Dispersal of foliar plant pathogens: mechanisms, gradients and spatial patterns

Spore dispersal

Fungi have many different methods of spore dispersal. We have mentioned some of them in the previous lecture. Here we will continue and focus on the dispersal by rain.

Dispersal by rain

Rain or spray irrigation can remove spores from infected leaves in run-off water or in splash droplets. The spores of many plant pathogens can be dispersed only by water because they are contained in mucilage which prevents dispersal by wind. However, raindrop impacts can also dislodge 'dry' spores from leaves to allow them to be dispersed by wind.

Water splash directly removes spores from leaf surfaces by incorporating them into splash droplets. Such droplets can travel more than a metre from the point of impact but most travel only a few centimetres. Consequently, dispersal gradients for splash-dispersed spores are generally much shorter than those for wind-dispersed spores. Splash can also transport inoculum vertically and can play an important role in vertical disease movement, for example in cereals. The effectiveness of splash in removing spores depends on the size and velocity of the incident drop and on the orientation and mechanical properties of the surface, but the physical mechanisms involved are not well understood.

Raindrop size influences both the removal of spores and the distances of dispersal. Large raindrops are more effective than small ones; they remove more spores and splash them further. Raindrops less than 0.5 mm in diameter contribute little to direct

dispersal by splash but can contribute to the wetting of leaf surfaces. Spore removal and dispersal are dependent on the force of impact or the kinetic energy of the incident water drops. Therefore, large slow-moving drops dripping from leaves may remove spores as effectively as small raindrops falling at their terminal velocity.

The potential for dispersal by rain-splash depends partly on the size distribution of the raindrops, which depends on the type of rainfall. For example, spores of *Septoria tritici* (anamorph of *Mycosphaerella graminicola,* cause of septoria tritici blotch of wheat) were splashed from the base of a wheat canopy to the upper leaves only during heavy summer showers. The texture, angle and flexibility of leaves and other surfaces in the canopy all influence the splash process and the amount of water splashed. This may then affect the energy imparted to the droplets and dispersal distances. Distances to which spores are dispersed also depend on the effects of canopy structure and density and mulching material, if present, on splash drop trajectories. The efficiency with which spores are incorporated into splash droplets also affects spore dispersal gradients and the number of spores carried per droplet is influenced by spore size. The incorporation of spores into splash drops can be modelled as the product of three functions of the droplet diameter, which may take similar forms for a range of pathogens: the diameter frequency distribution, the proportion of droplets carrying spores and the mean number of spores in each number category.

Most splash droplets that carry spores are very much larger than wind-dispersed spores and are therefore affected less by turbulence. When effects of turbulence are small, splash droplet trajectories can be computed using conventional Newtonian dynamics. The trajectory of a splash droplet is determined by solving the equation of motion which defines its velocity *v*:

$$m\frac{dv}{dt} = F_g + F_A + F_D + F_a$$

where *m* is its mass, *dv* and *dt* are change in velocity and time, respectively, *Fg* is the force of gravity, *FA* is a buoyancy force, *FD* is the drag force and *Fa* is a force due to acceleration of the droplet.

The distances travelled by primary splash droplets splashing directly from lesions are affected by crop canopy structure, position of the lesion in the crop, the nature of the water source (rain type, irrigation) and the leaf surface, and the wind speed. Crop canopy structure affects the deposition of splashed droplets and the potential for spread by secondary splash.

Primary dispersal is dominant at the beginning of a rain shower while the canopy is being wetted and the initial source of inoculum is being dispersed. Most of the bacteria that cause citrus canker were released within the first 10 minutes in simulated wind-driven rain experiments. However, as rain duration continues, secondary spread may begin to be important as previously splashed inoculum is transported by further splashes. If the rain persists for sufficient time to deplete the source, inoculum deposited may be lost by wash-off.

Spore deposition and disease gradients

Relationship between spore deposition and disease gradients

For both wind and splash-dispersed plant pathogen inoculum, deposition rates decrease with distance away from the inoculum source. Under environmental conditions favourable to infection, dispersed inoculum will produce further infections on susceptible hosts. The disease pattern that develops will also show a decrease in disease with increasing distance away from the source, i.e. a disease gradient. Disease gradients can also result from gradients in host or environmental

factors. The observation of a gradient, therefore, implies the existence of a local source of inoculum, since background inoculum from a large number of distant sources produces a uniform distribution of disease with distance across a crop. Vertical disease gradients (i.e. disease decreasing with height) can also be observed when inoculum sources are at ground level. Disease gradients produced by splash-dispersed inoculum are usually steeper than those produced by wind-dispersed inoculum, reflecting the differences in dispersal length scales between the two mechanisms.

