Aerobiology of foot-and-mouth disease (FMD): an outline and recent advances

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Summary: This paper describes how information obtained from epidemiological and meteorological analyses of outbreaks of FMD, together with experimental investigations on the excretion, survival and infection by airborne FMD virus, have been used to develop mathematical models which can be used to predict the probability of airborne FMD spread in the field.

KEYWORDS: Airborne infection - Aphthovirus - Cattle diseases - Epidemiology - Model - Statistics.

INTRODUCTION

In the era before the adoption of mass annual vaccination by countries on continental Europe in the mid-1960's, there were many occasions when FMD spread to the United Kingdom and Scandinavia. Frequently, such spread was preceded by the appearance of outbreaks on the nearby continent and often there was no history of contact linking outbreaks separated by seaways. Over the years, several authorities have attributed these episodes of unexplained distant spread to the carriage of virus on the wind (12, 13, 24, 25).

Although vaccination and other control measures have dramatically reduced the number of outbreaks of FMD in Europe during the last 20 years, there have still been occasions when the circumstances have suggested that airborne spread has taken place during epidemics. This has occurred both within and between countries (17, 18, 22).

Experimental studies on the aerobiology of FMD at the Animal Virus Research Institute have been in progress since the 1930's (14, J.T. Edwards, unpublished papers) but they were given a considerable impetus by the 1967-68 United Kingdom ("Oswestry") epidemic. In this epidemic more than 300 farms were affected during the first three weeks. This explosive start, attributed to airborne spread (21, 30), undoubtedly contributed to the subsequent enormous size of the epidemic which in total involved more than 2,300 farms. This experience identified a need to establish data on the quantitative aspects of airborne spread and to determine if such information could be used to develop the means of predicting airborne spread in future outbreaks so that improved control measures could be used.

As a consequence of experimental and epidemiological investigations and collaboration with the Meteorological Office, Bracknell, it has, in fact, been possible to

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develop mathematical models for predicting the airborne spread of FMD. The stages in the evolution of these models are outlined in this paper under the following headings: (i) sources of airborne virus; (ii) survival of virus in the air; (iii) airborne infection of susceptible animals; and (iv) operational use of mathematical models.

**SOURCES OF AIRBORNE VIRUS**

The duration and quantity of airborne FMD virus excreted by different species of domesticated and wild animals was determined by infecting groups of animals with a series of different strains of virus and then sampling the air in the rooms in which they were housed, using a range of air sampling devices. It was found that the quantity of airborne virus recovered was dependent on the species of animal, the strain of virus and the stage of disease. Infected pigs excreted by far the largest quantity of infectivity — the maximum amount recovered per pig per day being \( \log_{10} 8.6 \) TCID\(_{50}\) (7). The maximum amount of virus excreted during the same period by ruminants, domesticated or wild, was around 1,000-3,000 times less (10, 28). The duration of excretion with all species was generally 4-5 days. Inoculated sheep excreted most virus when only primary lesions were evident whereas cattle and pigs excreted maximally when vesicular lesions were at the early acute stage of generalisation. The strains which resulted in the highest yields of airborne virus were several O strains and C Noville (10).

These results demonstrated that infected animals, particularly pigs, are a probable source of airborne FMD virus during outbreaks. Other possible sources may include: the splashing of contaminated milk or faecal slurry; the spray disposal of infected slurry; rain falling onto contaminated ground; and the burning of carcasses on which vesicles are present. The quantities of airborne virus which these procedures could potentially generate have not, however, been determined.

Another possible source of airborne virus dissemination is from bulk milk tankers containing contaminated milk. During the filling of milk tankers it has been observed that the displaced air results in the production of milk aerosols near the air-outlet vent. However, the experimental seeding of milk tankers with spores as tracers and air sampling during venting suggested that the quantities of airborne FMD virus likely to be emitted by this source during outbreaks are not likely to constitute a serious hazard (G.J. Harper, unpublished results).

