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MINIREVIEW

Multiscale Airborne Infectious Disease Transmission

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ABSTRACT Airborne disease transmission is central to many scientific disciplines, including agriculture, veterinary biosafety, medicine, and public health. Legal and regulatory standards are in place to prevent agricultural, nosocomial, and community airborne disease transmission. However, the overall importance of the airborne pathway is underappreciated; e.g., the U.S. National Library of Medicine's Medical Subjects Headings (MESH) thesaurus lacks an airborne disease transmission indexing term. This has practical consequences, as airborne precautions to control epidemic disease spread may not be taken when airborne transmission is important but unrecognized. Publishing clearer practical methodological guidelines for surveillance studies and disease outbreak evaluations could help address this situation. To inform future work, this paper highlights selected, well-established airborne transmission events, largely cases replicated in multiple, independently conducted scientific studies. Methodologies include field experiments, modeling, epidemiology studies, disease outbreak investigations, and mitigation studies. Collectively, this literature demonstrates that airborne viruses, bacteria, and fungal pathogens have the ability to cause disease in plants, animals, and humans over multiple distances, from near range (<5 m) to continental (>500 km) in scale. The plausibility and implications of undetected airborne disease transmission are discussed, including the notable underreporting of disease burdens for several airborne-transmitted diseases.

KEYWORDS atmosphere, airborne infectious disease, aerosol, droplet nuclei, inhalation exposure

Air is not a sterile medium, as initially demonstrated in the early-19th-century experiments of Louis Pasteur. Bacteria and fungi are ubiquitous in the atmosphere and reach concentrations of about 10^4 and 10^3 cells m^{-3} in air, respectively (1–4). These facts are well understood and elucidated within the field of aerobiology, which has documented the life cycles, including the atmospheric transport and dispersion, of naturally occurring airborne viruses, microorganisms, and bioaerosols (5–7).

Both near-range and long-range airborne infectious disease transmission events are well documented in the plant biology, veterinary and agricultural biosafety, clinical medicine, and public health literature. However, these findings are not always widely disseminated across these specialties or to the wider scientific community. As a consequence, the true scope and characteristics of airborne disease transport can be underappreciated. This has practical consequences when airborne disease transmission is not recognized during a disease outbreak, and so precautions against airborne disease transmission to control epidemic disease spread may not be taken.

To assist the scientific community in better understanding the characteristics of long-distance airborne infectious disease transmission and its prevention and control, we provide here a selective, documentary review of well-established examples of airborne disease dispersions sorted according to transmission distance scale. The examples include the near-range-scale (<5-m) spread typically seen in clinical medicine up to continental-scale (>500-km) transmission. Due to its rapid development, this review

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does not review the severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2)/coronavirus disease 2019 (COVID-19) literature, but it highlights key prior coronavirus studies.

ATMOSPHERIC INFECTIOUS DISEASE TRANSMISSION

Near range (<5 m). In the medical context, near-range airborne disease spread (<5 m) is common and occurs when infected individuals generate large quantities of infectious droplet particles (and droplet nuclei) when coughing or sneezing (8, 9). Tuberculosis (TB) and measles virus (rubeola) have long been known to transmit over this distance (10, 11). *Bordetella pertussis* (whooping cough), varicella-zoster virus (chickenpox), mumps virus, rubella virus (German measles), and *Neisseria meningitidis* (bacterial meningitis) are additional examples (12, 13). This near-range airborne disease spread is known to contribute to the overall disease burden as lower respiratory infections and tuberculosis are the 4th and 10th leading causes of death worldwide (14). Finally, 2% of U.S. adults (6.5 million) are hospitalized each year for the treatment of community-acquired pneumonia caused in part by the near-range airborne transmission of common bacteria and viruses, including influenza virus (15). We note that the airborne disease transmission pathway can contribute to overall disease transmission, even when other—droplet (>5-μm-aerodynamic-diameter particles) and contact—pathways are important (e.g., see references 16 and 17).

