



Aerobiology and the global transport of desert dust

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Desert winds aerosolize several billion tons of soil-derived dust each year, including concentrated seasonal pulses from Africa and Asia. These transoceanic and transcontinental dust events inject a large pulse of microorganisms and pollen into the atmosphere and could therefore have a role in transporting pathogens or expanding the biogeographical range of some organisms by facilitating long-distance dispersal events. As we discuss here, whether such dispersal events are occurring is only now beginning to be investigated. Huge dust events create an atmospheric bridge over land and sea, and the microbiota contained within them could impact downwind ecosystems. Such dispersal is of interest because of the possible health effects of allergens and pathogens that might be carried with the dust.

Introduction

Dust clouds generated by storm activity over arid lands can result in soil particulates being transported to altitudes >5 km [1]. The Sahara–Sahel region of Africa is the largest source of aerosolized soil dust on Earth, contributing as much as one billion metric tons of dust yr⁻¹ to the global atmosphere [2]. Deserts continuously discharge dust, but it is the large-scale dust events, visible from space and capable of crossing oceans (Figure 1), that could have the biggest impact on the biology and ecology of downwind ecosystems. The intercontinental transport of African desert dust has been studied for decades [3], but, as we discuss here, research on the biological particles traveling between continents with the dust has only recently been initiated (Table 1). The topic has generated interest because of concerns about health effects of allergens carried in the dust [4–6] and the possible transport of pathogens [7].

Dust (and biology) in the wind

Several mechanisms contribute to the microbial load of African desert dust, in addition to the ~10⁶ bacteria g⁻¹ of soil estimated to occur naturally [8]: as they move across the continent, local winds lift large quantities of arid soil. Garbage disposal in many parts of Africa is accomplished by burning [9], which can contribute bacterial and fungal spores in the rising smoke [10]. Finally, the trade winds blow the dust out over the Atlantic Ocean, where additional marine microorganisms aerosolized by wave action can be picked up.

Wind-borne bacteria are typically transported <1 km from their source [11], however, dust-associated bacteria can be transported over 5000 km from Africa to the Caribbean [12,13]. Fungal spores and pollen are adapted for aerosol dispersal and can be transported thousands of kilometers in the presence or absence of dust [14]. Satellite images show that African dust is regularly transported west over the Atlantic Ocean to the Americas and Caribbean, as well as north over the British Isles to Scandinavia, across the Mediterranean to Europe, and into Southwest Asia (Figure 1). Similarly, Asian dust from the Takla Makan and Gobi deserts is blown eastward across Korea, Japan and the Pacific Ocean, affecting the Arctic, Hawaiian Islands and the west coast of the USA (Figure 2) [15]. Some exceptionally large dust events, such as the Asian dust storm that occurred during April 2001, can circumnavigate the northern hemisphere. The southern hemisphere is affected by Australian dust, which is deposited into the Tasman Sea and on New Zealand (Figure 2) [16].

These intercontinental dust events can facilitate long-distance dispersal (LDD) of dust-associated biological particles. The surprising lack of research into microbial LDD by dust is partly due to a common misconception that all microorganisms in dust clouds are killed by solar UV-radiation, lack of nutrients and desiccation during their multi-day journey. In fact, some genera of bacteria (e.g. *Bacillus*) and most fungi can form spores, a dormant state that is resistant to desiccation, heat, radiation and nutrient-poor conditions [17]. Many of the bacteria that are isolated from aerosol samples are highly pigmented, suggesting that pigmentation also helps shield the microbes from UV radiation [9,18,19], in addition to the protection afforded by clouds, fog, smoke and desert dust particles. The length of time spent in the atmosphere and the distance traveled varies, but what goes up must come down. Microbes, pollen and mineral dust particles are eventually removed from the atmosphere by gravity or precipitation [20,21].

