



Review

Microbiology of wind-eroded sediments: Current knowledge and future research directions



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ABSTRACT

Wind erosion is a threat to the sustainability and productivity of soils that takes place at local, regional, and global scales. Current estimates of the cost of wind erosion have not included the costs associated with the loss of soil biodiversity and reduced ecosystem functions. Microorganisms carried in dust are responsible for numerous critical ecosystem processes including biogeochemical cycling of nutrients, carbon storage, soil aggregation, and transformation of toxic compounds in the source soil. Currently, much of the information on microbial transport in dust has been collected at continental scales, with no comprehensive review regarding the microbial communities, particularly those associated with agricultural systems, redistributed by wind erosion processes at smaller scales including regional or field scales. Agricultural systems can contribute significantly to atmospheric dust loading and loss or redistribution of soil microorganisms are impacted in three interactive ways: (1) differential loss of certain microbial taxa depending on particle size and wind conditions, (2) through the destabilization of soil aggregates and reduction of available surfaces, and (3) through the reduction of organic matter and substrates for the remaining community. The purpose of this review is to provide an overview of dust sampling technologies, methods for microbial extraction from dust, and how abiotic, environmental, and management factors influence the dust microbiome within and among agroecosystems. The review also offers a perspective on important potential future research avenues with a focus on agroecosystems and the inclusion of the fungal component.

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1. Introduction

Wind erosion processes produce a significant impact upon global sustainability, health and environmental quality with estimates of global mineral dust emissions varying from 500 to about 3300 Tg yr⁻¹ (or 5.0 × 10⁸ to 3.32 × 10⁹ Mt yr⁻¹) (Shao et al., 2011). Although the majority of these emissions occur from non-anthropogenically influenced desert surfaces, agricultural soils can also represent significant regional dust sources (e.g. Lee et al., 2012; Ginoux et al., 2012). Tegen et al. (2004) postulated that about 10% of the total dust load is derived from agriculturally modulated sources alone, producing estimates of at least 50 million Mt of dust contributed to the global budget per year. Downwind transport of eroded sediment is often over great distances (Prospero et al., 2005, 2014) and carries with it a variety of mineral and organic materials including geochemicals, biochemicals, xenobiotics (e.g., pesticides), and microorganisms. Of these components, the microbial composition of dust is the least understood, in part due to the vast abundance and diversity of microorganisms found in soils. For example, one gram of an agricultural soil with relatively high contents of organic matter and clay (i.e., Iowa, USA) was found to contain 1.34 ± 0.38 µg DNA within the 0–0.3 m depth, with respective fungal and bacterial estimates of 1.03 × 10⁵ or 6.19 × 10⁷ colony forming units (Taylor et al., 2002). In terms of the variety of bacterial species, Roesch et al. (2007) estimated that up to 8.3 million species were present per gram of soil based on over 50,000 sequences of 16S rRNA evaluated for a forest soil from Canada and three agricultural soils from Brazil and the USA. By having the potential to remove vast numbers of soil microorganisms, wind erosion events on agricultural land such as Fig. 1 can exert profound impacts on the sustainability and productivity of soils that are subject to deflation by aeolian processes.

Microorganisms carried in dust are important in local, regional, and global processes including biogeochemical cycling of nutrients (Gardner et al., 2012; Li et al., 2007, 2008), pathogenicity (Griffin et al., 2001; Hara and Zhang, 2012; Prospero et al., 2005), and microbial biogeography (McTainsh and Strong, 2007; Smith et al., 2010, 2013) and there are discussions of their role in climate interactions and the formation of clouds (Konstantinidis, 2014). In his epic travels on *H.M.S. Beagle*, Charles Darwin and his associates collected airborne dust near the island of Santiago in Cape Verde and showed that it contained organic material subsequently identified by Darwin's associate, Professor Ehrenberg, as many forms of Infusoria, which are minute aquatic organisms (Darwin, 1845). Recent analysis of this dust shows that it most likely originated from the Sahara (Gorbushina et al., 2007). Darwin's pioneering study was one of the earliest to demonstrate the movement of microbial-rich dust as a result of aeolian entrainment and subsequent transport, and the potential wind-driven biodiversity loss of some ecosystems and enrichment of others.

Microbial communities lost from agricultural soils when carried away in dust are essential to the ecosystem functions, services and productivity of the source soil (Fig. 2). Microorganisms, for instance, play key roles in protecting soils from erosion and reduce soil erodibility potential through their influence in organic matter build up and aggregate stability. Thus, management practices that increase soil microbial biomass, C content and sequestration, will contribute to enhanced soil structure and reduce the erodibility of soils. Fungal growth, for instance, leads to the physical binding of aggregates and the production of cementing agents referred as glomalin, which glue soil particles together (Wright et al., 1996). Increases in soil organic matter that consequently lead to improved aggregate stability and increases in soil water holding capacity are the result of decomposition processes by both fungi and bacteria. Fungi, and to certain extent actinomycetes, degrade complex compounds to more simple forms that are sequentially used by bacteria (G+, G–), and these series of reactions not only incorporate and recycle several nutrients in soil, but will also lead to soil C sequestration. Bacterial species involved in symbiotic associations of N fixation (i.e., rhizobia) and fungal species (e.g., members of the

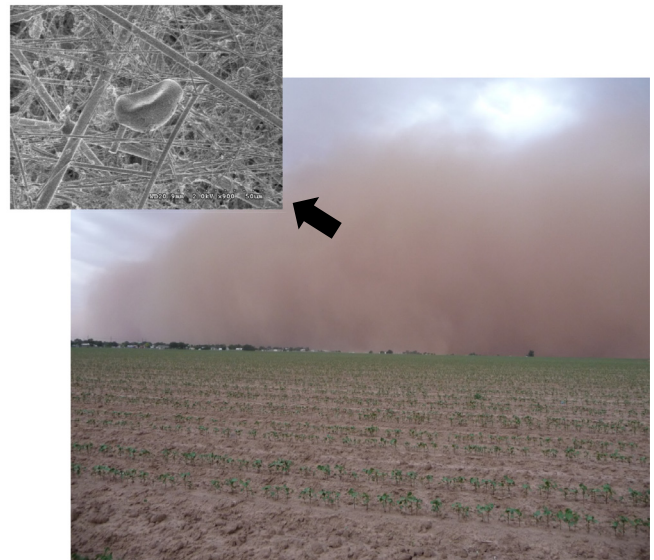


Fig. 1. Dust storm seen in September 3, 2011 in a semiarid agricultural region in the USA within the Southern High Plains in Texas. This region experiences high intensity rain events and high wind speeds (>9 m/s) particularly at planting time in the spring and at harvest in the fall when the crops and the soil are more susceptible to damage. The dust image (50 µm in size) shows pollen, fibers and fungal hyphae. The image was taken using a scanning electron microscope at *The Imaging Center of Texas Tech University* using a Hitachi S-4300SE/N (NSF MRI 04-511 The Texas Tech University A&S EOX Imaging Facility, Texas Tech University) by a Texas Tech graduate student Chenhui Li.

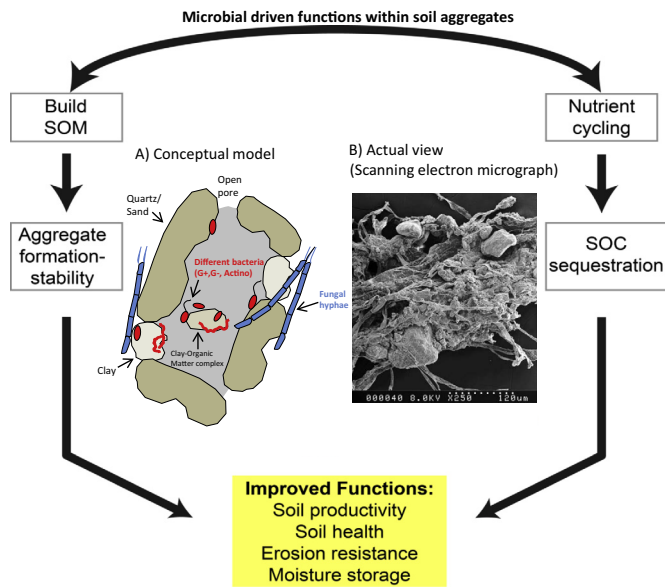


Fig. 2. Microbial communities of soil are located within aggregates and particles of different sizes. They play an important role in nutrient cycling and building soil organic matter (SOM) that lead to aggregate formation and stability and SOC sequestration resulting in improved functions that include soil productivity, soil health, erosion resistance and moisture storage. The conceptual model of an aggregate showing potential locations of microorganisms is modified from Paul and Clark (1989) (A) and the scanning electron micrograph was provided by Dr. Lisa Fultz, showing an intra-aggregate particulate organic matter fraction that has been associated with C sequestration and stable aggregate formation (B). The image was taken using a Hitachi S-4300SE/N (NSF MRI 04-511) at Texas Tech University A&S EOX Imaging Facility of Texas Tech University.

