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ORIGINAL PAPER

Science questions and knowledge gaps to study microbial transport and survival in Asian and African dust plumes reaching North America

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Abstract The Sahara in North Africa and the Gobi and Taklamakan deserts in Asia are the primary sources of mobilized dust in the atmosphere, with regional or global airborne transport estimated at 2 to 5 billion tonnes per year. Annual Asian dust plumes take about 7 to 10 d to cross the Pacific Ocean, and often reach the northwest USA between late February and May. In contrast, the peak season for the movement of African dust storms to the southeastern USA is typically June to August, and dust plumes take about 5 to 7 d to reach Florida. Although studies have documented that a wide range of bacteria, fungi, archaea, and viruses in dust plumes reach the USA each year, little is known about temporal and spatial variability in the microbial biodiversity in transoceanic dust plumes, or the effect on the deposition environments. A scoping study (called the Transoceanic Aerobiology Biodiversity Study) was conducted to develop field-based campaigns centered on examining the abundance, diversity, survival, and impact of microorganisms in transoceanic dust plumes arriving in the continental USA from Asia and Africa. This effort identified Science Questions (SQs) and Knowledge Gaps (KGs) that are highly relevant

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toward an understanding of the microbial diversity, transport, survival, and dispersal in transoceanic dusts. *Science Questions* were defined as broad science topics in transoceanic dust plume microbiology that were underexplored by the aerobiology community. *Knowledge Gaps* were defined as specific project-level research questions for each SQ that represented important topics in the study of transoceanic aerobiology.

Keywords Transoceanic dust · Aerobiology · Dust transport · Asian dust · African dust

1 Introduction

Large deserts like the Sahara in North Africa and the Gobi and Taklamakan deserts in Asia are the primary sources of annual mobilized dust in the atmosphere (Prospero 1999; Sun et al. 2001). The current estimate for the quantity of airborne dusts from deserts that make regional or global airborne migrations is 2 to 5 billion metric tonnes per year (Perkins 2001). While the Sahara and Sahel regions of North Africa are believed to be the dominant sources of dust on our planet (i.e., ~ 50 to 75% of the current estimate), there has been an increase in Asian dust activity over the past several decades due to climate change and desertification (Goudie and Middleton 2001; Zhang et al. 2003).

Asian and African dust plumes deposit at least 56 (Yu et al. 2012) and 50 (Prospero 1999; Yu et al. 2015a) million metric tonnes of dust annually on the northwest region of North America and on the Florida/Caribbean region, respectively. Although recent studies have demonstrated that bacteria, fungi, archaea, and viruses can be transported in transoceanic dust plumes (e.g., Griffin 2007; Gonzalez-Martin et al. 2014; Reche et al. 2018; Smith et al. 2013), few studies have attempted to characterize the long-term spatial and temporal changes in microbial biodiversity within the plumes. A recent study by Smith et al. (2013) showed that daily fluctuations in Asian dust storms were directly correlated with increased numbers of microbial species at the high-elevation Mt. Bachelor Observatory, 2.8 km above sea level (ASL) in central Oregon.

Dust-storm activity from Asia to the northwest of the continental USA peaks annually between February and May (Xiao et al. 2002) (Fig. 1). Asian dust events periodically can be massive, extending over much of the continental USA or even reaching central Europe. For example, a large dust event that impacted the west coast of North America in 1998 was reported as having reduced solar radiation at the surface by 30 to 40% and produced a geochemical fingerprint in soil extending inland to Minnesota (Husar et al. 2001). Asian dust storms can take between 7 and 10 d to cross the Pacific Ocean to reach the USA, and the dust events can extend from southern California to British Columbia (Husar et al. 2001). The dust is transported by mid-latitude storm tracks in the free troposphere, and the largest concentrations have been observed at high elevation sites in the western USA (Price et al. 2003; Uno et al. 2009). Asian dust frequently mixes with pollution from Asian industrial sources during transport (Chin et al. 2007), providing a way to track dust pollution plume origins (Jaffe et al. 2005).

