effect of physiology on the satellite-observed chlorophyll record (37, 38). One of these properties is the particulate backscattering coefficient, b_{bp} , which has been quantitatively related to phytoplankton carbon biomass, C_{phyto} (39, 40). Unlike chlorophyll concentration, C_{phyto} is insensitive to light- and nutrient-driven physiological adjustments

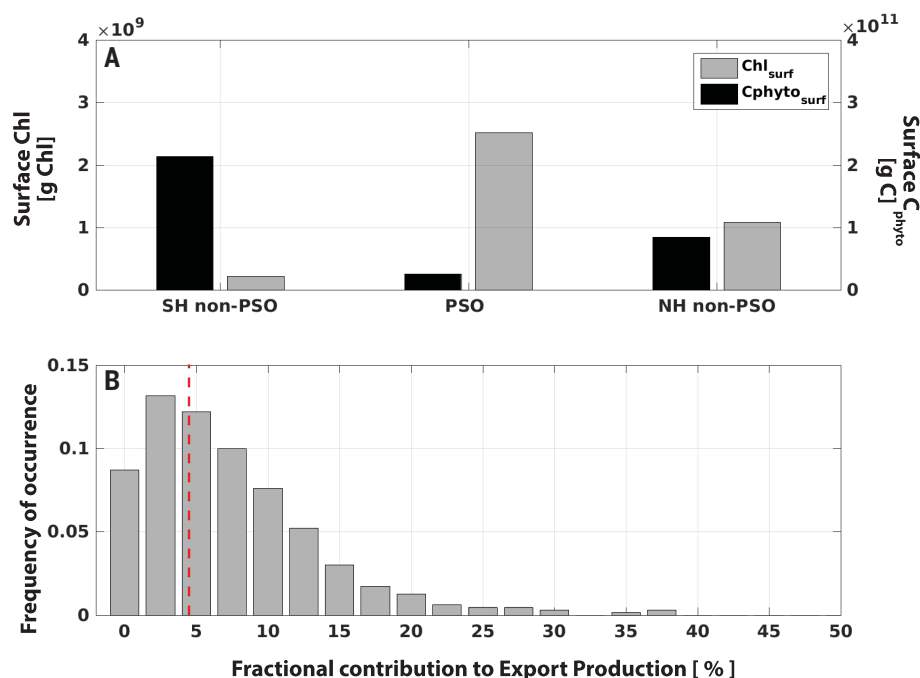


Fig. 4. Globally integrated effects of dust deposition on bulk ocean color properties and net primary production. (A) Median net effect of top 10% of dust events in three broad regions of the ocean on surface ocean chlorophyll (in units of grams of chlorophyll) and phytoplankton biomass (in units of grams of carbon). The three regions correspond to the PSO (annual SST $\geq 15^{\circ}\text{C}$), and the northern (NH non-PSO) and southern (SH non-PSO) areas of ocean outside the PSO. Values have been integrated over the top 10 m as a conservative estimate of the surface layer directly detected by satellite ocean color measurements. (B) Frequency distribution of the contribution of annual dust-mediated enhancement in NPP relative to corresponding export production (expressed as percentage) over all 5° -by- 10° bins ($N = 631$). Annual, integrated global contribution is indicated by the dashed red line and is equal to 4.5% (255 Tg of C per year). Corresponding global map is shown in fig. S5.

(41, 42). Reevaluating our top 10% of deposition events in terms of C_{phyto} anomalies (ΔC_{phyto}) (materials and methods), we find that observed changes in chlorophyll (Fig. 2B) are largely not indicative of increased biomass in the PSO (Fig. 3A). The two most notable apparent ΔC_{phyto} features in the PSO are the modest decreases in the tropical Atlantic west of Africa and in the northernmost Indian Ocean and Bay of Bengal (Fig. 3A). However, these two regions are notoriously dusty and are prone to errors in satellite b_{bp} retrievals (43, 44). In contrast to the PSO, higher-latitude regions exhibit notable increases in ΔC_{phyto} after dust events (poleward of black lines in Fig. 3A) in conjunction with the increases in ΔChl (Fig. 2B).

Results shown in Fig. 2B and Fig. 3A imply that dust depositions to the PSO primarily elicit improvements in phytoplankton physiological status without affecting standing stocks. More specifically, phytoplankton increase cellular pigment levels when dust events improve surface layer nutrient conditions—a response revealed in satellite $\text{Chl}:C_{\text{phyto}}$ anomalies ($\Delta\text{Chl}:C_{\text{phyto}}$) (Fig. 3B). We see, aside from the above-noted problematic regions west of Africa and south of India, broad re-