Evidence for LDD of microbiota via dust events

There is no doubt that microbes and pollen are contained within these large desert dust events; however, only recently have data been presented that implicate these dust events as mechanisms for transporting aerosolized microbiota around the globe. These data come from satellites and classical microbiology and molecular biology studies.

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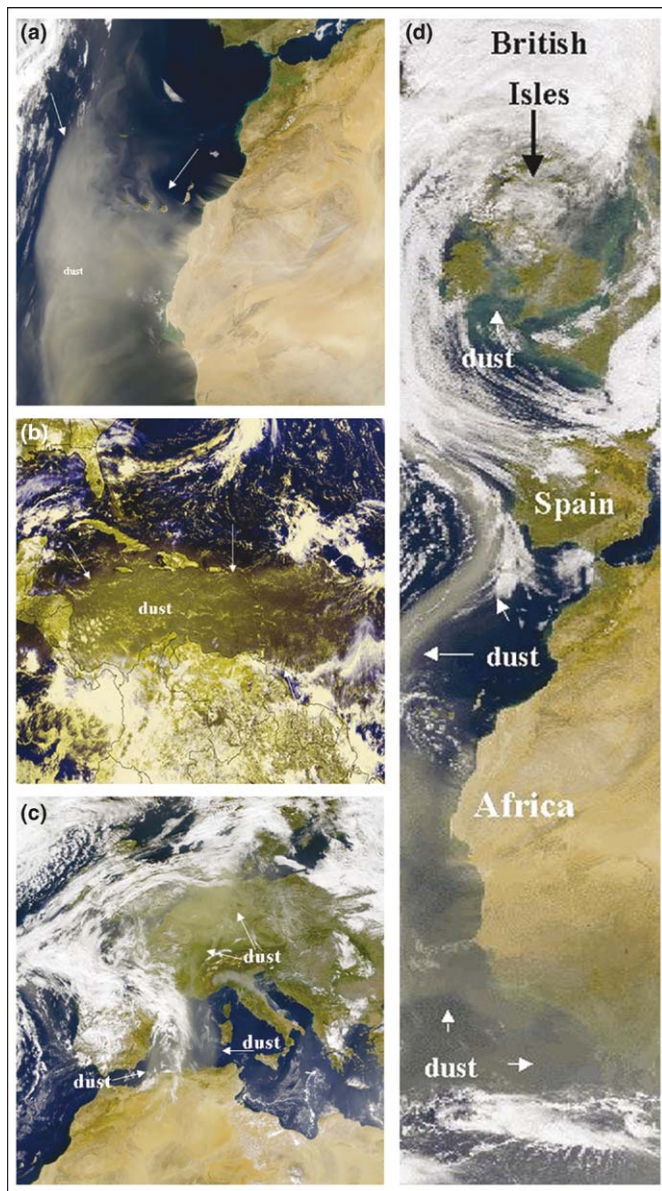


Figure 1. The intercontinental dispersal of African desert dust. Most of the dust moves westward in pulses from the Sahara–Sahel to the Caribbean and Americas, as shown in (a) and (b): (a) dust pours off the northwest African coast and blankets the Canary Islands, 11 February, 2001; (b) a dust cloud covering the entire Caribbean basin, 28 May, 1999. However, it is not unusual for dust from northern Africa to blow east into Europe and the Mediterranean as shown in this image from 13 October, 2001 (c). Less frequently, winds carry Saharan dust north over the British Isles, as on 13 February, 2001 (d). (a,c,d) reproduced with permission from the SeaWiFS Project, NASA Goddard Space Flight Center, and ORBIMAGE. (b) is an enhanced GOES 8 satellite photo reproduced with permission from NOAA.

Satellite data

Images from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS), carried by the OrbView-2 satellite, enable pulses of desert dust to be visually traced from their source to thousands of kilometers downwind (Figure 1a,c,d). These images document the huge mass of particulates (including bioaerosols) being ejected into the atmosphere; an image captured on February 26, 2000, of an African dust event the size of Spain precipitated commentary online, in the popular press, and in scientific articles (e.g. [22]).