Glomeromycota phylum) capable of sustaining mycorrhizal associations which increase plant water and phosphorus uptake are also important in soil functioning. In addition to bacteria and fungi, archaea have been found to play a greater role in nitrification than originally thought and thus, they are also an important microbial group in N cycling and productivity of agroecosystems (Qin et al., 2013). Thus, loss of microbial communities through wind erosion can reduce soil resistance to further erosion, introducing a notable feedback effect for rates of sediment loss.

The majority of the literature concerned with the microbial characteristics of wind eroded material has focused on long distance transport of microbes and the negative impacts to the environment (Griffin et al., 2001; Garrison et al., 2003; Griffin, 2004) or human health (i.e., Griffin et al., 2007; Polymenakou et al., 2008; Jeon et al., 2011). Much of this work has investigated the airborne transport of pathogens, and there is a relative dearth of research on the transport of soil microbial assemblages in relation to the eroded soil source, especially in agroecosystem landscapes (Burrows et al., 2009a, b). Increased research efforts in this area are of the essence given that current global climate models project more frequent droughts and extreme weather events, especially in many wind erosion prone areas (Dai, 2011). With an increased potential for wind erosion comes greater urgency to comprehend its effects on soil microbial communities, and the implications of wind-borne soil loss for soil functions and productivity. This paper provides an overview of our current knowledge and the most appropriate methods available for understanding the microbial characteristics of wind eroded sediments, drawing upon studies into the microbiology of dust on continental, regional and local field scales. Wherever possible, we discuss the relationship between the effects of wind erosion on soil quality and functioning and, given the relative scarcity of studies from agroecosystems, we provide a particular perspective on the future research

avenues for improving knowledge of agroecosystems and their management.

2. Drivers of soil erosion by the wind and soil biodiversity

2.1. Mechanisms of wind erosion

Soil erosion results in the detachment and transport of soil particles, aggregates and associated biota within the soil matrix and occurs due to the operation of several key mechanisms, often simultaneously. Aeolian erosion is caused by the combined effects of wind velocity and turbulence exerting shear stress at the surface (representing *erosivity*), and the availability of loose soil particles available for entrainment, together with insufficient soil surface protection (the surface *erodibility*). Rates of soil loss depend on a range of factors, with the wind speed and the particle size of the sediment acting as fundamental controls (Pye, 1987). Previous studies reported that it is possible for the erosion of soil and organic particles by wind to occur when wind speeds are as low as 3 m s^{-1} (Carroll and Vigleirchio, 1981), but soil erosion by wind is primarily initiated when wind speed exceeds the saltation threshold velocity for a given field condition. Soil particles are generally detached when the forces of drag and lift from wind overcome the gravitational and cohesive forces that hold particles to the soil surface (Zobeck, 1991a, b). When wind speeds reach approximately 6 m s^{-1} at 0.3 m above the soil surface, there is typically enough force to detach loose, dry soil particles that are not aggregated, and deflation occurs.

Soil particles are eroded by the wind through three main modes of transport related primarily to particle size: surface creep, saltation and suspension (Fig. 3). The first mode, surface creep, affects relatively large particles or soil aggregates (between 0.5 and 1 mm in diameter or $>500 \mu\text{m}$), which move by rolling or sliding along the soil surface. The second mode, saltation, affects particles about 0.07 to 0.5 mm in diameter ($70\text{--}500 \mu\text{m}$) and results in particles that bounce along the surface in a zone typically well under a meter in height. The ballistic impacts of saltating particles can also cause other particles to creep or splash at the surface via a process called reptation. Very small particles ($<70 \mu\text{m}$) with low settling velocities are typically carried in suspension, being held aloft for a period of time strongly related to particle size and therefore settling velocity (Tsoar and Pye, 1987). While direct (aerodynamic) suspension of fine particles can occur in soils with high silt content, such as those found in the Columbian Plateau of eastern

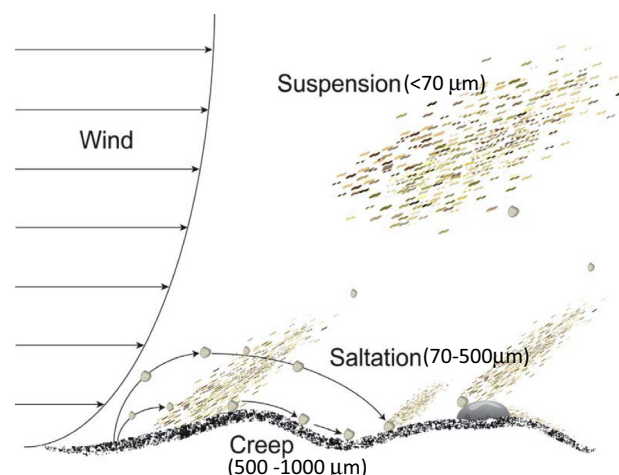


Fig. 3. Mechanisms of wind erosion involve suspension, saltation and creep movement of the soil particles related to their size diameter.

Washington (Kjelgaard et al., 2004), the impact of saltating sand-sized grains in ejecting fine particles into the airflow is an important contributor to suspension (e.g. Shao et al., 1993a). The bombardment of a crusted surface by saltation can liberate material susceptible to suspension, or silt and clay particles formed into saltation size aggregates can break down into finer sizes during saltation transport. The distance downwind from the source and the height that suspended dust can be transported is influenced by numerous factors but particle size is a major determinant. Suspended sediments greater than 20 μm (0.02 mm) diameter typically travel less than 30 km from their source of emission (Tsoar and Pye, 1987), but smaller particles may be carried in turbulent eddies and travel thousands of kilometers before being deposited (Chadwick et al., 1999; Goudie and Middleton, 2006; Bristow et al., 2007). Overall, saltation accounts for the majority of total sediments carried in the wind (50–70% of total), followed by suspension (30–40%) and creep (5–25%) (Lal, 2004).

2.2. The contribution of soil properties and land management to wind erosion

A combination of both physical and chemical soil properties influence the susceptibility of bare ground to wind erosion. For example, erosion potential is greatest in relatively coarse-textured soils (e.g., sandy loams and loamy sands) with low organic matter, moisture content and limited or weak aggregation (Gillette, 1977; Gillette et al., 1982; Zobeck, 1991b). Additionally, soil microbial community size and diversity are typically lower in these soil conditions, which can further contribute to overall lower resiliency (Acosta-Martínez et al., 2010). Thus, the ecological implications of wind erosion can vary between different types of soil. Both the number and types of microbes carried in wind eroded sediments away from a field will depend on the wind frequency, size of wind eroded sediment and climatic conditions, as well as the original microbial community composition of the soil source as affected by soil management. As wind eroded sediments are lost from a system, the structure and functionality of the microbial communities are impacted in three interactive ways: (1) through differential loss of certain microbial taxa depending on particle size and wind conditions, (2) by the destabilization of soil aggregates and reduction of available surfaces, and (3) through the reduction of organic matter and substrates for the remaining community.

Soil management activities such as land clearing, grazing, cropping and tillage are common contributors to increased soil erosion, resulting in erosion rates that exceed those of natural processes, particularly on slopes (Govers et al., 1994; Powlson et al., 2011). Tillage has been recognized as one of the major agents of wind erosion as the practice breaks aggregates making them more available for entrainment (Addiscott and Thomas, 2000; Bailey et al., 2013). Alternatively, cropping systems that reduce wind erosion include practices such as the use of cover crops, if possible, to maintain a cover on the soil surface and increase surface roughness, as well as techniques using windbreaks, shelterbelts, natural barriers, vegetative strips or retaining crop residue. When crop residues are not tilled into the soil, they offer the greatest protective effect when left standing, but residues flattened on the surface also provide effective shelter (Nordstrom and Hotta, 2004). Although not as effective as no-till cropping, cropping in strips is another wind erosion-sensitive approach that leaves rows of vegetative growth that protect the primary crop, especially during germination. These crop strips essentially function as a windbreak and typically remain dormant or are terminated, and remain in place throughout the year. Conservation efforts including reduced and no-till practices as well as specific government incentivized schemes (e.g., the Conservation Reserve Program in the US) can contribute to

an overall decrease in erosion rates on cropland (e.g., Stout and Lee, 2003).

New challenges due to climate change may increase the amount of land susceptible to wind erosion and alter patterns of wind magnitude and frequency. In agricultural areas where climate change models predict less frequent but more intense rain events, the prospect of longer drought periods may limit the use of vegetation cover or row crops. Lower soil moisture will also decrease the ability of the soil particles to bind together into larger, less erodible particle sizes (macroaggregates). Management strategies may require adaptations to climate change due to reduction in water availability with more frequent droughts and heat waves. This will make the selection of conservative management practices more challenging (tillage, crop rotations, application of organic amendments), especially for successfully maintaining cover crops.

