The Global Dispersion of Pathogenic Microorganisms by Dust Storms and Its Relevance to Agriculture

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Abstract

Dust storms move an estimated 500–5000 Tg of soil through Earth's atmosphere every year. Dust-storm transport of topsoils may have positive effects such as fertilization of aquatic and terrestrial ecosystems and the evolution of soils in proximal and distal environments. Negative effects may include the stripping of nutrient-rich topsoils from source regions, sandblasting of plant life in downwind environments, the fertilization of harmful algal blooms, and the transport of toxins (e.g., metals, pesticides, herbicides, etc.) and pathogenic microorganisms. With respect to the long-range dispersion of microorganisms and more specifically pathogens, research is just beginning to demonstrate the quantity and diversity of organisms that can survive this type of transport. Most studies to date have utilized different assays to identify microorganisms and microbial communities using predominately culture-based, and more recently nonculture-based, methodologies. There is a clear need for international-scale research efforts that apply standardized methods to advance this field of science. Here we present a review of dust-borne microorganisms with a focus on their relevance to agronomy.

1. INTRODUCTION

1.1 Origins and Causes of Dust Storms

Dust storms are a climatic phenomenon, originating in arid and desert regions of the planet, and are the main source of atmospheric dust on Earth (Middleton and Goudie, 2001). Mainly due to aridity and little plant coverage in those regions, winds over $8\,m\,s^{-1}$ are able to lift particles into the atmosphere through two different processes: saltation and suspension (Kim and Chung, 2010). Through saltation, aerosolized particles come back into contact with the ground at an impact speed capable of mobilizing particulates in downwind environments. Suspension is the injection into the atmosphere of particulates that may be transported significant distances through Earth's atmosphere due to particle size and wind speeds. Aerosolized particles may reach considerable altitudes (tropopause and lower stratosphere) (Kellogg and Griffin, 2006; Smith et al., 2010) and may be transported long distances before redeposition (Goudie, 2009; Middleton and Goudie, 2001).

Estimates of dust emitted to the atmosphere from these regions have a wide range (between 500 and 5000 Tg year^{-1}), depending on the study and the aerosol–modeling system used (Griffin, 2007; Huneeus et al., 2011; Perkins, 2001; Zender et al., 2004). Aerosol–emission data indicate that the main regions on the planet contributing to the global dust load are, as shown in Figure 1.1: North Africa (Sahara—Sahel); South Africa (west coast of South Africa and Namibia); the Arabian Peninsula; Central Asia ((Iran and desert areas of Turkmenistan, Mongolia, and North China (Gobi desert),
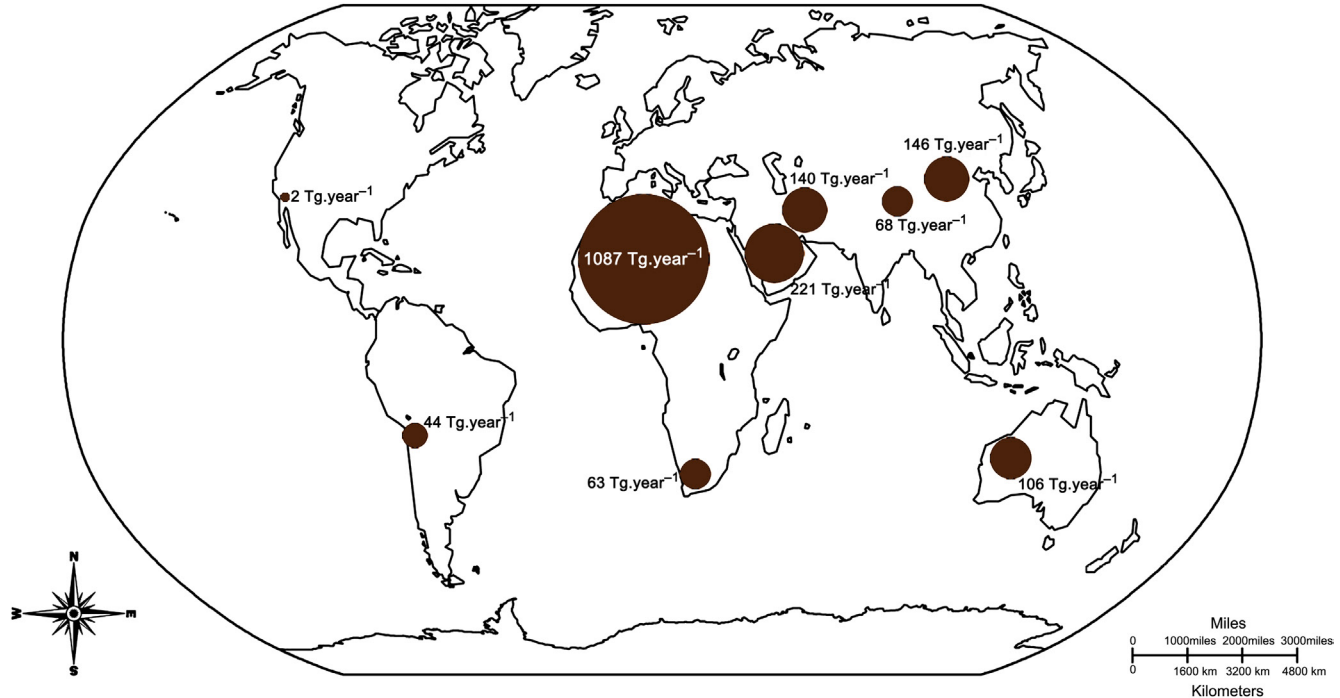
Figure 1.1 Global dust-load regions. *Annual averages based on data from Tanaka and Chiba, 2006.*

West China (Takla—Makan desert)); North America (Great American desert); South America (Atacama desert in Chile); and deserts of Australia (De Longueville et al., 2010). The main source region is the Sahara—Sahel area, responsible for more than 50% of the annual atmospheric dust load, which has been estimated to range between 204 and 2888 Tg year^{-1}, followed by the Asian deserts at 27–873 Tg year^{-1} (Huneeus et al., 2011).

African dust storms occur throughout the year but have seasonal route patterns. During summers in the Northern Hemisphere, dust is transported over the Atlantic Ocean and may reach the northern Caribbean and southern United States, whereas during winters, dust is more likely to impact environments in the southern Caribbean and South America (Prospero and Lamb, 2003; Shinn et al., 2003). It has been estimated that deposition in the Amazon basin is ~40–50 Tg year^{-1} (Kaufman et al., 2005; Koren et al., 2006). In the spring, African dust usually impacts the eastern Mediterranean and Middle Eastern countries and, on occasion, has been observed to impact North American air quality after passing over Asia and the North Pacific (Griffin et al., 2007; Israelevich et al., 2003; Kubilay, 2003; McKendry et al., 2007). African dust also frequently reaches southern Europe and the Mediterranean basin, and some events may reach more northern areas such as Scandinavia (Franzen et al., 1994; Moulin et al., 1997; Varga et al., 2013). On the other hand, Asian dust storms typically occur over a relatively short period from February to May. These dust storms usually impact air quality in proximal regions, such as China, Japan, Korea, or Taiwan. But large-event Asian dust storms may impact air quality in the Arctic and North America, over the Atlantic Ocean, and in Europe (Grousset et al., 2003; Han et al., 2008; Husar et al., 2001; Jaffe et al., 1999, 1997). Deposition of Asian dust in North America has been estimated at ~56 Tg year^{-1} (Yu et al., 2012b). Chemical-deposition fingerprints, obtained by isotope analyses of soils and snow, have confirmed long-range trans-Pacific transport from Asia to the Americas (detectable to date as far inland as Minnesota) and Europe (across America with fallout onto Alpine snowpacks) (Grousset et al., 2003; Husar et al., 2001).

