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Atmospheric Movement of Microorganisms in Clouds of Desert Dust and Implications for Human Health

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INTRODUCTION

The larger deserts on the planet, which include the Sahara and Sahel regions of North Africa and the Gobi, Takla Makan, and Badain Jaran deserts of Asia, are the primary sources of mobilized desert top soils that move great distances through the atmosphere each year (Fig. 1). The current estimate for the annual quantity of desert dust that makes regional or global airborne migrations is 0.5 to 5.0 billion tons (184). While it is believed that the Sahara and Sahel regions of North Africa have been and are the dominant sources of dust in the atmosphere (50 to 75% of the current estimate), there has been increased Asian dust activity over the last 20 years that has been attributed to climate change and desertification (73, 166, 191, 265). Between 1975 and 1987, the desertification rate in China was ~2,100 km^2 $year^{-1}$ (266). Other regions of known dust storm activity include the arid regions of the continental United States (the Great Basin), Central America, South America (Salar de Uyuni), Central Australia, South Africa (Etosha and Mkgadikgadi basins), and the Middle East (244). In general, high-energy wind conditions in arid regions can result in the mobilization of significant quantities of soils into the atmosphere, and large dust storm events are capable of continent-wide, transoceanic, and global dispersion (68, 193).

Dust emanates from North Africa year-round and at times throughout the year impacts air quality in Africa, the Middle East, Europe, Asia, the Caribbean, and the Americas (Fig. 2). Dust source areas in the Sahara and Sahel, primary latitudinal transport routes, and the influence of climate and climate systems (North Atlantic Oscillation and El Niño, etc.) on year-to-year dust flux have been previously reported (73, 74, 156, 166, 189, 191, 192, 212, 224, 235).

Dust storm activity in the deserts of Asia is seasonal, with the majority of atmospheric transport occurring during the spring (February to May) (258). Although Asian dust generation is seasonal, significant quantities are generated and can be dispersed universally in the Northern Hemisphere. A large Asian dust event in 1990 moved across the Pacific, the North American continent, and the Atlantic Ocean and was later identified in the French Alps via isotopic analysis of deposited particulate matter (84). A large dust event impacting the west coast of North America in 1998 reduced solar radiation levels by 30 to 40% and left a chemical fingerprint of deposited dust extending inland to the state of Minnesota (100).

Asian dust storms can take from 7 to 9 days to cross the Pacific Ocean. Dust storms moving off the west coast of Africa can take from 3 to 5 days to reach the Caribbean and Americas. As Fig. 1 illustrates, continuous transmission off the North African deserts can result in prolonged exposure of individuals living at considerable distances (the Caribbean and Americas) from the source of particulates. Using a handheld laser particle counter, I recorded a background particulate load of 2.6×10^6 airborne particles m^{-3} at a location south of Tampa Bay, Florida, on 15 July 2005. During an African dust event that occurred from 25 to 28 July 2005, the particle count in the same region south of Tampa Bay on 25 July was 26.1×10^6 particles m^{-3}. Ninety-nine percent of the particles were within a size range of >0.3 μm to <1.0 μm, the sub-2.5-μm fraction that can penetrate deep into the lung environment (Fig. 1C is an image of that dust event period). These data demonstrate the ability of dust storms to impact air quality at significant distances from their sources (Tampa Bay is >6,500 km west of the coast of North Africa). A higher risk to human health would obviously be associated with populations closer to dust

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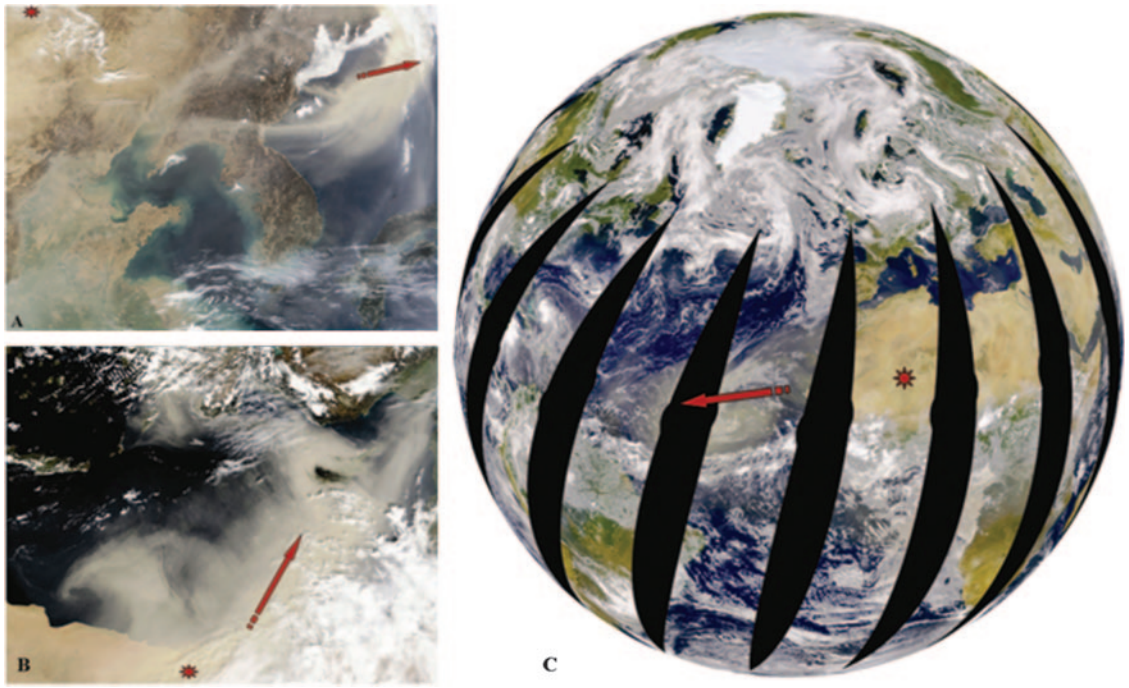

FIG. 1. African and Asian dust storms. Stars identify dust cloud source regions, and arrows identify dust clouds and the general direction of movement. (A) NASA image, via the moderate-resolution imaging spectroradiometer (MODIS) aboard the Terra satellite, of a dust storm blowing over the Sea of Japan on 1 April 2002. (Image courtesy of Jacques Descloitres, MODIS Land Rapid Response Team, NASA/Goddard Space Flight Center.) (B) NASA image, via MODIS, of a dust storm blowing out of Africa over the Mediterranean Sea in the direction of Turkey. The black spot in the tongue of dust is the Troödos mountain range of Cyprus, which protrudes through the top of the dust cloud. The image was taken on 25 February 2006. (Courtesy of Jeff Schmaltz, MODIS Land Rapid Response Team, NASA/Goddard Space Flight Center.) (C) NASA Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) image of a large dust cloud blowing across the Atlantic. The image was taken on 19 July 2005 and is courtesy of the SeaWiFS Project, NASA/Goddard Space Flight Center, and ORBIMAGE. This dust cloud impacted the air quality in Florida. Airborne particle measurements taken by the author with a handheld laser particle counter south of Tampa Bay, FL, went from 2.6×10^6 m^{-3} on 15 July 2005 (normal clear atmosphere) to 26.1×10^6 m^{-3} on 25 July 2005 (dust conditions). Over 90% of the particles ranged from >0.3 to 0.5 μm in size.

source regions, as this excerpt regarding the American Dust Bowl period illustrates:

> It is stated by some authorities that man breathes, on an average, approximately 25 pounds of air daily. Nelson's "Loose Leaf Living Medicine" says that a normal individual inhales 30.5 cubic inches of air at each breath and breathes 17 times per minute. Then with an average of 0.0368 g of dust per cubic foot of air over a period of ten hours (the average duration of the dust storms) the straining apparatus of the respiratory system is confronted with a very large task. From above figures it can be computed that an individual breathes 6.6240 g of dust during an average dust storm (18).

Every human breath taken is laden with particulate matter, and human evolution produced the most obvious and familiar front line of defense, nose hair. Less obvious are the mucus glands that line our airways. These glands function to trap and aid in the expulsion of particulates via secretion, ciliated transport, and ingestion or cough. Of particular concern are particles of <10 μm in size that can penetrate into the lungs and those of <2.5 μm that may penetrate into deep lung tissue and the subepithelial environment. These very small particles cause adverse health effects via oxidative stress (47, 52, 263). The deposition rate of ultrafine particles (<100 nm) in the lungs has been shown to increase as particle size decreases and to increase with exercise versus resting (46). Health studies conducted in urban and suburban environments have demonstrated mortality risk with exposure to particulate matter and have attributed this risk to anthropogenic particulates generated through automotive and industrial combustion versus those of crustal origin (130, 210). Several studies conducted to investigate the role of dust storms that consist of concentrated crustal particulates have shown an associated allergic, asthma, and silicosis/pulmonary fibrosis risk (36, 127, 173, 180, 202, 259). Areas impacted by desert dust storms, such as communities in the Middle East and the Caribbean, are known to have some of the highest incidences of asthma on the planet (8, 16, 96). On the Caribbean island of Barbados, the incidence of asthma increased 17-fold between 1973 and 1996, a period that coincided with increased flux of African dust to the area of the island (97, 188). Gyan et al. recently demonstrated a link between African dust and pediatric respiratory stress on the southern Caribbean island of Trinidad (85). Allergens commonly associated with dust storms include fungal spores, plant and grass pollens, anthropogenic emissions, and organic detritus (62, 103, 125).