Transoceanic dust plumes also emanate annually from North Africa (Fig. 2) and impact air quality in Europe, the Caribbean, and the Americas (Moulin et al. 1997; Prospero et al. 2014; Swap et al. 1992). The annual peak season for the movement of African dust to the Caribbean and southeast USA is June through August (Chiapello et al. 1999; Griffin et al. 2006). Dust storms moving off the west coast of Africa are transported somewhat slower than Asian dust, generally taking between 5 and 7 d to reach the Caribbean and Florida (Griffin 2007). From there, the plumes can reach into the Mississippi Valley, the Appalachian Mts., or extend to the eastern seaboard of North America. While the Sahel region of North Africa is a dominant source of dust, desert aerosols can also originate from populated, agricultural, and biomass burning regions in central and western North Africa, potentially carrying human, plant, and coral pathogens across the Atlantic (Gonzalez-Martin et al. 2014; Griffin et al. 2006; Shinn et al. 2003; Weir-Brush et al. 2004; Yu et al. 2015a).

Recent reports on microbial assemblages in transoceanic dusts have generally relied on culture-based approaches to determine bacterial and fungal diversity (De Deckker et al. 2008; Griffin 2007; Lee et al. 2009). For example, when African dust was visibly present in the Caribbean bulk atmosphere, isolates from 171 bacterial and 76 fungal species were cultured and

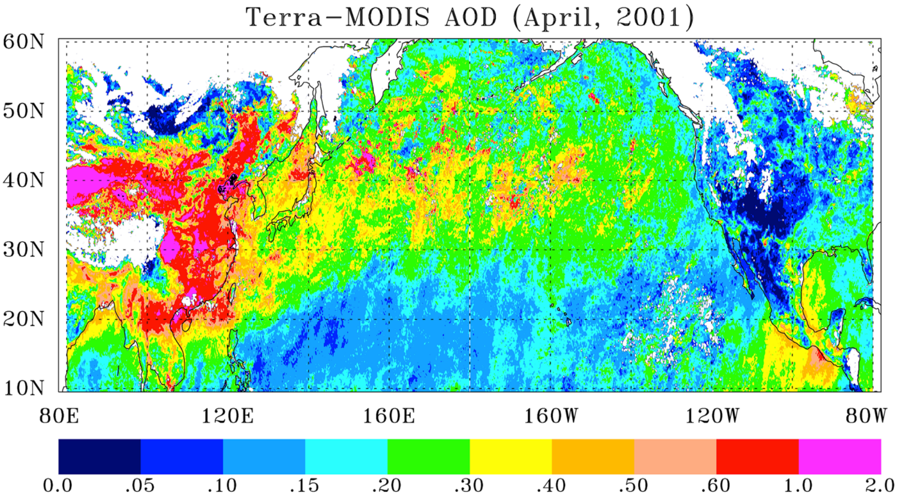

Fig. 1 Terra-MODIS observations of aerosol optical depth (AOD) in April 2001. Intense Asian dust plumes from the Taklamakan and Gobi deserts mixing with eastern Asian pollution swept across North Pacific and reached the west coast of North America in April 2001. AOD is a measure of columnar aerosol loading and was taken from the merged MODIS dark-target and deep-blue aerosol retrievals. (Color figure online)