Dust emissions vary every year due to many different factors, some of them a result of anthropogenic activity such as deforestation and overgrazing (Goudie, 2014; Griffin et al., 2012). There are two global atmospheric systems that largely influence the amounts of circulating dust, especially emanating from North Africa: the North Atlantic Oscillation (NAO) and El Niño–Southern Oscillation (ENSO). The predominantly positive phase of NAO since the late 1960s has coincided with persistent drought in North

Africa and with the increase in the quantity of dust emanating from the Sahara—Sahel (Griffin and Kellogg, 2004; Prospero and Lamb, 2003). An overall increase in transport typically follows ENSO events. Asian dust emissions are influenced by the Pacific Decadal Oscillation (PDO) and ENSO events. An increase in transport across the Pacific has been associated with negative-phase PDO years (Gao et al., 2003; Gong et al., 2006; Hara et al., 2006). El Niño and La Niña events influence the typical routes of Asian dust emissions with trans-Pacific transport occurring at ~45° during El Niño years (greater dust loads) and ~40° during La Niña years (lighter dust loads) (Gao et al., 2003; Hara et al., 2006). An increase in Asian dust activity over the last few decades has been attributed to climate change and environmentally harmful agricultural activity along the perimeters of Asian deserts (similar to what was observed during the American Dust Bowl years during the early-mid-twentieth century) (Griffin et al., 2012; Zhang et al., 2003).

1.2 Effects and Impacts on the Environment

1.2.1 Effects on Climate

Dust is considered the only atmospheric aerosol with the capacity to modify atmospheric temperatures and CO_2 levels (Foster, 2001). Consequences of these changes on climatic conditions are numerous and may have both positive and negative effects on the planet. Dust storms influence air temperature through absorption and dispersion processes of solar radiation. They may affect cloud formation, change rainfall patterns (Díaz et al., 2006; Toon, 2003), and modify hurricane formation and peak intensity in the North Atlantic Ocean (Evan et al., 2006). Dust-storm particulates may also serve as ice nuclei and may counteract acid rain, as has been observed in Japan with Asian dust (Stefanski and Sivakumar, 2009). High temperatures that regularly occur with dust storms may enhance desertification and desiccation processes along source-border regions and proximal downwind ecosystems (Han et al., 2008). Dust deposition and the resulting adsorption of solar radiation by dark particulates may increase surface temperatures and accelerate the loss of snowpack and ice (Bar-Or et al., 2008; Krinner et al., 2006).

1.2.2 Influence on Ecosystems

In marine ecosystems, dust storms play an important role in primary productivity (Ridgwell, 2003), and research has identified dust storms as a major source of iron for various areas of our oceans (Jickells and Spokes, 2001). Elements that are present in dust such as iron or phosphorus are crucial for phytoplankton development, but deposition can also cause harmful algae

blooms (Griffin et al., 2003; Lenes et al., 1998; Ramos et al., 2005; Schulz et al., 2012; Walsh and Steidinger, 2001). Dust deposition may also introduce pathogens into sensitive marine ecosystems, such as coral reefs (Shinn et al., 2000). Nutrient influx from dust storms is also important in sustaining forests. Stoorvogel et al. (1997) pointed out that African dust supports ~50% of the tropical forests in Ghana. Recently, mineral influxes from African dust storms in the Everglades of Florida (USA) have been shown to influence vegetation and primary production (Glaser et al., 2013; Mole, 2013). Dust deposition has also been identified as sustaining Amazonian and Hawaiian rainforests. Soils in those ecosystems are shallow, low in nutrients, and contain few soluble minerals. Heavy-precipitation rates deplete nutrients in surface soils, and without the external influx from atmospheric deposition of dust, sustainability would be compromised (Husar et al., 2001; Koren et al., 2006; Swap et al., 1992).

1.2.3 Effects on Soils

Dust deposition has been shown to play an important role in soil formation and alteration (Kohfeld and Harrison, 2001). African dust has been shown to contribute to the evolution of soils in nearby (Portugal, Ghana, and the Canary Islands) and distal regions (the Caribbean and southeastern United States) (Herrmann et al., 1996; Mann, 1986; Menéndez et al., 2007; Muhs et al., 1990; Tiessen et al., 1991). Other deserts of the world are known to contribute significantly to soil development in downwind environments, since allochthonous dusts occur in the southwestern United States and Australia (Chadwick et al., 1999; Hesse and McTainsh, 2003; Reheis et al., 2009). Dust deposition may enrich soils with a high variety of nutrients and may modify the availability of existing concentrations (Reynolds et al., 2001).

1.2.4 Effects on Human Health

In reference to human health, exposure to contaminants, allergens, and pathogens that may be carried by dust-laden air masses may be the cause of diseases and/or epidemics, as well as an aggravation of preexisting conditions, especially those that are respiratory and cardiac in nature (Griffin, 2007; Karanasiou et al., 2012; Kellogg and Griffin, 2006; Sultan et al., 2005; Yu et al., 2012a). This field of research has been recently reviewed (Goudie, 2014; Griffin, 2007).

1.3 Airborne Microorganisms Transported by Dust Storms

Bacterial concentrations in soils range from $\approx 10^3$ to 10^9 microorganisms per gram (Gonzalez-Martin et al., 2013; Griffin, 2007; Kellogg and Griffin, 2006).

Microbial–ecology studies have shown that the virus (bacteriophages) concentration in environmental samples is usually one to two logs greater than bacteria in water, whereas in desert soils they are typically equal to one to two logs less (Gonzalez-Martin et al., 2013). Many of these microorganisms can be aerosolized; most of them are probably transported only small distances due to their attachment to large soil-particulate matter, and many others may die or lose viability during transport due to stress (e.g., desiccation and UV stress). Some, however, are able to resist adverse conditions experienced during transport and reach new niches many miles away (Burrows et al., 2009; Griffin, 2007).

Ultraviolet exposure, dehydration, and absence or low availability of nutrients are factors that can hinder microbial survival during long-range atmospheric transport (Griffin et al., 2011). However, there are other factors that favor survival. A study conducted by the National Aeronautics and Space Administration (Herman et al., 1999) demonstrated that inside dust storms, UV exposure may be attenuated up to 50% due to the high content of suspended particulate matter. Additionally, most fungi and some bacteria are able to form spores or to stay in a latent stage until adverse conditions in the environment change and become beneficial to their development. Some bacteria are pigmented, which favors resistance to UV light and thus survival during atmospheric transport. Gorbushina et al., in 2007, published one of the most surprising studies in this area. They analyzed Saharan dust samples collected by Charles Darwin and his colleagues in the Atlantic in the 1830s. Those samples were originally sent to his colleague Professor Christian Ehrenberg (Berlin University) to be analyzed, and they are currently housed in the Natural History Museum of Berlin. The authors confirmed by geochemical analysis that the samples came from the Sahara, and they were able to culture viable bacteria and fungi from subsamples at concentrations up to 10^4–10^5 colony-forming units (CFUs) g^{-1} (Gorbushina et al., 2007).

Microorganisms may also form small aggregates that protect the more central or embedded isolates from UV damage or desiccation. Bacteriophages have a unique mechanism to avoid being exposed to adverse conditions. They can travel inside bacteria they infect, either with their genome integrated into the bacteria's genome or independent of the host's genome. This mode of transport can also have an adverse effect on plant and animal health. Although these viruses only infect bacteria, they are responsible for the exchange of genetic material among bacteria through a process known as transduction. Exchange of genes that impart resistance to antibiotics or

that convert a nonpathogen to a pathogen (virulence genes) may present risk to agroeconomic and human health in downwind ecosystems (Kimura et al., 2008).