Gradients of monocyclic or polycyclic diseases in crops can provide much information about the role of the wind-dispersed or splash-dispersed pathogen spores in the development of epidemics. Monocyclic diseases produce only primary disease gradients, in which all the lesions arise from the same inoculum source. For example, gradients of the phoma leaf spot stage of stem canker (causal agent *Leptosphaeria maculans*) can be produced by the wind-borne ascospores in winter oilseed rape crops in the autumn. However, spores of pathogens causing monocyclic diseases may be released over long periods of time so that the disease gradients gradually become less steep as the growing season progresses. This may explain why gradients of wheat eyespot in inoculated winter wheat plots became less steep with successive observations, although removal of inoculum suggested that there was no secondary disease spread.

Many studies on disease gradients have been done with polycyclic diseases spread by wind-dispersed spores, such as potato late blight, yellow rust of wheat or powdery mildew of barley. Typically, such diseases are first observed in a crop as primary disease foci resulting from a single lesion; by the time a yellow rust focus 1 m^2 in diameter is observed, four pathogen generations of infection, latent period and sporulation have occurred. Initially disease gradients away from these foci are steep

but spores which escape from the crop canopy soon establish secondary foci; primary disease gradients become more shallow as foci expand and, with the expansion of secondary foci disease, disease is soon distributed uniformly across the crop.

Spread of other polycyclic diseases involves both wind-dispersed ascospores, which initiate epidemics at the beginning of the growing season, and splash-dispersed conidia, responsible for subsequent cycles of disease spread. For example, initial horizontal gradients of white leaf spot (causal agent *Mycosphaerella capsellae*) in winter oilseed rape are caused by wind- dispersed ascospores but subsequent horizontal spread and vertical spread up the crop canopy is achieved by splash-dispersed conidia, with an estimated 9-13 pathogen generations per season. A similar pattern of disease spread is observed for septoria tritici blotch in winter wheat crops. Other pathogens with both ascospores and conidia are apparently monocyclic because either the ascospores (e.g. *Oculimacula yallundae*) or the conidia (e.g. *Leptosphaeria maculans*; anamorph *Phoma lingam*) seem to play little part in epidemics in practice.

Measurement of gradients

To measure a spore dispersal or disease gradient in a natural or experimental situation, measurements of spore numbers per m^3 (spore concentration gradient) or per m^2 (spore deposition gradient) (C) or disease incidence or severity (Y) at different distances (x) from the source are needed. Spore numbers can be estimated with artificial samplers but the choice of sampler and timing of sampling depend on the size of the spores, their mode of dispersal and concentration and the objective of the investigation. Generally, samplers need to be simple and easy to use because the measurement of gradients requires the use of at least 10-20 identical samplers simultaneously. To measure spore deposition gradients, passive samplers such as

horizontal slides under rain-shields for wind-dispersed spores or beakers for splash-dispersed spores can be used. Concentration gradients can be measured with volumetric samplers such as rotorods; vertical sticky cylinders can be used effectively for large spores, such as those of *B. graminis*. Rain-activated switches can be used to confine sampling to periods of rainfall for spores released by rain and sampling can be confined to specific times for spores with known diurnal or seasonal periodicities. Conventional spore samplers usually use microscopy to quantify concentration or deposition. This can be time-consuming and often restricts the number of samples that can be collected. Spore sampling methods based on the use of serological or molecular pathogen diagnostics are being developed. For example, PCR-based diagnostics have been used to detect air-borne inoculum of oilseed rape pathogens.

The disease component of disease gradients has been measured as numbers of lesions, numbers of infected leaves, numbers of infected plants, the percentage leaf area affected or the percentage of the population of plants which is affected. For most diseases, only some of these measurements are appropriate; for example, sorghum downy mildew (causal agent *Peronosclerospora sorghi*) infects plants systemically so cannot be assessed on individual leaves and barley leaf blotch lesions merge so that they cannot be assessed individually. It should be appreciated that whether disease is measured as incidence or severity affects the form of the gradient since incidence and severity gradients measured simultaneously can have different slopes.

The choice of distances (x) at which to assess spore numbers or disease is influenced by the geometry of the source, the scale of the gradient and the objectives of the investigation. Sources can be classified as point, line or area sources.