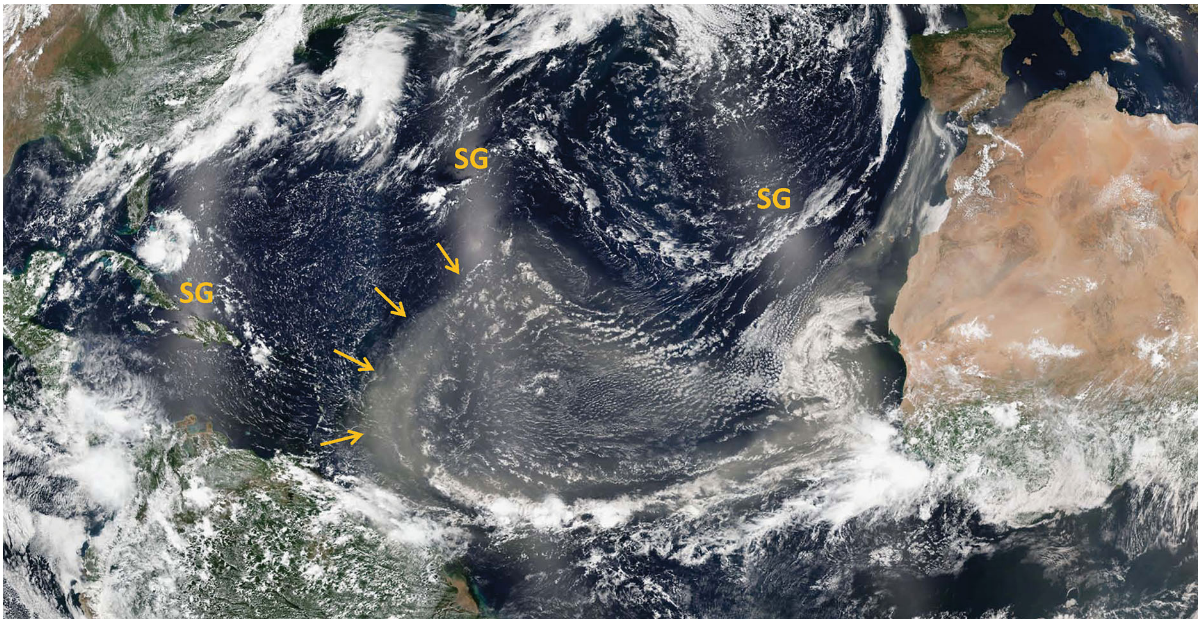

Fig. 2 Composite image obtained on August 01, 2013, by the Visible Infrared Imaging Radiometer Suite (VIIRS) satellite. The sunglints (SG) are from specular reflections of sunlight off of the Atlantic Ocean when the VIIRS satellite was in nadir positions for each pass. Arrows indicate the western extent of the African dust storm on August 01, 2013 (Image: vir_2013213_-Igr_08-01-2013, downloaded from https://earthobservatory.nasa.gov, and cropped to show an African dust plume traversing the Atlantic Ocean.) (Color figure online)

identified from collected dust samples (Griffin et al. 2001, 2003). During non-dust days, the biodiversity recovered in Asian and African air samples were reduced by 1–2 orders of magnitude compared to dusty days (Griffin 2007; Smith et al. 2013). More recently, metagenomic studies have been employed to characterize the biodiversity in Asian and African dust plumes (Gonzalez-Martin et al. 2014; Smith et al.

2013), revealing a taxonomic richness in the atmosphere that is comparable to most marine and surface environments. In the small number of studies ($\sim$ 20) published on Asian and African dust plumes to date, a broad range of organisms has been observed, including bacteria, archaea, fungi, and viruses. A few studies have suggested that human and plant pathogens may be co-transported with African dusts (Gonzalez-Martin et al. 2014; Griffin 2007; Griffin et al. 2001, 2006). Although Asian and African dust events are common, relatively little data exist on microbial biodiversity of the transoceanic plumes, and even less on spatial and temporal changes in microbial biodiversity and correlated health or ecosystem effects.

Between 2016 and 2017, we conducted a scoping study focused on questions related to dust source regions, microbial diversity and viability, remote sensing of dust, and atmospheric processing of dust and microorganisms with respect to microbial diversity in transoceanic dust plumes emanating from Central Asia and North Africa. A series of telecons and two workshops were held at Key West, FL (December 1–2, 2016), and Bend, OR (May 1–3, 2017), to develop the initial white paper on transoceanic dust plumes. The overarching goal of the Transoceanic Aerobiology Biodiversity Study (TABS) was to design a coordinated field campaign to characterize spatial and temporal distribution of microbial biodiversity in Asian and African dust plumes deposited on the continental USA, and to correlate variability in biodiversity to aircraft/satellite remote sensing measurements of global dust and the consequences to ecosystem health in the deposition regions.

We present here a summary of the key *Science Questions* (SQs) (i.e., broad science topics in transoceanic dust plume microbiology that are underexplored by the aerobiology community) and *Knowledge Gaps* (KGs) (i.e., specific project-level research questions for each SQ that represented important topics in the study of transoceanic aerobiology) that emerged during the course of the TABS scoping study. The goals of this paper are to engender discussions about important questions regarding the biodiversity, transport, survival, dispersal, and ecological consequences of transoceanic dust transport.