**SURVIVAL OF VIRUS IN THE AIR**

The concentration of airborne virus may be reduced by diffusion and sedimentation, i.e. by physical loss, and also by inactivation, i.e. by biological loss.

The effect of environmental factors on the viability of different strains of FMD virus has been investigated and it was found that the factor which had the greatest influence was the relative humidity (RH) (1, 4). In moist air (above 55% RH), airborne virus had a low rate of inactivation but in dry air (below 55% RH), the inactivation rate was high. For example, strain O\(_{1}\) BFS sprayed from tissue culture fluid decayed at a rate of \( \log_{10} 0.6 \) per hour at 60% RH whereas at 40% RH the rate was \( \log_{10} 4.2 \) per hr (1).
The fluid from which virus was aerosolised was found to influence subsequent decay rates. Physiological fluids generally were protective. For example, very low decay rates were obtained with virus aerosols from nasal fluid, milk or faecal slurry. An exception was bovine salivary fluid from which high decay resulted. A small dialysable, heat-resistant molecule was identified as being responsible for virus inactivation in bovine saliva (2, 5).

The respiratory tract was determined as the main source of airborne FMD virus from infected animals so the biological decay rates obtained with virus aerosolised from nasal fluid most probably approximate those which occur in nature.

Other environmental factors examined for their influence on the viability of airborne virus were daylight and atmospheric pollutants. Neither was found to be a strong inactivant under the test conditions used. In the case of daylight, virus held as droplets on microthreads and exposed for 30 min. was found to be photoresistant. The ambient RH was kept high during the tests to avoid the inactivation of virus by dehydration (6).

Airborne virus excreted by infected animals has been found to be associated with a range of particle sizes (8, 28). Between 65-71% of the total infectivity was associated with particles greater than 6 µm in diameter, 19-24% with particles 3-6 µm in diameter. It is considered that the physical decay rate of 6 µm and smaller particles will be small compared to the larger scale movements in the atmosphere which spread and dilute the particles (16).

Once airborne virus has been emitted from a source, a plume will be formed which will be subjected to dispersion in both horizontal and vertical planes. Prevailing climatic conditions, particularly windspeed and the vertical temperature structure in the lower atmosphere, will be the major determinants of physical decay. The roughness of the surface over which the air passes will influence the amount of turbulent mixing and topographical features will determine the direction the plume travels. Virus concentration is likely to be maintained for longer during travel over the sea than over the land.

The conditions under which the physical decay of airborne virus are likely to be minimal and, therefore, the potential for distant spread greatest are: in light winds; after a sea passage; when the air temperature over the sea exceeds the sea temperature i.e. little vertical dispersion; and when the humidity is high (17).

These theoretical considerations have been borne out by epidemiological and meteorological investigations of epidemics of FMD in the UK in which airborne spread is believed to have taken place. The determinant climatic factors in airborne spread have been identified as: wind direction (21, 26); wind speed (26, 30); wind veer (30) and high humidity (26). The furthest distance over which airborne spread is believed to have occurred is around 250 km for spread over the sea (9) and 60 km for spread over the land (21).

**AIRBORNE INFECTION OF SUSCEPTIBLE ANIMALS**

The amounts of virus which can initiate infection in cattle, sheep and pigs by the respiratory route are considerably less than those by the oral route. Henderson and Brooksby (19), for example, failed to infect cattle by feeding them $\log_{10}6.5$ ID$_{50}$ of virus in glass capillary tubes which the animals chewed, though Burrows (unpublish-
ed results) infected some cattle which were given log10 5.8-6.8 ID₅₀ of virus by mouth. In contrast, Eskildsen (11) found that an aerosol dose containing log10 2.7 mouse ID₅₀ was sufficient to infect a heifer, and in recent work cattle were infected following exposure to a dose of 25 TCID₅₀ of airborne virus (A.I. Donaldson, C.F. Gibson, R. Oliver, C. Hamblin and R.P. Kitching, unpublished results). The minimum dose reported to infect sheep by the respiratory route is 10 TCID₅₀ (15) but the minimum dose to infect this species by the oral route has not been reported. The lowest reported dose to infect a pig by the respiratory route is log10 2.6 ID₅₀ (29) and by the oral route log10 3.9 ID₅₀ (23).

