Highways in the Sky: Scales of Atmospheric Transport of Plant Pathogens

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atmospheric dispersal, disease spread, long distance transport, Lagrangian coherent structure, source localization, UAS, drone, LCS

Abstract

Many high-risk plant pathogens are transported over long distances (hundreds of meters to thousands of kilometers) in the atmosphere. The ability to track the movement of these pathogens in the atmosphere is essential for forecasting disease spread and establishing effective quarantine measures. Here, we discuss the scales of atmospheric dispersal of plant pathogens along a transport continuum (pathogen scale, farm scale, regional scale, and continental scale). Growers can use risk information at each of these dispersal scales to assist in making plant disease management decisions, such as the timely application of appropriate pesticides. Regional- and continental-scale atmospheric features known as Lagrangian coherent structures (LCSs) may shuffle plant pathogens along highways in the sky. A promising new method relying on overlapping turbulent back-trajectories of pathogen-laden parcels of air may assist in localizing potential inoculum sources, informing local and/or regional management efforts such as conservation tillage. The emergence of unmanned aircraft systems (UASs, or drones) to sample plant pathogens in the lower atmosphere, coupled with source localization efforts, could aid in mitigating the spread of high-risk plant pathogens.

MOTIVATION

Many high-risk plant pathogens are transported over long distances in the atmosphere (5, 17, 45). A relatively new strain of the fungus that causes wheat stem rust (*Puccinia graminis* f.sp. *tritici*) known as Ug99 is sweeping through Africa, and recently jumped the Red Sea into Yemen and Iran (94). Although a new resistance gene (*Sr33*) has been identified and characterized (70), the deployment of commercial varieties of wheat that are resistant to stem rust has not kept up with the regional and continental spread of the pathogen.

In 2004, Asian soybean rust (caused by the fungus *Phakopsora pachyrhizi*) came to the United States (90) from the tip of South America via hurricane Ivan (46). The plant pathogens *Peronospora tabacina* (causal agent of tobacco blue mold) and *Pseudoperonospora cubensis* (causal agent of cucurbit downy mildew) make long distance jumps along the eastern United States from one susceptible host to another throughout the growing season (11, 65). Large-scale information networks [e.g., the North Carolina Plant Disease Forecasting Center (62–64) and the Integrated Pest Management–Pest Information Platform for Extension and Education (IPM-PIPE)] have been established to track the atmospheric movement of pathogens across broad geographic regions, and these networks often use sophisticated atmospheric transport models such as HYSPLIT (25, 26, 78) and IAMS (46) to predict (or track back in time) their atmospheric movement. Such efforts are essential for establishing effective quarantine measures (particularly in the case of exotic pathogens such as Ug99) and forecasting disease spread (77).

The use of these atmospheric transport models for risk prediction is often limited by scale—a range of pathogen dispersal distances impacted by a suite of abiotic and biotic factors. Consequently, an increased understanding of the scales of atmospheric dispersal of plant pathogens along a transport continuum (pathogen scale, farm scale, regional scale, and continental scale) can assist growers in making plant disease management decisions, such as the timely application of appropriate pesticides (**Figure 1**) (see sidebar, Growers Need to Know the Who, What, When, Where, and How).

PROCESSES IN ATMOSPHERIC TRANSPORT

The transport of plant pathogens through the atmosphere involves processes of liberation (release and ascent), drift (passive horizontal transport), and deposition (landing) (**Figure 2*a***) (45, 46). Liberation is influenced by various ecological and environmental factors that dictate the timing and mechanism of release; drift is associated with the passive, directed movement away from the ground surface in turbulent air; and deposition involves settling (landing) at a new destination containing a susceptible host (45). Knowledge of these processes may assist stakeholders in making rational and informed disease management decisions (e.g., the application of a fungicide to control a specific plant pathogen) (3, 4).

GROWERS NEED TO KNOW THE WHO, WHAT, WHEN, WHERE, AND HOW

- Who is the pathogen in the atmosphere above my farm?
- What disease does it cause, and what crops might be threatened?
- When could the pathogen infect my crop?
- Where is the pathogen coming from?
- How can I control it?

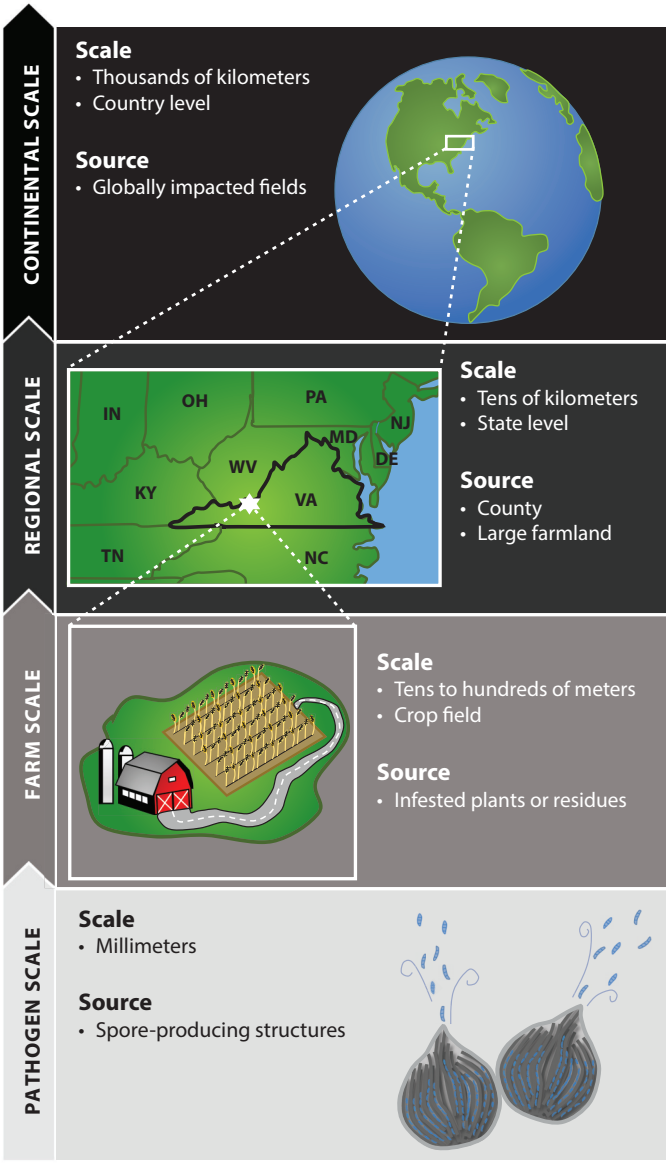

Figure 1

Scales of atmospheric dispersal of plant pathogens along a transport continuum (pathogen scale, farm scale, regional scale, and continental scale). Producers can use risk information at each of these dispersal scales to assist in making plant disease management decisions, such as the timely application of appropriate pesticides.