Knowledge about Saharan air-mass-transport routes and the potential for dispersal of microorganisms has driven multiple studies about the relationship between dust-storm events and pathogen dissemination. Studies conducted in the Virgin Islands and Mali (Griffin et al., 2001a; Kellogg et al., 2004) that analyzed microbial composition in air samples taken during dust storm and normal atmospheric conditions demonstrated that the presence of plant pathogens and opportunistic human pathogens in dust-associated samples ranged between 5% and 27% of the total culturable population. One of the clearest cases of the influence of dust storms on human health is the epidemic of meningitis that annually affects the area known as the "Sahel Meningitis Belt." This disease affects more than 200,000 people, mainly children, between February and May of every year (Sultan et al., 2005). In the last 15 years there have been ~800,000 cases, ~10% of which have been fatal (World Health Organization, 2012); in 2010, out of approximately 22,000 cases, there were 2,400 fatalities. During the winter, the increase of Harmattan winds creates conditions that favor outbreaks and cases of meningitis, because low humidity and the inhalation of airborne dust particles can compromise the integrity of the airway mucosa. This allows the pathogen, *Neisseria meningitides* that is residing as nasal flora or that may be present in the dust, access past the host's innate immune system. As soon as the wet season begins, the number of cases decreases considerably. The first epidemic studied was in 1841, and since then around 500 outbreaks have been registered in different regions of "The Sahel Belt" (Molesworth et al., 2003). Fungi spores, such as *Coccidioides immitis*, the causative agent of the human disease known as coccidiomycosis or "Valley Fever" (Welsh et al., 2012), are also common passengers in dust storms. This pathogen is a fungus exclusive to the Americas and is a common community member of the southwestern soils in the United States, where outbreaks of the disease have been shown to be due to regional dust-storm exposures (CDC, 2003; Jinadu, 1995). Viruses are also suitable for airborne transport; they may be more easily aerosolized due to their smaller size, but also may be more sensitive to adverse conditions during transport. There is, however, airborne transmission of viruses, some of them responsible for global epidemics such as influenza or the Severe Acute Respiratory Syndrome (SARS) (Booth et al., 2005; Tseng and Li, 2008). Hantaviruses, which regularly affect rodents and are shed in their feces, are known to occur in arid environments. When

the feces become desiccated, the viruses may become aerosolized and may infect exposed humans (Griffin, 2007). Recently, in September 2012, a Hantavirus outbreak occurred in Yosemite National Park, the United States, affecting 10 people, of which three cases were fatal (CDC, 2012). Bacterio-phages have been found to occur as high as 1.1×10^7 viruses per gram of soil in deserts; this demonstrates that viruses are a major biocomponent of any dust storm (Gonzalez-Martin et al., 2013).

The amount of dust emanating from desert areas and circulating around the planet has increased over the last few decades. Published studies related to dust and its consequences have sparked an international interest in inves-tigations into the field of dust storms and their influence on various ecosys-tems. Given the limited number of studies that exist in scientific literature, a clearly apparent need is the identification of optimal methods for sample collection and analyses for chemical, geochemical, and microbiological investigations.

2. METHODOLOGY

2.1 Sample Collection

Air sampling may be performed using a multitude of different devices, each of which presents benefits and drawbacks that have to be considered accord-ing to the research objectives. The methods are summarized in Table 1.1.

Gravity deposition is the simplest and cheapest of methods. It requires exposing a petri dish containing nutrient agar to the environment for a period of time. Although CFUs per volume of air might be estimated con-sidering the recipient surface area and time exposed, results may be biased by factors such as wind speed, petri dish size, and orientation of the dish to the wind (Buttner et al., 2002). Furthermore, larger particles are deposited more readily than smaller ones, which may contribute to misinterpretation of data (Grinshpun et al., 2007; Reponen et al., 2011).

Impaction devices entail the use of an air pump that drives the air toward a surface (adhesive tape, petri dish, cassettes, strips) with typical flow rates ranging from 10 to $700 \, l \, min^{-1}$ (Fang et al., 2007). Only particles with enough inertia will be captured onto nutrient agar or adhesive surfaces. Although this type of sampler is generally used for fungal spore counts or to determine the number of viable bacteria and fungi CFUs, slit samplers have been adapted to use a liquid medium that allows recovery of viruses and have been successfully used in the study of an SARS outbreak (Booth et al., 2005; Verreault et al., 2008).

Table 1.1 Advantages and Disadvantages of the Most Common Air Sampling Methods

	Advantages	Disadvantages
Gravity deposition	Inexpensive Insignificant cell death from impaction	Capture influenced by external factors Large particles are preferably deposited
Impaction	Easy use Portable Low cost Allows determination of culturable microorganisms per volume of air, in some devices, associated to size ranges	Loss of viability due to impact stress Low recovery of smaller particles (viruses) Low sample volumes due to low flow rates
Centrifugation	High flow rates Efficient capture	Loss of viability due to impact stress
Membrane filtration	Portable Inexpensive High efficiency	Loss of viability due to desiccation Predominance of spore-forming microorganisms
Impingement	Sample may used be for different types of analyses Portable	High cost Loss of collection fluid due to evaporation Loss of viability
Electrostatic precipitation	Consumes less power Collection efficiency up to 90% for particles of 0.3–0.5 μm Five to nine times higher recovery of culturable microorganisms compared to liquid impingement	Collection efficiency depends on the electrostatic field strength, sampling flow rate, and the electric charges of the microorganisms Low collection efficiency at high sampling flow rate

Centrifugation coupled with different containers (petri dish, wet or dry slides, etc.) has been used to collect airborne microorganisms, reaching flow rates of over $1000 \, l \, min^{-1}$ (Williams et al., 2001; Wust et al., 2003). Despite their capacity to sample large volumes, viability of the microorganisms may be compromised due to the physical stress associated with the process (Griffin, 2007).

Membrane filtration is one of the most utilized methods to collect microorganisms from air and can be used for both culture- and nonculture-based studies (Griffin, 2007; Peccia and Hernandez, 2006; Smith et al., 2013, 2012). The collection- and extraction-efficiency rates depend on

the material of the filter (cellulose, glass fiber, polycarbonate, etc.) and on their pore size, which typically has a lower range limit of $0.02\,\mu m$ (Bowers et al., 2012; Griffin et al., 2011). Filters may be put onto an agar plate to culture viable microorganisms, used for electron microscopy and standard microscopy (light and epifluorescence), and/or they can be used for nucleic acid extraction for assessments using molecular approaches (Smith et al., 2012).

Impingement consists of the collection of air into a liquid matrix using various flow rates, which allows the detection of low concentrations of microorganisms (Agranovski et al., 2005; Bergman et al., 2005). One of the main advantages with this technique is that the sample may be split for different analyses, including both culture- and nonculture-based. This methodology has been utilized in aerobiology studies using both low- and high-flow rates and was recently reviewed by Reponen et al. (2011).

Most recently, high-velocity devices called "aerosol-to-hydrosol samplers" have been developed (Gandolfi et al., 2013). In this case, air is forced through a porous filter membrane where the aerosols are collected, and flow rates may range from 1 to $1250 l\,min^{-1}$ (Xu et al., 2011). Similar to the benefits and problems experienced with impingers, the filters may be partitioned for different types of analyses, but high-flow rates compromise the integrity and health of cells and thus the ability to culture them.

A new type of aerosol sampler has been recently developed and is based on electrostatic precipitation (Han and Mainelis, 2008). This system converts aerosols directly into hydrosols and has demonstrated better recovery results than some liquid impingers under certain conditions (Yao and Mainelis, 2006). A recent adaptation has allowed concentrating the sample down to a volume of $5\,\mu l$. Moreover, an automated electrostatic sampler version has been demonstrated (Tan et al., 2011). This system collects the air continuously into a vesicle from which it is then routed to an onboard biosensor. This coupling of a sampler with a biosensor offers a promising option in automated bioaerosol monitoring. Future approaches may employ automation to collect, analyze, and report data in real time (Xu et al., 2011).