Desert dust cloud toxicity may be influenced by anthropogenic material as a result of particulate/pollutant aerosoliza-

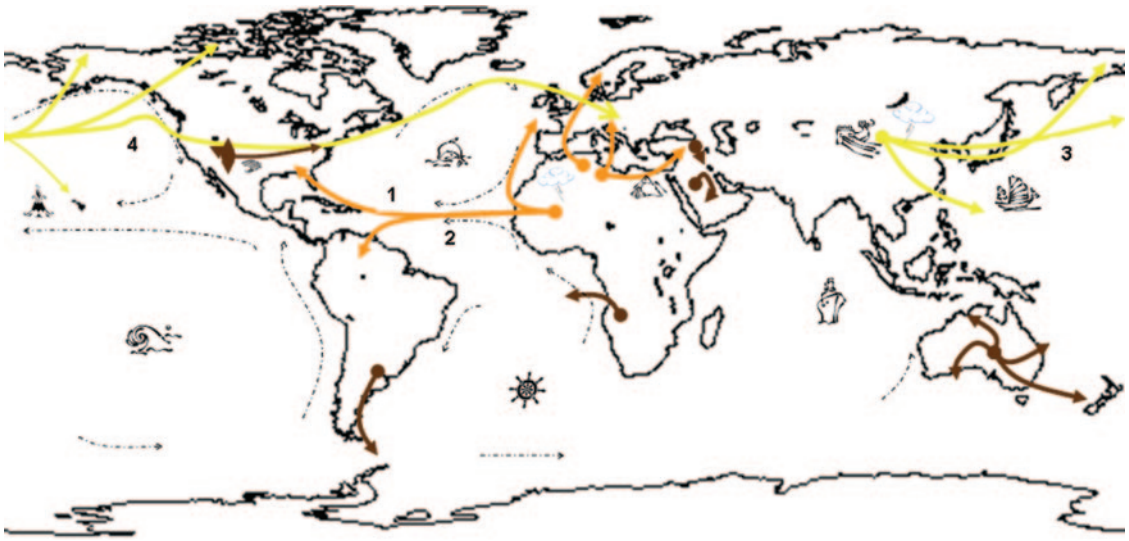

FIG. 2. Primary sources of desert dust and their atmospheric pathways. (1) During summer in the Northern Hemisphere (approximately June through October), African desert dust is transported across the Atlantic to the northern Caribbean and North America. (2) During winter in the Northern Hemisphere (approximately November through May), African desert dust is transported across the Atlantic to the southern Caribbean and South America. (3) The Asian dust season typically lasts from late February to late April. (4) Large Asian dust events can travel significant distances in the Northern Hemisphere. Yellow lines show Asian desert dust atmospheric routes, orange lines show African dust routes, brown lines show routes of other desert dust sources, and broken black lines depict wind patterns. (Base map image courtesy of NASA's Geospatial Interoperability Office, GSFC [http://viewer.digitalearth.gov/].)

tion during cloud formation or cloud capture during downwind transport (adsorption of pesticides, herbicides, and industrial emissions, etc.). Inherent toxicity is due to differences in native soil elemental composition (metals and naturally occurring or synthetic radioisotopes, etc.), atmospheric chemical alteration, size fractionation, and extreme particulate load (5, 44, 88, 131, 174, 176, 263). Toxic metals such as arsenic and mercury have been shown to occur in airborne desert dust in downwind environments at concentrations higher than regional crustal concentrations (93). In addition to the presence of these toxic metals, dust can indirectly impact human health by spurring toxic algal blooms in coastal environments (i.e., red tides, in which marine organisms utilize dust components such as iron as a nutrient in nutrient-depleted waters) (93, 138, 243). Dust clouds may contain high concentrations of organics composed of plant detritus and microorganisms (80, 108) and may pick up additional biological loads (fungal spores, bacteria, viruses, and pollen, etc.) as the clouds move through and sandblast downwind terrestrial environments and/or over aquatic environments through the adhesion of microbe-laden fine aquatic sprays to dust particles. All of these potential dust cloud constituents may negatively influence human health in regional and downwind environments, with the greatest risk factors being frequency of exposure, concentration of and composition of particulates, and immunological status. Dust-borne microorganisms in particular can directly impact human health via pathogenesis, exposure of sensitive individuals to cellular components (pollen and fungal allergens and lipopolysaccharide [LPS], etc.), and the development of sensitivities (i.e., asthma) through prolonged exposure. Dust-borne dispersion of microorganisms may also play a significant role in the biogeographical distribution of both pathogenic and nonpathogenic species, as long-range atmospheric transport routes and concentrations shift through time due to climatic and geologic change (148, 163).

OCCURRENCE

> Reflecting on the whole of this, I conclude that the germs float through the atmosphere in groups or clouds, and that now and then a cloud specifically different from the prevalent ones is wafted through the air. The touching of a nutritive fluid by a Bacteria cloud would naturally have a different effect from the touching of it by the sterile air between two clouds. But, as in the case of a mottled sky, the various portions of the landscape are successively visited by shade, so, in the long run, are the various tubes of our tray touched by the Bacterial clouds, the final fertilization or infection of them all being the consequence (236).

Bacteria

Desert topsoils are laden with viable and diverse prokaryote communities (29, 32, 53, 124, 177). Globally, a gram of topsoil contains ~10^7 (forest) to 10^9 (arid and other soil types) prokaryotes (247). These populations are believed to consist of ~10,000 bacterial types with ~0.1% of the total population composing ~99.9% of the diversity (67, 233, 234). Studies that have examined the number of culturable prokaryotes in desert soils have reported concentrations ranging from 0 to ~10^7 gram^{-1} (126, 144, 169).

Dominant phyla found in soils, as determined by their prevalence in sequence libraries, include the *Proteobacteria*, *Acidobacteria*, and *Actinobacteria* (110). Although this community

TABLE 1. Genera of bacteria and fungi found in dust storm samples where identified to at least the genus level[a]

Bacterial genus/genera	Fungal genera	Method of identification (bacterial/fungal)	Location (reference)	Dust source region
Arthrobacter, *Bacillus*, *Cryptococcus*, *Flavimonas*, *Kurthia*, *Neisseria*, *Paenibacillus*, *Pseudomonas*, *Ralstonia*, and *Staphylococcus*	*Alternaria*, *Cryptococcus*, *Mortierella*, *Penicillium*, *Phoma*, *Rhodotorula*, and *Stemphylium*	Fatty acid methyl esters and 16S rRNA gene sequencing/26S rRNA gene sequencing	Kuwait (141)	Middle East
Bacillus, *Pseudomonas*, and *Staphylococcus*	*Alternaria*, *Aspergillus*, *Botrytis*, *Cladosporium*, *Mortierella*, *Mucor*, *Penicillium*, *Pythium Ulocladium*, and *Verticillium*	Microscope/microscope	Saudi Arabia (126)	Saudi Arabia
Arthrobacter, *Corynebacterium*, *Microbacterium*, *Nocardioides*, *Planococcus*, *Saccharothrix*, and *Streptomyces*	*Alternaria*, *Cladosporium*, *Microsporum*, and *Penicillium*	16S rRNA gene sequencing/ microscope and 18S rRNA gene sequencing	Turkey (82)	Sahara
Arthrobacter, *Agrococcus*, *Bacillus*, *Curtobacterium*, *Duganella*, *Kocuria*, *Massilia*, and *Microbacterium*	*Acremonium*, *Alternaria*, *Cladosporium*, *Fusarium*, *Microsporum*, *Penicillium*, and *Trichophyton*	16S rRNA gene sequencing/ microscope and 18S rRNA gene sequencing	Turkey (82)	Middle East
ND	*Alternaria*, *Aspergillus*, *Cladosporium*, *Coleophoma*, *Fusarium*, *Libertella*, *Lophiostoma*, *Penicillium*, *Phoma*, and *Zygosporium*	NA/microscope	Israel (207)	Sahara
Acinetobacter, *Agrococcus*, *Arthrobacter*, *Aureobacterium*, *Bacillus*, *Corynebacterium*, *Deinococcus*, *Dietzia*, *Gordonia*, *Kocuria*, *Microbacterium*, *Micrococcus*, *Paenibacillus*, *Paracoccus*, *Planococcus*, *Rhodococcus*, *Saccharococcus*, *Staphylococcus*, *Streptomyces*, and *Zoogloea*	*Cladosporium*, *Alternaria*, and *Aspergillus*	16S rRNA gene sequencing/ 18S rRNA gene sequencing	Mali, Africa (117)	Sahara/Sahel
Actinomyces, *Bacillus*, *Brevibacterium*, *Cellulomonas*, *Frigoribacterium*, *Gordonia*, *Kocuria*, *Lechevalieria*, *Leifsonia*, *Lentzea*, *Novosphingobium*, *Pseudomonas*, and *Staphylococcus*	*Alternaria*, *Cladosporium*, *Dendryphion*, *Lojkania*, *Lithothelium*, *Massaria*, *Myriangium*, *Neotestudina*, *Penicillium*, *Phoma*, *Setosphaeria*, *Stachybotrys*, *Trichophyton*, and *Ulocladium*	16S rRNA gene sequencing/ 18S rRNA gene sequencing	Tropical mid-Atlantic ridge (83)	Sahara/Sahel
Actinosynnema, *Afipia*, *Agrococcus*, *Ancylobacter*, *Arthrobacter*, *Bacillus*, *Bosea*, *Curtobacterium*, *Frankiaceae*, *Fulvimaria*, *Hymenobacter*, *Kocuria*, *Kineococcus*, *Mesorhizobium*, *Nocardioides*, *Paracoccus*, *Propionibacterium*, *Pseudomonas*, *Rhizobium*, *Saccharothrix*, *Sphingomonas*, *Sinorhizobium*, *Streptomyces*, and *Taxeobacter*	*Acremonium*, *Aspergillus*, *Aureobasidium*, *Bipolaris*, *Chromelosporium*, *Chrysosporium*, *Cladosporium*, *Coccodinium*, *Cochliobolus*, *Geotrichum*, *Gibberella*, *Microsporum*, *Monocillium*, *Nigrospora*, *Oidiodendron*, *Paecilomyces*, *Penicillium*, *Pleospora*, *Rhizomucor*, *Scytalidium*, and *Trichophyton*	16S rRNA gene sequencing/ 18S rRNA gene sequencing	U.S. Virgin Islands (78, 79)	Sahara/Sahel
Bacillus	ND	Microscope/NA	Sweden (20)	North of the Black Sea
Bacillus	*Mycelia sterilia* (unidentified imperfect fungi with no known spore stage, 48% of isolates), *Alternaria*, *Arthrinium*, *Aspergillus*, *Cladosporium*, *Curvularia*, *Neurospora*, *Penicillium*, and *Periconium*	Microscope/microscope	Barbados (190)	Sahara/Sahel
ND	*Fusarium*, *Aspergillus*, *Penicillium*, and *Basipetospora*	NA/microscope	Korea (261)	Gobi/Takla Makan
ND	*Penicillium*, *Aspergillus*, *Nigrospora*, *Arthrinium*, *Curvularia*, *Stemphylium Cercospora*, and *Pithomyces*	NA/microscope	Korea (256)	Gobi/Takla Makan