Images from the Earth Probe-Total Ozone Mapping Spectrometer (TOMS) provide measurements of global aerosols [23]. TOMS aerosol data are currently being

used to track pulses of African dust during concurrent microbiological aerosol sampling [12,18,24]. At present, desert dust visualized by satellite imagery is used as a proxy for microbes and pollen, providing an indirect estimate of the geographical range of possible dispersal events. However, remote-sensing tools are being developed to model or monitor microbes directly in the marine environment (Box 1), and these tools could be adapted to monitor aerosolized microbes.

Enumerating dust-associated microbes

Only eight recent publications have investigated desert dust-associated microbes after long-distance transport, plus one additional study conducted in a desert source region specifically for comparison (Table 1). These papers address both the African and Asian dust systems (Figure 2) but a lack of standard methodology (Box 2) makes it difficult to compare results between or within systems. Different approaches have been applied to answer different questions as the focus of studies varies from allergens [5,6,25], to coral pathogens [26] and characterizing the dust-associated microbial community [12,13,18,24,27].

These studies all conclude that there are dust-associated microbes in that there are higher concentrations of aerosolized microorganisms during dust events. However, the magnitude of the concentrations and the specific microbes associated with the dust events remain topics of debate. As Table 1 shows, there are a wide range of values for concentrations of dust-associated microorganisms. A large part of the variability is due to the different collection methods; cultivation-independent methods, such as spore traps (which capture the fungal spores on an adhesive surface for counting by microscopy), will always generate higher counts than will a culture medium which selects for the subset of microorganisms capable of growing on it (Box 2). Additionally, numeric and taxonomic differences between samples might be due to heterogeneity or patchiness in the distribution of the microbial community within the dust event; for example, during dust events, the concentration of microorganisms (i.e. bacteria and fungi) does not correlate with the concentration of mineral dust particles [12].

Dust-associated fungi

Even when two research groups used the spore trap method to examine Asian dust at two different cities in Taiwan, the results were different [5,6]. Wu *et al.* [6] found no statistically significant difference between the concentration of fungal spores in dust versus background samples in Tainan City, but did note that some types of fungi (Basidiospores, *Aspergillus*, *Nigrospora*, *Arthrinium* and *Curvularia*; rusts, *Stemphylium*, *Cercospora*, *Pithomyces* and unidentified fungi) were between two and 12 times more abundant during dust events. Conversely, Ho *et al.* [5] found significantly higher total fungal spores associated with dust events ($p < 0.05$) in Hualien City, and different genera of fungi that occurred at higher concentrations during dust events (*Cladosporium*, *Ganoderma*, *Arthrinium*/*Poularia*, *Cercospora*, *Periconia*, *Alternaria* and *Botrytis*). The findings that *Periconia* and *Botrytis* concentrations were significantly higher during dust events,