2 Key science questions and knowledge gaps from the TABS project

We developed and refined six key SQs and up to 10 KGs for each SQ between late-2016 and mid-2017. Once a draft of the SQ and KG white paper was prepared and internally reviewed (completed December 2016), we circulated the suggested research priorities on the aerobiology of transoceanic dust plumes to 29 external and international reviewers in early 2017. From the original list of reviewers, we received 16 responses. The feedback from the general aerobiology community was integrated into the final draft of the SQ and KG document. The final SQs and KGs, plus reviewers comments, were forwarded to NASA's Biodiversity Office program on June 01, 2017. We present here a summary of the completed list of SQs and KGs for the study of transoceanic dust plumes.

2.1 Science Question-1

Are the biodiversities and geochemistries different between Asian and African dust plumes that reach the continental USA?

Rationale: The two transport corridors and transport histories are different in many aspects. The trans-Atlantic dust is transported to the southeastern USA in the summer in a Saharan air layer that is dry and generally below 6 km (Yu et al. 2015a). In contrast, Asian dust is co-transported with pollution during spring months, can be somewhat higher (up to 10 km; Chin et al. 2007; Uno et al. 2009; Yu et al. 2012), and likely transports different species of microorganisms than African plumes. Thus, if the biodiversities and geochemistries do differ between the different transoceanic sources, can the differences be used to measure and map the deposition rates of dust particles from both sources?

Knowledge Gaps:

1. What sampling protocols should be used for the aerial collection of Asian *versus* African dust plumes?
2. What molecular approaches are appropriate to detect microbiota in low biomass aerial samples?
3. Do the collection, sequencing, and bioinformatics protocols vary among target life-forms in the dust

plumes (e.g., bacteria, archaea, fungi, other eukaryotes, and viruses)?

4. How can biological or geochemical factors in the soils from source regions be used to track transoceanic aerosols?
5. Can biological, geochemical, or physical markers in dust plumes be used to distinguish transported microbiota from local airmass components?
6. How do atmospheric chemistry, dust geochemistry, and organic carbon composition affect the survival rates and/or growth of microorganisms during transit? How do these factors change with distance from source regions? How do these factors affect changes in community structure over transoceanic scales?
7. How do biodiversity, trace metal, nutrient, and organic carbon compositions change between source regions and target locations given diverse time/distance/environmental variables in the atmosphere?
8. Are microorganisms attached to dust particles during transport, or are microbial cells and spores transported as free-floating particles?
9. How are dust and microbial cells deposited at the Earth's surface in wet *versus* dry processes? What is the size distribution of the relevant atmospheric particles?

2.2 Science Question-2

How does biodiversity and viability change between source regions and target ecosystems? What are the spatial and temporal fluctuations in biodiversity within arriving transoceanic dust plumes?

Rationale: Few studies have attempted to characterize spatial and temporal changes in microbial biodiversity in Asian or African dust between source regions and deposition sites (e.g., Smith et al. 2013). Data on spatial and temporal changes in dust plume microbiology are required to predict the range of ecological effects along transport corridors. It is plausible that ecological impacts from transported microbiota will be affected by transport distance due to environmental impacts (e.g., UV irradiation, desiccation, diel temperature extremes) on the dispersed microbial cells or spores.

Knowledge Gaps:

1. How do transport altitude, UV exposure, desiccation, temperature, and atmospheric chemistry influence the survival of microorganisms as bioaerosols? Are Asian and African dust plumes exposed to different environmental conditions (altitude, temperature, UV exposure, RH, etc.) during transport that affect the survival of microbes?
2. How can the viability of dust-plume microbiota be assessed without dependence on cultivation methods?
3. How does cell/spore pigmentation affect resistance to UV during transoceanic transport?
4. How does cell viability vary by species?
5. What species of the total transported microbial biomass are viable on arrival?
6. What sampling transects are most effective for capturing dust plume characteristics? For example, can coastal islands be used as the primary upwind locations for sampling (e.g., Japan for Asian dust and Canary Islands for African dust) or should aerosol samples be collected in closer proximity to the source regions (e.g., Gobi desert in Asia and Sahel region in Africa)?
7. Does microbial diversity and viability of transported dust change with altitude? How can sampling be designed to develop 3-D models of dust plumes and transported microbiota?
8. What are appropriate sampling intervals (e.g., hours, days, weeks) required to characterize temporal heterogeneity in the arriving dust plumes?
9. How can microorganisms from source regions be differentiated from extant microorganisms present in downwind air masses and ecosystems?
10. What is the relationship between particle size, geochemical composition, and the abundance of viable microorganisms attached to the dust?