2.3. Survival strategies by microorganisms carried in dust and factors involved in likelihood of microbial redistribution

There is considerable evidence that a diverse assemblage of microbes is carried in dust for long periods of time and over wide geographical distances (Darwin, 1845; Bovallius et al., 1978; Gardner et al., 2012; Gonzalez-Martin et al., 2014) and that these assemblages are related to the characteristics and land-use of the soil source (Bowers et al., 2001a,b; Gardner et al., 2012). The survival rate of the microorganisms carried in dust and their success in colonizing a new environment are dependent upon several environmental and biotic factors. The persistence and fluctuations of climatic conditions (i.e., air humidity, temperatures, desiccation, UV light) and available resources during microbial transport will determine the microbial community composition of dust (Barberán et al., 2014). For example, dust can provide shadow protection and a protective environment (i.e., surfaces, clay, silt, and organic matter-clay complexes) able to capture humidity to help microorganisms survive the harsh conditions and strong desiccation during transport, especially those involving long distances (Tong and Lighthart, 1998; Yamaguchi et al., 2012). Dust also can physically protect microbial cells against damage from UV light and ozone (Milling et al., 2005).

In addition to the physical and biochemical protection imparted by dust particles, microorganisms employ numerous strategies to survive the harsh conditions during aerosol transport. These strategies include: endospore production (Nicholson et al., 2000), high G+C nucleic content, and enhanced DNA repair ability (Griffin et al., 2006). The ability of microorganisms to enter a dormant state, such as the formation of an endospore, must account for a significant pool of total cell dispersal across continents (Jones and Lennon, 2010). Upon entry into the new environment, cells that remain viable can recolonize the new habitat (Lenon and Jones, 2011). During the recolonization period, asexually reproducing organisms (e.g., all bacteria and many fungi) can form a new colony more quickly than those relying on sexual reproduction because of the rapid growth rates of these organisms (Brown, 1995; Barberán et al., 2014). Cells that do not survive can serve as nutrient sources for the colonizing population as well as the native population. Competition factors and the conditions of the deposition site are also important in the success of microbial colonization (Barberán et al., 2014).

3. Approaches for the collection of wind eroded sediments for microbiological analyses

3.1. Passive collection of wind eroded sediments during natural events

In-situ collection of wind eroded sediments can be most simply accomplished by a passive approach where samplers with clean

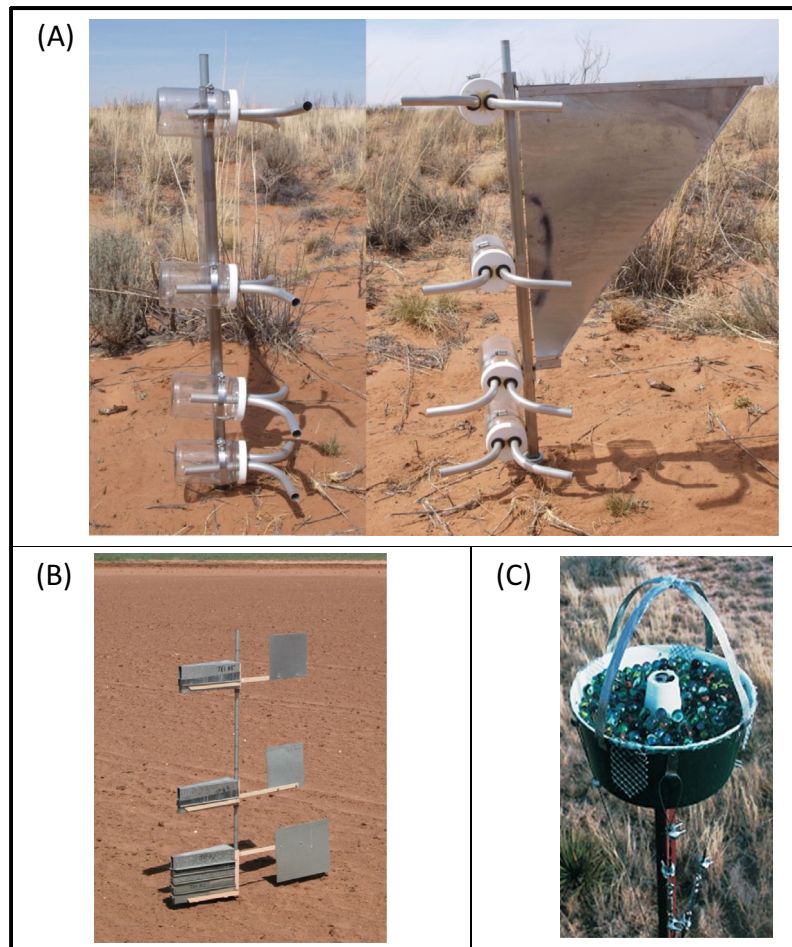


Fig. 4. Devices used for passive collection of wind eroded sediments during natural events: *Modified Wilson and Cooke (MWAC)* (A); *Big Spring Number Eight (BSNE) sampler* (B); *Marble Dust Collector (MDCO) system* (C).

surfaces collect the sediments during natural wind erosion events without particle size selection or the use of filters. The primary disadvantage of dry surface deposition is the ease with which the sample may be re-suspended by wind, but with careful adaptations the approach can allow eventual characterization of microbial properties from a soil source during active erosion events. One of widely used dust sampler for *in-situ* wind erosion research is the *Modified Wilson and Cooke (MWAC)* sampler as shown in Fig. 4a (Wilson and Cooke, 1980). The MWAC is easily made, inexpensive, and widely adaptable to a variety of sampling conditions, including its use to characterize microbial hitchhikers on dust from a region recognized as “the dustiest place on earth” (Warren et al., 2007; Bristow et al., 2007; Favet et al., 2013). Another field sediment sampler that is commonly used is the *Big Spring Number Eight (BSNE)* sampler shown in Fig. 4b (Fryrear, 1986). This passive air sampler has been verified under a variety of field conditions (Fryrear, 1986; Stout and Fryrear, 1989; Shao et al., 1993b) for collecting dust and saltating particles at different heights in the near-surface airflow. Goossens and Offer (2000) have compared the efficiency of the MWAC and the BSNE under a variety of wind speeds. These vertical samplers have been used since the 1970s and are accepted globally (Goossens and Offer, 2000; Goossens and Rajot, 2008). A wedge-shaped sampler similar to the BSNE but buried up to the intake has also been proposed for sampling coarse organic material and particles moving in creep mode (Ikazaki et al., 2009). Additionally, the *Marble Dust Collector (MDCO) system* described by Reheis and Kihl (1995) has been successfully deployed to collect deposited dust using low-cost

materials such as a Teflon-coated angel-food cake pan mounted on a steel fence post, glass marbles, and hardware cloth (Fig. 4c).

Although passive collection devices are inexpensive and simple to construct, they can only offer a qualitative overview of the microbial composition in wind-blown sediment as there is no way to quantify the volume of air from which the deposition took place.

3.2. Quantitative collection of dust from the ambient atmosphere

Devices designed to account for the airflow rates (e.g., liters/minute) which allow the quantification of the microbial loading in the atmosphere, including filters, impactors, cyclones, and impingers (Henningson and Ahlberg, 1994) as shown in Fig. 5. Previous studies have recognized strengths and weaknesses among these devices (Griffin, 2007), and a more common problem relies on the use of culture media. The availability of a variety of sampling methods, however, does also raise important issues regarding the validity of comparisons between studies, and some researchers have suggested that the employment of a standard sampling method would result in greater utility of experimental results (Kellogg and Griffin, 2006). A recent study, however, indicated that samples obtained using filtration, impingement, and impaction all resulted in the recovery of the same microbial community (Fahlgren et al., 2010).

Filtration is perhaps the most commonly used method to collect fine dust samples. Different types of filtration media from compressed glass and cellulose fibers to membranes composed of Polytetrafluoroethylene (PTFE), cellulose acetate, and