The atmospheric dispersal of plant pathogens comprises a complex series of events that are interconnected (3). Such events include life history stages of plant pathogens (e.g., production of spores, escape of spores from the crop canopy, survival of the spores while airborne, and landing of spores onto a host) (4). These events interact with a suite of biotic and abiotic factors (e.g., rainfall, atmospheric turbulence, wind patterns, UV radiation, etc.) that mediate effective dispersal (46). An increased knowledge of how these events and factors can change in time

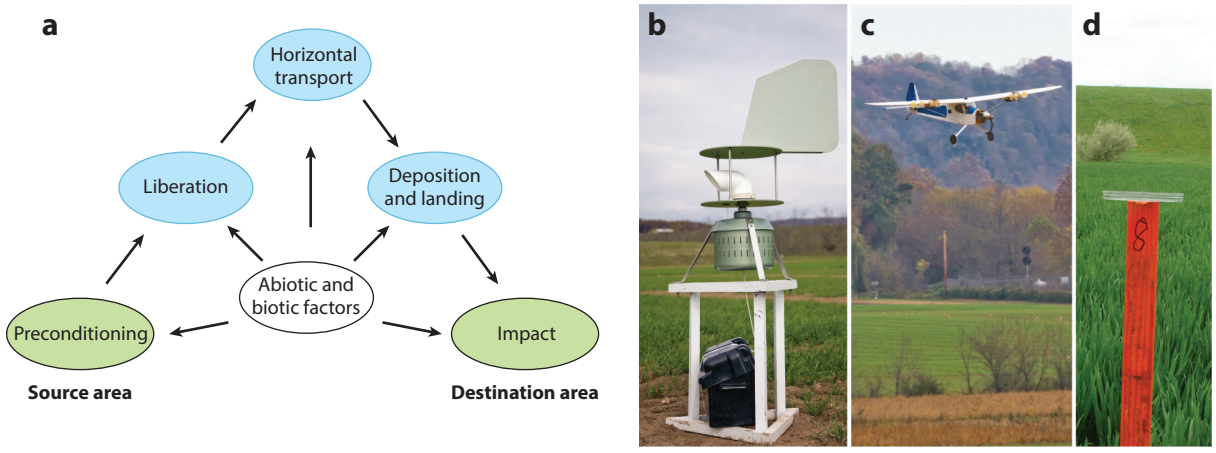

Figure 2

(*a*) The transport of plant pathogens through the atmosphere involves processes of liberation, horizontal transport, and deposition. (*b*) Active sampling devices such as the Burkard volumetric sampler have been used to monitor release, (*c*) unmanned aircraft systems (UASs, or drones) have been used to study horizontal transport, and (*d*) petri plates containing selective media and/or microscope slides have been used to study deposition and landing.

and space across large-scale biological and meteorological gradients may assist in forming an aerobiological process framework for understanding pathogen transport (46).

Historically, aerobiological research has focused on the processes of liberation and deposition, in part due to the availability and ease of use of tools that can sample plant pathogens at or near the surface of the earth [e.g., active samplers such as the Burkard Volumetric Sampler to monitor spore release (49, 55) (**Figure 2*b***) and passive samplers such as petri plates with selective medium to monitor spore deposition (84, 88) (**Figure 2*d***)]. The process of drift (horizontal transport) has largely been understudied, in part because of the lack of appropriate tools to sample the lower atmosphere for plant pathogens and due to the complexity of wind patterns. Although full-scale airplanes have been used to sample microorganisms in the lower atmosphere over broad agricultural regions (2, 18), these aircraft are expensive to operate and risk at least one human life during their operation. Within the past thirty years, a number of unique unmanned aircraft systems (UASs, or drones) (**Figure 2*c***) have been used to monitor the horizontal transport of plant pathogens in the lower atmosphere and help fill this knowledge gap (9, 34, 55, 57, 85, 87, 100, 101).

PATHOGEN SCALE

We define the pathogen scale as dispersal from a plant, residue, and/or soil environment through the laminar boundary layer—a thin column of air surrounding all natural surfaces (35, 66). In order to be dispersed through the remaining scales, a plant pathogen must first overcome the laminar boundary layer. Important components of this scale include the production of spore-bearing bodies (6) and the passive (wind or rain splash) or active release (forcible discharge) of spores into the air (10). The laminar boundary layer is generally only a few millimeters thick during turbulent conditions, extending at most to just a few meters during calm nights (35) (**Figure 3**). Consequently, the thickness of the boundary layer is important in determining whether or not a plant pathogen will escape the laminar boundary layer and be transported over long distances.

Spore production and release are tightly linked to abiotic factors, such as rainfall, wind, relative humidity, temperature, and light (6), although a detailed understanding of the mechanisms driven

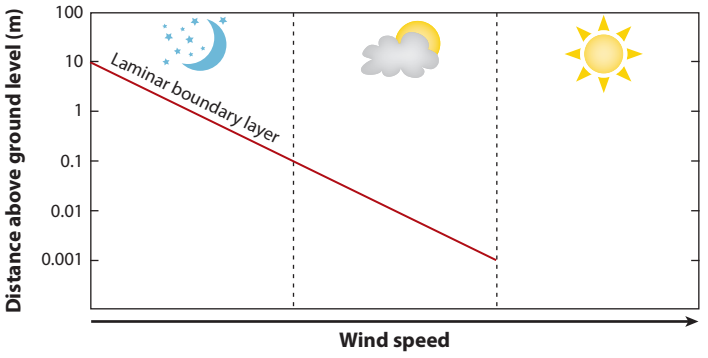

Figure 3

The relative thickness of laminar boundary layer during a clear night (*left*), a cloudy day (*center*), and a sunny day (*right*). In order to be dispersed beyond the pathogen scale, a plant pathogen must traverse the laminar boundary layer. The laminar boundary layer is generally only a few millimeters thick during turbulent conditions, extending at most to a few meters during calm nights. Adapted from Reference 35.

by these factors is unknown. In the case of *Fusarium graminearum* and the wheat disease Fusarium head blight (1), two reproductive structures (sporodochia and perithecia) may be produced on crops and residues (83). Perithecia generally form on the surfaces of residues of corn and small grains, and ascospores are discharged from residues at millimeter-scale distances (82) primarily during the nighttime hours (31, 69, 74). Ascospores are thought to initiate the primary infections on wheat (102). Sporodochia (cushion-shaped masses that produce macroconidia) may form on mature wheat plants, relying on wind and/or rain splash for dispersal (83).