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TABLE 1—*Continued*

Bacterial genus/genera	Fungal genera	Method of identification (bacterial/fungal)	Location (reference)	Dust source region
ND	*Alternaria*, *Arthrinium*, *Aspergillus*, *Botrytis*, *Cercospora*, *Cladosporium*, *Curvularia*, *Drechslera*, *Fusarium*, *Ganoderma*, *Nigrospora*, *Papulara*, *Penicillium*, *Periconia*, *Pithomyces*, *Stemphylium*, and *Ulocladium*	NA/microscope	Taiwan (92)	Gobi/Takla Makan

[a] All studies listed were culture based. ND, no data; NA, not applicable.

composition is determined by a number of factors, including pH, temperature, elemental composition, and nutrient and moisture content, members of other phyla also occur less frequently (67, 110). Pigments produced by desert soil taxa such as *Nostoc* sp. and *Scytonema* sp. are believed to provide UV shielding compared to less-pigmented community members (21). Novel or rare actinomycetes (*Citricoccus alkalitolerans*, *Jiangella gansuensis*, and species of *Nocardiopsis* and *Saccharothrix*) have been isolated from a number of desert soil samples collected in the deserts of both Africa and Asia (216, 267). Similar to the potential hazards of life in the soil, atmospheric sources of stress to airborne microorganisms include UV damage, desiccation (drying by wind), temperature (both low and high temperatures depending on the tolerance range of an organism), and atmospheric chemistry (humidity levels dependent on tolerance and oxygen radicals, etc.) (54, 76, 158). Dust-borne transport of microorganisms, particularly over aquatic environments, should be enhanced due to tolerable humidity levels and attenuation of UV by the particle load of the various dust clouds (78). NASA research has shown that the particle load of large dust clouds can attenuate UV by more than 50% (91).

Table 1 lists the genera identified in dust storm microbiology studies as described below. While it would be interesting to compare and contrast the diversity of isolates identified in each study, it should be noted that some relied on microscopy for identification while others employed molecular methods. It should also be emphasized that all were culture-based studies and few utilized like assays (i.e., collection and culture media, etc.), which restricts the comparison of data.

Desert dust research in Kuwait, which focused on "military personnel health protection," identified 147 bacterial CFU, which included representatives from 10 genera, by gas chromatographic analysis of fatty acid methyl esters and 16S rRNA gene sequencing in settled dust (141). Seven genera were isolated from the atmosphere over Erdemli, Turkey, during Saharan dust events in March 2002, with the most prevalent being species of *Streptomyces* (82). During a dust event of Middle East origin that impacted the same location in October 2002, species from eight genera were recovered, with the most prevalent belonging to the genus *Kocuria* (82). In Bamako, Mali, Africa, Kellogg et al. identified a small subset of the observed (n = 94 [by 16S rRNA gene sequencing]) airborne bacterial isolates collected during four dust events and one nondust event. These isolates were composed of 20 genera, and *Bacillus* sp. represented 38% of the isolates, followed by *Kocuria* sp. (12.8%), *Planococcus* sp.(8.5%), *Saccharococcus* sp. (7.4%), and *Micrococcus* sp. (6.4%) (117). Twenty-five bacterial isolates collected from the atmosphere over the mid-Atlantic ridge (~15°N, 45°W) during periods of elevated African desert dust concentrations consisted of 13 genera, with those dominant being *Bacillus* (32%), *Gordonia* (12%), and *Staphylococcus* (8%) (83). When African dust was visibly present in the northern Caribbean air, a subset of isolates from various samples was identified by 16S rRNA gene sequences as consisting of 25 genera (78, 79). The most dominant genera detected in these samples were *Microbacterium* (14.4%), *Sphingomonas* (7.2%), *Bacillus* (6.5%), and *Streptomyces* (4.0%). Eleven of the isolates (closest GenBank neighbor) had previously been identified in marine environments, demonstrating that aerosolized marine spray may adhere to dust particles as the clouds move over marine environments (78, 79). The few other dust storm-related studies devoted to the prevalence of bacteria in atmospheric samples were based on the presence of spores (in aerobic culture; i.e., species of *Bacillus* were identified) or other cellular morphologies (19, 126, 190) or on only reported CFU (39).

Concentrations of bacteria observed during dust storms are noted in Table 2. Between April and November 1934, 30 flights were conducted at altitudes of 0 to 7,772 m in the vicinity of Boston, MA, to collect air samples for microbial analysis (187). Flight 4 recovered samples at altitudes of 457 to 7,772 m at a time when visibility was hampered by dust transported within air masses from over the tropical Atlantic (area of the Sargasso Sea). These samples resulted in the growth of 16 to 266 bacteria (overall average of the five samples, 144) and 11 to 43 fungi (overall average of five samples, 23) m^{-3} of air (187). These CFU counts were by far the highest combined (bacterial and fungal) counts for all of the flights (for the other 29 flights, there were 137 samples yielding 0 to 138 bacterial CFU, average 14, and 0 to 267 fungal CFU, average 11). Flight 4 was the only flight of the 30 to be affected by Transatlantic dust (187). In Kansas, in 1935, numbers of bacteria on nutrient agar settle plates exposed to dust storms ranged from 2,880 to 42,735 m^{-2} min^{-1} (23). Images of a clear-day petri dish and a dust storm petri dish (both plates exposed to the atmosphere for 1.5 min.) showed fewer than 10 colonies isolated on the clear day and overgrowth on the dust storm plate (23). Atmospheric samples collected by plane from three altitudes (365, 1,280, and 2,500 m) over Junction, TX, demonstrated that the highest concentrations of bacterial and fungal isolates occurred when dust generated by frontal activity was present (66). Graph-based data showed >1,544 combined CFU m^{-3} at the 365-m altitude versus <450 combined CFU m^{-3} at each of the three altitudes during normal/no-dust conditions. The lowest CFU collections (<100 at each altitude) followed frontal precipitation events

TABLE 2. Concentrations of culturable bacteria and fungi and fungal spores in dust storms

Sample site (reference)	Dust storm source	Sampling method[a]	Concn[b] (bacterial CFU m^{-3}) (avg)		Concn[c] (fungal CFU m^{-3}) (avg)	
			Background	Dust	Background	Dust
Boston, MA (187)	Air mass from over the Sargasso Sea	Oil-saturated lens paper from a plane; altitudes, 0–7,620 m	0–138 (14)	16–266 (144)	0–267 (11)	11–43 (23)
Kansas (23)	Kansas	For background, 1.5 min; for dust storms, 5- to 15-s exposures of nutrient agar settle plates	Photograph of one plate with less than 10 colonies	2,880–42,735	ND	ND
Junction, TX (66)	Texas	Exposure of nutrient agar plates from a plane; altitudes, 365–2,500 m	<450 (avg) combined bacterial and fungal CFU; NS	>1,544 (avg) combined bacterial and fungal CFU; NS	See bacterial concn	See bacterial concn
Saudi Arabia (126)	Saudi Arabia	Dust plate trap followed by a dilution method (also 6-h nutrient agar settle plate counts)	ND	1,892 ± 325 (100× increase over background)	ND	869 ± 75 (40× increase over background)
Mali (117)	Sahara/Sahel	<1 h, low-flow rate; MF	200–1,100 (537)	720–15,700 (6,194)	0–130 (62)	80–370 (195)
Israel (207)	Sahara	25 min, 28.3 liters min^{-1}; Andersen sampler	79–108 (93)	694–995 (844)	31–115 (73)	205–226 (215)
Turkey (82)	Sahara/region	<1 h, low-flow rate; MF	0–41* (3)	0–59† (6)	0–291* (25)	0–703† (66)
Tropical mid-Atlantic (15°N, 45°W) (83)	Sahara/Sahel	<1–12 h, low-flow rate; MF	NA	0–24 (1)‡	NA	0–27 (3)‡
U.S. Virgin Islands (78)	Sahara/Sahel	<1 h, low-flow rate; MF	0–100 (12)	90–350 (203)	0–60 (15)	30–60 (48)
U.S. Virgin Islands (79)	Sahara/Sahel	<1 h, low-flow rate; MF	1–100 (13)	0–353 (80)	0–57 (13)	0–90 (31)
Barbados (190)	Sahara/Sahel	~24 h, low-flow rate; MF	0–(~10) (NS)	0–(~20) (NS)	0–(~4) (NS)	0–(~16) (NS)
Korea (39)	Gobi/Takla Mahan	Andersen sampler	105–1,930 (386)	225–8,212 (1,642)	100–8,510 (1,702)	336–6,992 (1,398)
Taiwan (92)	Gobi/Takla Mahan	Spore trap	ND	ND	4,839	6,078
Taiwan (256)	Gobi/Takla Mahan	Spore trap	ND	ND	28,683	29,038

[a] Low-flow rate, <20 liters min^{-1}; MF, membrane filtration.