Table 1. Comparison of dust-associated microbe studies

Dust system: approx. distance from source region ^a	Microbes	Collection method	Analysis ^b	Concentration of aerosolized microbes during dust event (range or average) ^{c,d}	Concentration of aerosolized microbes during background conditions (range or average) ^c	Refs
African (0 km)	Bacteria; fungi	Filtration	Culture, DNA sequencing of isolates	720–15 700 bacterial CFU m ⁻³ 80–370 fungal CFU m ⁻³	200–1100 bacterial CFU m ⁻³ 0–130 fungal CFU m ⁻³	[18]
African (5500 km)	Bacteria; fungi	Filtration	Culture, microscopy	0–20 bacterial CFU m ⁻³ 0–16 fungal CFU m ⁻³	0 bacterial CFU m ⁻³ 0 fungal CFU m ⁻³	[12]
African (6000 km)	Bacteria; fungi	Filtration	Culture, DNA sequencing of isolates	90–350 bacterial CFU m ⁻³ 30–60 fungal CFU m ⁻³ 0–185 bacterial CFU m ⁻³ 0–90 fungal CFU m ⁻³	100 bacterial CFU m ⁻³ 60 fungal CFU m ⁻³ 0–66 bacterial CFU m ⁻³ 0–40 fungal CFU m ⁻³	[24] [13]
	Fungi	Filtration	Culture, microscopy, DNA sequencing of isolates	50–83 fungal CFU m ⁻³	0–50 fungal CFU m ⁻³	[26]
Asian (2600 km)	Fungi	Impaction; filtration	Culture, microscopy	Not quantified	Not quantified	[25]
Asian (2700 km)	Bacteria; fungi	Impaction	Culture	225–3426 bacterial CFU m ⁻³ 336–2692 fungal CFU m ⁻³	105–621 bacterial CFU m ⁻³ 100–5929 fungal CFU m ⁻³	[27]
	Fungi	Spore trap	Microscopy	29 038 fungal spores m ⁻³ 6078 fungal spores m ⁻³	28 684 fungal spores m ⁻³ 4839 fungal spores m ⁻³	[6] [5]

^aDistances were estimated between West Africa, the Virgin Islands, and Barbados; and the Gobi desert, South Korea, and Taiwan using <http://www.mapcrow.info>.

^bDNA sequencing indicates partial sequencing of the 16S rDNA gene in bacteria and the 18S rDNA gene in fungi for identification.

^cAverages are provided when ranges could not be determined from the data.

^dCFU, colony forming units, assumed to have originated from a single bacterium or fungal cell.

whereas *Curvularia* and *Pithomyces* were significantly higher during background conditions, are the reverse of the findings of Wu *et al.* These differences were attributed to regional geographical differences and weather conditions in that Tainan is on the west coast of Taiwan facing

China, whereas Hualien is on the east coast, requiring that dust travel over Taiwan to reach it.

All nine studies (Table 1) agree that the composition of the aerosolized microbial communities varies dramatically during dust events and consist of a greater number of taxa

