MONITORING LONG-DISTANCE SPORE DISPERSAL BY WIND – A REVIEW

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ABSTRACT

Collection of meaningful data on long distance dispersal (LDD) of plant pathogens is very difficult because such events are very rare, and the strength and locations of pathogen sources are often unknown. This review of the different methods that have been deployed examines combinations of meteorological analyses and ground surveys, including spore trapping devices, collecting rainwater and identifying spores using real-time PCR. The relevance of these techniques is discussed in the context of surveillance and monitoring trans-Tasman dispersal of fungal spores.

Keywords: long-distance transport, spore dispersal, aerial dispersal.

INTRODUCTION

Plant pathogens are dispersed by contact, wind, water, vectors (e.g. insects and birds) and by humans through seed and infected plant material, clothing and introduction of biological control agents (Nagarajan & Singh 1990). Dispersal has three phases: spore liberation, transit and landing. Dispersal can occur a distance from a few centimetres or less between roots in soil to hundreds of kilometres between susceptible crops. For some pathogens, long-distance dispersal (LDD) is an important survival strategy enabling them to colonise new areas or survive between different seasons (Gage et al. 1999). The invasive potential of a pathogen can be largely explained by its ability to use atmospheric pathways for rapid spread into new areas. The ‘atmospheric pathway’ is a concept that explains how organisms move among geographic positions by utilising the dynamic but definable routes that are created by airflows that develop across landforms on the earth’s surface (Isard et al. 2005). Some plant pathogens can spread over very long distances, either between continents in a single step or by gradual spread (range expansion) within continents (Brown & Hovmøller 2002). LDD has been defined as occurring “when the pathogen is transported in a viable form capable of causing infection, and when the source is separated from the target by a distance of 1000 km or more” (Nagarajan & Singh 1990). These pathogens include obligately biotrophic fungi, such as those causing powdery mildew, downy mildew and rust diseases, which produce very large numbers of wind-dispersed spores (Brown & Hovmøller 2002).

The probability of viable spores reaching a susceptible host a continent away and causing infection is very low, but very real. Most of those reported in the literature involve rusts as their spores are relatively robust with thick walls and pigmentation to protect against UV radiation and can remain viable while transported over long distances (Agrios 1997). For example, *Hemileia vastatrix*, the cause of coffee rust, was thought to have dispersed from Angola to Brazil in 1970 by transatlantic winds (Bowden et al. 1971). Sugarcane rust, caused by *Puccinia melanocephala*, was almost certainly transported by cyclonic winds from Cameroon to the Dominican Republic in 1978 (Purdy et al. 1985). The introduction of two species of poplar rust from Australia to New Zealand in 1973 most likely occurred via high trajectory wind currents (Wilkinson & Spiers 1976; Close et al. 1978). Examples of seasonal spread are the “Puccinia Path” of wheat stem rust, caused by *Puccinia graminis* f.sp. *tritici*, from Mexico to the Prairie Provinces of Canada (Kolmer 2001) and the spread of *P. recondita* from South to North

India (Nagarajan & Singh 1990). The evidence for LDD of plant pathogens by wind has relied on the local appearance of new diseases in sites where they were previously unknown. Detailed analysis of meteorological data has provided supporting evidence of such long-distance transport events.

Because such events are so rare, and the strength and location of pathogen sources typically remain unknown, meaningful data collection about LDD can be very difficult (Nathan et al. 2003). Since it is almost impossible to mark individual pathogen spores at source, and so track their movement, the methods of monitoring LDD have relied on ground surveys, weather and climatic analyses, and remote sensing (Nagarajan & Ajai 1988). For study of LDD of plant pathogens, New Zealand's location approximately 1000 km south-east of Australia and the frequent westerly air currents makes for an ideal location. This literature review on the methodology used for studying LDD of plant pathogens via wind currents has been undertaken to facilitate research into the significance of Trans-Tasman transport of plant pathogens to New Zealand national biosecurity as a part of the Better Border Biosecurity (B3) programme. The review looks first at methods for monitoring spore dispersal that are relevant to Trans-Tasman transport and then considers the meteorological factors that contribute to spore dispersal.