Inoculum source potential, understood as the maximum number of spores that could be released, can be quantified and estimated, and is a critical input for mathematical models of disease spread (8). Using a series of laboratory and field experiments to ascertain perithecia production and ascospore release from natural (corn stalk) substrates, Prussin et al. (72, 74) provided estimates of the total number of spores present per acre in a field-scale source of *F. graminearum* inoculum. In addition, the number of spores released per acre per hour could be estimated, revealing a pattern that varies diurnally (**Figure 4*b***). Fine temporal resolution of spore release from a field-scale source of inoculum under field conditions is important for models of horizontal transport, given the temporal variability of wind speed and direction (73).

One of the biggest research needs for the pathogen scale is a more complete understanding of the environmental factors impacting pathogen release. Correlation and causality analyses can be applied to understand the environmental factors driving spore release (19), but such analyses may not be able to discern the individual contributions of each abiotic element. Often, experiments under controlled environmental conditions are needed to dissect the contributions of different abiotic factors to spore release at the pathogen scale. David et al. (19) developed a unique dual-chamber setup capable of controlling temperature, relative humidity, and light to assess spore release of *F. graminearum* as a function of environmental variables. In this unique design, different combinations of temperature (15°C and 25°C), relative humidity (80%, 90%, and 100%), and light (light or complete darkness) were applied, and the release of ascospores was monitored in real-time with an aerodynamic particle sizer. Trail et al. (103) used a wind tunnel to understand the effects of light and rainfall on the release of ascospores of *F. graminearum*, but these studies were unable to discern individual contributions of temperature and relative humidity to ascospore release, which are likely to be drivers of spore release.

Management strategies at the pathogen scale often involve targeted approaches for removing spore-producing structures (e.g., tillage) (24) and/or the reduction of inoculum in the absence of a susceptible host (e.g., the use of nonhost species in a within-field crop rotation) (37, 58). In the case of *F. graminearum*, tillage can control the availability of potential inoculum sources on the soil surface by incorporating residues of corn and small grains into the soil (24). This may provide some local (within-field) disease control, but inoculum still may be transported to the field from distant sources (57). Growers, however, may be hesitant to till residues of corn and small grains, in part due to high labor and fuel costs associated with this management practice. Rotations with nonhosts can allow some time for residues to decompose, which may reduce the inoculum potential for future growing seasons (37, 58). Multiple (integrated) management strategies are often implemented that combine tillage, resistant varieties, crop rotation, and/or chemical treatments.

FARM SCALE

We define the farm scale as the spread of a plant pathogen beyond a single plant or residue, within and across a field. This scale is generally confined to the surface boundary layer of the atmosphere, generally less than approximately 50-m thick during turbulent conditions (66) (**Figure 5**). Important components of this scale include rainfall and wind, which may actively assist in the movement of inoculum across a field over tens to hundreds of meters. Within-field sources of inoculum of plant pathogens can be water, soil, residues, seeds, or infested plant material (portions of tubers or transplants).

Dispersal kernel: a curve that gives the probability density function of the distance traveled by a plant pathogen from its source

At the farm scale, an important metric is the dispersal kernel, which is a curve representing the amount of spores deposited at a given distance from the source (**Figure 4*c***). This can be directly measured using an array of sensors (**Figure 4*a***) and compared with atmospheric transport models (e.g., Gaussian plume or Lagrangian stochastic models) to calibrate model parameters (7, 9, 73). The dispersal kernel provides the probability density function describing the average spatial distribution of spores from an inoculated field, and this is an important input for regional and continental scale epidemiological models to forecast future disease spread. Small changes in the fat tails of the dispersal kernel can cause dramatic changes in predicted spread rates; the dominant factor in predicting the rate of spread may be described by the tails of the kernel resulting from rare, long distance (>1 km) dispersal events.

One of the biggest research needs for the farm scale is a more complete understanding of the spread of plant pathogens from large area sources of inoculum (e.g., multiple plants and/or residues over a relatively large surface area). At this scale, release-recapture experiments can be used to discern the spread of unique isolates/strains of plant pathogens from known sources. Bennett et al. (12) infected wheat seeds with unique isolates of *Phaeosphaeria nodorum* (causal agent of *Stagonospora nodorum* blotch of wheat) and used a fingerprinting technique known as amplified fragment length polymorphism (AFLP) (104) to monitor the spread of these isolates to resulting plants and seeds. Keller et al. (47, 48) released unique isolates of *F. graminearum* on colonized corn debris in small, 1-m diameter plots, and used AFLPs to monitor the spread of the fungus to surrounding wheat plants up to 24 m from the inoculum sources. Prussin et al. (72) generated field-scale sources of inoculum of *F. graminearum* with a unique clone and used microsatellites to track the movement of the spores of the released clone up to 750 m from the source. Aylor et al. (9) generated field-scale sources of *Phytophthora infestans* (causal agent of potato late blight) and tracked the movement of sporangia up to 500 m downwind with ground-based sampling devices (towers equipped with Rotorods) and UASs (although this study was not able to unambiguously discern the released isolates from potential background sources). Future studies could use genetically tagged plant

