Assembling spatially explicit landscape models of pollen and spore dispersal by wind for risk assessment

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Models of windblown pollen or spore movement are required to predict gene flow from genetically modified (GM) crops and the spread of fungal diseases. We suggest a simple form for a function describing the distance moved by a pollen grain or fungal spore, for use in generic models of dispersal. The function has power-law behaviour over sub-continental distances. We show that air-borne dispersal of rapeseed pollen in two experiments was inconsistent with an exponential model, but was fitted by power-law models, implying a large contribution from distant fields to the catches observed. After allowance for this 'background' by applying Fourier transforms to deconvolve the mixture of distant and local sources, the data were best fit by power-laws with exponents between 1.5 and 2. We also demonstrate that for a simple model of area sources, the median dispersal distance is a function of field radius and that measurement from the source edge can be misleading. Using an inverse-square dispersal distribution deduced from the experimental data and the distribution of rapeseed fields deduced by remote sensing, we successfully predict observed rapeseed pollen density in the city centres of Derby and Leicester (UK).

Keywords: genetically modified crops; genetic modification; invasion; epidemic; spatial; fat-tailed dispersal

1. INTRODUCTION

There is a sustained interest in gene flow from genetically modified (GM) crops and, in the spread of fungal diseases, via spores. This paper centres on the selection of dispersal models for use in landscape-scale strategic, scenario-building or generic models involving the movement of pollen or disease propagules by wind. We use wind dispersal of oilseed rape (OSR) pollen from area sources as an example system. Several good physically based models of wind dispersal exist for use where topography and weather data are known (Berkowicz *et al.* 1986; Olesen *et al.* 1992; Carruthers *et al.* 1994; Giddings 2000; Aylor 2003). However, when deciding policy, it is often necessary to manage a threat arising at an unknown location and time, over spatio-temporal scales outside the practical capacity of such models. In such situations, authors have commonly used a generic dispersal curve (Peart 1985; Okubo & Levin 1989; Perry 2002). Two broad families of curves are commonly used successfully in pollen dispersal modelling: negative exponential or exponential power models with very rapidly declining probability of transport above a certain scale (Timmons *et al.* 1996; Lavigne *et al.* 1998; Damgaard & Kjellsson 2005) and inverse power-law models with fat tails (Austerlitz *et al.* 2004; Devaux *et al.* 2005), both of which may be justified on a simple physical basis (Stockmarr 2002; Katul *et al.* 2005). If a model with a tail declining exponentially or faster is chosen, it is possible to select a distance beyond which the probability of transport is negligible; for this reason, background levels cannot exist beyond a certain distance from a source.

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Many 'fat-tailed' probability density functions have been suggested with which to model dispersal. We suggest a simple form, based on heuristic physical arguments, for a probability density function that has power-law behaviour over sub-continental distances, but finite moments. We show that area sources affect the form of the dispersal function in addition to scaling of output to source size (e.g. Ribbens *et al.* 1994; Clark *et al.* 1999; Devaux *et al.* 2005). Greene & Calogeropoulos (2002) have shown that the dispersal curve will flatten with aggregation. With the form of the dispersal kernel we have chosen, we further show that by taking measurements from the centre rather than the edge of an area source, a single form of function incorporating the effective radius of the source can be used, regardless of the source size.

In this paper, we use simplified models of pollen dispersal to demonstrate that exponential family models are inconsistent with the existence of background pollen levels for wind-dispersed OSR pollen in the UK. We also show that the background levels observed are consistent with cumulative levels of individually negligible distant sources. These background levels may be comparable to relatively close single sources, so that the administratively convenient concept of a safe separation distance (Firbank *et al.* 1999; Ingram 2000; Agriculture & Environment Biotechnology Commission 2001) has limited value: the overall density and pattern of cropping are also important.

2. DATA

Data analysed here come from two sources. First, Timmons *et al.* (1995) provided daily pollen counts

during flowering of an adjacent rapeseed field. Volumetric spore traps were situated at 1, 100 and 360 m in the prevailing downwind direction from the edge of a 10 ha rectangular rapeseed field in 1992 and from a 3 ha field in 1993. Counts were converted to pollen grains per cubic metre of air per day. A background reference trap was positioned at 2500 and 1500 m from the nearest field in 1992 and 1993, respectively. Second, *Brassica* pollen counts were purchased for 2000–2002 from the National Pollen and Aerobiology Research Unit (University College Worcester, Worcester, UK), a network of volumetric traps in several city centres throughout the UK for pollen allergy research. Wind direction data were obtained from the British Atmospheric Data Centre (CCLRC Rutherford Appleton Laboratory, Oxford, UK).