[b] Values for the Kansas study are bacterial cells per square meter per min. NA, not applicable due to some level of dust always being present; ND, no data; NS, not specified (graph-based data); *, dust concentration below 12 μg m^{-3}; †, dust concentration at or above 12 μg m^{-3}; ‡, dust concentration above 6 μg m^{-3} at 10 m above sea level.

[c] Values for the Taiwan studies are mean numbers of spores per cubic meter. NA, not applicable due to some level of dust always being present; ND, no data; NS, not specified (graph-based data); *, dust concentration below 12 μg m^{-3}; †, dust concentration at or above 12 μg m^{-3}; ‡, dust concentration above 6 μg m^{-3} at 10 m above sea level.

(66). In Saudi Arabia, an increase of 100% over background levels was observed during dust storms with a settle plate technique. Kellogg et al. (117) reported background levels of 200 to 1,100 bacterial CFU m^{-3} in the atmosphere over Bamako, Mali, Africa, and dust condition levels ranging from 720 to 15,700 bacterial CFU m^{-3}. During two Saharan dust events impacting Israel's atmosphere (January and April 2004), airborne bacteria averaged 844 CFU m^{-3}, versus a 2-day background average of 93 CFU m^{-3}, and ratios of total CFU (bacteria and fungi) for dust days versus non-dust days were similar to those reported by Griffin et al. in the Caribbean (207). At Erdemli, Turkey, dust event bacterial concentrations ranged from 0 to 59 CFU m^{-3} (average, 6), versus background concentrations of 0 to 41 CFU m^{-3} (average, 3) (82). In the northern Caribbean (~18°N), normal background concentrations of bacteria in air samples collected over the islands and open water averaged 13.6 CFU m^{-3} (28 samples) (79). The same study noted an increase in airborne bacterial CFU (average, 80.1 CFU m^{-3} [15 samples]) when African desert dust was visibly present in the atmosphere, with the higher concentrations (average, 143.1 CFU m^{-3}; *n*, 8) occurring during late July and early August (79). Dust-borne microbial concentrations in the early summer (May, June, and early July) were not distinguishable above normal background levels in this Caribbean research site (79). To determine if bacteria and fungi being transported to the Caribbean in the early summer months of May and June could be detected in air samples at a site closer to the continent of Africa, a study was conducted over the mid-Atlantic ridge at 15°N over a 6-week period (22 May to 30 June 2003). Results showed that bacterial CFU ranged from 0.1 CFU to 23.7 CFU m^{-3} when culturable bacteria were recovered from the air samples (12 of 85 samples) (83). The U.S. Navy's Naval Aerosol Analysis and Prediction System, an atmospheric model that can determine airborne aerosol concentrations at various altitudes on a global scale (94, 114, 196, 209), demonstrated that most of the microorganisms recovered in the mid-Atlantic study were recovered during periods of elevated aerosol (dust) concentrations (83). On the island of Barbados, at ~13.1°N in the southern Caribbean, African desert dust-borne bacterial CFU (morphological iden-

tifications were via spore staining, and almost all were identified as *Bacillus* sp.) ranged from 0.0 to approximately 20.0 CFU m^{-3}, with the highest concentrations occurring primarily during the summer (190). During Asian dust events impacting air quality in Taejon, Korea, the bacterial CFU concentration increased on average 4.3 times over that observed under normal atmospheric conditions (39).

Fungi

The total number of fungal species has been estimated at 1.5×10^6, with approximately 7.4×10^4 to 1.2×10^5 having been identified (89). The number of fungi typically found in a gram of topsoil is approximately 10^6 (225). One of the genetic advantages that fungi have over many other microorganisms is that they are capable of producing spores. Spores enhance survival during transport and periods of prolonged environmental stress. Fungal spores are egg-like vesicles covered with a thin layer of hydrophobic proteins that provide protection from physical stresses such as UV exposure and desiccation (56). Viable fungi recovered from extreme altitudes in the atmosphere have demonstrated the ability to survive harsh conditions (77, 142, 143, 153, 200, 242). Mycological studies conducted in desert environments have demonstrated that diverse communities exist in desert topsoils worldwide (1, 2, 9, 165, 218). An early review of outdoor airborne concentrations of fungal spores reported that the highest concentrations typically occur in temperate and tropical regions (10^6 spores m^{-3} of air) and the lowest in desert environments (400 spores m^{-3} of air) (129).

In a survey of airborne fungi in the eastern and western deserts of Egypt, 44 genera and 102 species (*Aspergillus* was the dominant genus) were recovered, with the areas of highest fungal concentrations and diversity corresponding to increases in vegetative cover and anthropogenic activity (107). The most prevalent fungal genera in airborne dust samples collected from the atmosphere of Taif, Saudi Arabia, were (31 genera and 70 species) *Aspergillus*, *Drechslera*, *Fusarium*, *Mucor*, *Penicillium*, *Phoma*, and *Stachybotrys*, and it was noted that genus prevalence was dependent on the nutrient medium used (3). A similar study conducted in Egypt identified 27 genera (64 species), and again, prevalence was determined by the nutrient medium employed (4). While most studies have shown that desert environments harbor diverse mycological communities, fungi such as *Coccidioides immitis* and *Coccidioides posadasii* are known to be restricted geographically (the Americas in this case) (90). In contrast to microbial studies of soil or air environments, far fewer studies have been devoted to dust-borne transport of microorganisms. Table 1 lists those fungal genera found in dust storm studies where dust-associated isolates were identified to at least the genus level. Several studies, while identifying bacterial and or fungal isolates, did not distinguish those recovered during clear versus dust conditions and thus are not included in Table 1 (66, 187). As can be seen from Table 1, the dust-associated fungal community is diverse, and the true extent of diversity is probably much greater given that some of the more recent studies, which used molecular methods for identification, identified only a small fraction of the cultured isolates due to budget constraints (78, 79, 82, 117). Concentrations of fungal CFU and spores observed during dust storms at various geographical locations are noted in Table 2. In all cases, with the exception of the data reported by Choi et al. (39) (Table 2), the presence of desert dust in the atmosphere resulted in an increase in the concentration of culturable fungi or fungal spores relative to background or clear atmospheric conditions.

Viruses

Viral abundance in soil has been shown to occur at a concentration of $\sim 10^8$ per gram (198, 252). Certain desert soil characteristics (high temperatures, elemental composition [the ability of viruses to adsorb to soil particulates], soil chemistry [pH], and moisture content) are known to impact viral survival and thus community composition and concentration (260). Poliovirus and bacteriophage MS2 survival in seeded desert soil samples was limited in the summer months when temperatures of ~33.0°C and a decrease in soil moisture content (from 40% to <5%) were recorded (in comparison to winter survival) (222). Low pH, low moisture, and high concentrations of clay, cations, and total dissolved solids have been shown to enhance virus survival by increasing adsorption of viruses to other soil constituents (99, 215, 260). As in soil, milder temperatures and moderate to high humidity (50 to 80%, depending on the virus type) favor viral survival in aerosols, with atmospheric transport over open bodies of water (higher humidity versus that of overland environments) favoring long-range dispersion and infection (70, 104, 217). Bacteriophages that integrate their genome into the host genome (prophage) may be more apt to survive long-range atmospheric transport than are virulent phages (phages that directly replicate and lyse host cells following infection and therefore do not benefit from the shielding potential of a host cell). The scientific community has yet to address this topic of research. Since prophages are persistent in environmental bacterial populations and are important vectors of bacterial virulence factors (and other genomic material), these organisms may play an unforeseen role in the global dispersion of prokaryotic genomic information through long-range atmospheric dispersion (30, 146). Viral transmission in aerosols (influenza viruses and rhinoviruses, etc.) has been reviewed, and most of the documented cases have been limited to short-range laboratory tests (animal and human hosts) or indoor studies in hospitals (206). Data referencing long-range transmission of infectious viruses have been obtained only with aerosol models (no field detection of the aerosolized virus) (206). Several papers have hypothesized transoceanic movement of viruses through the atmosphere based on favorable atmospheric conditions (i.e., wind patterns, mild temperatures) and incidence of disease (81, 87). One research project that used a direct-count assay (use of a nucleic acid stain to count microorganisms via epifluorescence microscopy) to tabulate the number of virus-like particles in U.S. Virgin Island atmospheric samples reported a background concentration of 1.8×10^4 m^{-3} and an African dust event concentration of 2.13×10^5 m^{-3} (78). In summary, little research has been conducted to address the naturally occurring populations of desert soil viral communities, those viruses introduced by humans and other an-

imals, or occurrence and survival issues associated with airborne desert soils.