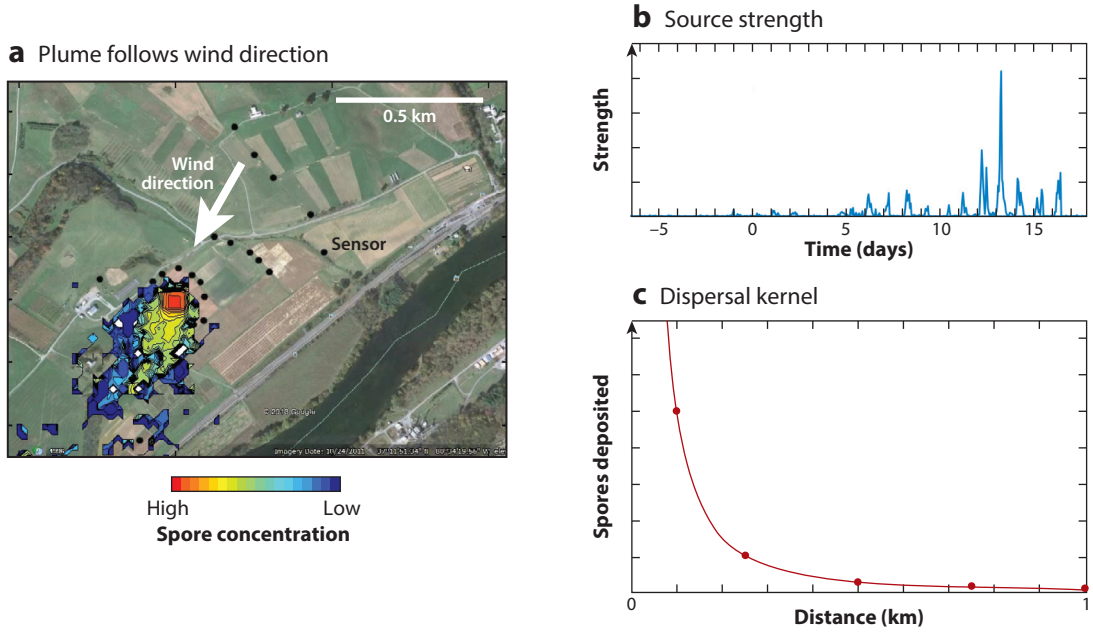

Figure 4

(*a*) With a sampler in the middle of a diseased field (*red square represents a large area source of inoculum*), one can monitor the number of spores released hourly, which we call (*b*) the source strength. The source strength is far from uniform, and over several days one sees instead a spiky pattern, which corresponds to nightly releases of spores, which start out small and then build up, until all the spores in the field have been released. The plume follows the wind direction (e.g., see Airborne Spread of Plant Disease: Lagrangian Stochastic Model; **https://www.youtube.com/watch?v=SDTkvXePtlU**). Using a mathematical model of how the spores are spread in the wind, one can predict where the spores will land on the ground (*a*). Comparing that with the measurements at sensor locations (*black dots*, *a*), one can predict the amount of pathogen spores deposited at a given distance. This curve, called (*c*) the dispersal kernel, is an important input for epidemic models of disease spread. Map data: Google, Commonwealth of Virginia, DigitalGlobe, USDA Farm Service Agency.

pathogens (e.g., 28) to unambiguously track the farm-scale dispersal of plant pathogens, but such studies would need to have appropriate approval from regulatory agencies.

Management approaches at the farm scale are generally focused on the use of resistant varieties (if available) and chemical and/or biological control applications (e.g., fungicides). These applications may be made in selected areas that contain isolated pockets of disease or may be applied across entire fields as a preventative measure, including areas that do not show disease symptoms.

REGIONAL SCALE

We define the regional scale as the spread of a plant pathogen over thousands of meters, often across county and even state borders. This scale includes transport in the planetary boundary layer of the atmosphere (66), tens to thousands of meters above the surface of the earth (**Figure 5**). Important components of this scale include wind, rainfall, and UV light (impacting the viability of spores) (4). Here, plant pathogens may be released from a large unknown source (e.g., an infested crop field) (86), and once they get high enough off the ground, winds can take them kilometer-scale distances through highways in the sky.

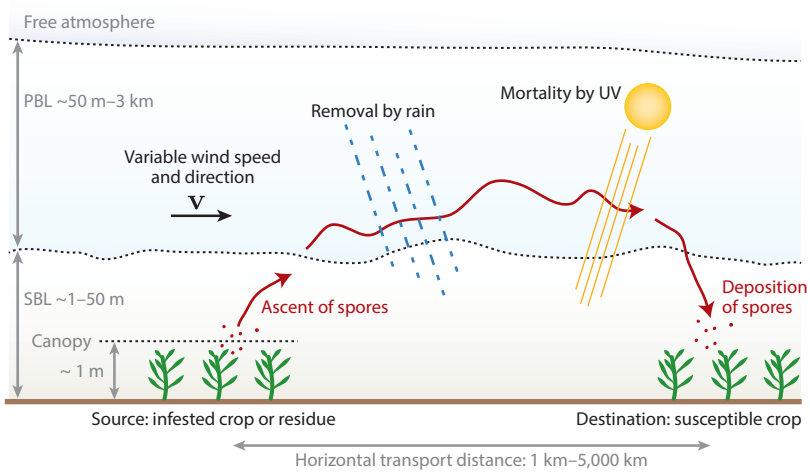

Figure 5

The farm scale is often confined to the surface boundary layer (SBL) of the atmosphere, generally less than about 50-m thick during turbulent conditions. Spores can spread beyond the farm, perhaps even crossing continents, riding on air currents. One of the major factors affecting the spread is the weather. Spores can be removed by rain, or they can be carried by a highway in the sky until they land on a susceptible plant or lose viability due to UV exposure. Abbreviation: PBL, planetary boundary layer.

At the regional scale, transport models may be used to predict the movement of plant pathogens in the atmosphere (25, 43, 44, 54, 81), but these models often fail to incorporate actual measurements of spore concentrations and spore viability along proposed particle trajectories. A number of UASs have been used to detect and monitor the long distance movement of plant pathogens in the lower atmosphere. Gottwald & Tedders (34) pioneered the collection of plant pathogens with UASs. They used a modified remote-controlled biplane platform called the MADDSAP (microbial agent dispensing drone for suppression of agricultural pests) equipped with two rotating drum samplers to collect spores of the fungal plant pathogens *Cladosporium caryigenum* (causal agent of pecan scab) and *Cladosporium carpophilum* (causal agent of peach scab) over pecan and peach orchards. This study showed the great potential for regional-scale transport for both of the *Cladosporium* spp. studied (as well as other microbes collected during the flights), particularly in the context of disease spread among peach and pecan orchards in the region.

Autonomous systems have been incorporated into some UASs, enabling teams of vehicles to perform complex atmospheric sampling tasks and coordinate flight missions with one another (100). Schmale and colleagues developed autonomous UASs to study the long distance transport of plant pathogens such as *P. infestans* (100) and *F. graminearum* (87) (**Figure 2*c***). Schmale et al. (87) showed that isolates of *F. graminearum* collected 40 to 320 m above the ground in Virginia caused disease (Fusarium head blight) and produced mycotoxins (deoxynivalenol, 3-acetyl-deoxynivalenol, 15-acetyl-deoxynivalenol, and nivalenol). One of these isolates produced a unique and dangerous mycotoxin (nivalenol) that had not been reported previously from ground-based studies of populations of the fungus in Virginia (89), suggesting at least some of the isolates originated from outside of the state. Lin et al. (54) conducted simultaneous sampling for fusaria at multiple heights in the atmosphere (a Burkard volumetric sampler at 1 m and a UAS at 100 m) and used concentration gradients to estimate the distance to the potential inoculum source(s). Interestingly, these distances to potential inoculum sources were on the

regional scale, approximately 1–4 km. Spore concentrations were higher in the fall, spring, and summer, and lower in the winter. The vertical concentration gradient also differed by season, suggesting near-farm sources (1–2 km) in spring, summer, and fall, and more distant sources in winter (4 km). Thus, there are opportunities to use UASs to validate and improve long distance transport models for plant pathogens at the regional scale.