It is evident, therefore, that sheep and cattle are especially susceptible to infection by the respiratory route and that the lowest dose which can initiate infection is similar for both species. Under experimental conditions when sheep and cattle were exposed to an environment containing airborne virus, the cattle became infected before the sheep (3). This was probably because cattle have a much higher respiratory tidal volume than sheep and thus sampled more air.

In epidemiological analyses of epidemics, cattle are the animals most frequently affected downwind during airborne spread of FMD and infected pigs are the animals most frequently identified as the source of airborne virus emission (9, 17, 18, 21, 26, 27). There is agreement, therefore, between the results obtained under laboratory conditions and in the field.

**OPERATIONAL USE OF MATHEMATICAL MODELS**

The mathematical models which provide an objective estimate of the area most at risk from airborne FMD spread in the event of an outbreak have been developed by a blending of the aerobiological characteristics of FMD and its causal virus, as described in the previous sections, with the mathematical and physical parameters governing the diffusion of particles in the atmosphere. Two separate models are available; one for short-range and the other for long-range prediction. The short-range model is computer-based and can be used to forecast the extent of dispersion of airborne virus over land within a 10 km radius of a known source. The long-range model is operated manually and is for analysing the dispersion of airborne virus across the sea over long distances.

The following input data is required for their operation: (i) an estimate of the daily airborne virus output from the infected animals; (ii) hourly or three hourly observations of windspeed, wind direction, RH, cloud cover and precipitation in the region of the outbreak; (iii) latitude and (iv) topographical features of the area.

The daily airborne virus output is estimated by determining the total number of infected animals at the source of virus release. This may be done crudely in the first instance but should be more accurate once an epidemiological team (9) or experienced clinician has been deployed to the infected premises. The start of the period of airborne virus excretion delineated for analysis can also be crudely estimated at first but should be more accurately defined by an experienced clinician once the age of the oldest vesicular lesions present on the affected animals at the premises has been established. When this has been done, the start of the airborne virus excretion period on the premises can be estimated. The period of excretion and total daily output having been determined, mathematical analysis and generation of plume
profiles can be done at the Meteorological Office*. Details of the equipment and programmes used have been given elsewhere (16).

Finally, plume profiles can be laid over animal distribution maps to identify the premises and herds which are potentially at risk. Epidemiological analyses have shown that cattle downwind, and especially those in large herds, are the species most likely to be infected during episodes of airborne spread (20).

The models have been tested on past outbreaks of FMD where there has been strong circumstantial evidence for airborne spread and a good agreement has been found between the spread of disease predicted by the models and that which actually took place (16, 17). The models were used operationally in March 1981 when a risk of spread from Brittany, France, to the United Kingdom, was successfully forecast (9).

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Résumé : L'auteur décrit la méthode adoptée pour obtenir des informations sur les foyers de fièvre aphteuse à partir d'analyses épidémiologiques et météorologiques. De même, grâce à des recherches expérimentales sur l'excrétion, la survie et le pouvoir infectieux du virus aphteux propagé par voie aérienne, il a été mis au point des modèles mathématiques utilisables pour prédire le risque de transmission aérienne de la maladie sur le terrain.


Resumen : Describe el autor el método adoptado para lograr informaciones sobre los focos de fiebre aftosa en base a análisis epidemiológicos y meteorológicos. Asimismo, merced a las investigaciones experimentales de la excreción, supervivencia y poder infeccioso del virus aftoso propagado por vía aérea, se han elaborado modelos matemáticos que se pueden utilizar para anticipar el riesgo de transmisión aérea de la enfermedad en el campo.

REFERENCES