3. STATISTICAL METHODS

Specific probability distribution functions were fitted to the cumulative empirical probability distribution functions describing daily pollen concentrations at each distance from the source field. Distributions regarded as convolutions of two sources were ‘deconvolved’ by dividing the Fourier transform of the convolved distribution by the Fourier transform of one of the presumed sources. Fourier transforms of distributions for which an analytical expression was not available were calculated by applying the fast Fourier transform algorithm (Press *et al.* 1992) to a series of points calculated along the fitted curve, including the range of very low concentrations which would all correspond to a zero observation.

4. MODELS

Two important classes of model for changes in mean pollen or spore concentration $t(r|\theta)$ with distance r from a point source along a given bearing θ are

$$t(r|\theta) \propto e^{-r/k}, \quad (4.1)$$

an exponential decline with a characteristic scale of k , and

$$t(r|\theta) \propto (c + r)^{-b}, \quad (4.2)$$

in which c is a small positive number with dimensions of distance, which avoids equation (4.2) becoming infinite at the origin, and b is a dimensionless constant. At sufficiently long distances from either a point or an extended source, equation (4.2) implies that concentrations obey

$$t(r|\theta) \propto r^{-b}, \quad (4.3)$$

so a plot of the logarithm of concentration against the logarithm of distance is a straight line with slope $-b$. Functions of the form of equations (4.2) and (4.3) are not valid probability density functions if $b < 1$, and do not have finite means if $b < 2$; this can be a problem in modelling since such values may nonetheless fit data well over the short distances that are experimentally observable. Neither of these models has usually been related to the underlying meteorological processes.

Three processes can be distinguished in air-borne dispersal. First, particles are carried by mean wind flow (advection). Wind speeds are typically between 1 and 10 m s⁻¹, with occasional extreme excursions far outside this scale (0–50 m s⁻¹; Shellard 1976; Kings & Giles 1997). Second, turbulence will lead to dispersal around

the average path of particles released at the same instant and place. If this turbulent dispersal is assumed to be a random walk or if turbulent processes are modelled in detail, this results in a Gaussian distribution about the mean advection (for an application to fungal spore dispersal see Spijkerboer *et al.* 2002); however, the scale length of this, for light particles, is much smaller than that resulting from advection. Third, propagules die or are deposited on the ground. The interaction of these three processes will give rise to the observed probabilities of moving from place to place.

If we imagine the particles to move in straight trajectories with a constant probability of deposition or death, we predict an exponential distribution of distance travelled along any given bearing. Since the probability of capture or deposition without rain is low, the length scale of this exponential is very long and is set by whether deposition or death is more rapid. For pollen or spores, which are typically viable for a mean time around 10–40 h (Gregory 1973), viability will make the scale of this exponential, measured by half-distance, roughly 50–2000 km. Oilseed rape pollen may remain viable up to 4–5 days (Mesquida & Renard 1982; Rantio-Lehtimäki 1995). In the event of rain, particles are removed rapidly and in this case, the question centres on the probability of encountering rain along a sample path, but again results in an exponential decline on a distance scale.

However, the exact advection encountered by any two particles will differ and we may visualize pollen or spores starting from a common point being blown into diverging trajectories. A reduction with distance in the probability of pollen or spore interception by an element of fixed size must occur, because of the smaller solid angle subtended by an area of element at right angles to the trajectory as distance from the origin increases. If we neglect vertical components of advection, this argument would suggest interception decreasing inversely with distance; Gaussian turbulence about the mean would tend to make this fall off slightly faster. If the vertical and horizontal components of advective trajectories separated at equal rates, the interception would fall off as an inverse-square law, just like light. However, dispersal in the vertical dimension will be limited, so that the angular separation of trajectories would not increase indefinitely with distance. In this case, the probability of intercepting pollen or spores should decline more slowly. These considerations suggest that the probability of transferring a particle by wind between the two points will be described by a function which has power-law behaviour with an exponent of between 1 and 2, until scales become so large that processes leading to exponential decline become significant.

Thus, we argue that a simple model of wind transport along a single bearing could be expected to have the general character

$$t(r|\theta) \propto (c + r)^{-b} e^{-r/k}, \quad (4.4)$$

with b in the range 1–2 and k in the range 100–1000 km. The constant c now represents the scale below which there is negligible divergence in trajectories, as well as avoiding a singularity at $r=0$. c and r have dimensions of length, but when equation (4.4) is normalized, the units of length m

Figure 1. Effect of an extended source on the relationship between pollen or spore concentration and distance. (a, b) Change in pollen concentration with distance from a circular field of radius 100 (open symbols) or 1000 (filled symbols) times the basic point source scale parameter; individual sources in the field obey equation (4.4) with $b=1$ (open circles), 2 (open squares) and 2.6 (open triangles). Fitted lines use equation (4.7) with b fixed at the value used for the basic point source. Dashed lines show the equivalent point source curves.