Management approaches at the regional scale often use early warning systems (77). These systems can provide a measure of relative risk of disease (e.g., atmospheric trajectories suggest a pathogen may be arriving into a growing region at a predicted time). There is an increasing need to improve these tracking and prediction tools, which are tightly linked to the timely reporting of disease by agricultural extension professionals and accurate collection and prediction of weather conditions. Growers depend on these tools to make informed disease management decisions, such as the appropriate application of fungicides.

CONTINENTAL SCALE

We define the continental scale as the spread of a plant pathogen between continents, sometimes over thousands of kilometers. These are generally rare events (17) but they do occur, and they remain a significant threat to the biosecurity on a continental scale (5, 94). Transdisciplinary research is needed to examine how pathogen-laden parcels of air are mediated by atmospheric mixing, particularly in the context of the spread of invading populations (42, 50). Natural environmental fluid flows such as those found in the atmosphere and oceans exhibit complex dynamics (14, 93). This complexity is actually a boon for the transport of plant pathogens because a rich dynamical structure makes possible efficient movement and dispersal (52, 79, 91, 98).

Continental-scale transport has usually been studied using a few sample trajectories (5, 21, 36). However, the study of individual trajectories cannot fully resolve the complex motion of the atmosphere nor the resulting changes in the observed concentrations of microorganisms in the lower atmosphere. Moreover, studies using individual trajectories may rely on long integration time (days to weeks) for the trajectories, which can lead to many uncertainties in trajectory computations. Trajectories are often chaotic and when viewed directly lead to confusing "spaghetti" plots (e.g., figure 2 in Reference 94). Rather than individual trajectories, the qualitative properties of entire air masses, approximated as a continuum of closely spaced trajectories, are more reliable. For example, visualizations can present the evolution of a patch of air parcel tracers from a desired release location at a desired time or display multiple trajectories originating from different release locations that sample the domain. Alternatively, trajectory data can be analyzed statistically to determine how initial release states relate to final locations, resulting in probability maps and connectivity charts (59, 80, 99).

We have previously proposed a more systematic, geometric framework for discussing the changes in atmospherically advected microorganism concentrations, based on computations of Lagrangian coherent structures (LCSs) (87, 98). LCSs act as organizing centers for divergent and convergent flow behavior (which are labeled repelling and attracting LCSs, respectively) and are robust transport barriers between otherwise complex mixing regions. The added value of the LCS-based approach is that it provides a new way to synthesize the data from a complex wind velocity field data set, uncovering key organizing structures that elucidate why and how atmospheric transport evolves the way it does (52, 91). Coupled with effective visualizations, LCSs can assist in the forecasting of the aerial transport of plant pathogens, thereby aiding decision-making strategies. Furthermore, whereas individual trajectories are usually complicated and highly sensitive to errors in the velocity field, the LCS are typically easier to visualize and more robust to uncertainty (40, 41, 53, 93).

Lagrangian coherent structure (LCS): a key organizing structure of the motion of air parcels in the atmosphere, often a boundary, or front, between two air masses with different histories and biotic (pathogen) compositions. Nearby air parcels converge onto attracting LCSs and diverge away from repelling LCSs