2.2 Microbial Identification

2.2.1 Microscopy

The study and identification of microorganisms by microscopy is one of the oldest microbiology tools still in use today (Griffin et al., 2007; Prospero et al., 2005). Standard light microscopy only allows a minimal level of identification since most species are not discernable based on morphology,

and this type of analysis requires expertise and is time consuming. However, detection and enumeration of culturable and nonculturable microorganisms can be made, and results can be obtained within hours after sample collection (Angenent et al., 2005; Buttner et al., 2002). It has been regularly used for identification of airborne fungi spores, usually to genus level (Ho et al., 2005; Wu et al., 2004). Staining may help differentiate unique features: Gram staining for bacteria and the use of lactophenol blue for fungi (Griffin, 2004; Tringe et al., 2008; Yamaguchi et al., 2012). Fluorescence microscopy enables the acquisition of additional data (metabolic state of the cell, direct counts of bacteria and fungi, etc.) through the use of different stains such as acridine orange, SYBR green, LIVE/DEAD staining, or DAPI (Albrecht et al., 2007; Fallschissel et al., 2010; Terzieva et al., 1996). The combined use of microscopy along with immunology or genetic methods allows identification to the species level. Fluorescence in situ hybridization may allow phylogenetic identification of bacteria (Amann et al., 1996; Korzeniewska and Harnisz, 2012). Electron microscopy has been used to enumerate smaller particles such as viruses and allows their classification based on their morphology (Hanssen et al., 2010; Kim et al., 2013; Whon et al., 2012; Yamaguchi et al., 2012).

2.2.2 Culture-Based Analysis

Cultivation is the primary method for the study of viable microorganisms. However, most bacteria in any given sample type are nonculturable (Burrows et al., 2009). Because of this, total concentrations and diversity are typically not attainable (Cho and Hwang, 2011; Ravva et al., 2012), although there are some studies that have demonstrated similar results when comparing molecular methods and culture-based approaches (Fahlgren et al., 2010; Urbano et al., 2011). Choosing the right cultivation assay may result in a better recovery rate of airborne microorganisms. In published studies, incubation temperatures and culture media type used have varied, although ambient temperature and use of a low-nutrient-agar medium seem to produce the best recoveries (Kellogg and Griffin, 2006). Results from culture-based studies are limited in determining the identification and number of CFUs of bacteria or fungi. The cultivation of airborne microorganisms is generally supplemented with other methodologies, such as microscopy and/or polymerase chain reaction (PCR)/high-throughput sequencing-based assays. Many published studies have used several methods (culture, direct count, flow cytometry, PCR, and sequencing) in order to obtain an accurate assessment of airborne microorganisms in different environments

(Giongo et al., 2012; Lim et al., 2011; Ravva et al., 2012; Temkiv et al., 2012; Vaïtilingom et al., 2012; Weir-Brush et al., 2004). With regard to viral viability assays, a known culturable host–cell line is needed, and since most bacteria have yet to be cultured, most viral assays are limited to some pathogenic viruses and known host/phage systems (Alexandersen et al., 2001; Zhao et al., 2013). This is an interesting emerging field of research, and metagenomic approaches will be needed to enhance our understanding of viral transport in aerosols (Fierer et al., 2007; McDaniel et al., 2013; Svraka et al., 2010).

2.2.3 Molecular Methods

PCR is one of the most powerful tools that allows sequence-based identification of microorganisms and microbial community members. Nested PCR, Multiplex PCR, RT-PCR, and real-time PCR, all variants of conventional PCR, have increased sensitivity and specificity, shortened analysis time, and allowed the distinction between live and dead organisms (Atkins and Clark, 2004; Capote et al. 2012; McCartney et al., 2003). Conserved genes are the usual targets when using conventional PCR for the identification of CFUs or community members (Griffin et al., 2007, 2006, 2003; Hervàs et al., 2009; Smith et al., 2010). Real-time PCR has provided a faster and a quantitative tool to estimate target and community–genome concentrations (Smith et al., 2012), and species-specific primers have been used to study spore dispersion of pathogen fungi (Carisse et al., 2009; Schweigkofler et al., 2004). Use of conserved genes together with cloning and sequencing has allowed microbial community composition studies, and although more powerful technologies (microarrays or next-generation sequencing) have been developed, cloning is still a common and affordable technique useful to evaluate communities (Fahlgren et al., 2010; Fierer et al., 2008). Combination of PCR with other techniques is also common, although some can be time consuming. PCR-ELISA (enzyme-linked immunosorbent assay), in situ hybridization (ISH)-PCR, ICC (integrated cell culture)-PCR, PCR-TGGE (temperature gradient gel electrophoresis), or PCR-DGGE (denaturing gradient gel electrophoresis) are some examples based on immunology aspects, ISH, tissue culture, and gradient gel electrophoresis. An ICC-PCR protocol that can be used to rapidly detect infectious viruses was developed by Reynolds et al. (1996). PCR-ELISA and PCR-DGGE have been used to enhance the detection of plant pathogens, like *Phytophthora* or *Pythium*, and to determine microbiological composition during dust storms (Bailey et al., 2002; Somai et al., 2002; Rytkönen et al., 2012; Lim et al., 2011).

Fingerprinting (also known as DNA profiling) uses sequences that are highly variable between individuals, to identify organisms at the species and in some cases the strain level, and has been used to assess airborne microbial communities (Maron et al., 2005). Included in this category, RFLP (restriction fragment length polymorphism) uses restriction enzymes to digest the DNA and electrophoresis to separate fragments, generating unique patterns specific for species and strains. Random amplified polymorphic DNA (RAPD) is a PCR-based assay that uses short generic primers that may bind to different regions of the target genome and ultimately create a unique fingerprint. Different authors have utilized RFLP to study airborne communities (Kuske, 2006; Lee et al., 2010; Polymenakou et al., 2008) and RAPD and to identify single-plant pathogens (McCallum et al., 1999; Zambino et al., 2000). Microsatellites are short sequences (one to six nucleotides) repeated in eukaryotic genomes, also known as simple sequence repeats or short tandem repeats. Their location and number of repetitions through the genome are random and unique; therefore, the pattern of amplification of these sequences may be used to identify individuals. This application has been used by Szabo and colleagues for the specific identification of the plant pathogen *Puccinia graminis* (Barnes and Szabo, 2007). Methods based on DNA hybridization are emerging with the development of microarray-based technologies. They allow the detection of multiple microorganisms in a single reaction, since arrays can harbor thousands of different genetic probes (Wilson et al., 2002). These chip-based assays can also be utilized to identify strains or to determine the endemicity of isolates (Cho and Tiedje, 2001). Airborne dust-storm communities have been successfully screened using this methodology (Leski et al., 2011; Smith et al., 2013).

Next-generation sequence technologies (454 GS-FLX (Roche), Illumina Hi Seq2000 (Illumina), Ion Torrent PGM (Applied Biosystems)) have provided powerful tools to study microbial communities. One of the primary journal articles on airborne metagenomics was published in 2008 by Tringe et al.; those authors reference the indoor urban environment. Rapid advances and improvements in these assays have resulted in interesting reports regarding airborne microorganisms and how they may be affected by factors such as seasonality or dust storms (Bertolini et al., 2013; Franzetti et al., 2011; Rastogi et al., 2012). These studies have primarily focused on airborne bacterial communities, and some are recently published references to airborne viruses (Bowers et al., 2011a,b; DeLeon-Rodriguez et al., 2013; Hall et al., 2013; Whon et al., 2012).

3. GLOBAL SCALE DUST STORMS, MICROBIAL PATHOGENS AND AGRONOMY

Dust storms may favorably impact some ecosystems, including those utilized for agriculture, via fertilization; although in the field of agronomy, most effects are negative in nature. In source areas, drought and harmful agricultural practices can contribute to dust-storm formation and loss of top-soils (Egan, 2006). This loss entails a decrease in nutrients, soil erosion, and acceleration of degradation and desertification processes. Severe droughts may cause the loss of grasslands along the perimeter of desert areas, and in some cases these pasture grasses can be overgrown with nonpalatable weeds (Christie, 1993; McTainsh and Strong, 2007). It has been estimated that 24% of cultivated and 41% of grazing areas have been lost to wind erosion at a rate of ~3600 km² year⁻¹ in northern China (Lacey and West, 2006; Womack et al., 2010). Agricultural regions that are frequently impacted by dust storms are subject to sandblasting plant injuries and loss of seeds and seedlings due to deposition and burial (Stefanski and Sivakumar, 2009). Many pathogenic plant viruses require a vector to move from one host to another, and they usually use biting or feeding injuries to access plant tissue. However, injuries caused by sandblasting may provide for an alternate route of infection. Unsheltered livestock may also be affected by dust through a reduction of growth and productivity and, in severe storms, fatalities (Egan, 2006; Stetzenbach et al., 2004). The Chinese Academy of Forestry Sciences estimated the loss of 120,000 head of livestock and 2.3 million hectares (Ha) of crops due to a heavy dust storm that occurred in May 1993 (Normile, 2007).