cancel, to make a dimensionally consistent equation. This is clearer in the following form

$$t(r|\theta) \propto \left(\frac{c}{m} + \frac{r}{m}\right)^{-b} e^{-r/k} \\ = \left(\frac{m}{c}\right)^b \left(1 + \frac{r}{c}\right)^{-b} e^{-r/k} \propto \left(1 + \frac{r}{c}\right)^{-b} e^{-r/k}. \quad (4.5)$$

In agricultural practice, point sources are relatively unimportant and we need to consider entire fields. A reasonable first approximation is to regard the field as a circular source containing a very large number of independent point sources and develop a dispersal curve to apply to the entire field. We did this for the family of curves represented by the power-law factor in equation (4.4), taking $c=1$ without loss of generality. In other words, we used units of length corresponding to the value of c for a point source—for an inverse square, this is the median dispersal distance. Each point source within a field was defined as a distance ρ from the field centre along a vector with an angular offset ϕ from θ , the bearing to the sink point. The distance from each point source to a point at distance r away from the edge of a circular field of radius R can be calculated using basic trigonometry. Substituting this into equation (4.5) and integrating over all values of ρ and ϕ within the field, the total pollen reaching the sink point is given, in polar coordinates, by

$$t(r|\theta) \\ \propto \int_{\phi=0}^{2\pi} \int_{\rho=0}^R \rho \left(1 + \sqrt{(R+r-\rho \cos \phi)^2 + \rho^2 \sin^2 \phi}\right)^{-b} d\rho d\phi. \quad (4.6)$$

For values of $b < 3$, the values of this integral were calculated at close intervals of r . The resulting curves were well approximated by a model of the form

$$\log(t(r|\theta)) = \alpha + b \log(\gamma(R) + r), \quad (4.7)$$

for all values of r and R (figure 1). Parameter values were estimated by least squares. The approximation was best for $b < 2$. At any given b the parameter α , determining the actual concentration at any distance, was proportional to field area, as expected. The constant of proportionality, A ,

was close to 1 but declined slightly with increasing b

$$A = 1 - 0.000760 e^{1.84b}. \quad (4.8)$$

At any given b , the parameter γ increased smoothly with R . Over the range $R=30$ –1000 m (roughly 0.25–300 ha) and for $1.4 < b < 2.4$, γ can be approximated as a straight line dependent on b

$$\gamma = (5.283b - 3.302) + (1.139 - 0.2955b)R. \quad (4.9)$$

The approximation holds reasonably well considerably outside this range.

Combining all the elements, the dispersal curve from an extended source of radius R is obtained from the point dispersal pattern in equation (4.4) by putting

$$c_{\text{extended}} = c_{\text{point}} + (5.283b - 3.302) \\ + (1.139 - 0.2955b)R, \quad (4.10)$$

and increasing the numerator in proportion to the field size. The error in this approximation is smallest for small values of b . We can use the approximation without knowing the exact value of c_{point} , provided it is negligible compared with the second term on the right-hand side of equation (4.10). In practice, field radii will be at least tens of metres, whereas measurements of local dispersal (McCartney 1987; van den Bosch *et al.* 1988; Aylor 1990) suggest that c_{point} is less than about 1 m.

The predictions of models at distances in the 1–1000 km range are important for setting isolation distances, especially if very low levels of contamination are of concern. In this case, there is an important distinction between models whose behaviour is dominated by the power-law component of equation (4.4), in which, in a large uniform habitat, long-distance effects dominate local sources, and models which have a more rapid decline in transport with distance, in which local sources dominate long-distance ones. The dominance of distant sources is especially important in models with power-law exponents b of 2 or less. By contrast, in the case where for some reason a short-range exponential substitutes for the power-law part of equation (4.4), local dominance is

extreme and it is possible to set a meaningful distance beyond which sources can be completely ignored.

A complete description of dispersal also requires consideration of how density will vary with θ . If wind is equally likely to blow from any direction, then variation with r is independent of θ and variation with θ is simply a uniform density on $[0, 2\pi)$. If the wind has prevailing directions, then the situation depends on the detail of how often the wind blows from each direction. On the basis of the argument we have put forward, the main reason for decreasing density with distance is geometric. This applies on a small scale around the particular direction in which the wind is blowing at any given moment; if the frequency distributions of wind speeds and forms occurring in any given direction are similar, then it is likely that only the constant of proportionality in equation (4.4) will be a function of θ . If both the frequency distribution of wind speeds and the frequency of blowing in the direction θ depend strongly on θ , then another approach—and very detailed data—would be needed. In this case, the advantage of a generic approach over detailed meteorological modelling would probably be lost.