PATHOGENS

Bacteria

Culture-based dust-borne microbiological studies have established that a diverse bacterial community can move through the atmosphere in clouds of desert dust, but no study has demonstrated the movement of a prokaryote pathogen and linked it to the occurrence of disease. The closest known associations of dust storms and human disease of microbial origin are the outbreaks of meningitis (primarily due to *Neisseria meningitidis* infection) that occur within the "meningitis belt" of North Africa (223). These outbreaks occur frequently in the Sahel region of North Africa between (and within) the months of February and May and affect as many as 200,000 individuals annually (160, 223). The conditions during this period are characterized as dry with frequent dust storms. Outbreaks usually cease with the onset of the wet season (160, 161). Dust storms are believed to promote infection via dust particles causing abrasions of the nasopharyngeal mucosa upon inhalation, allowing *Neisseria meningitidis* cells residing in the mucosa access to underlying tissue and blood, thus initiating infection (161). An additional and complementary hypothesis argues that cells of *Neisseria meningitidis* associated with the inhaled dust particulates are an alternate route of infection (80).

Five viable isolates of *Neisseria meningitidis* recently identified in settled-dust samples from Kuwait demonstrate that dust can serve as a carrier for the pathogen (141). Other pathogens were also identified in this project (141), including *Staphylococcus aureus* (wide range of infections), *Bacillus circulans*, (opportunistic), *Bacillus licheniformis* (opportunistic, peritonitis), *Pantoea agglomerans* (opportunistic, peritonitis), *Ralstonia paucula*, (opportunistic, septicemia, peritonitis, abscess, and tenosynovitis), and *Cryptococcus albidus* (opportunistic, disseminated) (13, 122, 136, 140, 159, 179). Given the current state of affairs in the Middle East, many of these opportunistic dust-borne pathogens may play a significant role in human health with regard to combat-related injuries, treatment, and recovery.

Bacterial species that are known human pathogens have been collected during dust events in Bamako, Mali (117). The species include *Acinetobacter calcoaceticus* (nosocomial respiratory tract infections), *Corynebacterium aquaticum* (urinary tract infections), *Gordonia terrae* (nervous system, skin), a *Kocuria* sp. found in advanced noma lesions in Nigerian children, and *Kocuria rosea* (bacteremia) (10, 28, 55, 117, 147, 181, 226). Additionally, *Acinetobacter calcoaceticus* has been linked to mad cow disease, and another isolate, *Staphylococcus xylosus*, was previously identified as the causative agent of septicemia in a loggerhead turtle in the Canary Islands (117, 229, 232). Of the 95 bacteria identified in this study, Kellogg et al. reported that approximately 10% were potential animal pathogens, 5% were potential plant pathogens, and 25% were opportunistic human pathogens (117). In the African dust corridor over the mid-Atlantic ridge, two of the human pathogens identified in the Mali dust study (83, 117), *Kocuria rosea* and *Gordonia terrae*, were also recovered when elevated concentrations of African dust were present in the atmosphere (83). Furthermore, atmospheric dust-borne bacteria isolated in this mid-Atlantic study that are recognized as pathogens included *Brevibacterium casei* (opportunistic, sepsis) and *Staphylococcus epidermidis* (opportunistic, endocarditis, urinary tract infections) (22, 254). In the atmosphere over the U.S. Virgin Islands, the opportunistic pathogen *Pseudomonas aeruginosa*, which can cause fatal infections in burn patients, was isolated when African dust was present (79). Additionally, identified microorganisms found in a Nigerian noma lesion study were also isolated (GenBank closest neighbor similarities: *Kocuria* sp., 97%; *Microbacterium arborescens*, 98%; *Sphingomonas* sp., 96%) (79). At Erdemli, Turkey, *Kocuria rosea*, *Corynebacterium aquaticum* (opportunistic, urinary tract infections, sepsis), and *Massilia timonae* (which has been isolated from the blood of an immunocompromised patient) were isolated during dust events (82, 133, 162, 226). Other desert dust studies included isolates of *Bacillus*, although no specific species-level pathogenic identifications were made (20, 190).

The bacterial endotoxin LPS can also directly impact human health via inhalation (205). LPS is a cell wall component of gram-negative bacteria and is commonly found in organic dusts (240). Human and animal inhalation trials have shown increases in neutrophils and lymphocytes with a reduction in alveolar macrophage phagocytosis (205). Short-term exposure can result in fever and reduced airflow. Long-term exposure can result in the development of lung diseases such as asthma, bronchitis, and irreversible airflow obstruction (240). Since gram-negative bacteria are dominant in marine waters, aerosolized marine bacteria that adhere to traversing dust particles may enhance dust cloud toxicity and affect human health in coastal environments that are typically impacted by significant quantities of desert dust. African dust reaches coastal communities in Europe, the Middle East, the Caribbean, and the Americas. Asian dust reaches Korea, Taiwan, Okinawa, Japan, regional islands, the Artic, and North America. Approximately half of the bacteria found in African dust studies conducted in the Caribbean were gram-negative bacteria. Given the volume of annual African dust exposure, LPS may contribute to the high incidence of asthma in the region (79, 96). Sea spray generation in near-shore environments may also produce elevated humidity levels in near-surface atmospheric layers, which can both concentrate and "rain out" dust-borne pathogens and toxins, thus increasing exposure and risk.

It is obvious from the few dust-borne microbiology studies that have identified pathogenic bacteria that there is some degree of human health risk associated with exposure to airborne desert dust. While most of the pathogens identified to date are opportunistic in nature, these are but a small number of culture-based studies, and as in most outbreaks of disease it is often the young, old, and immunocompromised who are within the higher levels of risk. These few studies provide a glimpse of risk evidence and highlight the need for non-culture-based assays to advance this field of study.

Fungi

In 1941 several air fields were established in the southern San Joaquin Valley. Coccidioidal infection was recognized to be a hazard, but it was preferred to

the hazards of mountains and fog in alternative locations. During the first year clouds of dust billowed over the fields, and a quarter of the susceptible personnel became infected. C. E. Smith, appointed consultant to the Secretary of War, proposed rigid dust control measures. Roads were paved, air strips were hard-surfaced, and swimming pools were substituted for dusty athletic fields. Lawns were planted by the acre, and military personnel were ordered, at risk of court martial, to avoid unprotected areas as much as possible (64).

The most well-known human pathogen associated with desert dust storms is the fungus *Coccidioides immitis* (64). This fungus has been found only in the Americas. Annual outbreaks following dust storms (the primary means of exposure) or dust clouds generated from natural disasters or anthropogenic activity (e.g., earthquakes and construction, etc.) are well documented (90, 113, 178, 208). An outbreak at a Naval Air Station in California following a large dust storm event resulted in a coccidioidomycosis incidence rate of 36 per 100,000 for personnel classified as white and 254 per 100,000 for those classified as nonwhite, indicating differences in racial susceptibility (250). In Arizona, an increase in annual cases from 33 per 100,000 in 1998 to 43 per 100,000 in 2001 was attributed to climate change (increased wind speed and drought), with peak periods occurring in the winter and the age group at highest risk being those ≥65 years old (33, 178). Of 128 studied cases of coccidioidomycosis that occurred between 1 September and 31 December 1991 in Tulare County, CA, males, Asians and blacks, and those over 20 years old were identified as the highest risk groups (57). In addition to wind-generated dust storms, an outbreak of coccidioidomycosis resulting in 203 cases and three fatalities followed exposure from earthquake-generated dust clouds (208). Between 1991 and 1993, medical expenses associated with outbreaks were estimated at $66 million (113).

While no other fungal outbreaks in human populations have been attributed to dust storm exposure, the cited fungal prevalence studies in desert soils and dust storms have demonstrated diverse communities composed of both nonpathogenic and pathogenic genera and species. In most of these studies, only a fraction of the observed culturable community was identified, or the methods employed for identification, such as morphological or spore identification, limited the ability to identify pathogenic species. As a result, research has produced only an indication of the true community structure in any of the dust source regions. While they have yet to be identified in dust storm studies, fungal pathogens such as *Histoplasma capsulatum*, the causative agent of histoplasmosis, often associated with exposure to dust originating from dried bird or bat feces, are certainly a potential risk factor (31, 164). Table 3 lists the dust storm studies in which fungal CFU or spores have been identified, the genera known to contain pathogenic species, and, where information was available, the pathogenic species. Information available on these genera indicates that most are cosmopolitan in nature. These pathogenic or opportunistic pathogens are known to cause a wide range of human diseases (mild to fatal disseminating infections). Some of the fungi in Table 3 are known to be mild or potent allergens (species of *Acremonium*, *Alternaria*, *Arthrinium*, *Aspergillus*, *Cladosporium*, *Curvularia*, *Emericella*, *Fusarium*, *Nigrospora*, *Paecilomyces*, *Pithomyces*, *Phoma*, *Penicillium*, *Torula*, *Trichophyton*, and *Ulocladium*). Outside of human disease, an outbreak of aspergillosis was documented in a captive locust population (~40% of the population) in Bikaner, India, following a dust storm (239). Sahara/Sahel dust storms have also been identified as long-range transport mechanisms for the pathogen responsible for the Caribbean region-wide outbreak of *Aspergillus* infections (*A. sydowii*) in seafans (213, 245). The long-range atmospheric dispersal of fungal crop pathogens has been well documented. Brown and Hovmøller present a review of those data (24).