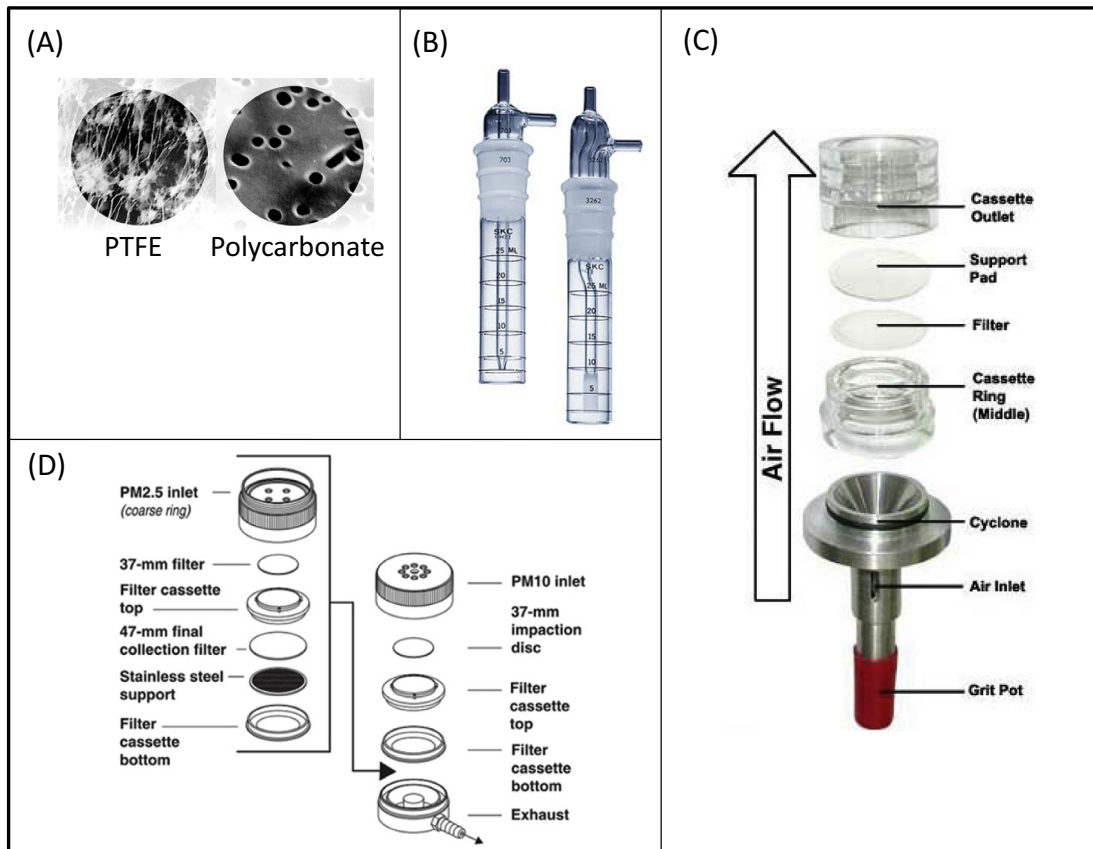


Fig. 5. Devices used for the quantitative collection of dust from the ambient atmosphere: filtration media composed of different materials including Polytetrafluoroethylene (PTFE) or polycarbonate (A); Impingers (B); Impactors (C); Cyclones (D).

polycarbonate (Fig. 5a) have been used to collect dust for subsequent microbial analyses (Kelly et al., 1951; Kellogg et al., 2004; Seedorf, 2004; Griffin et al., 2006, 2007; Miaskiewicz-Peska and Lebkowska, 2012; Favet et al., 2013). Filters are available in pre-sterilized holders and may be easily employed using an aspirated manifold that can be simply and inexpensively constructed. When returned to the lab, membrane filters may be washed and used for molecular (16S rRNA) or culturing assessments or placed directly onto agar culture media for quantification of colony forming units. Miaskiewicz-Peska and Lebkowska (2012) report that the collection efficiency of filters is slightly lower for bioaerosols than for mineral dust, especially at high flow rates. Disadvantages of using filtration to collect microbial samples include possible mechanical damage from fiber filters and desiccation from exposure to large volumes of air passing the cell (Henningson and Ahlberg, 1994; Griffin et al., 2007). By decreasing the sampling time, more viable microorganisms may be isolated, lending credence to the case for reduced desiccation (Griffin et al., 2011).

Impingement is another typically used method for collecting bioaerosols in less dusty environments (Yao et al., 2009; Griffin et al., 2011; Hara and Zhang, 2012). During impingement large volumes of air are drawn through a collection liquid, avoiding the mechanical damage and desiccation issues associated with filters (Fig. 5b). The liquid media may be water or a variety of culture media. One of the biggest advantages to collecting in a liquid medium is the ease with which samples may be split for multiple analyses (Griffin, 2007). The liquid media may also be dyed to stain the microbes and study damage patterns occurring in transport (Hara and Zhang, 2012). Among the disadvantages of impingers include the evaporation of the capture fluid, which must be evaluated constantly and replaced to maintain sampling efficiency, and losses of

microorganisms due to violent bubbling in high volume impingers. Griffin (2007), however, regards high volume liquid impingers as the most versatile and one of the most efficient bioaerosol capture methods available.

Impaction is also commonly used to collect bioaerosols in a highly variable range of environments and with many different design configurations (Fig. 5c). A simple impactor consists of a small plate coated on one side with a sterile sticky substance. Such samplers have been successfully employed on trans-continental and transoceanic flights at altitudes up to 20,000 m (Griffin, 2004, 2008; Smith et al., 2010). Once the collection is accomplished by inserting the impactor plate into the airstream, the organisms are counted by colonies resulting from the placement of the impactor plate on agar containing media. The culture media may also be the impactor plate itself (Kelly et al., 1951) and the collection efficiency is influenced by how completely the petri plate is filled with growth medium (Keller and Shields, 2014). Finally, attempts have been made to use electrostatic chambers on aircraft to precipitate microbe containing particles onto culture media (Kelly et al., 1951) resulting in low viability in the collected particles. More complex aspirated impactors are also used in air mass sampling for bioaerosols. These samplers are aspirated and the intake flow field is oriented so that the air flow is normal to the collection surface. The sampling efficiency with which these impactors operate is a function of the flow velocity and the distance from the orifice to the collection plate. In general, larger velocities and shorter distances to the plate result in greater collection efficiencies (Yao and Mainelis, 2006a,b). Recently, studies using these simple impactors to quantify colony forming units have been coupled with aspirated filter cassettes to allow for DNA analysis of the taxa collected, whether viable or not (Jeon et al.,

2011, 2013). Multi-stage cascade impactors have also been used to segregate particles by diameter classes prior to impaction on the growth media for studies in cattle feedlot environments (Wilson et al., 2002) and during dust incursion events (Schlesinger et al., 2006; Wang et al., 2012). The collection efficiency of many cascade samplers is influenced by wind velocity and constancy of direction and some losses may occur on the walls of the sampling inlet (Henningson and Ahlberg, 1994). Loss of microbial viability can also occur due to impact stress (Griffin, 2007).

Cyclones have also been used to collect bioaerosols (Fig. 5d). These specific devices rely on accelerating the airflow and bending it to force the impact of heavier particles with the cyclone wall. The cyclones may be either dry or have a water stream introduced to increase the collection efficiency (Henningson and Ahlberg, 1994) with the wetted wall cyclone representing a hybridization of the impaction and impingement sampling techniques. It has been noted that longer sampling time with wetted wall cyclones can result in reduced collection efficiencies due to loss on the walls of the cyclone above the wetted zone caused by splash of the circulating collection fluid (King et al., 2009). Significantly for fine dust studies, cyclones are not regarded as efficient collectors of particles less than 3–5 μm in diameter (Henningson and Ahlberg, 1994).

3.3. Collection of eroded sediments from laboratory dust generators and field wind simulators

Various environmentally controlled approaches have proved useful for soil erosion studies, notably the determination of surface erodibility, understanding the effect of soil properties on erosion, and in the collection of a wind eroded sediment sample suitable for investigation of microbiology. Controlled simulation of the

wind erosion process includes the ‘artificial’ generation of dust by agitation of disturbed soil surfaces in the laboratory (Fig. 6; Gill et al., 2006) or by the deployment of portable wind tunnels on natural surfaces in the field (Fig. 7; Van Pelt et al., 2010; Van Pelt, 2013). By providing controlled environments, both of these approaches help to quantify the relationship between microorganisms traveling in dust and those present in the soil source and the identification of microbial fingerprints of the soil source and potential soil functions impacted. These particular approaches can also facilitate the evaluation of how different soil management strategies vary in terms of losses of microorganisms due to wind erosion. Dust generators are especially useful in this regard as, by design, the purpose of these devices is to process straightforward bulk soil samples, thereby allowing a large number of samples, representing different locations, soils, and management practices to be tested (Acosta-Martínez and Zobeck, 2004). One drawback of dust generator systems, however, is that while effective in identifying the type of microbes and other characteristics of soil biology subject to loss by wind erosion, their findings cannot be directly related to actual erosion characteristics, for instance a particular wind speed and/or duration of a natural erosion event.