3.1 Historical Data

Links between dust transport and its biological load were made first during Ehrenberg's examination of Darwin's 1830s African dust samples (Darwin, 1846; Gorbushina et al., 2007). Approximately 100 years later, researchers such as Bernard E. Proctor, a Professor at the Massachusetts Institute of Technology and Fred C. Meier, a scientist with the U.S. Department of Agriculture, conducted a series of aircraft-based investigations focused on the intercontinental and transoceanic transmission of agricultural pathogens. Proctor noted that the presence of bacterial fungi and pollen should be expected at altitudes of up to ~6.1 km, based on his observations. He recorded the highest total CFU (bacteria and fungal) counts when visibility was impaired by dust being transported in air masses moving over

the Sargasso Sea (Proctor, 1935). Proctor noted, "*The height which is reached by some of these forms induces speculation regarding the horizontal movement of some of these microscopic forms. If they can go up three and four miles in the air it would seem likely that their travels in a horizontal plane might be almost limitless. Such considerations make it very easy to understand how plant diseases may be transmitted through the travels of spores*" (Proctor, 1935, p. 339). Meier believed transoceanic transport of crop pathogens was a viable and important route of transmission, and with the help of notable aviators such as Charles Lindbergh and Amelia Earhart, Meier collected numerous atmospheric samples and described their microbial content (Meier and Artschwager, 1938; Meier, 1936; Rogers and Meier, 1936). Unfortunately for the field of aerobiology (a term attributed to Meier), Meier was lost at sea during a trans–Pacific flight to China during World War II. After these and other related studies conducted during that period of the twentieth century, interest and efforts in the field of transoceanic microbial transport waned until the late 1990s.

3.2 Airborne Transmission of Plant Pathogens

Viruses, bacteria, and fungi are the main causes of plant diseases. Fungi alone are responsible for approximately 10,000 different pathologies (Kakde, 2012). Whereas viruses generally require a vector for their transmission, bacteria and fungi are more readily dispersed. Airborne transmission over short distances is a common route of dispersion. High-wind events are capable of dispersing fungi and bacteria, particularly spore formers, over vast distances. These wind events are the result of pressure in an encroaching front, and in arid environments the winds cause the generation of dust plumes that are capable of transporting biological material around the globe. Hurricanes are known to push or pull dust across the Atlantic, and agricultural studies have linked hurricanes to citrus canker outbreaks following storm landfall in Florida, USA (Gottwald and Irey, 2007; Gottwald et al., 2002). It has been hypothesized that the citrus canker pathogen could be transported to Florida in dust from Africa, where it is known to be endemic (Taylor, 2002). Interestingly, two pathogenic fungi, *Massaria platani,* the causative agent of Florida sycamore (*Plantanus occidentalis*) canker, and *Alternaria dauci*, a species known to infect Florida carrots, were identified in the mid–Atlantic in the transoceanic African dust trade-wind corridor when dust was present in the atmosphere during Leg 209 of the International Ocean Drilling Program (Griffin et al., 2006).

Intercontinental and transoceanic transport, either by winds, hurricanes, or in dust plumes, is thought to be responsible for historical dispersal/outbreak events of pathogens, as discussed and as shown in Figure 1.2
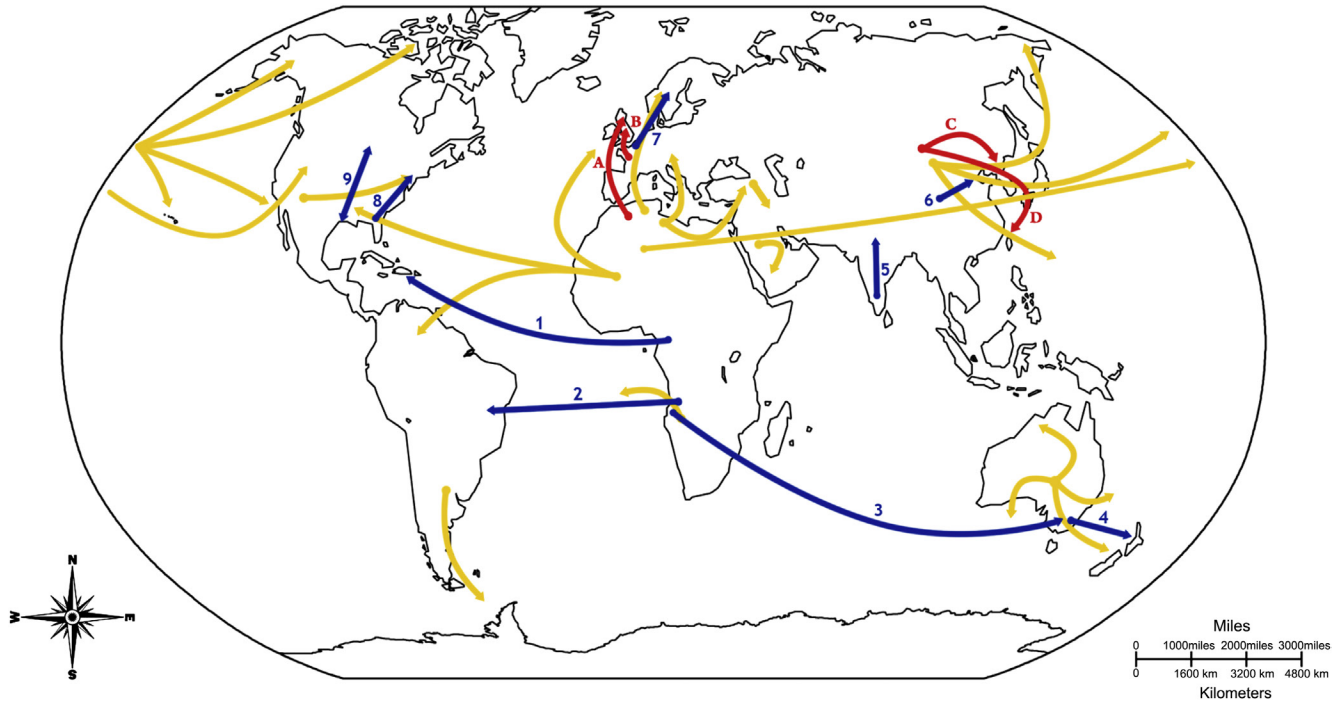
Figure 1.2 Dust-transport routes from the main global desert areas and hypothesized or known airborne dispersal of plant and animal diseases. Yellow lines indicate main dust-transport routes. *(Adapted from Griffin (2007).)* Blue lines indicate airborne dispersal of plant diseases. *(Adapted from Brown and Hovmøller (2002).)* (1) Sugarcane rust, (2) Coffee-leaf rust, (3) Cereal stem rust, (4) Cereal stripe rust, (5) Cereal stem and leaf rust, (6) Cereal stripe rust, (7) Cereal rusts, (8) Tobacco blue mold, (9) Cereal stem rust. Red lines indicate airborne dispersal of animal diseases. (A, B and C) Foot-and-mouth virus (Gloster et al., 2005; Griffin et al., 2001b; Joo et al., 2002; Ozawa et al., 2001; Sanson et al., 2011; Sørensen et al., 2000). (D) Avian Influenza (Chen et al., 2010).

(Brown and Hovmøller, 2002). Diseases caused by species of fungi within the genus *Puccinia* are responsible for most of the worldwide economic loss due to crop damage, especially in cereals (Narayanasamy, 2011; Strange and Scott, 2005). Many dispersion–modeling studies have been carried out in order to understand the airborne dispersion of these pathogens (Aylor, 2003; Aylor et al., 2011; Burt et al., 1999; de Jong et al., 2002; Isard et al., 2005; McCartney, 1994; Pan et al., 2006).