2.3 Science Question-3

Are transported microorganisms metabolically active during transoceanic transport?

Rationale: Metabolic activity and growth have been demonstrated at low pressures for bacteria between 10.0 and 0.7 kPa in both anoxic and oxygenated atmospheres that mimic pressure conditions in the lower troposphere and middle stratosphere, respectively (Schuerger et al. 2013; Schuerger and Nicholson 2016). However, it is unknown if metabolism and subsequent growth are possible when aerosolized microorganisms are exposed to high-UV irradiation and low-humidity conditions typically found in the middle-upper troposphere and stratosphere. If active metabolism and growth are possible for microorganisms during transoceanic transport, then it is plausible that microorganisms may persist by conducting cellular repair of DNA damage and adapt to the stressful conditions present during transport.

Knowledge Gaps:

1. Do Asian and African dust-plume microorganisms carry distinctive functional genetic capacities, i.e., do their metabolic capabilities differ?
2. Can metabolically active microbial cells repair DNA damage during transport caused by UV irradiation, desiccation, and atmospheric oxidants?
3. What protocols are appropriate for characterizing microbial activity in bioaerosols?
4. Can lofted microorganisms undergo genomic adaptation or evolution during transoceanic transport?
5. Can metabolic activity be measured at the moment of capture of transported microbial/dust aggregates?
6. What altitudes are conducive for metabolic activity and growth during transport?
7. How do atmospheric chemistry, dust geochemistry, and organic composition of dust particles affect the metabolic activity of microorganisms during transit?
8. How do microbial activity and metabolic properties change with distance from source regions?
9. What is the upper altitude of a metabolically active aerial biosphere? Conversely, does the atmosphere function only as a transport corridor for dormant microbial cells or spores?

2.4 Science Question-4

What are the ecological consequences from long-range transported microbial and dust deposition on downwind terrestrial and marine ecosystems in the continental USA?

Rationale: Several studies have demonstrated that geochemical nutrients (e.g., Fe^{+3}, PO_4^{-2}) in Asian and African dust plumes can impact marine and terrestrial ecosystems at downwind locations (e.g., Bishop et al. 2002; Yu et al. 2015b). However, few studies have described ecological changes caused by deposited microbial assemblages or communities in transported Asian and African dust. Examples of potential ecological disruptions by arriving African dust include the following: (1) a gorgonian coral disease caused by *Aspergillus sydowii* correlated with African dust deposition (Weir-Brush et al. 2004), (2) increased fluctuations in human pathogenic *Vibrio* spp. in marine waters following heavy dust deposition in south-Florida marine environments (Westrich et al. 2016), and (3) the global dispersion of agricultural pathogenic microorganisms by global dust storms (see reviews by Gonzalez-Martin et al. 2014; Griffin 2007).

Knowledge Gaps:

1. Can geochemical and/or biological inputs from transoceanic dust plumes affect ecological processes in deposition sites in North America, and on what timescales?
2. Do transoceanic dust plumes alter microbial diversity in soils or marine ecosystems on a seasonal basis, or are ecosystem changes only correlated with specific deposition events, and on short timescales?
3. Do seasonal dust plumes cause “microbial shock” to the target ecosystems? Microbial shock is defined as the influx of non-pathogenic microbial species that alter the normal functionality of a target ecosystem. And if microbial shock events occur, can the indigenous microbial communities recover?
4. While many microorganisms may be killed due to transport stresses, can their genomes be genetically scavenged by other microbial species in downwind environments?
5. Are the geochemical inputs from African or Asian dust plumes critical to the survival of specific marine or terrestrial ecosystems in North America?
6. During discrete dust deposition events within target locations, what is the spatial extent of the

dust influence? For example, in a tropical marine system, how does the influence of dust change between the surface microlayer (i.e., geochemistry and microbial community in the upper few centimeters), upper mixed layer (i.e., top 2 m), and benthos region (i.e., coral reefs and ocean floors)?