One apparatus to generate dust under controlled laboratory conditions is the *Lubbock Dust Generation, Analyses and Sampling System* (LDGASS; Fig. 6), and it has been used to evaluate chemical and biochemical dust characteristics as related to several soil sources (Amante-Orozco and Zobeck, 2002; Singer et al., 2003; Acosta-Martínez and Zobeck, 2004; Gill et al., 2006). Analysis of dust samples produced from the LDGASS identified for the first time the protein concentration and activities in dust of enzymes involved in C, P and S cycling and related this activity to the agricultural management history of the parent soils (Acosta-Martínez and Zobeck, 2004). Other dust generating devices include the

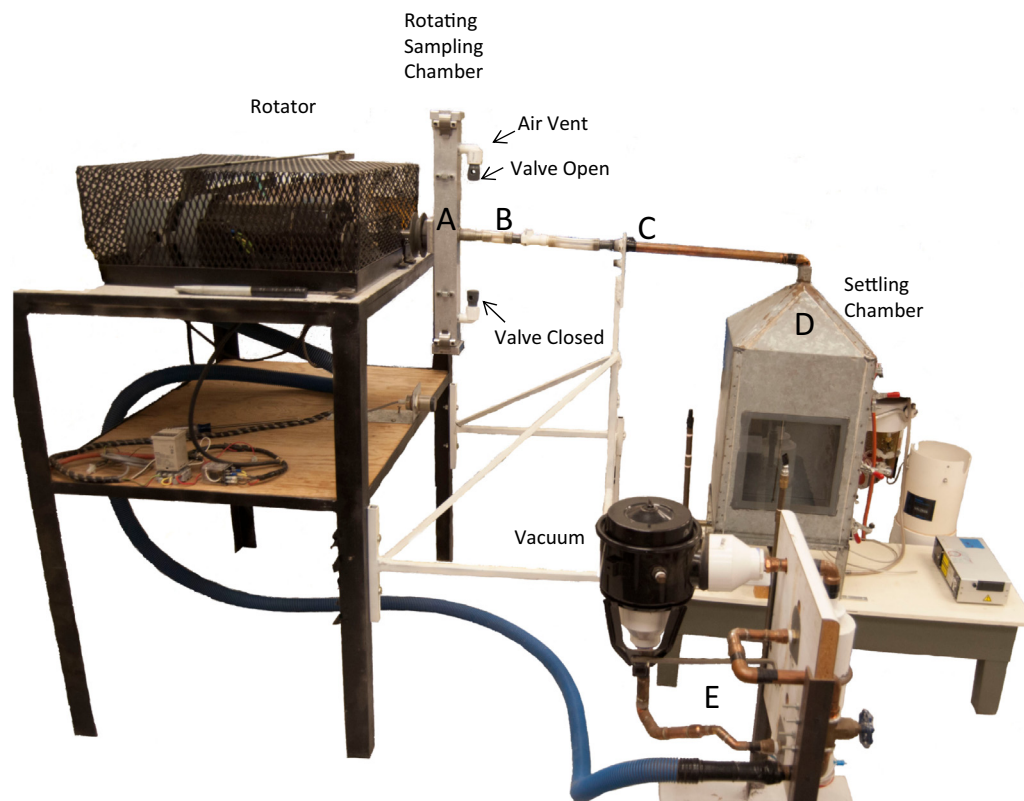


Fig. 6. Collection of eroded sediments can be accomplished from laboratory dust generators. The figure shows the Lubbock Dust Generation, Analyses and Sampling System (LDGASS), which contains: (A) a dust-generating tube, (B) two valves, (C) U tubing, (D) a settling chamber, and (E) two dust filters and an air flow meter to control attached vacuum.

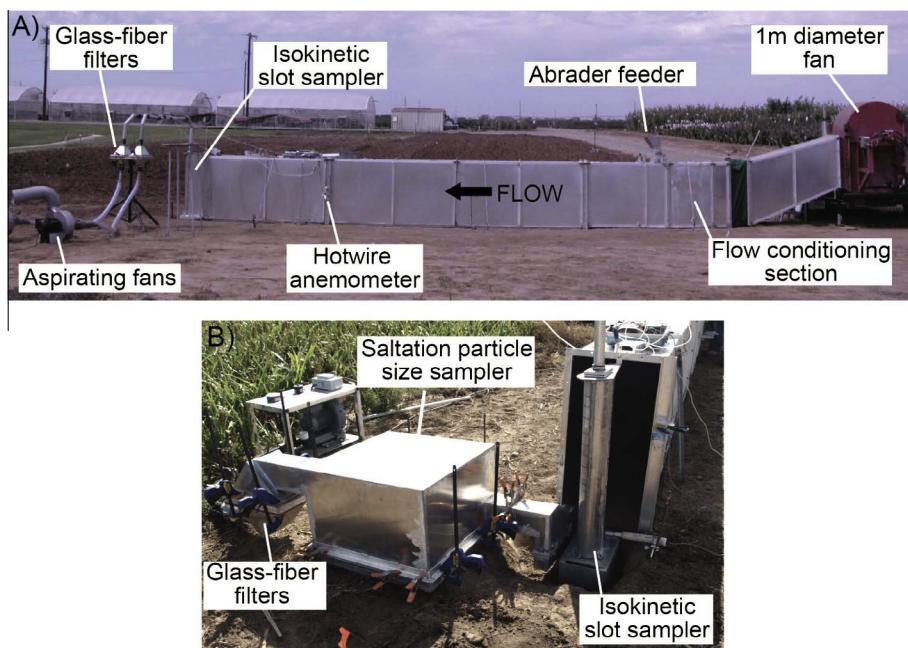


Fig. 7. Collection of eroded sediments in agricultural fields can be accomplished using wind simulators. The figure shows a portable wind tunnel operated by the USDA (A), which has been used in conjunction with an aspirated sediment collecting and separating device that isokinetically draws airflow and transported sediment from the mouth of the wind tunnel (B).

Abrader Cone (Chandler et al., 2002) and the *Easy Dust Generator* (Mendez et al., 2013), which have been used to compare the dust emission characteristics of surface soils.

To obtain wind-blown samples in the field, a portable wind tunnel operated by the USDA has been used in conjunction with an aspirated sediment collecting and separating device that isokinetically draws airflow and transported sediment from the mouth of the wind tunnel (Fig. 7). The sampler employs a series of traps and a large settling chamber to collect both saltation-sized and suspended particles at different sections of the sampler, with the finest suspension-sized material becoming captured on glass fiber filters. This wind tunnel system has been successfully employed to investigate the differences in microbiological characteristics (Gardner et al., 2012) and the chemical composition of organic matter and minerals (Padilla et al., 2014) found in coarse and fine fractions of wind-blown sediments. Such size-related distinctions are valuable as they provide information on the potential distances of sediment and microbiological redistribution.

4. Evolution of the methods to evaluate the microbial communities in wind eroded sediments

4.1. Culture-dependent techniques for dust analyses

Similar to general microbial ecological studies, the first approaches used to characterize the microbes carried in wind-eroded sediments have involved culturing. An important ecological advantage of this approach is that it can reveal how microbes present in aerosols and sediments are carried by wind regardless of their state (vegetative or spore-like) and provide insights into their potential to become active with deposition far from the source. Methods utilized for cultivation of environmental microbial communities have improved greatly in recent years, with the development of selective agars for enumeration of human pathogens and the utilization of growth inhibitors to promote enumeration of specific microbial groups (Kellogg and Griffin, 2006). Kellogg and Griffin (2006) suggested the use of a diversified culture

media such as R2A because it is also a low nutrient agar designed to cultivate stressed heterotrophic bacteria from water and the enumeration of dust-fungal colonies did not differ from other media used for the same dust samples. The main disadvantage of culture-dependent techniques is the fact that the overwhelming majority of microbial species do not grow on synthetic media in vitro and thus remain unexplored (Zengler et al., 2002). The use of culture-dependent techniques for dust analyses will be necessary depending on the purpose of the study and in combination with other techniques that facilitate identification (Smith et al., 2010, 2011).

4.2. Culture-independent or molecular biological techniques for dust analyses

The development of molecular biological techniques has provided the capability to better characterize the diversity of a sediment sample and the ecosystem it represents compared to culture-dependent techniques. Early methods (first generation or Sanger sequencing techniques) involved amplification of the universally conserved 16S ribosomal RNA (rRNA) gene with polymerase chain reaction (PCR), and separation of individual amplicons for sequence analysis using cloning techniques with *Escherichia coli* vectors. This approach, however, was labor intensive, required between months to years of work and it was still incapable of fully characterizing the complex microbial communities in environmental samples. The first generation of molecular methods included DNA fingerprinting approaches such as denaturing gradient/temperature gradient gel electrophoresis (DGGE/TGGE), quantitative or real-time PCR, and other approaches for assessing rRNA variation (ARISA, tRFLPs). TTGE patterns were used by Bruns and Scow (1999) to fingerprint bacterial communities of dust samples from agricultural soils with a history of wheat production at Central Valley of California in the USA. At that time, they pointed out the limitations involved to optimize TGGE conditions to obtain reproducible fingerprints from replicates. Air samples have also been analyzed with a PhyloChip approach (Smith

et al., 2013), which is a popular 16S rRNA gene microarray for microbial surveys. An advantage of rRNA-based phylogenetic DNA microarrays consist on the use of oligonucleotide probes that detect target microorganisms at multiple taxonomic levels of specificity (Loy et al., 2003).

More recently, second generation sequencing techniques allows for massively parallel, high-throughput sequencing (e.g., 454 pyrosequencing, Illumina platforms, and others), resulting in thousands to millions of 16S rDNA sequences. New high-throughput approaches have facilitated a more complete characterization of complex microbial communities, particularly in soil (see Roesch et al., 2007; Acosta-Martínez et al., 2010, 2014). The study by Gardner et al. (2012) pioneered the use of pyrosequencing to explore the diversity of wind eroded sediments. At the time of writing this review, there were only a limited number of studies identifying fungi and/or bacteria carried in dust using high-throughput sequencing techniques such as pyrosequencing (Griffin et al., 2001; Jeon et al., 2011; Gardner et al., 2012; Hara and Zhang, 2012; Favet et al., 2013) and there was no study using the Illumina platform to explore the microbial diversity of wind eroded sediments.