With respect to pathogenic coronaviruses, avian infectious bronchitis virus (IBV) disease was the first near-range airborne-spread disease to be clinically recognized in 1931. Currently, IBV is a high-mortality-rate upper respiratory infection with a global economic impact on poultry production (18). IBV has multiple routes of transmission, including inhalation, drinking of contaminated water, and direct contact (19). Vaccines are a mainstay of IBV disease control (20), with multiple strain-specific vaccines in routine use to improve morbidity and mortality. Live IBV vaccines are given by spray or aerosol or in drinking water (19). Humans can be infected, but human disease is not documented (21).

Human-pathogenic coronavirus infections were first identified in the early 1960s, and 4 strains (human coronavirus strain 229E [HCoV-229E], HCoV-OC43, HCoV-NL63, and HCoV-HKU1) are globally distributed (22, 23). These pathogens pose a substantial burden due to days lost from work and school and medical costs (23, 24). Infections occur at all ages, but disease is more severe in young children, the elderly, and patients with underlying medical conditions (25–28). While there is limited published research on the airborne transmission pathway, we note that these viruses are known to persist in the atmosphere (29) and collectively constitute the third most common cause of acute respiratory tract disease (30). Notably, a single population-based prospective community survey with active case finding documented a large HCoV-229E outbreak in which one-third of the community was infected and respiratory illnesses in the community doubled. Most cases were upper respiratory illnesses; however, 40% also had lower respiratory tract involvement (31).

Short range (5 m to 50 m). The airborne spread of human pathogens within buildings has been particularly well documented in both schools (32, 33) and medical care facilities (34–36). Indeed, Riley et al.'s experimental studies of clinically active tuberculosis are classic examples of airborne disease transmission. Air from a clinical TB ward of active human cases was routed to an animal exposure chamber located in the building ventilation duct system distant from the patients under treatment. Typical clinical disease subsequently developed in the test animals (10). In a follow-up study with a prospective case-control design, unprotected exposed animals again contracted tuberculosis, but an animal control group with UV-irradiated air did not (37). The latter study findings have been replicated (38, 39).

Separately, an expert panel review noted 10 studies documenting airborne disease transmission in medical settings (hospitals, clinics, and nursing homes) (34). These studies showed a direct contributory role of ventilation rates and building-related airflows in the pattern of the airborne spread of disease at distances farther than could

have been spread by an infected person coughing, sneezing, or breathing. Airborne outbreak examples included *Mycobacterium tuberculosis*, rubeola virus (measles), varicella-zoster virus (chickenpox), and variola virus (smallpox) (37, 40, 41). The U.S. Centers for Disease Control and Prevention also defines tuberculosis, measles, and chickenpox as airborne-transmitted diseases, which require formal isolation precautions in hospital settings (42).

We note that within hospital settings, high-infection-risk patient areas are designed with physical and ventilation barriers to minimize airborne infections. These building design features include, but are not limited to, permanently sealed hospital room windows and HEPA air filtration (34, 43–45). UV germicidal irradiation is also routinely used to reduce airborne disease risk in hospitals and other facilities, especially for tuberculosis control (46).

With respect to pathogenic coronaviruses, the 2003 Hong Kong SARS epidemic provided several notable examples of short-range airborne disease transmission. The first was a large hospital outbreak (34, 47, 48). Disease attack rates were highest (65%) in the same treatment bay (<5 m) as the index case (an undiagnosed SARS patient), slightly lower (52%) in a nearby treatment bay (10-m nominal distance from the index patient) that readily exchanged air with the index patient treatment bay, and much lower (18%) in patient areas (10-m nominal distance from the index patient) where the air was less well shared with the index patient treatment bay. The temporal and spatial spread of infection was consistent with computer modeling of building airflows and particle physics. Two other localized outbreaks were (i) transmission over a distance of several meters while flying on an airplane (49) and (ii) spread within high-rise residential buildings and between buildings 50 m apart (50, 51). Subsequently, the possibility of airborne disease transmission was investigated in a 2015 hospital outbreak of Middle East respiratory syndrome coronavirus (MERS-CoV) (52).