Early studies focusing on long-range wind-borne transport of plant diseases were focused on coffee leaf and sugarcane rusts, caused by the fungi *Hemilea wastatrix* and *Puccinia melanocephala,* respectively. Bowden and Purdy and their colleagues addressed the introduction of these two pathogens from Africa to America in the 1970s (Bowden et al., 1970; Purdy et al., 1985). Introduction of stem rust (*P. graminis*) from Africa to Australia in 1969 and stripe rust (*Puccinia striiformis*) from Australia to New Zealand in 1980 is also believed to have occurred via wind-borne dissemination (Watson and Sousa, 1983; Wellings and McIntosh, 1990). Reintroductions and recolonization events through long-range airborne transmission have been well documented (Aylor, 1999; Hamilton and Stakman, 1967; Hermansen et al., 1978; Nagarajan and Singh, 1990; Wan et al., 2000; Xie et al., 1993). In North America, there is a seasonal pattern of wind-borne dispersion of stem rust known as "The *Puccinia* Pathway," in which the spores are dispersed from south to north every spring and fall (Eversmeyer and Kramer, 2000; Hamilton and Stakman, 1967). Dispersal from south to north also occurs in India for both stem and wheat leaf rust (*Puccinia triticina*) and from central to east China with stripe rust (Nagarajan and Singh, 1990; Wan et al., 2000; Xie et al., 1993). More recently, Singh has addressed the spread of a virulent strain of *P. graminis* from eastern Africa to Middle East countries in which wind-borne dispersion may be playing a significant role (CIMMYT, 2005; Singh et al., 2011). Moreover, airborne introduction of soybean rust (*Phakopsora pachyrhizi*) to North America from Asia or South America has been considered (CIMMYT, 2005; Pan et al., 2006). Although the diseases named so far may be the most important for global agriculture, there are some other microorganisms that have been isolated from dust-storm samples, which may have negative effects in crops, as shown in Table 1.2. Prevailing fungi identified in air samples are the ubiquitous genera *Aspergillus*, *Cladosporium*, *Alternaria*, and *Penicilium*. Within the *Aspergillus* genus, which has been detected in dust samples collected in the North Atlantic Ocean and the Caribbean as well as in Korea, the species *Aspergillus niger,* the causative agent of black mold in onions, has been isolated in samples from Mali and

Table 1.2 Microorganisms Found in Dust Samples With Respect to Agronomy

References	Dust Origin	Collection Site	Pathogens Isolated	Related Diseases
Kwaasi et al. (1998)	Saudi Arabia	Riyadh, Saudi Arabia	*Pythium* spp.	Root rot (e.g., rice)
Griffin et al. (2001a)	Saharan desert	St. John, Virgin Islands	*Cladosporium cladosporioides*	Inhibition of growth (e.g., wheat, lettuce)
			Sphingomonas spp.	Brown spots (e.g., melons)
Yeo and Kim (2002)	Asian deserts	Seosan, Korea	*Fusarium* spp.	Keratomycosis (e.g., horses), toxicity in animals
				Rot, wilt (e.g., potatoes, tobacco, legumes, cucurbit, sweet potatoes, garlic, chickpeas)
			Aspergillus spp.	Aspergillosis (e.g., ruminants, bees, poultry)
			Penicillium spp.	Fruits blue mold rots, toxicity for animals
Griffin et al. (2003)	Saharan desert	Northern Caribbean	*Cladosporium* spp.	Scab (e.g., pecan, peach, cucumber)
				Inhibition of growth (e.g., wheat, lettuce)
			Microsporium spp.	Dermatophytoses (e.g., cattle, horses)
			Bipolaris spp.	Mycotic granuloma in cattle
			Aspergillus spp.	Aspergillosis (e.g., ruminants, bees)

Continued

Table 1.2 Microorganisms Found in Dust Samples With Respect to Agronomy—cont'd

References	Dust Origin	Collection Site	Pathogens Isolated	Related Diseases
Kellogg et al. (2004)	Saharan desert	Bamako, Mali	*Aspergillus niger* *Aspergillus versicolor*	Black mold in onions, Aspergillosis (e.g., ruminants, bees, poultry)
			Alternaria spp.	Early blight, leaf spots (e.g., beans, tomatoes, peas)
			Staphylococcus gallinarum	Bumblefoot disease in poultry
			Corynebacterium spp.	Lymphadenitis, ulcerative dermatitis and mastitis (e.g., sheep, goats, cattle)
			Cladosporium spp. *Cladosporium cladosporioides*	Scab (e.g., pecan, peach, cucumber) Inhibition of growth (e.g., wheat, lettuce)
Wu et al. (2004)	Asian deserts	Tainan, Taiwan	*Stemphylium* spp.	Leaf spot (e.g., alfalfa, garlic, onions)
Ho et al. (2005)	Asian deserts	Hualien, Taiwan	*Stemphylium* spp.	Leaf spot (e.g., alfalfa, garlic, onions)
Griffin et al. (2006)	Saharan desert	Atlantic Ocean (IDOP Expedition 209)	*Alternaria dauci* *Pseudomonas* spp.	Carrot leaf blight Skin and mucosal infections (e.g., sheep), bacterial canker in cereal
			Cladosporium spp.	Scab (e.g., pecan, peach, cucumber) Inhibition of growth (e.g., wheat, lettuce)
			Neotestudina rosatii *Massaria platani*	Mycetoma in animals Florida sycamore canker

Schlesinger et al. (2006)	Saharan desert	Haifa, Israel	*Pleospora tarda*	Leaf spot (e.g., tomato)
			Aspergillus flavus	Aspergillosis (e.g., ruminants, bees, poultry)
			Aspergillus fumigatus	
			Cladosporium cladosporioides	Inhibition of growth (e.g., wheat, lettuce)
			Alternaria alternata	Leaf spots, rot, blight (e.g., tomato, carrots)
Griffin et al. (2007)	Saharan desert	Erdemli, Turkey	*Alternaria* spp.	Early blight, leaf spots (e.g., beans, tomatoes, peas)
			Acremonium spp.	Mycetoma, onchomycosis in animals, and diverse symptoms in plants (e.g., strawberries, muskmelons)
			Microsporum spp.	Dermatophytoses (e.g., cattle, horses)
			Trichophyton spp.	Dermatophytoses (e.g., cattle, mammals)
			Streptomyces spp.	Scab (e.g., potatoes, sweet potatoes)
			Pleospora herbaceum	Purple spot (e.g., asparagus)
Polymenakou et al. (2008)	Saharan desert	Crete, Greece	*Sphingomonas* spp.	Brown spots (e.g., melons)
Hervàs et al. (2009)	Saharan desert	Pyrenees, Spain	*Sphingomonas* spp.	Brown spots (e.g., melons)
			Acinetobacter spp.	Coinfection along with other pathogenic bacteria (e.g., tomatoes)

Continued

Table 1.2 Microorganisms Found in Dust Samples With Respect to Agronomy—cont'd

References	Dust Origin	Collection Site	Pathogens Isolated	Related Diseases
Kakikawa et al. (2009)	Asian deserts	Dunhuang, China	*Agrobacterium tumefaciens*	Crown gall disease
			Nyssopsora echinata	Spignel rust
			Staphylococcus spp.	Mastitis in cattle, sheep, goats
			Pseudomonas spp.	Skin and mucosal infections (e.g., sheep), bacterial canker in cereal
			Rhodococcus spp.	Pneumonia (e.g., foals, pigs, cattle)
Smith et al. (2010)	Asian deserts	Pacific Ocean	*Bacillus* spp.	Mastitis, anthrax in mammals
			Penicillium spp.	Fruits blue mold rots, toxicity for animals
Chen et al. (2010)	Asian deserts	Wan–Li and Shin–Jhuang, Taiwan	*Avian influenza A/H5*	Avian influenza (poultry)
Chuvochina et al. (2011)	Saharan desert	Mont Blanc, France	*Curtobacterium flaccumfaciens*	Vascular wilt of beans
			Bacillus pumilus	Rarely cause of mastitis in cattle
Lim et al. (2011)	Australian desert	Canberra and Melbourne, Australia	*Bacillus* spp.	Mastitis, anthrax in mammals
			Pseudomonas spp.	Skin and mucosal infections (e.g., sheep), bacterial canker in cereal
Munday et al. (2011)	Australian desert	Victoria, Australia	*Curtobacterium flaccumfaciens*	Vascular wilt of beans
			Psychrobacter pulmonis	Respiratory infections in lambs
			Bacillus spp.	Mastitis, anthrax in mammals
			Bacillus pumilus	
			Bacillus subtilis	