5. RECONSTRUCTION OF POLLEN DENSITIES

Satellite data showing the barycentre and areas of flowering rapeseed fields in central and eastern England in May 2001 were obtained from three Landsat images, covering central, eastern and southeast England. Approximately 10 000 fields were located on the basis of spectral characteristics described in [Wilkinson *et al.* \(2003\)](#). The pollen densities at each point on a grid 100×100 km with a grid spacing of 500 m centred on Leicester were calculated by summing the contributions from each field in the satellite images. The concentrations were calculated based on three models: an exponential model with median dispersal distance of 100 m, and inverse power-laws of powers 2 and 1.6. Based on equations (4.4) and (4.10) as fitted (equations (6.1) and (6.2)) to the Scottish data, taking the effective field radius for each field as R and the distance between the field centre and the grid point as $R+r$. Edge effects were minimized by using all located fields in the integrations. To assess the extent to which wind direction was critical in determining background levels ([Giddings *et al.* 1997](#); [Stockmarr 2002](#)), we constructed windroses for sites in the study area where hourly data were available for May during 1990–2000, from the UK Meteorological Office automatic weather stations. On an average over all sites and years, wind in the southwest and northeast quadrants was almost three times as common as in the northwest and southeast. However, in any given year, there were substantial differences between the sites. Furthermore, when averaged over sites the preferred wind directions, if any, varied substantially between years. In the absence of detailed meteorological information, there is therefore no simple way to allow for the effect of wind, at least in this region at this time. Therefore, we chose to test whether we could obtain approximately correct results in a year not in our dataset by assuming that dispersal was the same along all bearings. This assumption is in common with the studies of [Perry \(2002\)](#) and [Devaux *et al.* \(2005\)](#). The pollen levels calculated for grid points at the centres of Derby and Leicester were compared with the means of the lognormal

Figure 2. Frequency density of 24 h pollen catches and the best-fitting lognormal distribution with spread parameter fixed at 1.91. (a) 1 m, 1992; (b) 360 m, 1993 (the worst fit). In each case, the inset shows the lower range of the curve at a larger scale.

distributions for pollen count data in those cities for pooled data from May 2000, 2001 and 2002. (Outside the May flowering period of rapeseed very little pollen was caught.)

6. RESULTS

The distributions of catches at each site in both the city-centre data and the experiment are closely fitted by lognormal distributions ([figure 2](#)), with R^2 more than 0.992 in every case. This allows description of each site using the two parameters of the lognormal distribution. The location parameters decrease with distance, while there is no trend in the spread parameters. This is slightly unexpected since air-parcels carrying pollen should spread and become more dilute as they travel further. However, to improve the stability of the estimates, the distributions were re-fitted assuming a constant spread parameter equal to the average for all the data, 1.91. Changes in goodness of fit were small and no systematic differences to the residual patterns occurred. The total pollen deposited at each experimental site will be proportional to the mean of this distribution. We used the mean of the fitted lognormal as our estimate of this mean to minimize the effect of individual extreme observations.

We now consider how concentrations change with distance from source. Initially, we assume that background concentration, not originating from the source field, has negligible influence on the transect data. With this assumption, the data do not fit an exponential model ([figure 3a](#)). However, they are very well fit in both years by a model of the form of equation (4.7), with slope $b = -0.5$. (A two parameter fit with $\gamma = 0$, with degrees of freedom directly comparable to the exponential fit, is also good.)

Figure 3. (a) Natural log (ln) of estimated mean catches at different distances from the field edge, with the best fitting exponential decline curves. (b) Natural log (ln) of estimated mean catches after subtracting background at different distances from the field edge with a spread parameter fixed at the average observed. Lines are the best-fitting curves for extended sources of the two known field sizes. Single-parameter fit, made by adjusting vertical position of the curves only, with power-law exponent, b , fixed at 2.

A slope of -0.5 represents an extremely shallow dispersal curve, and suggests a contradiction: if it were the correct power-law relationship, the background concentration could not be negligible, because distant sources would inevitably have a major effect.

Therefore, we assume that each experimental site receives pollen from both background and local sources; the observed pollen count is the sum of these, in unknown proportions. This means that the distribution of counts is the convolution of a background and a local count distribution. If we can posit or estimate the background distribution we can derive the local distribution by taking Fourier transforms, dividing the coefficients of the transform of the observed distribution by those of the distant distribution, and then inverting the resulting transform.

To proceed further, we need to determine the background concentrations. Concentrations in the centre of Invergowrie have a greater mean than those at the background locations in the experiment; this makes it impossible to find a local spread that could add to them to produce the observed value. Further, in 1993 there was a negligible difference between catches at 360 and at 1500 m. The 2500 and 1500 m data are, therefore, the best available estimate of background at the location of the experiment.

Removing this background from the 1, 100 and 360 m data as explained in § 3, the corrected distributions remains very close to lognormal, but the spread of concentrations found increases steadily with distance.