gions of elevated $\Delta\text{Chl}:C_{\text{phyto}}$ after depositions (red pixels in Fig. 3B), indicative of increased phytoplankton photosynthesis and division rates (45, 46). A physiological interpretation of the ΔChl response in the PSO is further supported by concurrent and widespread decreases in observed chlorophyll fluorescence quantum yields ($\Delta\phi_f$) (Fig. 3C) (materials and methods). As nutrient stress commonly enhances fluorescence yields in phytoplankton (47), these observed decreases in $\Delta\phi_f$ are consistent with improved surface nutrient conditions. At latitudes poleward of the PSO (black lines in Fig. 3), $\Delta\text{Chl}:C_{\text{phyto}}$ was modestly depressed after dust events (Fig. 3B) and $\Delta\phi_f$ was slightly elevated (Fig. 3C). Although further investigation is warranted, these unexpected findings could reflect a preferential increase in accessory photosynthetic pigments in the diverse phytoplankton communities found at these higher latitudes (48). Similar to results for ΔChl (Fig. 2C), random sampling of low-deposition periods during our 14-year record yielded ΔC_{phyto} , $\Delta\text{Chl}:C_{\text{phyto}}$, and $\Delta\phi_f$ values close to zero (fig. S3).

Results presented here provide observational evidence for global ocean ecosystem

responses to prevalent but modest-scale dust depositions. By investigating a variety of phytoplankton properties now retrieved from ocean color remote sensing, we find a distinctly different signature of deposition responses between the PSO and higher-latitude seasonal seas. When integrated across the PSO, the deposition events were associated with an average elevation in surface chlorophyll levels of 2.5×10^9 g of Chl while having a negligible effect on phytoplankton biomass (Fig. 4A). This finding is consistent with current understanding of lower-latitude plankton ecosystems. Across the open ocean PSO, seasonal changes in growth conditions are muted, and variations in phytoplankton division rates are tightly coupled to loss rates. Accordingly, modest dust-stimulated increases in phytoplankton division rates are paralleled by increased loss rates, thereby rapidly conveying enhanced primary production to higher trophic levels. A similar finding was reported for phytoplankton responses to climate variability in the PSO, wherein observed variations in chlorophyll were associated predominantly with physiological adjustments in $\text{Chl}:C_{\text{phyto}}$ rather than C_{phyto} (38). By contrast, growth conditions at higher latitudes are constantly changing over the seasons, and this variability sustains a greater degree of decoupling between phytoplankton division and loss rates (49). Stimulation of phytoplankton division by atmospheric nutrient inputs has a greater chance of affecting phytoplankton stocks, which, for the dust events evaluated here, amounted to average increases in C_{phyto} and Chl of 8.5×10^{10} g of C and 1.1×10^9 g of Chl for the north polar and subpolar region and 2.1×10^{11} g of C and 2.3×10^8 g of Chl for the south polar and subpolar region, respectively (Fig. 4A).

The satellite ocean color measurements used in our analysis only detect properties of plankton a few meters below the surface (e.g., Fig. 2B and Fig. 4A). If the Chl and C_{phyto} responses to atmospheric deposition reported here are applied to a contemporary ocean net primary productivity (NPP) model and scaled to the total annual dust deposition, we find that dust-mediated NPP amounts to 255 Tg of C per year. This enhancement results from externally provided (“new”) nutrients and can be compared with the total annual ocean exportable production of 5.7 Pg of C per year (50) (see supplementary materials for discussion). Thus, 4.5% (red dashed line in Fig. 4B) of globally exportable carbon is attributable to dust deposition, but this dust contribution varies widely by location from just a few percent to ~40% of the annual total within any 5° -by- 10° bin (Fig. 4B and fig. S2). Although considerable uncertainty remains in this assessment, it does provide an observation-based, order-of-magnitude quantification for the contribution

of atmospheric nourishment to global ocean ecosystems.

The productivity and health of Earth's biosphere are intimately linked to the functioning of the coupled land-ocean-atmosphere systems as well as to human activities. For global plankton, climate warming poses direct threats through its effects on upper ocean thermal gradients, currents, and seasonal cycles. However, human emissions and warming may also influence ocean ecosystems through their effect on atmospheric aerosols. Changes to atmospheric circulation, precipitation patterns, and soil moisture and the advance or retreat of freshwater bodies associated with climate warming or other human activity may be associated with substantial future change in aerosol deposition to the ocean. Concurrent alterations in the atmospheric load of pollutants and smoke emissions may also influence chemical transformations of dust during transport from source regions to deposition sites, further complicating predictions of impacts on ocean biology. The current analysis demonstrates measurable ocean biological responses to a wide dynamic range in atmospheric inputs (Fig. 2A). Although these responses represent only a modest contribution to total plankton stocks or annual net primary production, they nevertheless are an important component of ocean production that is likely to change in the face of a warming planet.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S5
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Editor's summary

Most of the nutrients that fuel primary production in the oceans come from water upwelled to the surface from deeper depths, but atmospheric aerosols have long been recognized as another potential source. Westberry *et al.* used measurements of ocean color made by satellites to show that the global distribution of phytoplankton is affected by dust deposition, with impacts that vary from region to region. Climate change is expected to alter the relative importance of this mechanism. —H. Jesse Smith

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