Palmero et al. (2011)	Saharan desert	Almeria, Spain	*Fusarium* spp. *Fusarium solani* *Fusarium equiseti* *Fusarium dimerum*	Rot, wilt (e.g., potatoes, tobacco, legumes, cucurbit, sweet potatoes, garlic, chickpeas)
			Fusarium proliferatum *Fusarium oxysporum*	Keratomycosis (e.g., horses), toxicity in animals
Giongo et al. (2012)	Saharan desert	Bahaï Wadi, Chad	*Pseudomonas* spp.	Skin and mucosal infections (e.g., sheep), bacterial canker in cereal
			Cochliobolus lunatus	Leaf spot (e.g., maize)
			Fusarium spp.	Keratomycosis (e.g., horses), toxicity in animals
				Rot, wilt (e.g., potatoes, tobacco, legumes, cucurbit, sweet potatoes, garlic, chickpeas)
Griffin (2012)	African desert	Atlantic Ocean (IDOP Expedition 336)	*Trichophyton verrucosum*	Ringworm in cattle
			Exhopiala/Wangiella spp.	Abortion in cattle, phaeohyphomycosis (e.g., ruminants, poultry)
			Curvularia spp. *Pseudallescheria* spp. *Acremonium* spp.	Mycetoma, onchomycosis in animals and diverse symptoms in plants (e.g., strawberries, muskmelons)
			Cladosporium spp.	Inhibition of growth (e.g., wheat, lettuce)

Table 1.2 Microorganisms Found in Dust Samples With Respect to Agronomy—cont'd

References	Dust Origin	Collection Site	Pathogens Isolated	Related Diseases
			Alternaria spp.	Early blight, leaf spots (e.g., beans, tomatoes)
				Scab (e.g., pecan, peach, cucumber)
			Aspergillus spp.	Aspergillosis (e.g., ruminants, bees)
			Aspergillus nigrans	
			Aspergillus niger	Black mold in onions
Grishkan et al. (2012)	Saharan desert	Haifa, Israel	*Alternaria alternata*	Leaf spots, rot, blight (e.g., tomato, carrots)
			Phlebia spp.	White rot (e.g., onions)
			Cladosporium cladosporioides	Inhibition of growth (e.g., wheat, lettuce)
			Penicillium spp.	Fruits blue mold rots, toxicity for animals
			Aspergillus niger	Black mold in onions
			Aspergillus versicolor	Aspergillosis (e.g., ruminants, bees, poultry)
			Aspergillus fumigatus	
			Pleospora tarda	Leaf spots, pod rot (e.g., legumes)
Smith et al. (2012)	Asian deserts	Oregon, USA	*Alternaria infectoria*	Leaf black spot (e.g., wheat)
			Chaetomium globosum	Necrosis in roots (e.g., barley)

Yamaguchi et al. (2012)	Asian deserts	Japan Sea	*Actinobacteria*	Canker, wilt, galls, etc., (e.g., tomato, beans, wheat, etc.)
				Tuberculosis (e.g., cattle, sheep, goats, etc.)
			Bacilli	Anthrax, mastitis in mammals
			Sphingobacteria	Brown spots (e.g., melons)
Maki et al. (2013)	Asian deserts	Suzu, Japan	*Bacillus* spp.	Anthrax, mastitis in cattle and abortions in sheep
			Bacillus subtilis	
Sánchez de la Campa et al. (2013)	Saharan desert	Andalusia, Spain	*Escherichia* spp./ *Shigella* spp.	Gastrointestinal infections
			Acinetobacter spp.	Coinfection along with other pathogenic bacteria (e.g., tomatoes)
			Bacillus spp.	Mastitis, anthrax in mammals
			Rhodococcus spp.	Pneumonia (e.g., foals, pigs, cattle)
Smith et al. (2013)	Asian deserts	Oregon, USA	*Pseudomonadaceae*	Skin and mucosal infections (e.g., sheep), bacterial canker in cereal
			Sphingomonadaceae	Brown spots (e.g., melons)

In those cases in which the identification is at the genus/family level, diseases cited are caused by species within that group.

the North Atlantic Ocean (Griffin, 2012; Griffin et al., 2003; Kellogg et al., 2004;Yeo and Kim, 2002). *Cladosporium* spp. may cause inhibition of growth and scab in vegetables such as lettuces and cucumbers and have been frequently isolated by Griffin and his colleagues when analyzing air samples from a variety of regions affected by African dust storms, e.g., northern Caribbean, Mali, Atlantic Ocean (Griffin et al., 2006, 2001a; Kellogg et al., 2004). The species *Cladosporium cladosporioides*, which causes inhibition of growth in wheat or lettuce, has been identified in both clear atmosphere and dust (at higher concentrations) samples collected in Haifa, Israel, an area also influenced by African dust (Grishkan et al., 2012; Schlesinger et al., 2006). *Alternaria* is commonly detected, and it is related to leaf spots, blight, and rot in many plant species (e.g., tomatoes, carrots, radishes, sprouts) (Griffin, 2012; Griffin et al., 2007; Kellogg et al., 2004). Four species within the *Alternaria* genus have been identified in three regions affected by Saharan and Asian dust. *Alternaria alternate* and *A. dauci* have been identified in air samples collected in Israel and in the middle of the Atlantic Ocean during African dust–storm events (Griffin et al., 2006; Grishkan et al., 2012; Schlesinger et al., 2006). *Alternaria infectoria* and *Alternaria japonica* have been isolated from air samples collected atop Mt. Bachelor in Bend, Oregon, USA, an area affected by Asian dust storms during the spring season (Smith et al., 2012). Species within the genus *Penicillium* cause blue molds in fruits, and this ubiquitous genus is frequently recovered in dust studies (Grishkan et al., 2012;Yeo and Kim, 2002). *Fusarium* spores are also frequently recovered in air and dust samples, and several species, such as *Fusarium solani* or *Fusarium oxysporum*, are known to cause rot and wilt in potatoes or legumes (Palmero et al., 2011). Leaf spots are a common disease in plants caused by a variety of fungal species, some of them detected in air samples during dust events. *Stemphylium*, *Pseudocercospora*, *Pythium* and species such as *Pleospora tarda*, *Pleospora herbaceum*, or *Cochlibolus lunatus*, are among the fungi that can produce leaf spots in rice, tomatoes, asparagus, bananas, or maize crops (Giongo et al., 2012; Griffin et al., 2007; Grishkan et al., 2012; Ho et al., 2005; Kwaasi et al., 1998; Schlesinger et al., 2006;Wu et al., 2004). *Phlebia, Curvularia, Acremonium,* and *Pseudallescheria* have also been isolated from air samples collected in the middle of the Atlantic Ocean and in Israel and may cause diverse symptomatology in strawberries, muskmelons, and onions (Griffin, 2012; Grishkan et al., 2012). Species such as *Nyssopsora echinata* and *Chaetomium globosum*, responsible for spignel rust and necrosis in roots, respectively, have been identified in Asian dust samples collected in China and Oregon, USA (Kakikawa et al., 2009; Smith et al., 2012).

Although bacterial infections are less common among plants, there are some that may cause damage to crops. *Agrobacterium tumefaciens* causes crown gall disease, and *Curtobacterium flaccumfaciens* is the causative agent of vascular wilt in beans. Both have been isolated from air samples collected in China, France, and Australia, under the influence of Asian, African, and Australian dust storms, respectively (Chuvochina et al., 2011; Kakikawa et al., 2009; Munday et al., 2011).