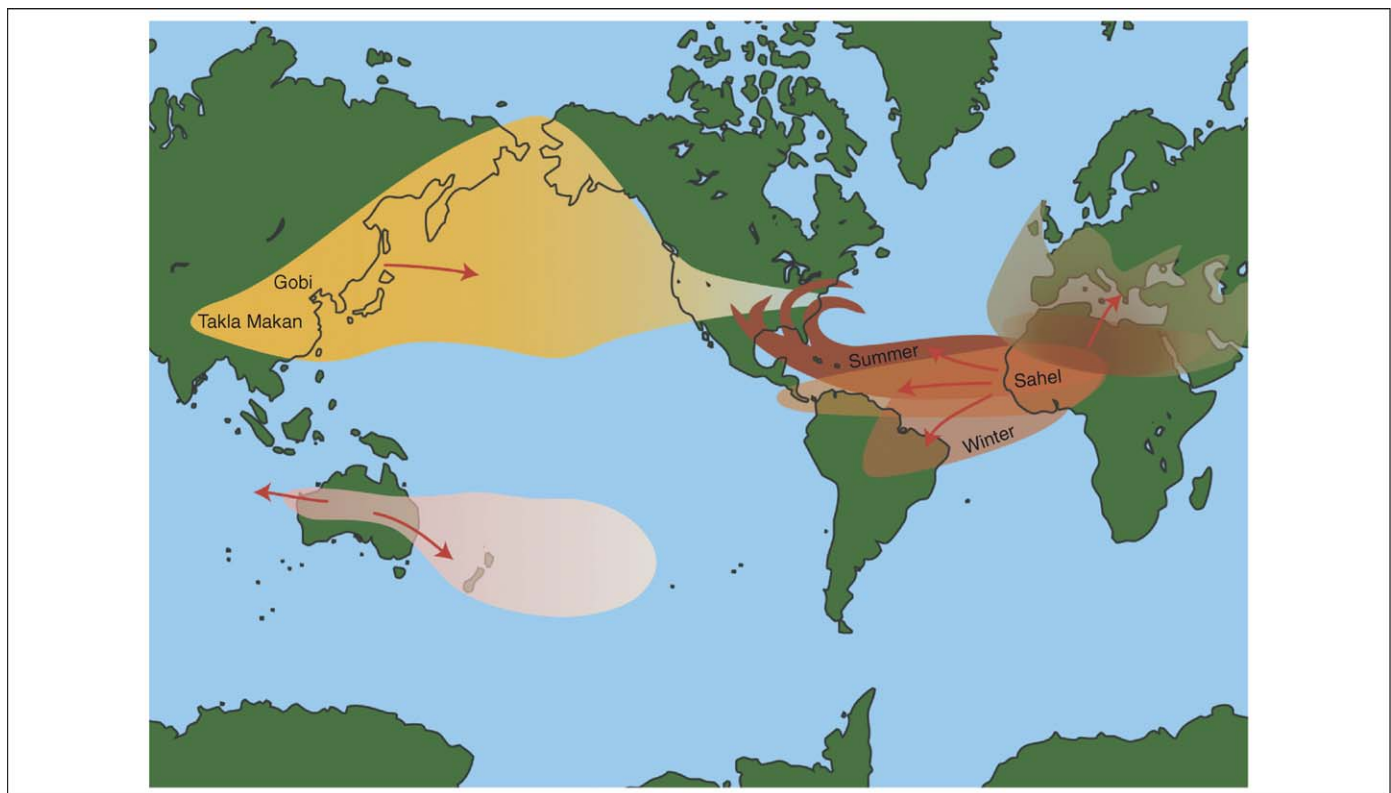


Figure 2. Principal ranges of the two major global dust transport systems. The African dust system (red–orange) has a strong seasonal component; in the summer (c. May–November) trade winds carry Saharan dust to the Caribbean and USA. In the winter (c. December–April) the African dust-flow is shifted to South America, where air-plants in the Amazon rainforest derive nutrients from the dust. Throughout the year, pulses of dust from northern Africa cross into the Mediterranean and Europe, impacting air quality. The Asian dust system (yellow) exports dust primarily during the spring (March–May). These dust events can incorporate emissions from factories in China, Korea and Japan, carrying a ‘brown smog’ across the Pacific to the west coast of North America. Occasionally, extremely large Asian dust events can travel across the entire USA and then impact Europe, making an almost complete circuit of the globe. Although not an intercontinental dust source, Australian deserts (pink) produce large dust storms that can reach New Zealand and halfway to South America. This updated version of a figure from [9] is reproduced with permission.

Box 1. Applying satellites to microbial ecology

Remote sensing, the use of satellites to monitor processes on broader regional scales, is being applied to microorganisms [52,53]. Most satellite methods involve using a proxy, such as sea surface temperature (SST), sea surface height (SSH), ocean color, and so on, to track the microorganisms. For example, *Vibrio cholerae* concentrations in the marine environment correlate very closely with temperature. The bacteria also are closely associated with marine plankton, and SSH is a good indicator of incursions of plankton-rich waters into near-shore bays. By combining satellite data on SST and SSH, a statistically significant correspondence can be made with the incidence of cholera in Bangladesh [54]. Thus, satellite data can be used to estimate the location and concentration of *V. cholerae* as well as to predict areas of cholera outbreaks. There are rare examples of more specific detection, mainly of marine phytoplankton, which can be detected by algorithms based on multiple color bands that distinguish the unique fluorescence spectra of the photosynthetic pigments of the microorganism [55].