The 360 m data in 1993 are uninformative since they are indistinguishable from background. These corrected data were fitted to a model of the form of equation (4.7), with γ set to the value in equation (4.10) and two free parameters: b and the overall constant α . The difference in concentration between the 2 years is too large to be accounted for solely by the different field size: fitting a single curve to both datasets with no information at 360 m in 1993 artificially flattens the dispersal curve, so separate values of α are needed for each year. The best estimate of b in the 1992 data is 1.6 and this also fits the 1993 data well, although it is clear that little weight can be placed on this. However, at 100 and 360 m, data values are strongly influenced by the inferred spread parameter. To test the effect of this, we refitted the corrected catch distributions with a fixed spread parameter equal to that found in the raw data. In this case $b=2$, an inverse-square decline of spread with distance, matches best with the data (figure 3b).

To summarize this argument, the probability of pollination at a given distance from a pollen source cannot be described by an exponential, since there would be no background unless the scale of the exponential were larger than is allowed by the data. If we assume that the most distant measurements are dominated by background, the exponent of a power-law describing the change in probability with distance along a given bearing is in the region of 1.5–2. Our best estimates of the two possible distributions for the pollen count per cubic metre of air at a distance r from a field of equivalent radius R , both measured in metres, are therefore

$$t_1(r|\theta) = \frac{0.65\pi R^2}{(5.2 + 0.66R + r)^{1.6}} \quad (6.1)$$

and

$$t_2(r|\theta) = \frac{3.24\pi R^2}{(7.3 + 0.55R + r)^2}. \quad (6.2)$$

To show the difference between the models and test the deduced dispersal distributions, we calculated the expected OSR pollen density in central England using rapeseed field data for 2001 obtained from satellite images. Away from fields, the predicted density is zero with the exponential model and no pollen is expected in Derby and Leicester city centres, contrary to observations. Using an inverse square law with pollen output scaled to field size, which is consistent with the Scottish data, we find the ratio of concentrations in Derby and Leicester to be 1.33, compared to the actual value of 1.57 (figure 4). Furthermore, and most convincingly, the observed concentrations are in reasonable agreement with those deduced from the model: Derby 1.1 against 1.9 measured; and Leicester 1.4 against 3.0. Using $b=1.6$ leads to overwhelming backgrounds with values of 13.6 and 17.8 in Derby and Leicester, respectively.

7. DISCUSSION

The results presented here demonstrate the application of our modelling approach to a simple dataset with a limited number of data points. Nevertheless, the general principles described would be expected to hold true for other pollen or spore dispersal datasets from area sources with similar propagule buoyancy. So far, all dispersal functions based on mechanistic models incorporate approximations,

Figure 4. Contours of deduced pollen concentration in central England, based on the locations of oilseed rape fields in 2001 and using dispersal kernels fitted to the Scottish trap data, assuming power-law behaviour with $b=2$ (equation (6.2)).

which make them, in effect, justified empirical models. Our approach is parameter-sparse, physically motivated although not mechanistic and has led us to some new insights and predictions.

(a) *Other function types*

We have fitted a particular functional form to our rather sparse data; an infinite variety of other functional forms would of course fit as well or better. We do not argue that the inverse power-law is the unique best function nor an exact fit. However, it economically summarizes the extent to which the (unknown) real underlying function is fat-tailed, through a single parameter; it is in some sense the ‘simplest’ way to do this. For example, [Clark *et al.* \(1999\)](#) suggest the dispersal kernel

$$f(r) = \frac{\kappa}{(u + r^2)^{p+1}}, \quad (7.1)$$

where we have absorbed various constants into the single κ , u corresponds to our c_0 and p is a parameter. When $r \gg \sqrt{u}$, i.e. once the function is declining steadily, this approaches κ'/r^b (with $b = 2(p+1)$), where κ' is a constant. Similar reasoning applies to all inverse power functions, e.g. if $Q_s(r)$ is a polynomial with a highest power of s , not necessarily integer and

$$f(r) = \frac{1}{Q_s(r)^{p/q}}, \quad (7.2)$$

then at longer distances, the function will become indistinguishable from $\kappa''/r^{sp/q}$, where κ'' is a constant. However, functions of the form $f(r) = \kappa''' \exp(Q_s(r))$ eventually always decrease faster than any power-law. This may be irrelevant in a finite world, but it does suggest that we should be looking for generic characteristics of dispersal kernels rather than the detail of individual functions. In the present paper, we have tried to pare

our dispersal functions down to the minimum required to capture the overall characteristics of air-borne pollen or spore dispersal; this could, of course, have been done in an infinitude of other ways differing in detail.

[Bullock & Clarke \(2000\)](#) fitted a variety of equations, empirical and based on simplified physical models, to data on seed dispersal from ericaceous species. Seeds of the order of 500 μm in diameter are around 3 orders of magnitude larger than pollen grains. Despite this, they found that the tails of the dispersal distribution were best fitted by equations that were asymptotically power-laws. Although seed density close to the source fell faster than the long-distance power-law would predict, this is consistent with our procedure.