Some studies have been able to identify the bacteria only to the phylum, e.g., Actinobacteria and/or genus, e.g., *Sphingomonas*, levels. In both of these cases, pathogenic species are known to exist that may cause plant diseases such as canker, galls, wilt, and spots (Hervàs et al., 2009; Polymenakou et al., 2008; Smith et al., 2013; Yamaguchi et al., 2012).

3.3 Airborne Transmission of Animal Pathogens

Viruses, bacteria, and fungi are also common etiologic agents in livestock. Unlike plant diseases in which fungi tend to be the dominant cause of morbidity and mortality, bacterial and viral infections tend to be the dominant agents in livestock. The most common routes of transmission are fecal-oral for gastrointestinal diseases and close contact for respiratory infections. Whether a pathogen is shed in feces or in other secretions, it can be aerosolized and effectively transmitted through the atmosphere. Airborne transmission of pathogens is well known to occur over short distances, e.g., influenza transmission. In 1989, Hammond and colleagues hypothesized the transmission of this viral pathogen from Asia over the North Pacific to North America, given the typical influenza season and corresponding atmospheric conditions that would favor long-range dissemination (Hammond et al., 1989). Since then, many authors have considered dust plumes and strong winds to be carriers for some important animal diseases, as shown in Figure 1.2. The most studied to date is foot-and-mouth disease (FMD) caused by an *Aphthovirus.* First indications of airborne transmission were in 1967–1968 in the United Kingdom, when around 300 outbreaks developed in downwind areas from the original outbreak site (HMSO, 1968). In the 1980s, rapid spread of the disease over vast distances in Europe spurred the development of models to evaluate the possibility and extent of wind-borne dispersion. Gloster demonstrated that under certain circumstances, long-range atmospheric transmission of the virus was possible (Gloster, 1982; Gloster et al., 1981). Later, Griffin hypothesized the possible transmission of FMD virus from Africa to the United Kingdom, via African dust storms, based on timing of the outbreak following an African dust event that impacted

air quality in the UK prior to the outbreak and on the serotype similarity between the virus causing the outbreak and viruses found in domestic cattle in the dust-storm source region (Taylor, 2002). This possibility of dust-storm transmission of FMD has been also considered in Asia, where heavy dust storms have been followed by outbreaks of the disease. However, analyses performed to identify the virus in air samples yielded negative results (Joo et al., 2002; Ozawa et al., 2001). Nevertheless, recent studies using statistical methodology have confirmed the airborne transmission in outbreaks in the United Kingdom (Gloster et al., 2005; Sanson et al., 2011).

Among diseases affecting poultry, avian influenza has gained great importance in recent years. Massive economic losses due to this infection plus the known threat of transmission to humans have brought studies of avian influenza viruses to the forefront. Chen et al. (2009) reported the quantification of avian influenza in environmental samples. A year later, those authors collected air samples during normal atmospheric conditions and when Asian dust was present over Taiwan. In those samples, the virus was only detected during dust-storm days. Outbreaks in downwind areas after the occurrence of dust storms implicates effective transmission via dust storms (Chen et al., 2010).

Bacillus anthracis is a dangerous animal and human pathogen of bioterrorist concern, and studies have been conducted to evaluate long-range airborne transmission. Short-range airborne transport is a common route, but long-range transmission of this disease has been reported for an outbreak in Sverdlovsk, Russia, in 1979. This outbreak affected around 100 people, 68 of whom died, and livestock in villages up to 50 km away from the source were also affected (Meselson et al., 1994; Turnbull et al., 1998). Various species of *Bacillus* are commonly recovered in dust-storm microbiology studies (Griffin, 2007).

Table 1.2 lists microorganisms able to produce animal diseases that have been identified in dust samples. Mastitis is one of the most common ailments for the dairy industry. *Staphylococcus aureus* is the primary causative agent, although other *Staphylococcus* species and different genera of bacteria may also cause mastitis, e.g., *Staphylococcus epidermidis*, *Corynebacterium*, or *Bacillus*, all of which have been isolated from dust samples in various geographic regions (China, France, Mali, and Japan) (Chuvochina et al., 2011; Kakikawa et al., 2009; Kellogg et al., 2004; Maki et al., 2013). Additionally, the species *Staphylococcus gallinarum*, which is the causative agent of bumblefoot in poultry, and isolates of the genus *Corynebacterium* that may also cause lymphadenitis and dermatitis in cattle, sheep, and goats, have been isolated from dust samples collected in Mali (Kellogg et al., 2004). Actinobacteria

is a phylum that contains many pathogenic species, which may cause diseases such as tuberculosis or pneumonia in cattle and has been identified in numerous dust-storm studies (Kakikawa et al., 2009; Sánchez de la Campa et al., 2013; Yamaguchi et al., 2012). In addition, *Pseudomonas* species, frequently reported in dust samples, may produce skin and mucosal infections (Giongo et al., 2012; Griffin et al., 2006; Kakikawa et al., 2009; Smith et al., 2013). *Rhodococcus* spp. have been identified in samples collected in China, Oregon (USA), and Andalusia (Spain), and although rare, this bacteria may cause pneumonia in foals, pigs, and cattle (Kakikawa et al., 2009; Sánchez de la Campa et al., 2013). Furthermore, *Psychrobacter pulmonis* has been isolated from dust samples in Victoria, Australia. This bacterium has been related to respiratory infections in lambs (Munday et al., 2011). Fungal infections are less numerous, although aspergillosis and toxicity caused by *Aspergillus*, *Fusarium,* and *Penicillium* species, regularly found in atmospheric samples and in dust-storm studies, can affect the health of ruminants and poultry (Giongo et al., 2012; Griffin et al., 2003; Grishkan et al., 2012; Kellogg et al., 2004; Palmero et al., 2011; Yeo and Kim, 2002). Dermatophytoses is also a fungal disease that affects cattle. *Microsporum* and *Tricophyton* are some of the fungi responsible, which have been isolated from dust samples (Griffin et al., 2007, 2003). *Acremonium, Curvularia, Pseudallescheria,* and *Neotestudina rosatii* may cause mycetomas in cattle, and all of them have been detected in air samples collected in the middle of the North Atlantic Ocean (Griffin, 2012; Griffin et al., 2006). Other fungal infections, such as mycotic granuloma or phaehyphomycosis in cattle, caused by *Bipolaris* and *Exophiala* species, may be transmitted through the atmosphere, since they have been recovered from air samples collected in the northern Caribbean and North Atlantic Ocean (Griffin, 2012; Griffin et al., 2003).

3.4 Future Perspectives

The role of dust storms in dispersing pathogens around the planet may ultimately prove to be an important transmission route, given the yet realized influence of climate change on future dust loads and the recognized threats associated with the widespread use of monoculture crops. A basic understanding of these various atmospheric dust corridors and their ability to route microorganisms across continents and oceans has only recently been recognized. Although standard methodologies for aerobiological studies have yet to be adopted, the recent emergence of collection techniques such as electrostatic concentrators and identification/molecular activity assays such as high-throughput sequencing and molecular probes should provide

for rapid advancements in the field. Adaptation of collection and analyses tools for use on drones would greatly facilitate investigations of air masses from distant locations. Advances in remote sensing and modeling have contributed significantly to our understanding of the 'big-picture' nature of this field, and further capabilities and refinement of existing tools are needed.

Since the transoceanic aerobiology work of Bernard E. Proctor and Fred C. Meier in the 1930s and 1940s, agricultural agencies have largely dismissed the relevance of this potentially important route of transmission. With an estimated 60 million tons of Asian dust impacting North America each year through a corridor that overlies the breadbasket region of the United States, this research field should be given funding priority. Regardless of the dust-source region or the agricultural region being impacted, the economic and possible human consequences that may result from ignoring obvious transoceanic routes of dispersion may be significant and, more importantly, may directly affect the ability of a region to optimally produce and sustain food supplies.

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