It has been suggested that aerobiological dispersal processes (for organisms as diverse as birds, insects, viruses, bacteria, fungi, pollen and seeds) can be studied by an ecological scaling approach. That is, examining dispersal events as they relate to larger geographical areas and time scales, for example by utilizing topographic maps and satellite data of vegetation change [56]. Many of the factors that affect atmospheric microbial transport and survival, such as temperature, humidity, precipitation and wind strength and direction can be monitored by existing meteorological and satellite systems [53]. As more types of sensors become available and microbiologists provide a better understanding of how individual microbial species are affected by environmental parameters, the current framework can be expanded to use these global tools to better study the phenomenon of long-range microbial dispersal in the atmosphere.

than do the background samples. In several of the studies [5,6,13,18,24], *Cladosporium* was the numerically dominant fungal genus detected during dust events; however this could be because *Cladosporium* is both ubiquitous and commonly found in aerosol samples [28]. *Aspergillus* species were also found to be associated with dust events [6,12,13,18,25,26]. Although this genus is also frequently observed in aerosol samples, the species are of interest because of their roles as allergens, and in one case (*Aspergillus sydowii*), as a coral pathogen [26].

Dust-associated bacteria

Four studies of African dust identified bacterial isolates [12,13,18,24]. Most of the bacteria are Gram positive, and many are spore-formers, making them more resistant to desiccation. It is possible that the filtration methodology used in these studies has a selection bias for desiccation-resistant microbes, however, these are the types of microorganism that are most likely to survive transoceanic transport in a dust event. *Bacillus* [12,13,18] and *Microbacterium* [13,24] were the numerically dominant genera of bacteria isolated.

Dust-associated viruses

To our knowledge, there is only one study that mentions virus-like particles being associated with a transoceanic dust event [24]. This report is based on epifluorescent microscopy of filters stained with a nucleic-acid specific stain. An order of magnitude increase in virus-like particles, from 10^4 m^{-3} to 2.10^5 m^{-3} was observed between

Box 2. The need for standardized methods

Many dust-related studies (Table 1, main text) use culture-based analyses to isolate microorganisms not only because culturing is relatively easy and inexpensive, but also because it was of interest to show that microbes were viable after being transported several thousand kilometers, and therefore capable of causing an infection or establishing a niche in downwind environments. Culturing a microbe also enables additional assays to characterize its biochemical and physiological capabilities (e.g. antibiotic resistance profiles, [18]). However, the use of diverse culture media (e.g. R2A, blood agar, malt extract or potato dextrose) renders many of the culture enumeration data non-comparable. Each type of nutrient agar creates a slightly different selection bias, and even if the bacterial and fungal counts are identical between agars, counts can represent a different mixture of species. R2A, a low-nutrient agar designed to cultivate stressed heterotrophic bacteria from water and which has been used in several aerobiology studies [13,18,20,24,57], is recommended as a standard general medium. Enumeration of dust-associated fungal colonies on R2A resulted in counts that did not significantly differ from those of identical samples grown on malt extract agar and Sabouraud's agar [12,18].

It is also necessary to determine standard methods of collection and molecular analysis to reveal the true diversity in microbial aerosol communities. Only 1–10% of environmental bacteria are culturable on any given medium [58]; culture-independent methods provide access to the viable-but-not-culturable bacteria, as well as fungi, archaea and viruses that are presently not detected in dust events. Microbial-community DNA extraction followed by the creation of 16S rRNA gene sequence libraries has been accomplished with non-dust aerosol samples [59,60] and it is expected that data of this type will shortly be generated from dust-events. However, collection methods do differ: one study used a filtration system and then extracted DNA from the filter [60], whereas the other utilized a liquid impinger system where the aerosol particles were trapped in a liquid buffer [59]. Capturing bioaerosols in a liquid medium simplifies division of the sample, which can then be analyzed by multiple methods, including culture, direct DNA extraction, and enumeration by microscopy [61].

background and dust conditions in the Caribbean. Total bacterial counts from these same filters were almost identical to the viral counts. This was surprising because, in soil and marine environments, there are typically an order of magnitude more viruses than bacteria (in those cases, most of the particles are bacteriophages, or bacterial viruses). It might be that fewer viral particles are able to survive the high UV radiation and dry air associated with long-distance transport in dust events.