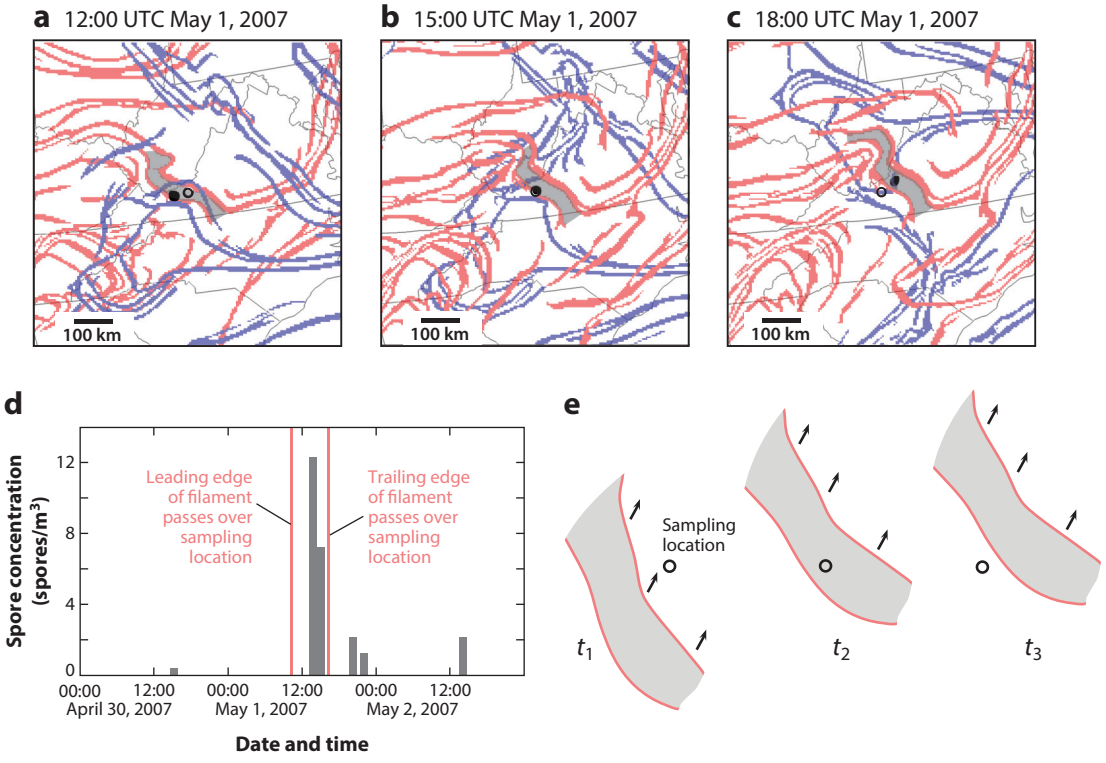

Figure 6

Lagrangian coherent structures (LCSs) [repelling (divergent flow) LCS shown in pink and attracting (convergent flow) LCSs shown in blue] in the atmosphere (the 900-mb pressure surface) for the time surrounding the "spike" in concentration (shown in panel *d*) at 14:00–15:00 UTC (coordinated universal time) on May 1, 2007. LCSs act as organizing centers for divergent and convergent flow behavior (which are labeled repelling and attracting LCSs, respectively) and are robust transport barriers between otherwise complex mixing regions. (*a*) 12:00 UTC on May 1, 2007, (*b*) 15:00 UTC on May 1, 2007, and (*c*) 18:00 UTC on May 1, 2007. The gray region represents an air mass filament of high spore concentration (here, for fungal spores) "sandwiched" between two repelling LCSs. The corresponding schematic is shown below in panel *e*. The open circle is the sampling location at Kentland Farm. The filled circle in panels *a*, *b*, and *c* and in the schematic in panel *e* represents the portion of the air mass sampled at 15:00 UTC on May 1, 2007. Adapted with kind permission from Springer Science and Business Media; Schmale DG, Ross SD, Fetters TL, Tallapragada P, Wood-Jones AK, Dingus B. 2012. Isolates of *Fusarium graminearum* collected 40-320 meters above ground level cause Fusarium head blight in wheat and produce trichothecene mycotoxins. *Aerobiologia* 28: 1–11, figure 4.

LCSs are moving fronts, or boundaries, between air masses, and thus could play a significant role in the movement of microbes between habitats (**Figures 6** and **7**). Plant pathogens moving passively are not likely to cross the evolving LCSs, which delimit the past and future movement of a pathogen-laden air mass, often a tendril or filament (**Figure 6**). LCSs can be predicted and tracked, based on forecast models and observations, using dynamical systems methods and concepts such as invariant manifolds and almost-invariant sets (13, 22, 23, 39, 40, 92, 105).

LCSs can be large scale (hundreds of kilometers in length) but with effects observed locally. For example, the air mixture, including plant pathogens, on either side of an LCS is expected to be discontinuous (**Figures 6** and **7**). Therefore, LCSs are likely to be an important mechanism by which punctuated changes in the structure of plant-pathogen assemblages can be understood at fixed geographic locations and also at different locations at different times. An analysis of UAS

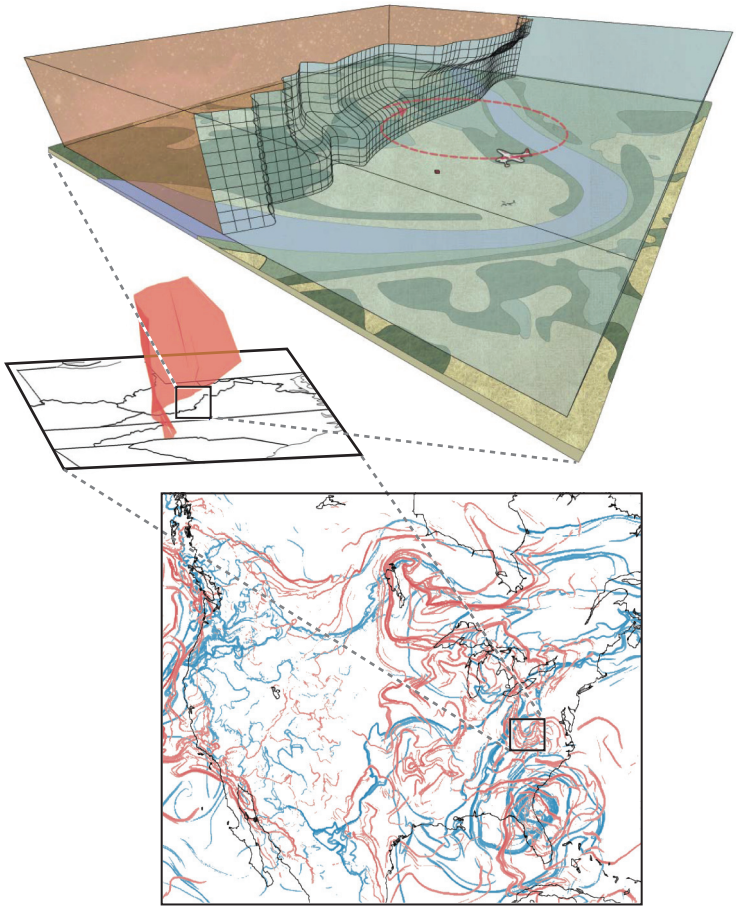

Figure 7

Atmospheric Lagrangian coherent structures (LCSs) are large-scale features with local effects. An LCS (shown as undulating mesh in the upper figures) separates two volumes of air as it moves over topography, shown schematically on a scale of several kilometers near a sampling site at Virginia Tech's Kentland Farm in Blacksburg, Virginia. Autonomous unmanned aircraft systems (UASs) are used to collect pathogen spores on both sides of an LCS. Mixed assemblages of spores in the lower atmosphere may be mediated by LCSs, which are fronts between well-mixed air masses. This LCS is just one of a large-scale network of fronts on the continental scale (*bottom*). Repelling LCSs shown in pink and attracting LCSs shown in blue. The continental outline is shown as a thin black line. See the video version at **https://www.youtube.com/watch?v=p0HnjYMC6pI**. Adapted with permission from Tallapragada P, Ross SD, Schmale DG. 2011. Lagrangian coherent structures are associated with fluctuations in airborne microbial populations. *Chaos* 21:033122. Copyright 2011, AIP Publishing LLC.

flight collections of *Fusarium* showed a significant relationship between punctuated changes in concentrations of *Fusarium* and the passage times of LCS fronts (98). Furthermore, the temporal variation of viable spores at a fixed geographic location suggests a coherence timescale consistent with clouds of spores with horizontal dimensions on the scale of 20–100 km (54), compatible with the filamentary structure seen on the continental scale (**Figures 6** and **7**) (87).

On the continental scale, LCSs provide a useful framework. The fronts are short-lived, appearing for just hours or days before disappearing (**Figure 7**). Although they are computed using

weather data, LCSs are not all related to obvious weather phenomena like storms or cold fronts. Although early work recognized a relationship between atmospheric fronts and atmospheric populations of microorganisms (33), the new language of LCS provides us with a powerful conceptual tool to further explore such relationships. Work is underway to start cataloging the variety of formations and their possible role in microbial dispersal (79), but more work is needed, especially regarding the limits of forecasting. Using current techniques that utilize ensemble forecasting (15) and experimental fluid mechanics (75, 76), one can predict in real-time (with a lead time of 12–14 hours) the passage of an LCS front over a given geographic point with an accuracy of approximately 2 hours (16). These efforts could assist in predicting the potential movement of invasive and/or quarantined plant pathogens from source continents (e.g., the movement of Ug99 from Africa to Australia) (94) and provide important linkages to regional-scale risk management efforts.