In plant biology and biosafety studies, short-range (<50-m) airborne particle and pathogen transmissions are thought to be the most frequent scenarios. For example, initial median windborne (anemochorous) plant seed dispersals are typically short (<10 m), but the 95th percentile for airborne seed dispersion occurs over longer distances and varies significantly by species (53–55). In plant pathology studies of wheat stripe rust (*Puccinia striiformis* f. sp. *tritici*) and the wind-dispersed banana plant fungus *Mycosphaerella fijiensis* (56, 57), single-field experimental studies are used to model initial local-plot/field-level airborne pathogen dispersal and clearly demonstrate short-range airborne infection transmission. These studies have also been used to develop source (emission) estimates for larger-scale, long-distance disease spread and propagated epidemics (57).

Medium range (50 m to 500 m). Epidemiological disease outbreak studies provide human data for medium-range airborne disease transmission. Well-documented examples include ongoing community-level outbreaks of Legionnaires' disease (*Legionella pneumophila*) from building cooling towers (58–66), Q fever (*Coxiella burnetii*) transmission from livestock farms to their surrounding communities (67), as well as histoplasmosis (*Histoplasma capsulatum*) and *Aspergillus fumigatus* and *A. flavus* dispersions from construction work or sites where contaminated soil is disturbed (68–74). On this spatial scale, best practices and regulatory standards aim to reduce the risk of the airborne transport of infectious particles. Guidelines exist to control occupational and environmental construction-associated dust during building renovations. In regions of endemicity, these guidelines are codified into law to reduce infections (75, 76).

Newcastle disease (ND) virus, an avian paramyxovirus, is one well-known example of an airborne disease. It is a commercially important pathogen globally in poultry production (77–80). ND has the potential to transmit over medium-range distances, as demonstrated by positive viral cultures of air samples at 60 m in field experiment studies (80). Recent experimental work has reconfirmed an airborne transmission route for ND virus (78), and some live-virus vaccines are delivered via fine aerosolized powders (79). While vaccines are a mainstay of disease control, the disease remains endemic in

many countries (78). Studies have shown that negative air ionization and dilute viricidal chlorine aerosols are useful in preventing ND virus infections (81, 82).

Porcine reproductive and respiratory syndrome virus (PRSSV) disease in swine also has global economic impacts despite the availability of vaccines (83). Medium-range PRRSV airborne transmission at distances of 80 to 120 m has been clearly demonstrated in experimental field studies (84, 85). Field studies and a long-term controlled production model prospective study with positive and negative controls demonstrated the efficacy of air filtration to protect animals in farm buildings from airborne PRRSV (84). Indeed, air filtration of farm buildings is effective at controlling pandemic PRRSV infections, even when conventional controls, intended to protect against other infection pathways, have failed. Building air filtration systems have since become an industry standard in U.S. pig breeding and production (86). Filtration has also shown efficacy in reducing emissions of airborne methicillin-resistant *Staphylococcus aureus* (MSRA) from farm buildings (87).

Furthermore, with respect to potential medium-range airborne disease transmission, there is also a long-standing, yet still evolving, literature that supports existing regulatory standards aimed at protecting workers and nearby communities from airborne pathogen dispersal from environmental sites such as composting facilities, sewage processing and wastewater aerosols, agricultural gray water aerosols, livestock feed yards, and land applications of manure (88–96). As one example, a protective ring of up to 250 m is commonly specified under the assumption that existing air monitors detect little to no viable infectious airborne material beyond that point (92, 93, 97).

Long range (500 m to 500 km). Long-distance atmospheric infectious disease dispersions, termed LDD in the plant biology and agricultural biosafety literature, have been shown to play crucial ecological roles in plant species invasion, migration, and survival as well as plant pathogen dispersal (98–104). In veterinary biosafety studies, this field is well advanced in its understanding of the connection between airborne pathogen transport and dispersion and disease epidemics (105–108).

Biosafety experimental field studies also clearly demonstrate kilometer-range dispersion of plant pathogens. For example, fungal plant pathogens are an increasing threat to world food security (109). A wind-dispersed banana plant fungus (*Mycosphaerella fijiensis*) field experiment documented 1-km airborne dispersal in one generation (56). Studies such as these together with the above-mentioned plant biology and biosafety literature demonstrate that airborne infection probability initially decreases rapidly with distance, which is then followed by a regimen of lower-probability kilometer-range LDD events (termed a "long dispersion tail").