LAND-BASED AND AERIAL METHODS FOR MONITORING SPORE DISPERSAL

Sampling from the ground is a fundamental tool frequently used to study LDD of plant pathogens (Nagarajan & Ajai 1988). However, evidence that the spores found have indeed originated from distant places is difficult to obtain and is often circumstantial, being based on presence of airborne soil and dust particles (Davis 1987). More specific information on spore dispersal can be obtained with various spore-trapping devices, such as Petri dishes, filters, sticky cylinders, suction traps, rotorod traps, live traps, jet spore samplers and rain samplers (Nagarajan & Singh 1990). Limpert et al. (1999) determined the spore dispersal of barley mildew propagules using a volumetric jet spore sampler (Burkard Manufacturing, Rickmansworth, Herts., UK) installed 25 m above ground level. Within the trap, the aerosols were carried through a jet to an orifice at the top of a sedimentation chamber, where the spores settled on segments of primary leaves of a susceptible barley cultivar exposed in a Petri dish containing agar. Presence of the pathogen was assessed by counting the colonies on the leaf segments after incubation. Live trap plants can be used in a similar way. Another method of obtaining spore samples from a wide area is by driving across the region(s) of interest with a jet spore sampler mounted to the car roof.

Bioaerosol samples are used in industrial, hygiene and environmental applications to quantify the number of culturable micro-organisms in a sample (Griffiths et al. 2001). Sterile microbiological cellulose nitrate filters have been used to collect and then identify cultures of bacteria and fungi transported in the wind. For example, Prospero et al. (2005) provided rare evidence of LDD of micro-organisms from Africa to Barbados, West Indies, by collecting daily filter samples in 1996-1997 from the top of a 17 m walk-up tower located at the easternmost coast of the island and culturing the filters to identify fungi and bacteria. The location of the tower was carefully selected and the protocols (e.g. smoke tests and computer controlled pump) specifically designed to minimise the possibility of impacts from local sources. They showed that significant concentrations of viable bacteria and fungi were transported with African dust across the Atlantic, but air masses from the North Atlantic, North America and Europe did not yield viable bacteria or fungi. The transport of bacteria and fungi to Barbados followed a clear meteorological and seasonal pattern. The authors suggested that it should be possible to model the transport process and also predict transport events.

In Central Texas, USA, Mims & Mims (2003) studied the micro-organisms contained within smoke that drifted from Yukatan, Central America. In 2002, they placed microscope slides on a 4 m meteorological tower in an open field to quantify carbon particles and fungal spores. Two nutrient media films (3M Petrifilm™), one for bacteria and one for

fungi, were hydrated and exposed for 15 min on the tower and incubated to identify bacteria and fungi. In 2003, a passive air sampler was flown from a kite over a Texas beach on days when smoke from Yukatan was either visible or not visible to eliminate interference from any Texan spores. For both sampling methods, spores were identified by morphological features. The same research team also ran an experiment in which they sampled the air over various kinds of burning plant materials, using nutrient film, which was subsequently incubated. They found that the nutrient films exposed to smoke had significantly more colony-forming units than those exposed in ambient air. They suggested that agitation of leaves during burning may have dislodged spores, which were then carried upward with the warm plumes of air, or that turbulent air rushing in to feed the flames on the ground may have carried spores into the smoke plume. Mims & Mims (2003) suggested that major fires, which can produce smoke plumes 3 km or more high, could be much more effective in launching spores into the troposphere than surface wind storms. They speculated that the transport of sugarcane rust to the Dominican Republic in 1978 (Purdy et al. 1985) may have been initiated by burning of the sugarcane after harvest in Cameroon.