In addition to the use of new techniques for the characterization of the microbial communities of wind eroded sediments, it is important to consider the sampling approach behind the collection of the wind eroded sediments (discussed in Section 3). Depending upon the sampler used to obtain dust samples, it may be possible to use a commercially available DNA extraction kit. With direct collection of sediment, a number of DNA kits designed for soil samples may be used. Liquid samples maybe filtered and DNA may be extracted with water DNA kits. With filter media, members of our team have successfully extracted DNA from large $8 \times 10''$ glass fiber filters by cutting them into strips, eluting with buffer coupled with vortexing and sonication and filtering the elutant through a membrane filter. The filter was then loaded directly into the water DNA extraction kits. Regardless of the approach, we recommend contacting the technical services from DNA kit companies to best fit the sampling approach and type of sample. Similar to soil samples, we also advise storing dust samples at -80°C until extraction or extracting the DNA immediately and storing the DNA at -80°C until sequencing (Lee et al., 2007).

4.3. Future approaches for the characterization of the microbial communities of dust

A potentially beneficial future research direction in wind erosion would see complementary approaches that, in combination with previously used techniques, could provide information not only on the identification of microbes but also on the activity levels (Griffin, 2007; Hoose et al., 2010). Such a focus would address persistent knowledge gaps on the role played by different microbes in the environment, especially in sustaining soil functions (Acosta-Martínez et al., 2010, 2014). In this regard, various ‘-omics’ techniques including metagenomics, metatranscriptomics, proteomics, and volatilomics will aid in identifying the interactions between microbial communities carried in wind-eroded sediments and both the environmental and management factors affecting ecosystem functioning. For example, methods utilizing messenger RNA as a measure of both diversity and activity are showing promise. While extraction of mRNA from soils can be fraught with difficulties and is highly susceptible to contamination by RNA-degrading enzymes (Hurt et al., 2001), mRNA extraction kits are now commercially available and widely used in research laboratories. These kits could become a useful tool to determine the genes expressed by microbial populations present in different dusts. Advances in “-omics” will permit specific linkages to be established between the microbiome and function relevant to

ecological services (e.g., amino acid metabolism, phosphorous transformations, etc.). We recommend using books on “omics” for soil analyses because they explore the specific problems in the application of various omics technologies to soil science and discuss future research necessary to overcome current limitations in this area that will likely be applicable to the study of wind eroded sediments (e.g., “Omics in Soil Science” released in 2014 edited by Nannipieri, Pietramellara and Renella). We believe that as current limitations on the application of metagenomics, metatranscriptomics, and proteomics to soil science are overcome, the field of dust microbiology will benefit significantly in terms of better establishing links between wind erosion, global soil biodiversity and effects on soil functionality.

5. Studies of microbes carried in wind eroded sediments at trans-oceanic or continental scales

Wind is considered the principal agent for the long distance transportation of microorganisms (Yamaguchi et al., 2012) and microorganisms with both beneficial (e.g., nutrient cycling, N fixing, decomposers, antibiotic producers, etc. (Bristow et al., 2007)) and pathogenic capabilities (i.e., human, animal, and plant pathogens) can be transported up to global scales in this way (McTainsh and Strong, 2007; Goudie, 2014) (Fig. 8a). This section will not review in detail microbial transport across continents (see Griffin and Kellogg, 2004; Kellogg and Griffin, 2006; Griffin et al., 2007; Gonzalez-Martin et al., 2014), the global dust cycle (Shao et al., 2011) or the full ecology of dust and its global implications (Field et al., 2009). Our goal is to further highlight the global routes of microbial-dust transport and provide updated findings since the previous reviews (Fig. 9).

An impressive and complex example of microbial transport in dust at the largest scale is the route that begins with North African dust sources, crosses the Atlantic Ocean, and results in deposition in the Caribbean, Southeast United States and the Amazon basin as shown in Fig. 9, route 1 (Swap et al., 1992; Prospero, 1999; Prospero et al., 2005). Over a decade of research by the US Geological Survey (USGS), (Griffin et al., 2001, 2003; Gonzalez-Martin et al., 2014) has documented that hundreds of bacteria and fungi, particularly spore-forming examples, are capable of surviving considerable distances in trans-ocean dust events taking 5–6 days to traverse the Atlantic Ocean. The USGS started the Global Dust Project in 2000 to investigate the relationship of coral reef decline across the Caribbean and the increase in African dust (monitored in Barbados) motivated by a suspected link with the microbial assemblages carried in the dust (Shinn et al., 2000; Griffin et al., 2001, 2011). The causative agent of sea fan coral disease has been identified as a fungi (*Aspergillus sydowii*), shown to be present in air samples taken during periods of greater dust occurrence and carried in by African mineral aerosol outbreaks (Prospero and Nees, 1986; Geiser et al., 1998). Air dust sampling in the Virgin Islands during African dust events reported that the amount of airborne microorganisms can be 2–3 times greater than that found during clear atmospheric conditions (Griffin et al., 2001). Among the microorganisms identified in the Virgin Islands, 25% were plant pathogens and 10% were opportunistic human pathogens (Griffin et al., 2001).

More research on African desert dust in the Caribbean has reported that *Cladosporium* is a dominant fungi detected during dust events (Kellogg and Griffin, 2006), but this may be due to the ubiquitous nature of this taxa in aerosol samples. Kellogg and Griffin (2006) summarize that, among bacteria, mostly Gram-positive bacteria are present, which are known to be more resistant to extreme conditions than other microbial groups due to their capacity to sporulate and are more capable of survival in

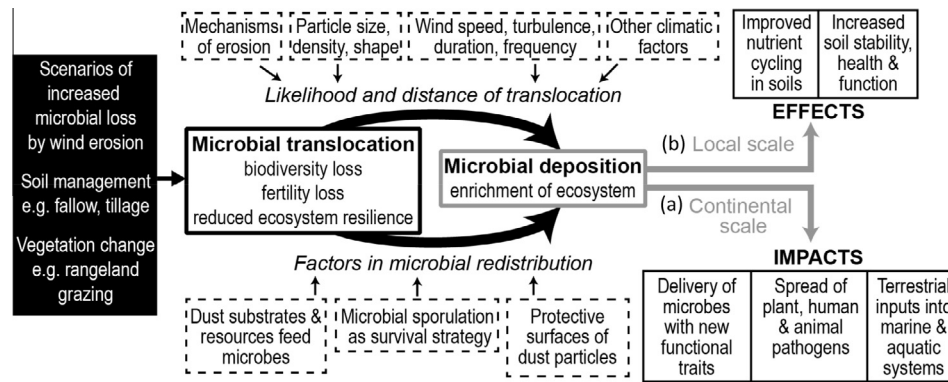


Fig. 8. Implications of wind erosion in terms of microbial translocation and deposition through continental (A) and local (B) scales and factors that affects likelihood and distance of translocation and microbial survival/redistribution.

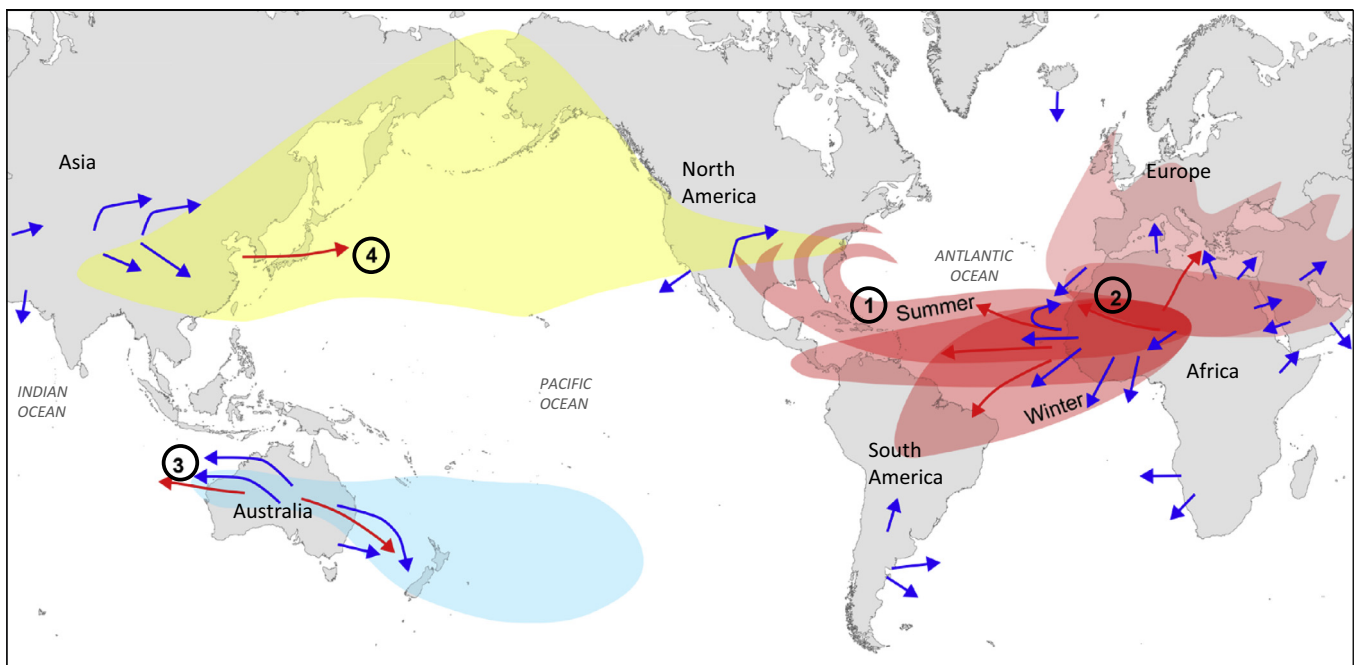


Fig. 9. Map illustrating four major global dust transport-routes (blue arrows and color shaded regions). Our review found descriptions of the microbes transported in pathways indicated by the red arrows within each of the four major routes (Adapted from Kellogg and Griffin, 2006; Muhs et al., 2014).