In the United States, long-range airborne spread of economically significant plant disease across the landscape is an ongoing concern. Predictable seasonal airborne pathogen incursion pathways across the continent are well identified and routinely monitored to protect crop yields. These continental-scale incursions typically proceed in a stepwise series of shorter (long-range) airborne dispersions. Chief examples are the seasonal airborne south-to-north U.S. dispersion incursion pathways across the Midwest Great Plains for wheat stem rust (*Puccinia graminis* f. sp. *tritici*), the pandemic spread of tobacco blue mold spores (*Peronospora tabacina*) across the eastern United States, and seasonal U.S. airborne invasion by soybean rust (*Phakopsora pachyrhizi* Sydow) (103, 110–113).

In the veterinary literature, there are many examples of probable kilometer-range airborne infection transmission. For example, Newcastle disease virus, equine influenza (A/H3N8) virus, highly pathogenic avian influenza A (H7N7) virus, PRRSV, and *Mycoplasma hyopneumoniae* are important ongoing diseases, and each has evidence for long-range airborne transmission (114–119). The best-described long-range airborne-transmitted disease in animals is foot-and-mouth disease virus (FMDV), an economically significant disease of veterinary livestock. Long-range FMDV aerosols have contributed to a number of costly, regional-scale disease outbreaks in Europe, including airborne transmission from continental Europe to the United Kingdom (120, 121).

FMDV research has motivated the development and testing of scientific models and forecasting capabilities for long-range infectious aerosol dispersions with the aim of limiting epidemic spread (105–108, 122–126).

In the human epidemiology literature, many well-documented examples exist for airborne disease transmission over distances of >1 kilometer downwind. *Coxiella burnetii*, an endemic disease of ruminants and livestock, is also the cause of Q fever in humans (127). Long-range outbreaks of airborne disease spread from animal farms to human populations have been documented in many European countries (128–132). Notably, the recent regional-scale Q fever epidemic in 2007 to 2010 in the Netherlands was caused by infectious aerosols emitted from small-animal farms (133–137). The epidemic resulted in 4,000 clinical cases and 2,700 hospitalizations (135). A more recent 2018 follow-up of this outbreak showed that among the 519 chronic Q fever cases identified, 86 patients had died (138).

Legionella pneumophila dispersions from building cooling towers are also an ongoing source of kilometer-range community Legionnaires' disease outbreaks despite the introduction of preventive legal regulations for cooling equipment maintenance (63, 139). Significant kilometer-range airborne Legionnaires' disease outbreaks have been reported in many countries, including the United States, France, Norway, Sweden, and Spain (58–62, 64–66, 140–143), and airborne disease models have been developed (144).

The fungal pathogens *Histoplasma capsulatum* and *Coccidioides immitis* and *C. posadasii* cause significant human disease when inhaled (histoplasmosis and coccidioidomycosis [valley fever], respectively). Both are endemic in the United States: histoplasmosis in the eastern and midwestern states and coccidioidomycosis in the American West and Southwest (72, 145). Based on observational epidemiological studies, citywide airborne outbreaks of histoplasmosis are suspected to have occurred, two at a community level (146–148). A series of three large-scale histoplasmosis outbreaks that occurred in urban Indianapolis, IN, may also have resulted from airborne dispersion (149–151).

Coccidioidomycosis occurs after inhalation of fungal spores, which are widely distributed in southwestern U.S. soils (152, 153). Forty percent of exposed persons will have clinical symptoms, ranging from an influenza-like illness to disseminated disease and chronic meningitis. Symptomatic disseminated disease requires aggressive treatment and has increased rates of hospitalization and mortality (154, 155). Desert dust cloud dispersions containing *Coccidioides* spores are an important ongoing cause of disease, and legal standards prevent high-risk persons from being assigned to prisons in areas of endemicity (156). In addition, long-range airborne dust cloud *Coccidioides* dispersal events triggered by natural disasters have caused significant regional coccidioidomycosis outbreaks in the U.S. state of California (157). Kilometer-scale airborne transmission occurred in the Los Angeles area following the 1994 Northridge earthquake, where strong aftershocks generated landslides on the slopes of the Santa Susana Mountains, resulting in large, contaminated dust clouds (158–160). These clouds were blown by ambient winds into the urban Simi Valley and Ventura County areas, causing a coccidioidomycosis outbreak (203 total cases, 55 hospitalizations, and 3 fatalities).