Pfender et al. (2006) used a complex air pollution model (CALPUFF) to estimate dispersal and deposition of *Puccinia graminis* spores (which cause grass stem rust). When a 1 m diameter circular area in the centre of a ryegrass plot was inoculated with urediniospores, emission of urediniospores from the diseased ryegrass was measured using an array of samplers set in an arc downwind from the plot. The samplers were rotary impaction devices that collected airborne particles on square polystyrene rods whose leading edges were coated with silicone grease. The numbers of *P. graminis* urediniospores per sampling rod, determined by microscopic examination, were incorporated into a model showing that most spores were deposited in the field or nearby, but 12.5% of the spore biomass was carried aloft and horizontally beyond 200 km in the air.

Various devices have been created to sample air high above ground. Maldonado-Ramirez et al. (2005) measured the relative abundance of viable spores of *Gibberella zeae* (causal agent of fusarium head blight of wheat) in the planetary boundary layer (PBL) at 60 m above ground level using remote-piloted vehicles (RPV). Each RPV had a wingspan of 2.4 m and was fitted with four spore sampling devices that were opened and closed by remote control from the ground. The sampling devices consisted of vertically mounted Petri plates containing *Fusarium*-selective media. Each sampler had the capacity to sample around 8 m³ of air per minute. Sampling was conducted over agricultural fields in Aurora, New York, from spike emergence through to grain formation of local wheat in May/June. A total of nearly 13,000 viable spores of *G. zeae* was collected over 158 sampling flights in the four consecutive years of sampling (1999–2002). They found that long-distance transport of inoculum of *G. zeae* was important in regional epidemics of fusarium head blight and should be taken into consideration when developing prediction models and management strategies for fusarium head blight.

Specific evidence for LDD can be obtained through analysis of genotype distribution patterns in comparison with the patterns at the assumed sources or origins. These methods, however, have some limitations as they assume that there is no selection, no mutation, all populations are created equal with a constant number of individuals and equal contributions to the migrant pool, there is no spatial structure, and everything is at equilibrium (Whitlock & McCauley 1999). In addition, as species become more widespread it becomes more difficult to determine the sources of particular populations (Nathan et al. 2003). Samples for genotype analyses can be obtained by a wide variety of sampling methods, such as trap plants or plots, leaf samples or devices that collect the rain in a target area. Stukenbrock et al. (2006) analysed the distribution of genetic diversity within and among populations of *Phaeosphaeria nodorum* (leaf blotch and glume blotch on wheat). A total of 639 *P. nodorum* strains isolated from wheat crops in five continents, Australia, China, South Africa, Central and North America and Europe, were included in the analysis. The genetic structure of *P. nodorum* populations showed

moderate population differentiation consistent with high levels of gene flow among continents. These findings suggested that LDD of *P. nodorum* has contributed to the genetic structure of the pathogen on a global scale. Molecular methods, such as real-time PCR, have been used to detect presence of spores in samples of rain water. Barnes et al. (2005) found that this method could provide an early warning system for the movement of *Puccinia graminis* in the USA.

Several of the techniques described above are appropriate to use for monitoring spore dispersal across the Tasman Sea to New Zealand. For example, spores can be trapped with various spore trapping devices and appropriate placement for these can be found by studying 30-year records of simulated wind trajectories from Australia.

ANALYSIS OF METEOROLOGICAL FACTORS

Detailed analysis of meteorological data, together with ground surveys, is essential to provide evidence of LDD and to facilitate estimation of its impact. Of particular importance to LDD is the role of occasional intense meteorological events, such as thunderstorms, tornadoes and hurricanes, as these events cause strong vertical winds that may lift up spores. Weather or earth resource satellites can provide essential meteorological data that can be integrated with information from ground surveys for use in prediction modelling. NASA (National Aeronautics and Space Administration, www.nasa.gov/) and NOAA (National Oceanic and Atmospheric Administration, www.ncdc.noaa.gov/) provide satellite and weather data, some of which is freely available. Lidar instrumentation and acoustic radar have increased the capacity to study microscale atmospheric motions in the surface boundary layer and PBL. If coupled with microbiota sampling, they could be used to study the role of atmospheric structures in initiating the movement of organisms in the atmosphere (Westbrook & Isard 1999).

