Dispersion: A Spore's Journey in Vineyards

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Pathogen movement

To better utilize scouting data to manage disease, an understanding of pathogen movement through a vineyard is needed. Exactly how an airborne pathogen spreads in a vineyard is a highly chaotic and complex process that involves interactions among the plant, pathogen, and the topology and microclimate of a vineyard. Understanding how these interactions influence four key events (Fig. 1) that comprise the airborne portion of many plant pathogens' life cycles will aid you in utilizing disease scouting information to refine disease management decisions.

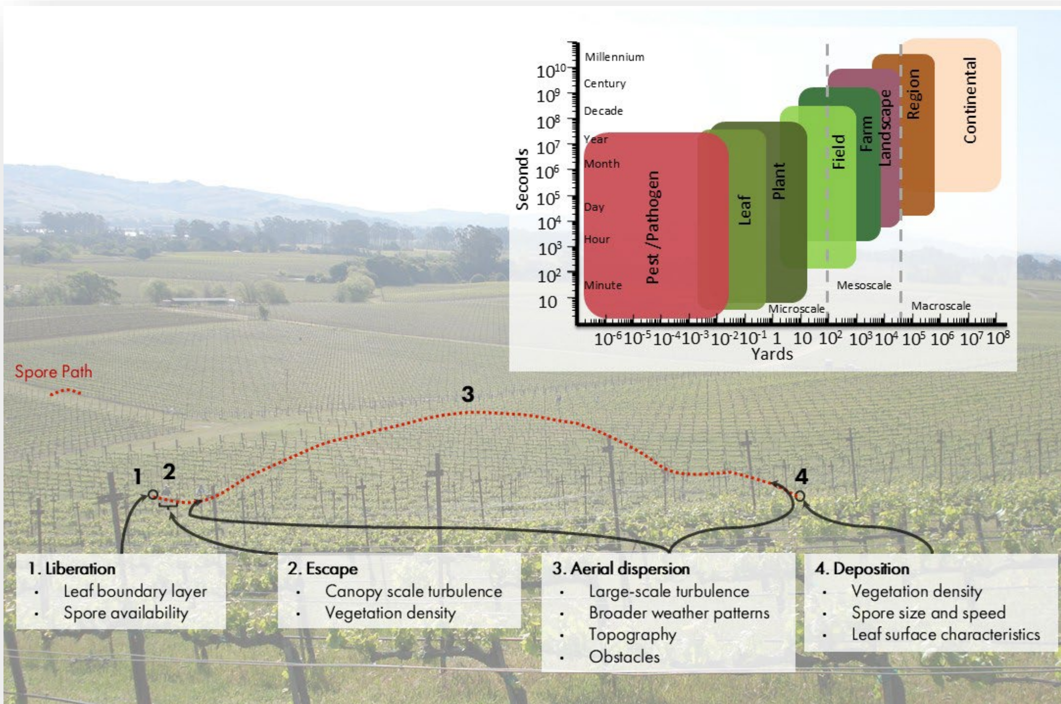

Figure 1: The four main stages of pathogen dispersion and the main factors influencing them. Inset: Schematic representation of the spatial and temporal scales involved in pathogen spread (adapted from Mahaffee et al. 2022)

While each event has some key factors listed in Fig. 1, there are many more factors and interactions that influence how a pathogen moves through a vineyard. The first event is *liberation*, where the spore leaves the plant surface it was generated from and crosses the leaf's *boundary layer.* Next, the spore must *escape* the region around the original host plant without the spore being deposited back onto the host plant. Once the spore is airborne, it experiences many competing turbulent forces that dictate how far it will be transported in the air (*dispersion*) before contacting and adhering to a hospitable leaf surface (*deposition*).

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1. Liberation

The first obstacle a spore faces when leaving a leaf surface is the leaf boundary layer, a thin blanket of laminar slow-moving air near the leaf that behaves in a more viscous manner (thicker) than air further away from the leaf (Fig. 2). Think of throwing a ball underwater— it travels a lot slower and shorter distance than in air.

When this leaf boundary layer gets disrupted (i.e., made thinner), spore liberation is easier. Two phenomena that can disrupt the boundary layer are leaf fluttering or high-energy turbulent air moving into the canopy (a common wind pattern seen in crop fields). How the disruption of the boundary layer influences liberation is largely a factor of the pathogen and how spores are produced.