[Stockmarr \(2002\)](#) showed that, in the direction of the wind, a simplified physical model of the interplay of advection and turbulence gave rise to an inverse power-law with an exponent $-3/2$ along the wind. Using a more detailed physical approach, [Katul *et al.* \(2005\)](#) derived a model applicable especially to particles, such as most plant seeds, with a terminal velocity that is large compared with mean vertical wind speeds. This model has an exponential cut-off and within this power-law behaviour with an exponent of $-5/2$ along a single bearing, assuming isotropic wind directions. They show that this fits many measured datasets; however, the dispersal scale at which exponential cut-off becomes important is several orders of magnitude smaller than is appropriate for very small particles, and the approximations they use may not be appropriate for small particles.

(b) *Fat-tailed dispersal kernels and background*

We have shown that an exponential model with a range comparable with the experimental data does not fit

experimental pollen dispersal curves well and is inconsistent with the observed existence of background pollen counts. We have also shown that inverse power-law models fit experimental data well with exponents in the region 1.5–2 and that a power-law with an exponent close to two provides reasonably accurate predictions of observed background levels of air-borne pollen. This has important implications for the fitting of fat-tailed curves, since it becomes imperative to separate the background from the local tail to maintain model consistency. This is most reliably achieved by direct measurement (for seeds, see Bullock & Clarke 2000).

(c) *Treatment of extended sources*

Greene & Calogeropoulos (2002) demonstrated that dispersal curves will flatten with increasing aggregation of point sources. We demonstrate that for a power-law function this effect can be quantified simply by field size. While the total output of fields has been taken into account (e.g. Devaux *et al.* 2005), the scaling effect of source size on the dispersal function itself has often been ignored. Even when dealing with individual trees (Clark *et al.* 1999; Austerlitz *et al.* 2004) this should be considered, as they will vary considerably in size over their lifetime. Additionally, we show that measuring from the centre of an area source, taking radius into account can simplify the choice of equation to describe dispersion and modelling using these equations.

We treat area sources as disks, which is an assumption valid only when the source has reasonably similar dimensions in all directions. Azimuthally variable dispersal would be expected for extremely asymmetrical sources (Greene & Calogeropoulos 2002). However, systematic variation in the wind direction is likely to be a much larger source of error in agricultural applications.

(d) *The role of insects*

Here, we deal exclusively with wind dispersal. It is reasonable to assume that wind pollination will usually be proportional to the composition of the pollen cloud. In addition, the effect of insect pollination must be considered when deriving a complete pollination kernel. The general character of pollen dispersal by insects is likely to depend on the mix of pollinators in a particular region. However, it is likely that the scale and form of functions describing insect dispersal will be similar to those derived for wind dispersal. Cresswell *et al.* (2002) chose an exponential power model to represent bumblebee pollination, but a fat-tailed model may offer an explanation for the non-zero paternity further from the source. Furthermore, smaller pollinators may in fact be blown by the wind as much as actively disperse. For example, pollen beetles can disperse over long distances with fat-tailed distributions (Skogsmyr 1994). Ramsay *et al.* (2003) recorded the presence of pollen beetles on fertilized plants 26 km from the nearest OSR field.

(e) *Implications for policy*

Rieger *et al.* (2002) measured pollen-mediated gene flow from herbicide-tolerant rapeseed into conventional crops in Australia, finding small amounts of pollination as far as 3 km from source fields, with no perceptible fall with distance. This is consistent with the very shallow dispersal

curves measured suggested above. By contrast, conventional breeders' guidelines suggest separation of fields by only a few hundred metres ensures adequate purity. However, this does not imply that cross-pollination will continue to drop rapidly as separation increases.

It is a consequence of the power-law curves that separation distances should explicitly refer to the size of field involved, since the median dispersal distance depends on the field size. For an inverse square power-law, the required separation for a 20 ha field will be twice that of a 5 ha field. A further implication of the very shallow dispersal curves deduced above is that no completely 'safe' separation between fields is possible on a landscape scale; there will always be a low, but real, probability of pollen arriving from very distant sources. Using a fixed safe distance between GM and organic fields, Perry (2002) showed that only a small area of the UK could be used for production of GM rapeseed without risking gene flow to organic crops. For the 100 km square area modelled here, a number of distinct regions with different background levels emerge from around 7 to around $40 \text{ m}^{-3} \text{ d}^{-1}$, depending on the density of rape cropping. Within such an area, there would be unavoidable background 'gene flow', assuming that air-borne pollen causes fertilization (figure 4). These values are of similar magnitude to those expected within 200 m of isolated fields, so background levels may be equivalent to those within the recommended buffer zones for crop isolation developed from small-scale studies. In this case, gene flow levels would depend on the average proportion of GM fields, rather than only the distance to the nearest GM field. Importantly, the near homogeneous, but low, levels of background pollen observed (and predicted) mean that the *location* of hybrids arising from them would be very unpredictable and therefore difficult to manage. This principle even applies across national boundaries.