BLENDING SCALES THROUGH SOURCE LOCALIZATION

Source localization (discerning where something came from) for chemicals and biota carried by fluids is an important problem at multiple scales (e.g., bacterial chemotaxis, pheromone localization for insects, green sea turtle migration, contaminant tracking in urban environments, forecasting of plant disease epidemics, etc.) (56, 61, 68). In the context of plant pathogens, sophisticated statistical methods have been developed and tested for source localization on the scale of a field or farm (a few meters up to 1 km) by modeling a plume using a Gaussian approximation or Lagrangian stochastic model (29, 32, 38). However, over long distances (>10 km), plumes become turbulent and form patchy, highly concentrated tendrils (67), rendering common localization techniques ineffective (27).

Over continental distances (several hundred kilometers), previous source localization work has either provided only directional information [e.g., finding the direction from which most air masses came via clustering analysis (43, 44, 81)] or used a geographically dispersed array of sensors [e.g., >100 sensors spread over Europe (106)], each sensor sampling concentration with a high temporal resolution. This sets the stage for some promising new methods that rely on the overlap of turbulent back-trajectories to localize potential sources. In this application, time and location can be used to initialize an ensemble of back-trajectories to construct a probable source region for a given sample of air containing a plant pathogen. If there is an overlap between the probable source region for two air samples, these samples are likely to contain a common plant pathogen reflecting a common source (**Figure 8**).

To find the common source, back-trajectories of sampled spores (well-approximated by passive particles) moving in the lower atmosphere can be numerically integrated backward in time, using the available velocity data (NOAA's North American Mesoscale product) for past time steps,

$$\mathbf{x}(t_0 - \Delta T) = \mathbf{x}_0(t_0) + \int_{t_0}^{t_0-\Delta T} \mathbf{v}(\mathbf{x}, \tau)\, d\tau,$$

where t_0 is the time when the sampled spores were collected, ΔT is the backward integration duration, and x_0 is the sampling collection point. The result of this integration can be used to generate hypotheses about the potential source region for each air sample. The available velocity data can be used for interpolation to find the unknown velocity at arbitrary points inside the domain of the field. When stochastic effects are ignored (e.g., a subgrid scale turbulent velocity component, to be discussed below), then there is a single back-trajectory. This single trajectory provides a first approximate guess as to the source, which could be anywhere along the trajectory. An important note is in order here. One might think that a specific source point, and thus time since release from source, could be determined by considering when the three-dimensional back-trajectory

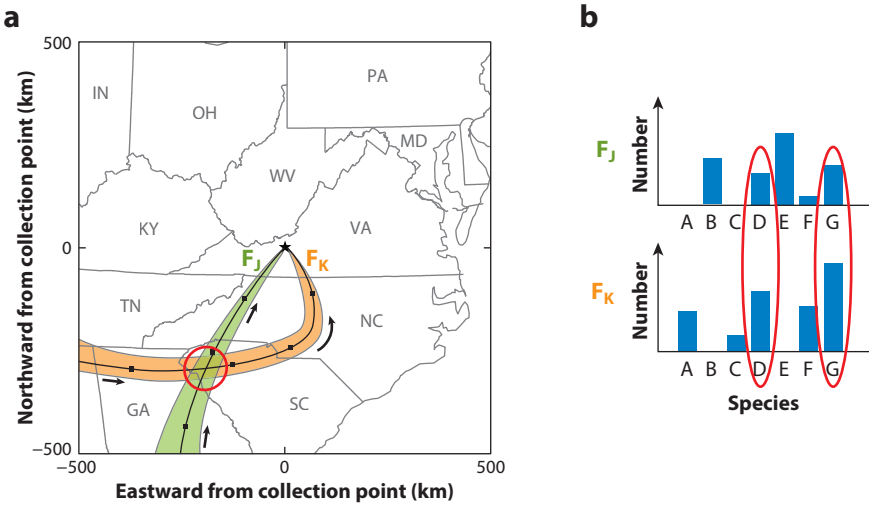

Figure 8

(*a*) The point of collection at Kentland Farm in Blacksburg, Virginia, is given by the star. Swaths of back-trajectories for two unmanned aircraft system (UAS) sampling flights, F_J and F_K, show an overlap, highlighted by the red circle in western South Carolina approximately 300 km to the southwest of the collection point, which could represent a common source. (*b*) Because the flights sampled air with a potential common source, we can hypothesize that this will be reflected in some common species within the sampled populations of each flight, e.g., species D and G, highlighted by red ovals.

returns to the ground (0-m AGL), which would be the point of release. However, resolving the vertical velocity component to the level needed over the horizontal scale we are considering (much greater than 1 km from the collection point) is currently beyond the state-of-the-art capability of meteorological data and simulation (95, 96). Thus, we do not model the vertical velocity and instead make a well-mixed assumption in the vertical direction, assuming the bulk air motion is horizontal and occurring along a two-dimensional constant pressure surface of 850 mb (a transport layer with varying height above the ground that coincides with that of our aerial collection point) (20, 98). We are thus making an assumption that air parcels (and the spores they carry) can join the proxy back-trajectory at any point along the trajectory—that is, we assume plant pathogens we sampled are equally likely to be released at any point along the back-trajectory (**Figure 9**). There are biological limitations to travel time, however, based in part on spore viability. Spores may lose their viability due to UV exposure, which can result in survival times (airborne travel times) of hours to days, depending on the species (4, 73). Additional work is needed to discern the critical irradiation dose for many high-risk plant pathogens.

Whereas the vertical velocity components are unreliable, the horizontal velocity components are more reliable. However, for the meteorological data that are available, the deterministic assumption is considered no longer valid and to obtain the true motion of pathogen-laden air parcels, we must incorporate turbulent motion to assist in the calculations of the trajectories and the identification of potential source regions. The potential source in general no longer provides a single trajectory but a fattened trajectory or swath, consisting of an ensemble of possible paths (this is similar to how predictions of future paths of hurricanes are depicted in the news media). Unresolved turbulence is defined as the components of the velocity that cannot be described as a deterministic function of the grid point data; consequently, stochastic models must be used to obtain a reasonable estimate. This refers to the probabilistic motion of particles that could occur with