Continental range (>500 km). Continental-scale airborne dispersion events, especially plant seed dispersions, have been well studied and influence the spread of invasive species, metapopulation dynamics, and plant diversity (54, 100, 101, 161). Continental-scale transport of common environmental bacterial species, either on normal atmospheric air currents or in association with dust cloud dispersions, has also been well demonstrated (2, 162–164). As one example, bacterial communities from the Saharan desert are known to travel airborne to high European Alpine lakes (165, 166). Pathogenic bacteria have also been observed in the ambient atmosphere, including plant, animal, and human pathogens (167–169). Furthermore, airborne transmission of *Neisseria meningitidis*, a major cause of meningitis worldwide, is under investigation in

the endemic Sahel region of North Africa as outbreaks occur most often in dry months with frequent dust storms (164, 168).

Airborne continental-scale disease spread often proceeds as a series of sequential long-range airborne transmission events over the landscape (saltatory transmission). However, individual continental-scale airborne disease transmission events, i.e., a single airborne plume transporting pathogens more than 500 km, are also documented in the literature (98, 110, 170, 171). Most but not all of the existing examples are from agricultural biosafety studies where these events are termed "single-step" LDD pathogen invasions (98). These types of events are thought to be rare and often associated with extreme weather events or natural disasters (110, 157). However, routinely occurring, single-step LDD events could be more frequent, although this possibility has not been systematically investigated. For example, a sentinel LDD study of airborne plant-pathogenic fungi (*Erysiphe graminis* f. sp. *hordei* [barley mildew] and *Erysiphe graminis* f. sp *tritici* [wheat mildew]) demonstrated transmission over a distance of 650 km across the North Sea from Great Britain to Scandinavia (171). Samples were obtained using disease-free receptor plant populations and compared to unexposed control plants, and a multiyear series of samples was obtained in the regions with the highest-expected-transmission probability.

A major weather-related single-step LDD event was the 2,000-km airborne dispersion of Asian soybean rust (*Phakopsora pachyrhizi*) across the Caribbean from northwestern South America to the United States during Hurricane Ivan (110). This 2004 event marked the invasion of Asian soybean rust into the North American continent. The event was anticipated as the spread of Asian soybean rust from Brazil northward in South America was being monitored and Brazil had lost a significant fraction of its soybean production to this pathogen. Among other measures (and prior to the event itself), predictive atmospheric dispersion modeling for potential airborne transport to the United States during tropical cyclone seasons was conducted, and the U.S. Department of Agriculture deployed disease forecasting systems and field tested a detailed response plan for use in the event that soybean rust was identified (110). Soybean rust was detected infesting soybean fields in Louisiana (as predicted) within 2 weeks after Hurricane Ivan had passed. Subsequently, Asian soybean rust has remained endemic in many southern states, especially in the initial epidemic outbreak area (172).

A clear human disease example of single-plume continental-scale airborne disease transmission is the 600-km dispersion of *Coccidioides immitis* spores in California, which resulted in widespread coccidioidomycosis outbreaks (173). In this 1977 event, a 160-km h^{-1} windstorm scoured 15 cm of *Coccidioides immitis*-contaminated topsoil from Kern County, located in the southernmost basin of California's San Joaquin Valley, carrying a resulting dust cloud to an altitude of 1,500 m (see the JPEG image [890 by 690 pixels] at https://geochange.er.usgs.gov/sw/impacts/geology/dust/desertdust.jpeg). The dust was transported northward and dispersed over an 87,000-km^2 area (150, 170, 173, 174), burying freeways and shutting down interstate transportation. There were 3 immediate storm-related fatalities, and 3 firefighters died in a forest fire spread by the strong winds. Sacramento, a low-endemicity area 500 km to the north, experienced a large coccidioidomycosis outbreak (115 cases and 6 fatalities reported versus a background incidence of 0 to 6 cases per year). Overall, 15 California counties northward in the dust cloud dispersion area reported a 10-fold increase in coccidioidomycosis cases, and 9 counties reported lesser increases (173). This 1977 *Coccidioides immitis* dispersion, with a total of more than 379 reported cases, serves as a historical benchmark for the potential magnitude of coccidioidomycosis cases from a significant dust storm (170). Integrated coccidioidomycosis case surveillance and dust storm forecasting are currently standard in U.S. areas of endemicity (175).