Descriptive and measurement terms for modelling LDD of plant pathogens include: numbers of spores released at the source and the source characteristics; structure of the vegetation at the source; time when individuals become airborne; height of the vegetation where aerial movement is initiated; favourable wind speed and direction; airborne travel time; dilution of the spore cloud by turbulence; and loss of viable inoculum from the air column either by mortality or by physical removal by wet and dry deposition processes (Aylor 1986, 1999). Modelling and quantifying spore escape from the plant canopy to the air above is difficult and complex. The factors that determine this process are vertical position of spores in the canopy and the ratio of spore settling velocity to ambient turbulence: the number of spores escaping from the canopy increases with wind speed, turbulence level and source height (Aylor 1999). Atmospheric mixing is required to lift spores to altitudes for LDD, and is mainly confined to the planetary boundary layer and varies within diurnal and seasonal cycles (Westbrook & Isard 1999).

According to Aylor (1990), empirical descriptive models and spatial contact models have been used to describe population spread whilst dispersal of spores in the atmosphere can be modelled using Eulerian advection diffusion models, Lagrangian stochastic (LS) simulation models or Gaussian plume or puff models. The first two models are more accurate and versatile than Gaussian models but require detailed meteorological data, which are often not available. Gaussian puff models are suitable when modelling something far from a source and well above a vegetated surface (Aylor 1986, 1999). The most widely used model for aerobiological applications is HYSPLIT (HYbrid Single-Particle Lagrangian Integrated Trajectory; Isard et al. 2005). Coupling of detailed atmospheric models, for example the high resolution large eddy simulations (LES), with regional atmospheric models results in very useful hierarchical models (Nathan et al. 2005). Predictive models help to better understand the mechanics and patterns of LDD and assist in risk analysis to identify pathways of entry for wind-dispersed pathogens. Quality of inputs remains a limiting factor in constructing accurate risk maps (Magarey et al. 2007).

An example of incorporating weather data with ground information in an integrated aerobiology modelling system is one described by Isard et al. (2005). This system

was designed to forecast invasion and spread of soybean rust (caused by *Phakopsora pachyrhizi*) in the United States. It incorporated observation and knowledge (meteorological, biological and physical) into relational databases that were linked with socioeconomic data to assess risk of movement. The decision support system (DSS) assessed field observations, model results and information on ecosystem susceptibility and socioeconomic impacts. Community users, such as farmers, scouts, policymakers and scientists, had access to the DSS through GIS and other tools on the internet. This DSS guided the scouting operations after the rust was first found in Louisiana and it correctly predicted the spread of this pathogen to other southeastern states.

Despite advances in the study of movement of organisms via atmospheric pathways, this mechanism remains one of the least understood ecological processes on earth (Isard et al. 2005). Future challenges include integrating biological knowledge and monitoring techniques using information technology into an aerobiological framework capable of anticipating the threat of invasive species with a DSS to manage the pathogen. In addition, new sensor systems to quantify flows of organisms in the atmosphere, and cost-effective techniques for monitoring spore (and other organism) movement with standardised measurements and efficient databasing procedures are required (Isard et al. 2005). It is important not to ignore alternative pathways of introduction from Australia and Tasmania, mainly human-assisted dispersal, otherwise useful and regulatory strategies (e.g. sanitation and quarantine) could be overlooked (Aylor 2003).

CONCLUSIONS

Knowledge of the processes involved in LDD will assist in the study of trans-Tasman transport of plant pathogens to New Zealand. Identification of conducive weather conditions to LDD, together with ground-based information on possible pathogens that pose a threat to New Zealand's border biosecurity, could provide advance warning to primary producers about the possible arrival of new pathogens. It can also help target the resources required to respond to incursions more effectively.

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