7. How do local meteorological conditions that coincide with deposition events interact with the biological and geochemical structures of dust plumes to affect marine or terrestrial ecosystems?
8. What are the effects of sea state (e.g., calm seas with stratified water column *versus* windy conditions with a well-mixed water column, water temperature) on microbial survival in marine environments?

2.5 Science Question-5

Are pathogens for human, animal, plant, or other terrestrial or marine species present in transported Asian and African dust plumes?

Rationale: Potential human, animal, and plant pathogens have been reported in Asian (e.g., Smith et al. 2013) and African (e.g., Griffin et al. 2003, 2006) dust samples. Species in a wide range of bacterial, fungal, and viral families have been identified by DNA sequencing of recovered isolates. For example, Griffin et al. (2006) suggested that approx. 20% of all fungal isolates recovered from African dust particles were human, plant, or animal pathogens. In addition, a positive correlation was observed between arriving African dust storms and increased incidence of aspergillosis in gorgonian corals in the U.S. Virgin Islands reefs, but the direct transport of the pathogen, *Aspergillus sydowii* (Weir-Brush et al. 2004), in the dust was not demonstrated. Thus, the increased disease incidence might have been caused by other factors (e.g., increased influx of geochemical inputs to the reef systems by the arriving dusts) and not by direct deposit of the pathogen. These and other studies (see reviews by Gonzalez-Martin et al. 2014; Griffin 2007) have not yet conducted appropriately designed pathogenicity assays to confirm Koch's Postulates (Agrios 2005) for specific strains, and thus, the identified species should be labeled only as presumptive pathogens at this time. However, it should be noted that many plant pathogens have been transported over long distances in the atmosphere (see review by Schmale and Ross 2015). For example, Asian soybean rust came to the southeastern USA in 2004 from South America via Hurricane Ivan (Isard et al. 2005). And, a devastating strain of wheat stem rust recently crossed the Red Sea from Africa into Iran and Yemen (Singh et al. 2011). Additional work is needed to assess the ecological impacts of potential pathogens in aquatic, terrestrial landscape, agricultural, marine, or human habitats in the continental USA.

Knowledge Gaps:

1. Are human, animal, plant, or other terrestrial or marine species pathogens transported in transoceanic dust plumes?
2. Do pathogen diversities and bioloads differ between Asian and African dust plumes?
3. What is the total biomass and spatial distribution of viable pathogens into North America via dust plumes?
4. Are there long-term ecological effects to host species correlated with the influx of emerging pathogens to North America?
5. Do outbreaks of emerging pathogens correlate with transoceanic dust plumes? And do these pathogens become endemic within a target region or remain episodic with dust deposition events?
6. Are pathogenic genetic elements from source regions (e.g., antibiotic resistance or toxin production) laterally transferred to endemic species in downwind ecosystems?
7. Can exposure to atmosphere stresses during transport change the virulence of pathogens?
8. Can specific pathogens detected in transoceanic dust plumes be linked to unique source regions (e.g., dust source regions, countries, oceans, other territories).
9. Can paleo-records (e.g., ice, lacustrine mud cores) be used to characterize the impact of human activity on the prevalence and abundance of pathogens in transoceanic dust plumes?

2.6 Science Question-6

Can ground (e.g., up-looking LIDAR), aircraft, and satellite remote sensing measurements be used to develop a global dust/microbiology dispersal and *survival model using dust particles as proxies for microbial biodiversity in transoceanic dust plumes?*

Rationale: Modeling the global dispersal of microorganisms is still in a nascent stage of development. Microbial transport models will require the development of emission inventories for microbes and an adequate characterization of their sizes and potential changes along the transport route. In contrast, capabilities of remote sensing and numerical modeling the transoceanic dust transport have been substantially enhanced in the last two decades (e.g., Yu et al. 2013), and some lines of evidence exist that microbes may be co-transported with dust. Thus, what is the feasibility of using transported dust as a proxy for fluctuations in microbial abundance in Asian and African dust plumes using the remote sensing of aerosols that can be tracked via total column (e.g., MODIS AOD), vertical profile (e.g., LIDAR), or in situ (e.g., aircraft) measurements?