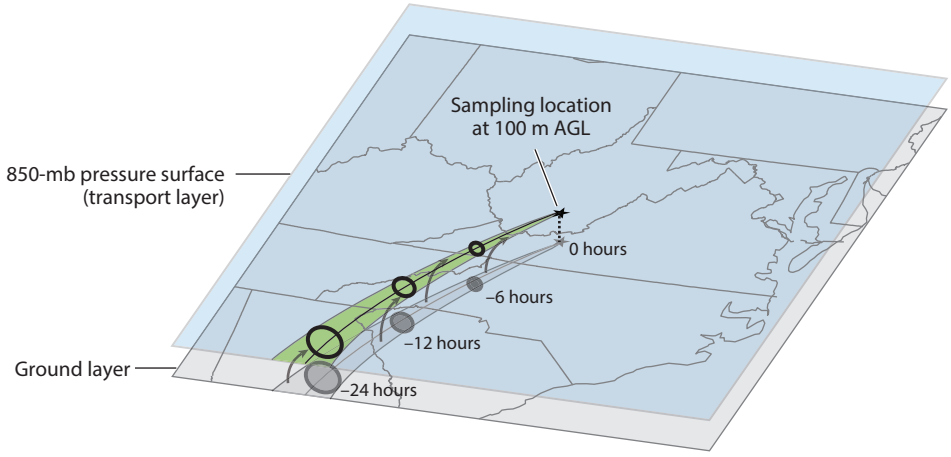

Figure 9

A schematic of a swath of trajectories (*green*) along the airborne transport layer, 850-mb pressure surface (*blue*) is shown, along with its projection on the ground layer (*gray*), showing the location of air parcels 24 hours prior to an unmanned aircraft system (UAS) sampling flight for fungi in the genus *Fusarium*. The arrows going from the ground layer to the transport layer represent our assumption that air parcels (and the spores they carry) can join the swath of probable back-trajectories at any point along it. The height of the pressure surface above the ground layer is shown exaggerated for illustrative purposes only. Probable source regions at 6, 12, and 24 hours prior to sampling are shown schematically as ellipses but will likely be irregular shapes because of nonuniform winds. Abbreviation: AGL, altitude above ground level.

respect to the constraints imposed from the existing velocity data at each node and at discrete time steps. For the calculation of the probabilistic source regions, we used stochastic models suitable for atmospheric flows that describe the time-varying unresolved velocity components stochastically based on available data on each grid point,

$$\mathbf{v}(\mathbf{x}, t) = \bar{\mathbf{v}}(\mathbf{x}, t) + \mathbf{v}_t(\mathbf{x}, \bar{\mathbf{v}}, t),$$

where $\bar{v}(x, t)$ is the background deterministic velocity and $v_t(x, \bar{v}, t)$ is the unresolved turbulent velocity that is a function of the background velocity field as well as the position and time. The spatiotemporal dependence of the stochastic velocity component to the time-varying deterministic background velocity field (25, 30, 51) plays an important role in the determination of the swath of likely back-trajectories. We note that the mathematical model used is similar to the HYSPLIT simulation platform (25), but the HYSPLIT platform does not allow for the obtainment of probabilistic source regions, so we have developed this capability in-house (15, 16, 87, 97). Owing to the stochasticity of this model, we simulate the trajectories of many individual and independent particles (i.e., a Monte Carlo approach) to obtain an approximately converged probability distribution, represented schematically in **Figure 9** as a swath. Collectively, these approaches can help identify potential source regions for high-risk plant pathogens, which could help in downstream disease management efforts.

ROUNDUP

New tools and approaches are needed to study the scales of plant-pathogen dispersal. Such work is important for contributing to our understanding of invasions of plant pathogens; new strains

of plant pathogens introduced into the United States could interbreed with native strains, and individual traits [such as the production of unique mycotoxins (87)] could be incorporated relatively quickly into the existing populations and efficiently dispersed throughout the country. Methods for source localization at continental scales via sparse aerobiological sampling at a single geographic location can provide powerful tools for growers and producers to identify areas of risk. Given the emergence of UASs as platforms for aerobiological sampling, with costs low enough to make it practical even in developing countries (71), the ability to do source localization at a single sampling location could aid in halting the spread of airborne plant diseases, which are sweeping through the developing world and affecting wheat and other staple crops (94).

SUMMARY POINTS

1. The air is teeming with microbial life. Some of these microbes are plant pathogens, traveling thousands of kilometers from their sources (infested plants, soil, or residues) to successful final destinations (susceptible host crops).
2. Knowledge of the scales of atmospheric dispersal of plant pathogens along a transport continuum (pathogen scale, farm scale, regional scale, and continental scale) can assist growers in making plant disease management decisions, such as the timely application of appropriate pesticides.
3. With release and recapture experiments from a known inoculated source, one can experimentally determine the dispersal kernel over the farm scale, which provides an important input for disease models at the farm and regional scales.
4. The dynamics of atmospheric assemblages of plant pathogens (e.g., *Fusarium*) reveal temporal correlations on the scale of 6–9 hours, corresponding to coherent cloud sizes of 20–100 km, which are portions of large-scale atmospheric filaments bounded by LCSs.
5. At the regional and continental scales, there is an atmospheric transport network of evolving air masses that is relevant for large-scale spatiotemporal patterns of plant-pathogen dispersal.
6. Invasive microorganisms have been documented to travel on large-scale weather phenomena (such as hurricanes), and likely move about due to more subtle weather phenomena as well.
7. Airborne measurements of plant pathogens at a single location are sampling a web of dispersal plumes from innumerable sources, but new source localization techniques are coming online that take advantage of shifting wind patterns to pinpoint sources.
8. The challenges of understanding and predicting the airborne dispersal of plant pathogens over multiples scales are broad in scope, encompassing plant pathology, geosciences, applied mathematics, and computational and information science and engineering.

FUTURE ISSUES

1. What are the local environmental conditions that initiate plant-pathogen dispersal? How can these processes be mechanistically modeled and effectively incorporated into disease risk management strategies?

2. Lagrangian methods for uncovering, quantifying, and predicting key atmospheric transport processes have been limited because of high computational cost and limited spatiotemporal meteorological data resolution. What breakthroughs are needed in the atmospheric and computational sciences to perform real-time prediction of four-dimensional (3D + time) pathways of plant-pathogen dispersal?
3. How can real-time prediction of weather-based LCSs and related Lagrangian methods inform better management practices (e.g., the timely application of pesticides)?
4. The long-range aerial dispersal of plant pathogens may be limited to spore viability, in part because of UV exposure. Given that different pathogens may have different levels of resistance to UV light, what are appropriate transport times for agriculturally important pathogens such that spores can arrive alive on a susceptible crop?
5. How might climate change impact the routes of dissemination for airborne plant pathogens?
6. Weather and climate have played a role in plant-pathogen dispersal; could the reverse also be true? What role do plant pathogens play in weather (e.g., encouraging precipitation as ice nucleators) (60)? What role have plant pathogens played in the evolution of climate over geological time?
7. What is the role of rare, continental-scale dispersal events?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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