long distance dust outbreaks. Numerically, there was a predominance of *Bacillus* and *Microbacterium* (Griffin et al., 2003; Prospero et al., 2005). Garrison et al. (2006) also explained it is possible that, in general, we have more information on plant pathogens transported in dust than animal pathogens, and their consensus was that most of the infectious invaders are fungus because of the spores' capacity to resist exposure to UV light and other extreme conditions during transport more than bacteria. Within their examples, most disease outbreaks from dust storms were linked to fungi including potato blight fungus (*Phytophthora infestans*), Lentil anthracnose (*Colletotrichum truncatum*), fungal wheat pathogen (*Puccinia graminis*), sugarcane rust (*Puccinia melanocephala*), coffee rust (*Hemileia vastatrix*) and banana leaf spot (*Mycosphaerella musicola*; Brown and Hovmoller, 2002).

Recent research has characterized the microbiology of dust deflated specifically from the Bodélé Depression in the Republic of Chad, a source area identified as the dustiest place on Earth, as transported to the Cape Verde Islands (Warren et al., 2007; Favet et al., 2013), which correspond to route 2 in Fig. 9. Using high

throughput sequencing techniques combined with classical microbiological methods, Favet et al. (2013) reported a large variety of microbes well adapted to the harsh conditions in deserts. Within fungal populations, they reported that *Ascomycota* was the overwhelmingly dominant fungal group followed by *Basidiomycota* and traces of *Chytridiomycota*, *Microsporidia* and *Glomeromycota*. They found four most abundant bacterial groupings: (1) *Firmicutes-Bacillaceae*, (2) *Actinobacteria-Geodermatophilaceae*, *Nocardiodaceae* and *Solirubrobacteraceae*, (3) *Proteobacteria-Oxalobacteraceae*, *Rhizobiales* and *Sphingomonadaceae*, and (4) *Bacteroidetes-Cytophagaceae*. They also explained the importance of finding *Bradyrhizobium* spp. that nodulate and fix nitrogen in *Acacia* species, the predominant trees of the Sahara, as well as *Herbaspirillum* (*Oxalobacteraceae*), a group of chemoorganotrophic free-living soil inhabitants that fix nitrogen in association with Gramineae roots. An interesting outcome of their study is the identification of relatively few pathogenic strains from which they postulated that African dust may not pose a large threat to public health in terms of microbiological loading.

Australia is a significant source of dust in the Southern Hemisphere and different fingerprints have shown that depending on the transport pathway, Australian dust can be deposited into the Tasman Sea, Southern Ocean, Indian Ocean or terrestrially on New Zealand and Antarctica (Bowler, 1976; Hesse, 1994; McGowan and Clark, 2001; De Deckker et al., 2010). Microbiological evaluation of dust from Australia that traveled from eastern sources via a north-west pathway (corresponding to route 3 in Fig. 9) revealed the presence of Gram-positive bacteria and distributed within the phyla of *Proteobacteria* (25%) and *Bacteroidetes* (23%) (De Deckker et al., 2008). Recent work by Abed et al. (2012) evaluated the microbial communities of dust deflated from inland saline lake sediments and adjacent biological soil crusts of Southern Australia, reporting the presence of *Actinobacteria* and the spore-forming *Firmicutes* in both dust and its sources, but with *Firmicutes* more associated with saline lake sediments.

In the USA, recent research (Smith et al., 2010, 2013) has sampled air in the troposphere (heights up to 7000 m) in the Cascade Mountains of central Oregon with possible origin across the Pacific Ocean, including from Asia as shown in Fig. 9-route 4. The study by Smith et al. (2013) reported DNA concentrations (derived from quantitative PCR assays) of 4.94×10^{-5} ng DNA m⁻³ for bacteria and 4.77×10^{-3} ng DNA m⁻³ for fungi. The researchers explained that the aerosols occasionally corresponded with microbial abundance, most often in the Spring and that viable cells were recovered from 27.4% of bacterial versus 47.6% of fungal samples with 49 different species identified by rRNA. This work indicated that diverse, viable microbial populations including potential plant pathogens such as *Alternaria infectoria* and *Chaetomium globosum* were present after 10 days' transport across the Pacific Ocean in the free troposphere. The study by Smith et al. (2013) identified bacterial assemblages and a number of marine archaea for the first time during the Transpacific wind/plumes and reported higher concentrations of taxa already in the background air such as *Proteobacteria*, *Actinobacteria* and *Firmicutes*. We also found a study that could track several halotolerant bacteria in dust collected in Japan with Asian dust events in 2005–2006 (Hua et al., 2007). The study reported sequence similarity of the 16S rRNA gene for strains of *Bacillus subtilis*, *Bacillus licheniformis*, *Staphylococcus epidermidis*, *Gracilibacillus* sp., and *Halomonas venusta* in dust collected in Japan and Asia.

According to our review of the literature, more research would be beneficial in other dust transport and deposition regions of the world, as the research has been limited by the lack of techniques, resources or attention. However, work continues to evolve, especially as high-throughput sequencing techniques become available to facilitate the analyses of dust and enable better comparisons between regions and across spatial and temporal scales. A recent study provided information of microbial transport in dust from the Saharan that is deposited in NE Spain (Barberán et al., 2014). The study emphasized the seasonal variability found in the microbial communities carried in dust (i.e., communities from the same season tended to resemble each other more than those from different seasons). Their findings also suggested that the three habitats examined (i.e., parent soil, deposition, air–water interface) harbored distinct microbial communities, although airborne samples collected in the Pyrenees Saharan dust outbreaks were closer to Mauritanian soil samples than those collected during no Saharan dust episodes, and overall the three habitats shared 1.4% of the total number of sequences in the dataset. This route identified two (*Alpha- and Beta-Proteobacteria*) or four (*Alpha- and Beta-Proteobacteria*, *Actinobacteria* and *Bacteroidetes*) as predominant taxa in atmospheric deposition and lake neuston communities, respectively, while archaea were minor predominant taxa. Another study identified distinct patterns of microbial richness

and diversity, using pyrosequencing for 16S and 18S rRNA genes, for two dust storm events at the Southeast Mediterranean (southern Israel) according to the origin of the air masses (Katran et al., 2014). For example, an event that had European origin was rich in *Betaproteobacteria* and *Embryophyta* while an event that originated in north-Africa (corresponding more to route 2 of Fig. 9) contained significantly more *Actinobacteria* and fungi (without conifers). At the time of reviewing the literature, studies on the microbiology of dust in South America and Russia seemed to be particularly lacking.

6. Microbial assemblages carried in dust in shorter routes or agricultural field scales

6.1. Studies evaluating microbial communities carried in dust and significance to soil functioning and productivity

A difference from trans-oceanic aerobiology, where the long range dispersal of microbial activity depends on large-scale wind patterns and the stratospheric fate of microbes including pathogens over periods of several days, the impacts of wind erosion also requires consideration at a local scale (Fig. 8b). The focus at this smaller scale can relate in particular to how function and productivity of the source soils are affected by losses of beneficial microorganisms through wind erosion. This area of research has been almost unexplored, with the major limitation being collecting enough dust material to perform culture-independent analysis used to characterize soil microbial communities (see Section 4 on the evolution of methodology for microbial analyses of dust and soil). Currently, DNA extraction kits require less material for analysis and second generation sequencing techniques allows high-throughput sequencing, which will facilitate more studies at this scale for the comparison of microbial communities in both soils and dust. Important areas of studies include investigation of the loss of soil microbial diversity and agronomical-relevant microbial assemblages due to wind-induced soil erosion such as microbes contributing to biogeochemical cycling, carbon sequestration, and stabilization of soils including bacteria involved in nitrogen fixation (e.g., *Rhizobium* and *Bradyrhizobium*) and other pathways of nitrogen cycling (*Nitrosomonas*, *Nitrobacter*, *Nitrospira*, *Nitrovibrio*, spp. etc.) as well as phosphorus transformations (e.g., *Patulibacter*). The evolution of high-throughput sequencing approaches have allowed evaluation of management associated with increases on beneficial microbial assemblages to degradation of lignin and cellulose including fungi and bacterial members of the *Actinobacteria* family, aggregation and phosphorus acquisition (e.g., *Glomeromycota*) (Davinic et al., 2012; Roesch et al., 2007; Acosta-Martínez et al., 2014). Notably, our literature review revealed relatively few studies offering an evaluation of the microbial communities carried in dust from agricultural soils.