Viruses

Transport of infectious human viruses in dust storms has not been investigated. Hammond et al. hypothesized that long-range transport of human influenza virus from Asia to the Americas could occur in the winter months given the prevailing wind patterns over the Pacific and the low dose of virus required for infection (87). With the annual peak of the Asian dust season occurring in March and April, the attachment of infectious viruses to dust particles moving across the Pacific may serve to enhance long-range host-to-host transport, as virus survival studies (water and air based) have shown a relationship between particle association/attachment and enhanced survival (41, 45, 128, 194). Obviously, short-range transmission (person to person) of infectious viruses such as the influenza viruses and rhinoviruses is an evolved means of movement. Short-range atmospheric transmission via dried aerosolized rodent excreta (dust) is the primary route of hantavirus infection, and elevated risk has been documented in the arid American southwest during droughts that follow El Niño events (59). Evidence of longer-range transmission (building to building) of the severe acute respiratory syndrome virus has been documented (262), but what about even longer-range transmission? Is there a range limit with various human viral pathogens that are transmitted through the air? How does the limit vary between viral pathogens, and what is the evidence that long-range transmission occurs?

In livestock populations, dust storms have been identified as a possible source of foot-and-mouth disease virus outbreaks that occurred in Korea and Japan. Some of the outbreaks followed Gobi/Takla Makan dust events (115, 175, 203). Although two studies (115, 175) screened dust samples for the presence of foot-and-mouth disease virus by reverse transcriptase PCR (>400 samples) with no positive results, the authors suggested additional testing before ruling out the transmission route. Griffin et al. hypothesized that foot-and-mouth disease virus outbreaks in Europe could result from long-range transmission in African dust based on the similarity of endemic (Africa) and outbreak serotypes, dust events and outbreak occurrences, and a favorable atmospheric route (over water) (81). Evidence of regional (European) airborne transmission of foot-and-mouth disease virus to downwind locations within the United Kingdom, from France across the English Channel to the United Kingdom, and from Germany over the Baltic Sea to Denmark, has been well documented (51, 69, 71, 72, 157, 217). Using an atmospheric model and inputting optimal climate and topography, Sorensen et al. estimated that 1,000 pigs

TABLE 3. Fungi capable of affecting humans[a]

Organism	Location(s) (reference[s])[b]	Dust source region(s)	Miscellaneous information[c]	Disease(s)[d]
Acremonium	USVI, Turkey (82, 83)	Sahara/Sahel, Middle East	Common in soil, on plants, and indoors	Mycetoma (colonization of tissue/bone), onychomycosis (colonization of nail), mycotic keratitis, a number of different allergen-related disease types in the immunocompromised
Alternaria	Mali, Africa, mid-Atlantic, Barbados, Taiwan, Saudi Arabia, Israel, Turkey (82, 83, 92, 117, 126, 190, 207, 256)	Sahara/Sahel, Gobi/Takla Makan, Middle East	Common in soil, on plants, and indoors	Cutaneous phaeohyphomycosis (colonization of skin), potent allergen (common cause of extrinsic asthma)-related disease, deep tissue infections in the immunocompromised
Alternaria infectoria	Turkey (82)	Sahara	Common environmental isolate	Phaeohyphomycosis
Arthrinium	Barbados (190)	Sahara/Sahel	Common environmental isolate	Allergen-related disease
Aspergillus	Mali, Africa, USVI, Barbados, Taiwan, Saudi Arabia, Israel (79, 83, 92, 117, 126, 207)	Sahara/Sahel, Gobi/Takla Makan, Saudi Arabia	Common in soil, organic detritus, and indoors	Aspergillosis (pulmonary [allergic and colonizing], disseminated, central nervous system, cutaneous, nasal-orbital, and iatrogenic), a number of different allergen-related disease types in the immunocompromised
Aspergillus clavatus	Barbados (190)	Sahara/Sahel	Common environmental isolate	Invasive aspergillosis
Aspergillus flavus	Barbados, Israel (190, 207)	Sahara/Sahel	Common environmental isolate	Invasive aspergillosis
Aspergillus fumigatus	Barbados, Israel (190, 207)	Sahara/Sahel	Common environmental isolate	Invasive aspergillosis
Aspergillus niger	Mali, Africa, Barbados, Israel (117, 190, 207)	Sahara/Sahel	Common environmental isolate	Invasive aspergillosis
Aspergillus terreus	Barbados (190)	Sahara/Sahel	Common environmental isolate	Invasive aspergillosis
Aspergillus ustus	Israel (207)	Saharan	Common environmental isolate	Rare, invasive aspergillosis
Aspergillus versicolor	Mali, Africa, Israel (117, 207)	Sahara/Sahel	Common environmental isolate	Invasive aspergillosis
Aureobasidium	Mid-Atlantic, USVI (79, 83)	Sahara/Sahel	Distributed in temperate areas; common on plant tissue and indoors	Cutaneous phaeohyphomycosis, invasive disease in the immunocompromised
Bipolaris	USVI (79)	Sahara/Sahel	Common plant and indoor isolate	Pansinusitis, meningoencephalitis, chronic pulmonary disease
Cladosporium	Mali, Africa, mid-Atlantic, USVI, Barbados, Taiwan, Saudi Arabia, Turkey (78, 79, 82, 83, 92, 117, 126, 256)	Sahara/Sahel, Gobi/Takla Makan, Middle East	Most commonly isolated fungus in outdoor studies	Cutaneous phaeohyphomycosis, chromoblastomycosis (subcutaneous skin infections), mycotic keratitis, potent allergen-related disease
Cladosporium cladosporioides	Mali, Africa, USVI, Israel (78, 117, 207)	Sahara/Sahel	Common environmental isolate	Cutaneous phaeohyphomycosis, chromoblastomycosis
Cladosporium sphaerospermum	Israel (207)	Sahara	Common environmental isolate	Cutaneous phaeohyphomycosis, chromoblastomycosis
Chrysosporium	USVI (79)	Sahara/Sahel	Common environmental isolate	Opportunistic, infecting brain, nasal and skin tissue
Curvularia	Taiwan, Barbados (92)	Gobi/Takla Makan	Common environmental isolate	Allergen-related disease, opportunistic, pneumonia, disseminated
Emericella nidulans	Mid-Atlantic (83)	Sahara/Sahel	Common in tropical and subtropical environments	Allergic alveolitis
Fusarium	Taiwan, Turkey (82, 92, 256)	Gobi/Takla Makan, Middle East	Common soil and indoor isolate	Invasive cutaneous (erythematous lesions and nodules), systemic granulomatous disease, allergen-related disease
Microsporum	USVI, Turkey (79, 82)	Sahara/Sahel, Middle East	Some species are geographically restricted	Dermatophytosis (i.e., ringworm)

Continued on facomg page

TABLE 3—*Continued*

Organism	Location(s) (reference[s])[b]	Dust source region(s)	Miscellaneous information[c]	Disease(s)[d]
Mortierella	Saudi Arabia (126)	Saudi Arabia	Common environmental isolate	Rare, cutaneous
Mucor	Saudi Arabia (126)	Saudi Arabia	Common environmental isolate	Rare, opportunistic, pulmonary, disseminating, cutaneous
Neotestudina rosatii	Mid-Atlantic (83)	Sahara/Sahel	Common environmental isolate; Africa, Australia, India	Mycetoma
Nigrospora	USVI, Taiwan (79, 92, 256)	Sahara/Sahel, Gobi/Takla Makan	Common in soil, organic detritus, and indoors	Allergen-related disease
Paecilomyces	USVI (79)	Sahara/Sahel	Common in soil, organic detritus, and indoors	Mycotic keratitis paecilomycosis, pneumonia, allergen-related disease
Pithomyces	Taiwan (92, 256)	Gobi/Takla Makan	Typically found on dead plant detritus	Allergen-related disease
Phoma	Mid-Atlantic (83)	Sahara/Sahel	Common plant pathogens	Allergen-related disease
Pythium	Saudi Arabia (126)	Saudi Arabia	Common plant pathogen	Pythiosis
Penicillium	Mid-Atlantic, USVI, Barbados, Taiwan, Saudi Arabia, Turkey (79, 82, 83, 92, 126, 190, 256)	Sahara/Sahel, Gobi/Takla Makan, Middle East	Very common in temperate regions, common in soil and indoors	Bronchopulmonary penicilliosis, potent allergen-related disease (hypersensitivity and allergic alveolitis)
Penicillium brevicompactum	Turkey (82)	Sahara	Common environmental isolate	Rare, necrotic lung ball
Penicillium chrysogenum	Israel (207)	Sahara	Common environmental isolate	Rare, endocarditis, necrotizing pneumonia
Penicillium spinulosum	Israel (207)	Sahara	Common environmental isolate	Allergen-related disease
Phoma cava	Israel (207)	Sahara	Common environmental isolate	Subcutaneous phaeohyphomycosis
Rhizomucor	USVI (79)	Sahara/Sahel	Common environmental isolate	Rare opportunistic, pulmonary, disseminating, cutaneous zygomycosis
Stachybotrys	Mid-Atlantic (83)	Sahara/Sahel	Commonly found in soil and decaying plants	Rare, toxin producer, pulmonary
Stemphylium	Taiwan (256)	Gobi/Takla Makan	Common plant pathogens	Phaeohyphomycosis
Torula	Taiwan (92, 256)	Gobi/Takla Makan	Common environmental isolate	Allergen-related disease
Trichophyton	Mid-Atlantic, USVI, Turkey (79, 82, 83)	Sahara/Sahel, Middle East	Commonly found in soils and indoors	Dermatophytosis, allergen-related disease
Ulocladium	Taiwan, Saudi Arabia (92, 126)	Gobi/Takla Makan, Saudi Arabia	Found in soil, on plants, and in high-moisture environments	Phaeohyphomycosis
Ulocladium botrytis	Mid-Atlantic (83)	Sahara/Sahel	Found in soil, on plants, and in high-moisture environments	Allergic alveolitis