Point sources may be individuals or small groups of infected plants; ideally a point source should have a diameter of less than 1% of the length of the gradient although the diameter is often 5-10% of the length in practice. Line sources may be hedges containing infected alternative host plants or strips of a susceptible cultivar. Area sources may be infected fields, although such area sources may become point sources if the distance over which the gradient is measured is kilometres rather than metres. Gradients from sources above ground level are generally less steep than those from ground level sources. For measuring gradients, a minimum of five distances should be sampled. Ideally there should be at least 10 distances, selected on a logarithmic scale with more samples near to the source for gradients within crops, and more distances for gradients between crops or over longer distances. Generally, it is easiest to measure gradients over short distances within crops, although gradients have been measured over km distances, for example down river valleys. It may also be possible to observe gradients within crops from above using remote sensing techniques, such as infra-red aerial photography and optical techniques from satellite or tractor-mounted platforms. Long distance transport of spores over 100s of kilometres is important in the spread of some epidemics, such as black stem rust (caused by *Puccinia graminis*) in North America; such spores can be sampled at heights of 1000 m with samplers on aircraft but are generally dispersed by wind and deposited by rain in relatively uniform clouds so that gradients are not observed.

When plotted on a linear scale, spore dispersal and disease gradients are generally hollow curves, which are difficult to compare. Therefore, to compare gradients, the empirical negative exponential (Equation 1) or inverse power law (Equation 2) models (previously mentioned in page 16) are generally log-transformed to give the forms for disease (Y):

$\ln(Y) = \ln(Y_0) - \alpha x$

and

$\ln(Y) = \ln(A) - \beta \ln(x)$ …… (2)

where: x is the distance from the source and α, A and β are constants. The coefficients α and β determine the rate of decrease in spore concentration (or deposition) with distance.

When the models are fitted in these forms, linear regression can be used to estimate parameters to describe and compare gradients. When disease gradients are fitted by an exponential model they can also be expressed as a half-distance. If disease incidence is expressed as the proportion of individual plants affected, then a multiple infection transformation must generally be used to account for multiple infections of the same plant by different spores:

$N_i = N_t(1 - e^{-y_{i/N_t}})$

This allows calculation of the probable number of infections *Yi* that occurred when *Ni* leaves are diseased out of a total of *Nt* plants or leaves. Although only one new infection among 100 plants is required to increase the percentage of plants diseased from 1 to 2%, 69 new infections are required to increase it from 98 to 99%. A problem which arises in using these transformed models is that log-transformation cannot be used if the value of Y or C is zero. This can be overcome by adding a small quantity to each value.

Field experiments to study horizontal or vertical spore dispersal or disease gradients are difficult to design and to do. The experimenter has to contend with the unpredictability in the occurrence, direction and strength of the wind or rain. Consequently, some experiments on dispersal have been done in controlled wind

tunnel or rain tower conditions; results obtained with these model systems have then been compared with those obtained in field crops. In controlled conditions, it is possible to replicate treatments in time but this is rarely feasible under natural conditions.

Experiments with wind-dispersed pathogens, such as *Puccinia polysora* (cause of maize rust, *P. infestans* or *B. graminis* have used point sources of inoculum to study horizontal dispersal and disease gradients. When inoculum has been placed in the centre of plots, disease assessments have been made at points on concentric circles around the source.

Uses of spore dispersal and disease gradients

Measurement of disease or spore gradients can be extremely important for identifying sources of disease, for identifying inoculum dispersal mechanisms, for assessing the effectiveness of some disease control strategies and for interpreting the results of field experiments. Since the observation of a disease gradient implies the existence of a local source of inoculum, gradient measurements can be used to identify inoculum sources.

Dispersal gradients can be used to infer inoculum dispersal mechanisms; shallow gradients suggest wind dispersal and steep gradients imply splash dispersal. Primary gradients of mummy berry disease (causal agent *Monilinia vaccinii-corymbosi*) in blueberry crops were shallower downwind than upwind, suggesting that the ascospores causing the infections were wind dispersed. In contrast, secondary disease gradients, caused by conidial infections, were generally shallower upwind than downwind, suggesting that conidia might be dispersed by insect pollinators. Gradients have also been used to assess the relative importance of primary and secondary inoculum in disease development. Gradients of pod rot (caused by

Botrytis cinerea) at harvest of beans (*Phaseolus vulgaris*) were similar to spore dispersal gradients observed in inoculated plots during flowering, although the spore dispersal gradients had become much flatter by harvest. This suggested that the primary inoculum during flowering was the main cause of the pod rot.

The effectiveness of mixtures of susceptible and resistant cultivars in decreasing the rate of spread of epidemics can be influenced by disease gradients. Simulation models suggested that such mixtures would be most effective against pathogens with shallow spore dispersal gradients; these predictions were confirmed in experiments with the wind-borne barley powdery mildew pathogen. By contrast, such mixtures were relatively ineffective in decreasing spread of the splash-dispersed wheat glume blotch pathogen (*S. nodorum*), which has steep spore (conidia) dispersal gradients.

Disease spread: modelling development of foci

References of this lecture

- Biology of fungi, by Jim Deacon, 4th edition, 2006, p 193 - 221.
- The Epidemiology of Plant Diseases. Edited by B.M. COOKE, and B. KAYE, Second Edition, 2006.