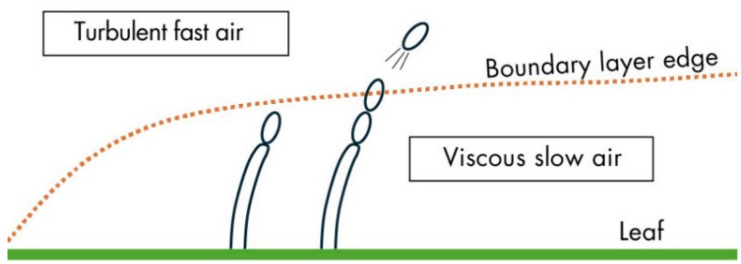

Figure 2: Liberation of an *E. necator* spore (asexual sporulation). The dotted line represents the top of the boundary layer, a region of slow-moving air near the leaf surface.

Fungal pathogens have evolved multiple mechanisms that aid spores in crossing this boundary, from active propulsion to passive structural features. Some pathogens have spores that are primarily released by wind (powdery mildew conidia) while others are often assisted by additional mechanical forces (e.g., downy mildew and botrytis).

2. Escape

The next challenge for a spore is to "escape" the immediate vicinity of the leaf it just left and either move within the plant canopy or leave the canopy for the surrounding air (Fig. 3).

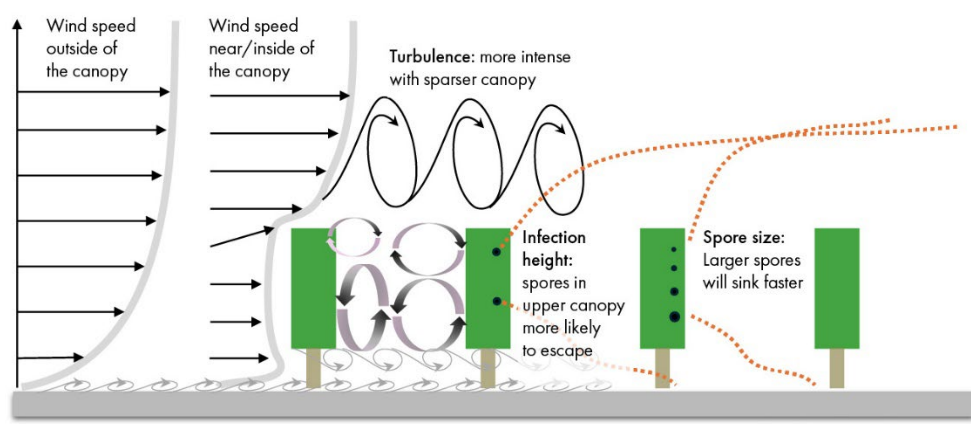

Figure 3: Factors influencing escape. Typical turbulent wind patterns inside vineyards are shown with black arrows. Potential spore trajectories are shown with red dotted lines.

In grapevines, as the canopy grows and becomes denser, wind velocities in the canopy are lower and the ability of turbulence to move spores around gets weaker. This will likely result in disease incidence and severity increasing in the adjacent canopy with little spread to neighboring plants because of the reduced airflow and the eddies that are formed in the space between rows. These eddies (turbulent structures) strengthen and have more influence on spore movement the greater the distance between rows. Typically, these eddies sweep spores from the trunk or lower canopy downward to the ground, while they eject spores originating from tissue in the mid to upper canopy to the air moving above the canopy. They are then carried some distance away. The distance traveled depends on numerous factors other than wind speed, including terrain and presence of obstacles (e.g. buildings, trees, windbreaks). The row structure also influences wind direction within the canopy by channeling air and thus air movement up or down the row. These are reasons why disease is often found aggregated to a few vines and appears to move up and down a row.

Since an airborne spore must fight gravity to stay aloft long enough to escape the canopy, spore size dramatically affects the chances of escape. In still air, a 1-micron particle may stay aloft for 10 hours while a 20-micron particle settles after only a minute or two (Table 1). Many pathogen spores are larger than 20 microns, making the transport conditions during first few minutes of flight critical in determining how it will escape the canopy and the distance it will travel. Particle shape is also important; non-spherical spores (e.g., powdery mildew conidia, downy mildew sporangia) introduce lift and drag forces that can help keep it moving with the air mass.

Spore size and settling times for common grape pathogen spores

	Erysiphe necator (Powdery Mildew)	*Plasmopara viticola* (Downy Mildew)	*Botrytis cinerea* (Botrytis Bunch Rot)
SPORE SIZE	~30 micron	5-20 micron	~10 micron
SETTLING TIME	~20 sec	~60 sec	~4 min

How a pathogen liberates from the leaf boundary layer also offers clues about how far it will ultimately travel. Spores released during high-shear wind events (e.g. gusting or high velocity) are likely to travel farther than those released by leaf flutter caused by raindrops or other mechanical forces. Faster moving wind is more likely to carry spores so that they have enough momentum to escape the plant canopy and be caught in an eddy that moves them further from the canopy. Spores liberated by leaf movement or other mechanical forces are more likely to be pushed back to the original host by the surrounding slow-moving air.