In general, we argue that generic ecological models of the behaviour of air-borne viruses, bacteria, fungal spores and pollen should use functions which are broadly of the type of equation (4.4). While the exponential component represents the reality of death and deposition of spores, this may be on such a long distance scale that much interesting biology is dominated by power-law behaviour, with exponents of two (with the same long-distance behaviour as a Cauchy distribution) or less. In practice, this may also be true of other organisms (Viswanathan *et al.* 1996; Bullock & Clarke 2000; Paradis *et al.* 2002), but we do not know of general arguments as to why.

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REFERENCES

- Agriculture and Environment Biotechnology Commission 2001 *Crops on trial*. London, UK: Department of Trade and Industry.
- Austerlitz, F., Dick, C. W., Dutech, C., Klein, E. K., Oddou-Muratorio, S., Smouse, P. E. & Sork, V. L. 2004 Using

- genetic markers to estimate the pollen dispersal curve. *Mol. Ecol.* **13**, 937–954. (doi:10.1111/j.1365-294X.2004.02100.x)
- Aylor, D. E. 1990 The role of wind in the dispersal of fungal pathogens. *Annu. Rev. Phytopathol.* **28**, 73–92. (doi:10.1146/annurev.py.28.090190.000445)
- Aylor, D. E. 2003 An aerobiological framework for assessing cross-pollination in maize. *Agric. Forest Meteorol.* **119**, 111–129. (doi:10.1016/S0168-1923(03)00159-X)
- Berkowicz, R., Olesen, H. R. & Gislason, K. B. 1986 The Danish Gaussian air pollution model (OML): description, test and sensitivity analysis in view of regulatory applications. In *Air pollution modelling and its applications* (ed. V. C. De Wispelaire, F. A. Schiermeier & N. V. Gillani), pp. 453–481. New York, NY: Plenum Press.
- Bullock, J. M. & Clarke, R. T. 2000 Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia* **124**, 506–521.
- Carruthers, D. J., Holroyd, R. J., Hunt, J. C. R., Weng, W. S., Robins, A. G., Apsley, D. D., Thomson, D. J. & Smith, F. B. 1994 UK-ADMS: a new approach to modelling dispersion in the earth's atmospheric boundary layer. *J. Wind Eng. Ind. Aerodyn.* **52**, 139–153. (doi:10.1016/0167-6105(94)90044-2)
- Clark, J. S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J. 1999 Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* **80**, 1475–1494.
- Cresswell, J. E., Osborne, J. L. & Bell, S. A. 2002 A model of pollinator-mediated gene flow between plant populations with numerical solutions for bumblebees pollinating oilseed rape. *Oikos* **98**, 375–384. (doi:10.1034/j.1600-0706.2002.980302.x)
- Damgaard, C. & Kjellsson, G. 2005 Gene flow of oilseed rape (*Brassica napus*) according to isolation distance and buffer zone. *Agric. Ecosyst. Environ.* **108**, 291–301. (doi:10.1016/j.agee.2005.01.007)
- Devaux, C., Lavigne, C., Fenentin-Guyomarc'h, H., Vautrin, S., Lecomte, J. & Klein, E. K. 2005 High diversity of oilseed rape pollen clouds over an agro-ecosystem indicates long-distance dispersal. *Mol. Ecol.* **14**, 2269–2280. (doi:10.1111/j.1365-294X.2005.02554.x)
- Firbank, L. G., Dewar, A. M., Hill, M. O., May, M. J., Perry, J. N., Rothery, P., Squire, G. R. & Woitwod, I. P. 1999 Farm-scale evaluation of genetically modified crops. *Nature* **399**, 727–728. (doi:10.1038/21516)
- Giddings, G. D. 2000 Modelling the spread of pollen from *Lolium perenne*. The implications for the release of wind pollinated transgenics. *Theor. Appl. Genet.* **100**, 971–974. (doi:10.1007/s001220051378)
- Giddings, G. D., Sackville Hamilton, N. R. & Hayward, M. D. 1997 The release of genetically modified grasses. Part 2. The influence of wind direction on pollen dispersal. *Theor. Appl. Genet.* **94**, 1007–1014. (doi:10.1007/s001220050508)
- Greene, D. F. & Calogeropoulos, C. 2002 Measuring and modelling seed dispersal of terrestrial plants. In *Dispersal ecology: the 42nd Symp. of the British Ecological Society, University of Reading, 2–5 April 2001* (ed. J. M. Bullock, R. E. Kenward & R. S. Hails), pp. 3–23. Oxford, UK: Blackwell.
- Gregory, P. H. 1973 *The microbiology of the atmosphere*, 2nd edn. London, UK: Leonard Hill.