[a] The fungi were cultured and identified—to the species level, where the information was available—in atmospheric desert dust samples. Where no species is given, disease information is relevant to pathogenic strains.
[b] USVI, U.S. Virgin Islands.
[c] See references 199 and 221.
[d] See references 199 and 221 and http://www.doctorfungus.org.

excreting foot-and-mouth disease virus could infect cattle located 300 km downwind (217). Modeling was also used to demonstrate the 1988 atmospheric spread of pseudorabies virus between swine herds over an area of 150 km^2 in Decatur County, IN (40, 75).

Unknown Agents

> Cattle went blind and suffocated. When farmers cut them open, they found stomachs stuffed with fine sand. Horses ran madly against the storms. Children coughed and gagged, dying of something the doctors called "dust pneumonia." In desperation, some families gave away their children. The instinctive act of hugging a loved one or shaking someone's hand could knock two people down, for the static electricity from the dusters was so strong. Ike Osteen's life spans the flu epidemic of 1918, the worst depression in American history, and a world war that ripped apart the globe. Nothing compares to the black dusters of the 1930s, he says, a time when the simplest thing in life—taking a breath—was a threat (58).

Incidence of pneumonia of unknown etiology in populations exposed to airborne desert dust storms has been reported throughout the course of time (18, 23, 121, 174, 248). In the American Dust Bowl era of the 1930s, the numbers of cases of pneumonia were 50 to 100% higher during dust periods than during previous low-dust years (23). In dust storm-impacted regions around the Aral Sea, pneumonia rates are the highest

in the former USSR, and 50% of all childhood illnesses are respiratory (105, 237). Pneumonia from dust storm exposure has also been reported in the Middle East, especially those cases pertaining to deployed military personnel (14, 34, 121, 214). Of 15,459 surveyed military personnel who were deployed in Afghanistan or Iraq during 2003 and 2004, 69.1% reported some form of respiratory illness (204). Pneumonia acquired from exposure to inorganic and organic material in dust storms has been termed Al Eskan disease, Persian Gulf syndrome, Persian Gulf War syndrome, Gulf War syndrome, and desert dust pneumonitis (50, 109, 120, 121). In addition to pneumonia, adverse health conditions reported by military personnel who were deployed in the area include fatigue, fever, respiratory stress, arthromyoneuropathy, and neurological impairment, and epidemiological studies demonstrated higher prevalence in exposed/deployed groups than in controls (14, 50, 65, 86, 108, 116). In contrast, a number of studies designed to identify the incidence of disease in deployed versus nondeployed groups noted no identifiable differences between the groups (101, 106, 118, 134, 201). In China and the Himalayas, studies have shown that indigenous populations in dust areas have higher incidences of silicosis than do populations residing in nondust or low-dust areas (173, 202, 259). Cell culture studies have demonstrated that dust storm constituents can inhibit defense functions of alveolar macrophages and increase reactive oxygen species, causing DNA base damage (61, 186). Mouse- and rat-based inhalation studies have shown that desert dust causes increases in the levels of neutrophils, lymphocytes, eosinophils, interleukin-2 and -6, and tumor necrosis factor alpha and that responses are dose dependent (102, 137).

DETECTION

One of the most striking characteristics of aerobiological studies, and more specifically of the few on dust storm microbiology cited in this article, is the different techniques used to collect and analyze air samples, as previously reviewed (27, 255). The only instances of dust storm microbiology research that employed "like protocols" are those papers published by the same research groups. Due to the drawbacks of various collection and evaluation assays, comparisons of results among studies that utilized different techniques can answer only the most basic of questions: that, yes, a diverse community of culturable bacteria and fungi is capable of surviving long-range atmospheric transport in clouds of desert dust. The limited number of dust-borne projects, in addition to the lack of a recognized or standardized protocol, has and will impede progression in this field of study. Moreover, there is a clear need for culture-independent analysis of dust-borne microbial communities (16S and 18S rRNA gene sequencing), without which we will never be able to see the "big picture" (98). For a comprehensive review of aeromicrobiology methods, see Buttner et al. (27).

Collection

Protocols that have been used to collect microorganisms in the atmosphere include impaction, impingement, centrifugation, filtration, and gravity deposition (27, 54, 219). Gravity deposition is one of the simplest methods of collecting airborne microorganisms and involves exposing nutrient agar to an open-air environment for some period of time. The benefits of this protocol are that it is inexpensive and cell death from impaction is insignificant, and yet it has been shown to be an unacceptable method in comparison to volumetric assays (26, 76). Impaction of microorganisms onto surfaces such as tape, nutrient agar, or hard surfaces coated with an adhesive fluid such as oil is commonly utilized for the collection of airborne microorganisms. Exposure of a petri dish containing nutrient agar or a small metal surface coated with glycerol to an air stream has been used to collect airborne microorganisms from aircraft for morphological identification of airborne biological constituents or culture-based studies (77, 152, 154, 155). While a reliable estimate can be made of the volume of air sampled based on the collector surface area, air speed, and time exposed, particle capture on the surfaces can be negatively influenced by wind speed, impactor shape, and presentation angle (collector surface angle to wind/flight direction) (76). Impaction of spores or pollen onto adhesive tape via an air pump-driven system such as a Burkard spore trap (Burkard Manufacturing Co. Ltd., Rickmansworth, United Kingdom) is an efficient means of obtaining total counts of fungal spores (and identifications based on spore morphology), as demonstrated by Ho et al. and Wu et al. in their Taiwan-based Asian dust studies (92, 256). The primary limitations of spore traps are restricted use in the analysis of other microbial types (bacteria and viruses) and the fact that morphology-based identifications are limited to genus level classification.

Another method of impaction is the use of an air pump to move air over the surface of a petri dish (cassettes and strips are also used) containing nutrient agar. Airflow over nutrient agar is controlled by slits or holes that are arranged to distribute the airflow evenly over the agar surface and in some cases to control for particle size ranges. Numerous companies manufacture air pump devices, including the portable handheld Millipore M Air T Air Tester (Millipore Corporation, Bedford, MA) and the popular Andersen six-stage sampler (Andersen 6-STG; Graseby Andersen, Smyrna, GA) (12; K. R. Lentine, N. Le, J. Lemonnier, A. Entzmann, and M. Pickett, presented at the 99th General Meeting of the American Society for Microbiology, Chicago, IL, 30 May to 3 June 1999). The benefits of these types of samplers are ease of use, portability, cost, assessment of culturable populations of bacteria and fungi per volume of air, and, as in the case of the Andersen 6-STG-type sampler, the ability to determine the numbers of microorganisms associated with various size ranges of airborne particulates. Drawbacks to the use of these impactors are loss of viability due to impact stress, loss of recovery efficiency due to microorganisms not adhering to agar surfaces, low sample volumes due to low flow rates, and low recovery of ultrafine biological matter in the size range of viruses (220). Centrifugation has been used to collect microorganisms on container walls, wet or dry slides, or nutrient agar (petri dishes and strips, etc.) (249, 251, 257). The benefits of centrifugal concentration are the use of high flow rates (>100 liters min^{-1}) and efficient capture (251). The drawback of this method is the loss of viability due to impaction stress (257).

Impingement of microorganisms into a liquid matrix (via bubbling) is another method of capture used in aeromicrobiology (7, 27, 227). A widely used liquid impinger is the AGI-30

(Ace Glass Inc., Vineland, NJ), which utilizes a low flow rate to bubble air through a liquid matrix. Research has shown that the AGI-30 is a low-cost and efficient method of collecting aerosolized microorganisms for culture- and non-culture-based analyses (227). However, this impinger is constructed of glass and can be easily broken in the rigors of field studies. High-flow-rate liquid impinger units have been developed to detect low concentrations of microorganisms in the atmosphere and have also been utilized for culture- and non-culture-based analyses for the presence of bacteria, fungi, and viruses (17). The benefit of using liquid impingers for aeromicrobiology studies is that the liquid matrix can be split for various analyses to include media cultures, direct counts, molecular assays, and cell cultures. The drawbacks of liquid impingement include the low capture rate of some low-flow-rate impingers (the use of large-bore air lines and, thus, large bubble production in the liquid matrix), high cost (high-flow-rate impingers), loss of collection fluid to evaporation and violent bubbling (some of the high-flow-rate impingers limit this loss), low capture rate of virus-sized particles, and loss of viability (i.e., viral inactivation due to bubbling) (6).