Dust-associated pollen

A recent study investigated pollen transported from North Africa to Spain via Saharan dust, and found that pollen for five species of non-native plants were exclusively detected during dust events [29]. In another study, exotic *Casuarina* pollen found in New Zealand peat and soil samples is believed to have been deposited via atmospheric transport from Australia [30].

DNA sequence evidence of LDD

Although the increased number and taxa of microorganisms detected during dust events is indicative of a dust-associated microbial load, it is still difficult to determine specifically which microorganisms arrived with the dust and which were present in the local atmosphere. The main problem is insufficient identification. Many of the studies

were limited to the genus-level identifications possible by microscopy. However, microbial biogeographical distinctions require identifications to the species or even strain level [31]. Four studies identified some of their cultured isolates by partial sequencing of the 16S rRNA gene (bacteria) and 18S rRNA gene (fungi) [13,18,24,26]. Comparisons between these small sample sets show that 19 bacterial isolates from dust events sampled in the Caribbean were of the same genus and species as isolates from dust events sampled in an African source region [18,24]. Comparison of 16S sequences between Caribbean and African samples revealed that there was one bacterium (*Kocuria erthyromyxa*) with 100% sequence identity, and another (*Bacillus pumilus*) with 99% identity [18]. Comparing fungal isolates, 18S sequences for all four of the *Cladosporium* isolates from the Caribbean samples were 99–100% identical to an isolate from dust samples collected in Africa [18]. However, it has recently been shown that bacteria with identical 16S sequences can have significant differences in their genome and physiological capabilities [32]. Therefore, although these genetic similarities are suggestive of LDD from Africa to the Caribbean, our limited understanding of microbial biogeography makes these data preliminary at best.

Consequences of the LDD of desert dust

Interest in the LDD of desert dust has been increasing as questions have arisen about the potential effects of associated chemical pollutants and pathogenic microbes on human health and ecosystems [9,33,34]. Recent work in this area raises issues of pathogen transport and the biogeography of microbes and pollen.

Transport of pathogens

There are economic and agricultural concerns raised by the possibility of intercontinental dust events enhancing the spread of plant and animal diseases. The limited genetic diversity of many modern crops increases the risk that a disease outbreak could quickly achieve worldwide distribution given that many of the plants are clones with identical susceptibility [35]. Of the microorganisms identified from African dust aerosols in three studies, 5–25% have the potential to be plant pathogens; that is, the genus or species identified is known to contain members that cause disease [13,18,24]. Examples include *Bacillus pumilus*, which can cause bacterial blotch in peaches, and *Bacillus megaterium*, which can cause ‘wetwood’ disease in trees.

Transoceanic or intercontinental aerosol transmission of a livestock pathogen has not yet been reported. However, there have been reports of the foot-and-mouth disease virus (FMDV) being transmitted by aerosols from Germany to Scandinavia, and from France to England [36,37], which led to speculation that FMDV could be carried from Africa to Britain or South America via desert dust [38]. It has also been suggested that FMDV has traveled from China to Korea in Asian dust [33].

A hypothesis has been offered that infectious agents in African dust could be linked to widespread episodes of coral reef morbidity and mortality occurring across the Caribbean basin [7]. This hypothesis has been supported

by the discovery of the fungus *Aspergillus sydowii*, causative agent of sea fan aspergillosis, in Sahelian soil [39] and African dust events sampled in the US Virgin Islands [26].

Although opportunistic human pathogens, such as *Aspergillus fumigatus*, *Aspergillus niger*, *Staphylococcus gallinarum* and *Gordonia terrae*, have been identified in African dust [12,13,18,24], there are no reports as yet of human infectious diseases related to LDD of desert dust. However, correlations between African dust events and increased incidences of asthma in the Caribbean have been proposed and confirmed [40,41].