3. Dispersion

Once aloft above the canopy, a group of spores travels downwind in a wedge-shaped pattern called a plume (Fig. 4). The plume is aligned with the wind direction and widens based on the amount of turbulence caused by weather, topography, row orientation, canopy density, and other obstacles.

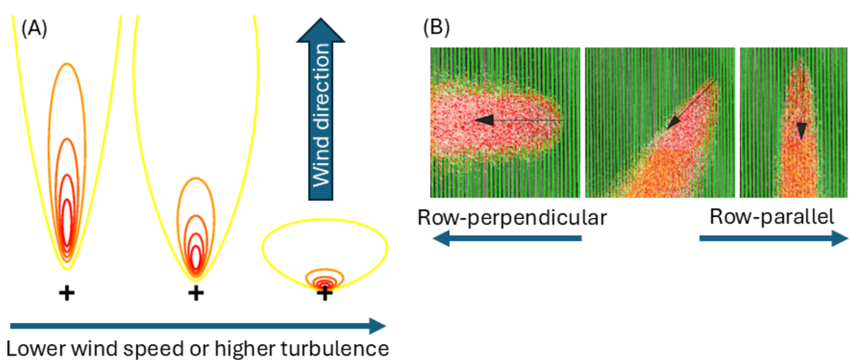

Figure 4: (A) Gaussian plumes in different wind conditions. Spore origins are marked by black crosses. The redder the color, the more likely a spore is to end up in that location. (B) As wind direction (with respect to row direction) changes, plume width and shape change. Computer-simulated spores are shown.

Factors Causing Deviations from Idealized Plume Behavior

DIURNAL WEATHER VARIATION

Every morning as the sun rises, air near the Earth's surface warms up, becomes less dense, and begins to rise. Cooler air takes its place. This churning process is called convection and is a major source of atmospheric turbulence. As the sun sets, the atmosphere cools and returns to a stratified (layered) state with much less turbulent mixing. The substantial turbulence of daytime convective periods enhances spore liberation and escape compared with the relatively calm overnight stable periods. Knowledge of a pathogen's daily cycle (i.e., growth and spore availability) is critical to determine how diurnal winds impact disease spread. Are spores available for transport during convective or other high-turbulence periods? This happens with the grape powdery mildew pathogen, where spores mature and are ready for release 4-6 hours after sunrise. Some spores are mostly released at night. These tend to be smaller, around 4 microns (e.g. trunk disease pathogens)

TOPOGRAPHY

Sloped terrain produces diurnal wind patterns, with upslope winds in the mornings caused by warming air near the surface, and downslope winds in the evenings as the Earth cools off. It is critical to understand the characteristic wind flow patterns caused by hills, valleys, and ridges for a given growing region, as these flow patterns can create high or low risk disease zones. Certain topographical features like valleys or depressions can cause cold air pooling; aside from promoting frost, these also create a low-velocity "dead zone" where spores can congregate. Other features such as sloping valleys or notched ridgelines can channel and accelerate the flow.

ROW ORIENTATION

The orientation of the vineyard rows with respect to typical wind directions impacts spore transport. A vineyard experiencing row-parallel winds will have higher velocities and more mixing than the same vineyard in row-perpendicular winds. In row-diagonal winds, spore plumes channel down the row direction, becoming misaligned with the overall wind direction.

OBSTACLES

Wakes behind trees, windbreaks, buildings, or topographical features are low-velocity regions where spores will congregate and deposit.

4. Deposition

As a spore plume moves through a vineyard, the vines filter out spores being carried in it via deposition. Denser canopies will result in more deposition, decreasing the overall concentration of spores and decreasing the distance the remaining spores in the plume can travel. In addition, as spore velocity and density increase so does deposition. Imagine trying to hit a target on a windy day with a ball— this will be easier using a baseball thrown at top speed than a ballon the same size.

What this means for vineyard disease management

You can use this information to develop intuition for where disease may travel next, once it is found. An understanding of spore dispersion can help in interpreting spore trap data (e.g., due to settling and deposition, the vast majority of spores released from a leaf will only travel around 3-5 rows away, so trapped spores are likely from nearby plants) and in deciding where to place traps (e.g., the more vegetation near the trap, the less likely a spore will be able to reach it before depositing, but too far away from the vegetation and you will intercept fewer spores).