A wind tunnel study simulating wind erosion on organic soils under onion production in Michigan revealed a high diversity of bacteria traveling in the wind-blown sediments, i.e., up to 3000 sequences on each sample of eroded sediment (Gardner et al., 2012). In this study, the predominant bacteria in the sampled dust were those typically found in the parent soil, including *Bacteroidetes*, *Chloroflexi*, *Firmicutes*, *Proteobacteria* and *Acidobacteria*. The implications of the loss of these bacterial groups in wind eroded sediments from agricultural soils are critical for their productivity. For example, members of the bacteria phylum *Proteobacteria*, are a genetically and ecologically diverse group of bacteria which perform key ecological transformations of carbon and nitrogen. The specific role of these bacteria in nutrient cycling and in promoting soil fertility is of ecological significance given their detection and evidence of removal in dust-sized eroded

sediments. In Gardner et al.'s (2012) study, *Actinobacteria*, known to be important in the degradation of complex compounds, tended to be more predominant in the parent soils than in the eroded sediments. This finding indicated relatively less predominance of these bacteria in the wind eroded sediments compared to other bacteria.

Other work concentrating on local impacts of erosion includes the study by Acosta-Martínez and Zobeck (2004) which assayed the activities of enzymes involved in C, P and S cycling in samples obtained from the dust generator described in Section 3.3. Looking at three agricultural soils collected under different management practices from a semiarid region, they found a linear positive correlation between the enzyme activities detected in the dust with their soil source. Significantly, this finding indicated that the lower enzyme activity value in a soil sample with a tilled monoculture management history would also be matched by low enzyme activity in its eroded dust sample. These trends provided preliminary information on the suitability of soil microbial-produced enzymes as a biochemical fingerprint of the soil management history, and demonstrated that the fine particle fraction of soil can carry the proteins of the source soil several hundreds of kilometers away. Additionally, the study illustrated the negative impacts of wind erosion on the soil fertility and biogeochemical potential of agricultural soils. Further studies are still required to identify the microbial assemblages and their enzymes carried in agricultural soil dust during actual erosion events in order to translate this information to the function and productivity of the agricultural soil.

Among agricultural landscapes, microbial transport within cattle feedlots is highly confined and localized. In these locations, microbial emissions and transport are more related to uncompacted soil/manure mixtures in open surfaces that are subject to trampling (Grelinger and Lapp, 1996) rather than broader scale to wind induced soil erosion. The impacts therefore have been more associated to health implications for the animals and people directly exposed to the operations of these facilities (Razote et al., 2006; Dungan and Leytem, 2009).

6.2. Microbial distribution within different-sized wind-eroded sediments at local scales

Particle-size is a key determinant of the potential distance for sediment transport by aeolian processes, and soil scientists have recently recognized the importance of aggregate and particle-size distribution on the stratification of soil microbial communities for agricultural land (Davinic et al., 2012). Thus, studies that target microbial population distribution as related to different particle sizes in sediment can reveal important implications for wind erosion on ecological functionality (e.g., Gardner et al., 2012). For example, the preferential association of certain microorganisms with smaller particles provides potential for their transport over greater distances than those carried within coarse particles. Therefore, as the transport of microbial communities varies with particle size, community characteristics will also vary over scales ranging from local redistribution within or between fields to transcontinental distances. Gardner et al. (2012) used 454 pyrosequencing to explore the bacterial composition in wind-eroded sediments generated from three different organic-rich agricultural soils in Michigan using the wind tunnel described in Fig. 7. Not all bacterial assemblages identified in the source soil were detected in the eroded sediments. Some bacterial assemblages were found in both the coarse eroded fraction (>106 µm) and in a finer fraction while others were specific to only the finer dust. Overall, bacterial diversity was higher in the coarser wind-eroded sediment than the finer dust. In general, *Proteobacteria* and *Acidobacteria* were more predominant in the coarse sediment while *Bacteroidetes*, *Cloroflexi*

and *Firmicutes* were more predominant in fine dust. There are certain differences in the findings of the study by Gardner et al. (2012) at local scales compared to a bioaerosol study representing a major dust event within trans-oceanic or continental scales (source Africa) which impacted a coastal city on the eastern Mediterranean Sea by Polymenakou et al. (2008). For example, Polymenakou et al. (2008) reported that large particles were dominated by spore-forming bacteria (e.g., *Firmicutes*) while Gardner et al. (2012) found this group was more predominant in the fine dust from the agricultural soils evaluated. Despite different methodologies of sample collection and analyses, both Polymenakou et al. (2008) and Gardner et al. (2012) found that members of *Bacteroidetes*, which potentially tolerate more extreme and unique environmental conditions (e.g., desiccation and UV radiation), were more abundant in fine particles compared to coarse particles. The redistribution of these organisms as well as those carried in coarse sediments can be of particular ecological significance in the areas where they become ultimately deposited. For particles >100 µm this will be restricted within the eroding field system, or environs immediately downwind of it meaning they may still become lost from a system and negatively impact agronomic productivity.

The growing evidence of different distribution of microorganisms within different sized eroded sediments demonstrates another significant reason for using conservation management practices for agroecosystems that better protect soils from wind erosion. The observed differences from diverse studies indicate that the size-resolving of microbiological analyses is an essential aspect of their study. Tying microorganisms to eroded particle size will allow those microorganisms predominant in dust-sized sediment, and therefore prone to removal by longer range suspended transport, to be distinguished from those more likely to be locally redistributed by saltation flux.

7. Future studies and research directions

Estimates of the cost of wind erosion have been evaluated at approximately \$37.6 billion each year in the US (Uri, 2000). However, this estimate does not account for the loss of ecosystem services associated with the impacts of erosion on soil biota (Baxter et al., 2013). For the soil ecosystem, we found an estimate of the economic benefit derived from soil biodiversity that is around 1.546 trillion US dollars (Maron et al., 2011); this emphasizes the urgency to better understand the impacts of wind erosion in soil biodiversity. More research is necessary to identify unique microbial assemblages that are associated with, for example, a specific region, crop management history, and climate in order to accurately determine the impact of wind erosion on both the soil functions of agroecosystems as well as human health. This information will be critical toward maintaining or increasing soil productivity in order to support future population growth in a changing climate. For regions where climate projections predict an increase in magnitude and frequency of dust activity, declines in soil and air quality due to the aeolian transport of microbial communities may be a significant contributor to threatened food security and human and animal health.

As wind erosion research develops and strives to better understand the sensitive denudation of the soil microbiological component by wind, future progress clearly requires a multi-disciplinary effort that includes sophisticated microbiological assessments of the dust microbiome and the functional traits carried in wind-eroded sediments. Future teams should involve wind erosion scientists (e.g., soil scientists, geomorphologists, agricultural engineers, etc.), soil microbiologists, and atmospheric scientists to fully understand the interactive characteristics between

soil and surface, site management and cropping, wind speeds and weather patterns, and the complex nature of the microbiome. Information is urgently needed to better characterize the dust microbiome for different source soils, for a range of wind-blown particle sizes, and under different land management scenarios responding to climate change. Most simply, sediment samples can be selectively partitioned into different sizes using passive collectors located at different heights in a field (e.g., BSNE or MWAC techniques) or with active samplers (e.g. impactors). Sampling at different heights and/or particle sizes provides particularly valuable information regarding the potential transport distances. Furthermore, the relative ease of sample generation under laboratory (e.g., LDGASS) or controlled field conditions (e.g., using wind tunnels) permits eroded sediment to be readily collected from a range of soils. This is a route toward compilation of a 'source soil library' populated as broadly as possible, allowing for the fingerprinting of potential source soils through their chemical, physical, and microbial properties.

This review has highlighted numerous approaches that are available for the successful characterization of the microbial community in dust and soil samples. Less research has been conducted on the fungal composition of wind-eroded samples despite the recognition of this microbial group in a variety of key ecological services as well as pathogenic effects. Some insights have been gained (e.g., into the variable impact of UV) but it will be of considerable interest to further distinguish the influence of aeolian transport patterns on the relative persistence of dust-carried fungi compared to bacteria. Recent advances in high-throughput sequencing, computational biology, and many "omics" technologies (including genomics, metabolomics, proteomics, etc) are enabling exploration of the composition, function and activities of the communities traveling in dust. Continued technological advances of this type will drive wind erosion research as we seek to better understand the dynamics between microbial translocation and deposition and thus, the effect of aeolian soil loss on soil quality and functioning for agroecosystems.

Federal statement

"Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture." "USDA is an equal opportunity provider and employer."

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