Biogeographical patterns of microbial diversity

Microbiologists have been arguing for over 70 years about whether microbes exhibit biogeographical patterns [42,43]. The historical view, dating back to the early 1900s, is summed up by a quote attributed to Martinus Beijerinck: ‘Everything is everywhere, the environment selects’ [44]. The assumption is that microorganisms must have a cosmopolitan distribution owing to their enormous population sizes and ease of dispersal and, therefore, the microbial species found in a given habitat are a function of the selective properties of that environment and have no link to historical factors (e.g. previous desert dust events) [44]. Although there is evidence supporting this view [44], the idea presupposes (i) successful dispersal; (ii) successful colonization, and (iii) survival, none of which are guaranteed [45,46]. For example, spore-formers, such as *Bacillus* spp., are more likely to survive long-distance, dust-associated dispersal than are many Gram negative bacteria and, accordingly, are among the most commonly isolated genera in downwind dust samples [12,18]. Invasion or colonization capabilities will thus vary by species if not by strain.

Evidence of geographically distinct microbial populations has been offered: a study of fungi in Australian desert soils demonstrated that genetic divergence between fungi from different locations increased with the geographical distance between them [43]. In another study, strains of *Sulfolobus islandicus*, a species of thermophilic archaea isolated from hot springs in North America, Russia and Iceland, were found to cluster genetically according to where they were isolated [46] (the strains were all 99.8% identical based on 16S sequencing; the geographical grouping was based on sequence divergence at nine chromosomal loci). This type of evidence has led to discussion of the importance of isolation to microbial diversity and evolution [47].

Against this backdrop, the questions linked to LDD of microbes by desert dust are; (i) Are microbial species geographically restricted and if so how? (ii) What are the mechanisms that drive microbial distribution? (iii) What are the limits of adaptation? Given that most of the clay soil on carbonate Caribbean islands is derived from African dust [48], is it possible to distinguish between ‘African’ microbes and ‘Caribbean’ microbes, assuming that microorganisms have been crossing the Atlantic with desert dust for centuries?; and (iv) What genomic, molecular, or biochemical tools are best suited to distinguish these biogeographical distinctions?

Does hybridization occur?

The movement of pollen in desert dust events [29] raises the possibility of hybridization of downwind plant species by non-native populations [49]. Models predict that 'pure' native plant displacement by genetic assimilation can occur rapidly when selection favors the hybrid [49]. However, we are unaware of any reports of hybridization resulting from dust-associated pollens. From a biogeographical perspective, dust events that transport pollen long-distances (e.g. from North Africa to Scandinavia) introduce a potential for error in paleoecology studies that interpret past local vegetation based on presence of pollen [50].

Future directions

While more work is clearly required on both Asian and African dust systems, it would be of interest to have microbiological and pollen data from the large Australian dust events that impact New Zealand and the southern Pacific. Each dust system is likely to have unique microflora owing to regional geographical influences; once standard methodologies have been defined (Box 2), it will be of interest to compare the three systems.

The community composition and frequency of occurrence data generated by these efforts could then be integrated into an interdisciplinary, multiscale modeling framework [51] to predict and quantify aerial LDD of microbes and pollen in dust events. Finally, it would be beneficial to have more scientists with an ecological background focusing or collaborating on what is essentially an Earth surface process being studied mainly by geologists, atmospheric chemists and microbiologists.

Summary

Huge dust events create an atmospheric bridge over land and sea. Although satellite images leave no doubt that desert dust particles have an intercontinental distribution, we are only now beginning to address the questions relating to the dust-associated biological particles that also make this trip (how many, how often, and even which types). Data suggest that dust events can transport pathogens and allergens with the potential to impact the health of downwind populations and ecosystems. The desire to determine conclusively the source of dust-associated microorganisms compliments efforts to characterize microbial diversity in terms of biogeographical patterns. More work is needed to characterize the long-distance dispersal of microbes and pollen by these large-scale desert dust events and the consequences of this transport on distant ecosystems.

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