DISCUSSION

Historically, the importance of the airborne disease transmission pathway has been well recognized (11, 176–178), but more recently, work in this area has not been

prioritized. Prior reviewers have suggested that the motivation to understand the airborne infectious disease transmission pathway has waned over time due to (i) the availability of antibiotic therapy and immunizations for key diseases of interest and (ii) the difficulty in detecting infectious pathogens in airborne particles relative to water, surfaces, or large-droplet sprays (179).

Regardless of the cause, the multiscale transmission of airborne disease is likely currently underappreciated, even though the cumulative body of literature across the scientific disciplines is large. Our experience is that it is quite difficult to locate all pertinent papers in the medical and public health literature, even for a single disease. A contributing cause may be the lack of standard indexing terms for airborne disease transmission. As an example, the U.S. National Library of Medicine's Medical Subjects Headings (MESH) indexing system lacks MESH terms for airborne disease transmission. For comparison, there are MESH terms for "fomite," "waterborne diseases," "vectorborne diseases," "sexually transmitted diseases," and "foodborne diseases." Currently, MESH terms in use to code airborne transmission articles are generic ones such as "air microbiology," "respiratory tract infections/diseases," and "inhalation exposure." To facilitate Internet searches in the future, we suggest that authors add the phrase "airborne disease transmission" or "airborne infection transmission" to article abstracts.

Most of the reports cited here are epidemiology studies where the airborne pathway is the predominant means of disease transmission and where researchers have excluded other disease transmission pathways, i.e., single-pathway outbreaks. There are relatively few published reports documenting airborne transmission as a secondary, contributory cause of disease, although important examples exist (e.g., see references 115, 119, and 180). For opportunistic pathogens, in which a disease can transmit through multiple pathways, not investigating or reporting instances of secondary airborne disease transmission may serve to reduce the number of airborne disease reports in the literature. Airborne transmission as a partial cause of disease outbreaks may be common, and more attention to this topic is warranted in the literature.

Our knowledge of the infectious disease population impacts is primarily based on surveillance systems that rely on reported, diagnosed cases. These systems are useful for monitoring trends over time and for identifying disease outbreaks. However, they can underreport population incidence and prevalence and so risk creating the impression that a particular disease is uncommon and lacks a significant population-level impact. This impression could be a disincentive to disease-specific research and airborne transmission pathway research in general.

As an example, Q fever is thought to be uncommon; however, U.S. nationally representative data show that 3% of the population have positive Q fever serology at any one time, which corresponds to an estimated 6 million adults (181). Similarly, Legionnaires' disease pneumonias are believed to be 10 times more common than what is currently being diagnosed (182). Notably, histoplasmosis, like coccidioidomycosis, has clear potential for airborne disease transmission and is widely endemic across the eastern, midwestern, and southern United States. We note that there have been no literature reports of longer-range airborne histoplasmosis outbreaks in the United States since the 1980s.

CONCLUSIONS

Airborne transmission of infectious disease has been demonstrated in multiple, independently conducted field experiments and observational epidemiology studies across distances ranging from meters to continental in scale. Furthermore, multiscale airborne disease transmission has been demonstrated for viruses, bacteria, and fungi across a wide range of relevant scientific disciplines, including plant biology, agricultural and veterinary biosafety, medicine, and public health. While historically, the importance of the airborne disease transmission pathway has been well recognized, this area has not been prioritized until the recent COVID-19 outbreak. Consequently, the scientific literature may underestimate the prevalence, importance, and key features of

airborne disease transmission. Greater awareness of the potential for airborne disease transmission and dissemination of methodological guidelines for surveillance studies and disease outbreak investigations could help address this situation.

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