Membrane filtration in which air is pumped through a porous membrane is also utilized in aeromicrobiology and has been used by a number of researchers in desert dust microbiology (27, 78, 79, 83, 117, 190). This method can be employed for both culture- and non-culture-based studies, is inexpensive, can be portable, and is highly efficient at trapping microorganisms larger than the pore size on the filter surface (111, 145). Filters commonly utilized for collection include cellulose-based, nylon, and glass fibers with pore sizes down to 0.02 μm (for viral analysis) (78). The drawbacks of filtration include desiccation of the microorganisms on the filter surface due to filtration rate and time (higher flow rates and longer filtration times), the preferential concentration of spore-forming microbes over other community members as non-spore formers are desiccated during rapid or long filtration times (culture-based studies), filter size (37 mm versus 47 mm; i.e., larger diameters limit stacking of cells in a high particle load environment), and filter type (a thicker filter can wick nutrients to cells, thereby limiting close-contact nutrient shock of stressed cells) (27, 83, 111, 150, 231).

In regard to these currently used methods of recovery, use of a high-volume liquid impinger for aeromicrobiology studies in general is the most versatile and arguably one of the most efficient capture methods available. While the capture efficiency of virus-range particles is a concern with today's machines, virus-based analyses are still possible. Furthermore, advances in technology should enhance the capture of all microbial size fractions and at the same time allow what no other isolation assay currently does: rapid large-volume sampling for the full suite of microbial types and the ability to split a single sample for multiple analyses.

Identification

Microorganisms collected in samples (soil, aquatic, air, and clinical, etc.) are characterized by culture-based assays (for CFU counts and identification via substrate utilization) and/or non-culture-based assays (morphology-based identification; cell, spore, physiological, and nucleic acid stains; identification via nucleic acid amplification and/or hybridization; immunological identification; direct counts; and fatty-acid analysis). Usually, in any environment, less than 1.0% of the bacterial community is culturable under the most favorable (low-stress) conditions, and thus any data obtained from this approach are limited in regard to community composition (11). For culture-based studies of airborne microorganisms, particularly in the case of long-range transport studies in which a majority of the community may be stressed by desiccation, temperature, and UV exposure, selection of a nutrient source and incubation temperature that will maximize recovery is critical. It is known that both nutrient and temperature shock can negatively impact the ability to culture stressed bacteria (197). Numerous studies comparing low-nutrient broths or agars (diluted high-nutrient recipes or low-nutrient recipes such as Reasoner's 2 agar [R2A]) have shown superior recovery rates of culturable bacteria versus rates with high-nutrient agars in different settings (water, air, soil, and serum, etc.) (15, 95, 112, 149, 195, 238). The incubation temperature can significantly impact culturability (in general, a temperature close to the environmental temperature from which the sample was taken gives better recoveries), and most dust-borne culture-based studies have used moderate temperatures for growth (~23.0°C [room temperature]) (43, 79, 83, 117, 170, 185, 190). Several nutrient-based identification assays, such as the Analytab System (Analytab Products, Syosset, NY) and BioLog plates (Hayward, CA), are utilized in environmental studies. Although these are low-cost assays, they are subject to variation (i.e., reproducibility issues due to variation in cell densities and physiological state, etc.) and false-positive results (previously unclassified organisms producing similar or like carbon utilization patterns) (25, 119, 135). Recent advances in culture technology, such as the employment of single-cell encapsulation into microdroplets containing naturally occurring nutrients, have demonstrated improved recovery rates and hold promise for future studies (264).

Microscopy is one of the oldest tools used for the study of bacteria and fungi. Identifications or descriptions are based on staining characteristics, cellular morphology, spore shape, the presence or absence of spores, and pigmentation. At the microscopic level, many organisms cannot be identified, due to similarities among species and genera and to significant differences in the education and experience of the investigator. Species- and strain-specific identifications are possible with the use of immunological (antigen-specific antibodies tagged with a reporter) and genetic (i.e., fluorescence in situ hybridization [FISH]) tools, as well as direct-count assays and physiological studies using nucleic acid or cellular stains, respectively (37, 48, 172, 183, 228, 241). Whereas stains that utilize direct-count assays are invaluable in assessing total cell counts in a sample, certain cells are known to resist staining, and similar-sized particles that are not cells may take up the stain, resulting in false-positive counts (27). Another limitation is that more than 10^4 cells per sample are required for useful data (27). The result is that microscopic methods can be prone to error. Such methods also require expertise and can be time-consuming (27).

Although sequence-based identification assays, such as those using oligonucleotides (dot blot assays and FISH, etc.), have served microbial ecologists well, the invention of nucleic acid

amplification protocols such as PCR and nucleic acid sequence-based amplification has enabled researchers to assess community composition at the strain level efficiently and to detect organisms in the community that occur in very low numbers (42, 167, 182). Nucleic acid amplification methods target regions of conserved genes, such as those found in the ribosomal genes, for use in identification (42, 167). Once the target gene is amplified, the community amplicon can be evaluated with ecology-based gene chips or through the classical approach of clone library production and analysis (35, 253). Several other widely used types of postamplification analysis include denaturing gradient gel electrophoresis and temperature gradient gel electrophoresis (168). These assays produce a microbial community fingerprint that can be analyzed with specific group probes for individual band identification, or individual bands can be excised and sequenced directly. The primary benefits of PCR-based assays are ease of use as DNA and RNA extraction kits, PCR amplification kits, cloning kits, the availability of commercial sequencing facilities, and information on the community (culturable and nonculturable) are obtained. The primary drawbacks are the cost of cloning kits, the required expertise in sequence interpretation, debate among mycologists on the appropriateness of relying on DNA sequences alone to identify fungi, and the lack of a universal gene for virus ecology (211).

Phospholipid ester-linked fatty acid and intact phospholipid profiling can also be utilized to identify bacteria and fungi in both culture- and non-culture-based studies via unique lipid structures (63, 132, 246). The benefits of these assays are that they address viable biomass due to rapid phospholipid turnover (63, 246). The drawbacks are costs of analysis, overlapping profiles, biomass to cell count conversion, and compositional shift from variance in growth conditions (63).

With the rapid progression of technology, new and emerging tools, such as optical tweezers, phylogenic gene chips, chip use in cross-hybridization studies, cellular circuits, mass spectrometry, and the miniaturization of existing equipment, should greatly enhance our understanding of dust-borne microbial ecology through availability, affordability, adaptation, and use (38, 60, 123, 151, 171, 230, 253).

CONCLUSIONS AND PERSPECTIVES

Two common misconceptions are that desert soils are too inhospitable to host a diverse microbial community and that those microorganisms that are present cannot withstand the physical stresses (UV, desiccation, temperature) of atmospheric transport. Research in the twentieth and twenty-first centuries has shown that microorganisms mobilized into the atmosphere along with desert soils are capable of surviving long-range transport on a global scale. As with the better-known pathogens that use aerosolization to move from host to host (*Bacillus anthracis*, *Yersinia pestis*, *Mycobacterium tuberculosis*, *Legionella pneumophila*, *Histoplasma capsulatum*, influenza viruses, and rhinoviruses, etc.), the microbiological research conducted to date has identified a wide range of dust-borne pathogenic microorganisms that move great distances through the atmosphere. In light of the few dust-oriented studies outlined in Table 2, which are based only on culture or spore-counting techniques, it is clear that we have only begun to grasp the true numbers of microorganisms capable of using the atmosphere as an infectious route or as a means of extending the limit of their dispersion.

The prime question, of course, is related to risk: do microorganisms in dust clouds pose a risk to human health? The evidence of outbreaks of coccidiomycosis following dust storm exposure in the Americas demonstrates risk. Outside of this example, the risk from other pathogenic microorganisms is unknown, due to the limited number of studies and study design (all to date have been culture based, and none have been risk oriented). While some of the dust storm microbiology studies cited in this review have identified pathogenic microorganisms, information relative to concentrations over a realistic period of exposure does not exist, nor do we know the full extent of fate and survival issues as they relate to geographical variance and seasonal influences. The adaptation of existing and emerging molecular techniques will give us a clearer understanding in future studies. We need non-culture-based studies to advance this field in regard to issues in microbial ecology, biogeography, pathogen prevalence (fungal, bacterial, and viral), epidemiology, bacteria as carriers of potentially harmful genetic elements (i.e., phage related), microbial fate and survival, and risk. Integrated and global-scale collaborations need to be advocated and supported to allow multiple purchases of appropriate equipment (i.e., high-volume liquid impingers) for "true" matched studies in source and downwind environments. We also do not know what roles the synergistic influences of the many different constituents of dust play in human health. How does exposure to dust storms differ between source regions? When individuals who have never been exposed to desert environments (or dust storms) visit them (or are deployed in them), how is their health impacted in both the short and long terms? With the advent of the industrial age and the resulting widespread use and release of anthropogenic chemicals and emissions, are modern dust clouds more of a health threat than those that blew around the planet before the influence of humanity? How will climate change influence dust emissions and their associated microbial communities? The questions are many.

As if this point has not been made enough, I close this review with a quotation from a paper published by Fred C. Meier and Charles A. Lindbergh in 1935:

> While it is generally known that bacteria, spores of higher fungi and pollen grains are present among dust particles in the atmosphere near the earth's surface, much detailed information of practical value remains to be revealed by further research (154).

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