Knowledge Gaps:

1. What methods are appropriate for correlating dust physical and chemical parameters with co-transported microbiota?
2. How can a global microbiology dispersal and survival model be developed using the existing framework of global dust models?
3. How are microorganisms lofted or injected into the atmosphere? What are the emission fluence rates of the microbial cells from desert environments?
4. What are the optimum approaches of constraining the models through convolving ground, unmanned aerial systems (UASs), and aircraft dust/microbial sampling with up-looking ground LIDAR and down-looking aircraft and satellite remote sensing?
5. What are the optimum airborne and orbital spaceborne assets that are required to characterize major dust properties and transport pathways of high relevance to microbial transport and survival?
6. What modeling approaches are appropriate for integrating all data into one global dust/microbe dispersal and survival model?
7. Can a global dust/microbe dispersal and survival model also explain regional fluctuations in airmass aerobiology?
8. What are the spatial scales for the microbial dispersal models, and at what scales do the models perform with high degrees of accuracy?
9. Can microbial dust transport and survival models be used to predict human, plant, marine, or other ecosystem health risks?
10. Which (if any) existing aerosol modeling tools can be used as a reliable proxy for tracking the dispersal of transoceanic airborne biomass?

3 Discussion

North America annually receives a large amount of transoceanic dust (up to 110 million tonnes per annum (Prospero 1999; Yu et al. 2012) from African and Asian source regions. However, only a few systematic studies have been published on the microbial diversity in these dust plumes (e.g., Gonzalez-Martin et al. 2014; Griffin 2007; Smith et al. 2013), or the consequences of microbial deposition in aquatic, terrestrial, or marine ecosystems (e.g., Weir-Brush et al. 2004; Westrich et al. 2016). It is the high mass of the transoceanic dusts arriving in North America per annum that underpins the urgency for characterizing the microbial bioloads in the transported dusts. In particular, questions relating to ecological impacts of the arriving dust/microbe aggregates must be emphasized in case emerging pathogens or microbial shock events occur more often than are currently understood.

As far back as the mid-1930s, atmospheric samples were collected by aerial platforms (i.e., airplanes and balloons) at ever increasing altitudes (e.g., Rogers and Meier 1936) in an effort to characterize the upper boundary of the active biosphere. However, the upper limit of the active aerial biosphere has not been established, although some data suggest that this limit may be ≤ 41 km (see review by Smith 2013). Others have raised the question of whether the atmosphere acts like an ecosystem or merely as a conduit for aerial transport between ecosystems (Diehl 2013; Smith 2013). Recently, two potential metabolically conducive regions have been proposed in the lower troposphere (up to 7 km) and upper stratosphere (between 30 and 45 km) based on the interactive effects of low-temperature (− 18 °C; see Rummel et al. 2014) and low-pressure (0.7 kPa; see Schuerger et al. 2013) limits for microbial growth (Schuerger and Nicholson 2016).

The aerobiology SQs and KGs introduced here are offered as a set of organizing concepts in the study of transoceanic dust/microbe transport in order to generate a conversation in the aerobiology community on research priorities and methods to identify the upper boundary of the active biosphere and to characterize the ecological effects of deposited dust/microbe aggregates. The SQs and KGs introduced here are not a definitive list of all possible research questions that could be addressed by aerobiologists. Instead, the conceptual analysis offered here is intended as an initial framework for evaluating priorities in the rich research landscape of transoceanic dust/microbe transport, survival, activity, ecosystem impacts, and transport modeling.

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Authors contribution The study was initially conceived by AS, DJS, and DG. AS coordinated all aspects of the work, including preparation of the original draft of the manuscript, compiling all editorial suggestions by the coauthors and external reviewers (see Acknowledgments section), and the preparation of the figures. HY assisted in compiling data and creating the graphics in Figs. 1 and 2. All coauthors contributed to the creation and editing of individual Science Questions and Knowledge Gaps through a series of telecons, email exchanges, and two TABS workshops held in Key West, FL (December 2016), and Bend, OR (April 2017).

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Compliance with ethical standards

Conflict of interest All coauthors have confirmed via emails to the corresponding author that there were no conflicts of interest in participating in the TABS Scoping Study; the TABS workshops in Key West, FL, and Bend, OR; nor the preparation of the manuscript.

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