- Ingram, J. 2000 *Review of the separation distances between genetically modified and other crops*. London, UK: Ministry of Agriculture, Fisheries and Food.
- Katul, G. G., Porporato, A., Nathan, R., Siqueira, M., Soons, M. B., Poggi, D., Horn, H. S. & Levin, S. A. 2005 Mechanistic analytical models for long-distance seed dispersal by wind. *Am. Nat.* **166**, 368–381. (doi:10.1086/432589)
- Kings, J. & Giles, B. 1997 The midlands. In *Regional climates of the British Isles* (ed. D. Wheeler & J. Mayes), pp. 111–130. London, UK: Routledge.
- Lavigne, C., Klein, E. K., Vallée, P., Pierre, J., Godelle, B. & Renard, M. 1998 A pollen-dispersal experiment with transgenic oilseed rape. Estimation of the average pollen dispersal of an individual plant within a field. *Theor. Appl. Genet.* **96**, 886–896. (doi:10.1007/s001220050816)
- McCartney, H. A. 1987 Deposition of *Erysiphe graminis* conidia on a barley crop. *J. Phytopathol.* **118**, 258–264.
- Mesquida, J. & Renard, M. 1982 Etude de la dispersion du pollen par le vent et de l'importance de la pollinisation anemophile chez le colza (*Brassica napus* L., var. *oleifera* Metzger). *Apidologie* **4**, 353–367.
- Okubo, A. & Levin, S. A. 1989 A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* **70**, 329–338.
- Olesen, H. R., Løfstrøm, P., Berkowicz, R. & Jensen, A. B. 1992 An improved dispersion model for regulatory use—the OML model. In *Air pollution modelling and its applications IX* (ed. H. van Dop & G. Kallos), pp. 29–38. New York, NY: Plenum Press.
- Paradis, E., Baillie, S. R. & Sutherland, W. J. 2002 Modeling large-scale dispersal distances. *Ecol. Model.* **151**, 279–292.
- Pearl, D. R. 1985 The quantitative representation of seed and pollen dispersal. *Ecology* **66**, 1081–1083.
- Perry, J. N. 2002 Sensitive dependencies and separation distances for genetically modified herbicide-tolerant crops. *Proc. R. Soc. B* **269**, 1173–1176. (doi:10.1098/rspb.2002.2007)
- Press, W. H., Flannery, B. P., Teukolsky, S. A. & Vetterling, W. T. 1992 *Numerical recipes in C: the art of scientific computing*, 2nd edn. Cambridge, UK: Cambridge University Press.
- Ramsay, G., Thompson, C. & Squire, G. 2003 *Quantifying landscape-scale gene flow in oilseed rape. Final Report of DEFRA project RG0216: an experimental and mathematical study of the local and regional scale movement of an oilseed rape transgene*. London, UK: DEFRA p. 50.
- Rantio-Lehtimäki, A. 1995 Aerobiology of pollen and pollen antigens. In *Bioaerosols handbook* (ed. C. Cox & C. Wathes), pp. 387–406. Boca Raton, FL: CRC Press.
- Ribbens, E. J., Silander, J. A. & Pacala, S. W. 1994 Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* **75**, 1794–1806.
- Rieger, M. A., Lamond, M., Preston, C., Powles, S. B. & Roush, R. T. 2002 Pollen-mediated movement of herbicide resistance between commercial Canola fields. *Science* **296**, 2386–2388. (doi:10.1126/science.1071682)
- Shellard, H. C. 1976 Wind. In *The climate of the British Isles* (ed. T. J. Chandler & S. Gregory), pp. 39–73. London, UK: Longman.
- Skogsmyr, L. 1994 Gene dispersal from transgenic potatoes to conspecifics: a field trial. *Theor. Appl. Genet.* **88**, 770–774. (doi:10.1007/BF01253984)
- Spijkerboer, H. P., Beniers, J. E., Jaspers, D., Schouten, H. J., Goudriaan, J., Rabbinge, R. & van der Werf, W. 2002 Ability of the Gaussian plume model to predict and describe spore dispersal over a potato crop. *Ecol. Model.* **155**, 1–18. (doi:10.1016/S0304-3800(01)00475-6)
- Stockmarr, A. 2002 The distribution of particles in the plane dispersed by a simple 3-dimensional diffusion process. *J. Math. Biol.* **45**, 461–469. (doi:10.1007/s002850200157)

- Timmons, A. M., O'Brien, E. T., Charters, Y. M., Dubbels, S. J. & Wilkinson, M. J. 1995 Assessing the risks of wind pollination from fields of genetically modified *Brassica napus* ssp. *oleifera*. *Euphytica* **85**, 417–423. (doi:10.1007/BF00023975)
- Timmons, A. M., Crawford, J. W., Charters, Y. M. & Wilkinson, M. J. 1996 Risks from transgenic crops. *Nature* **380**, 487. (doi:10.1038/380487a0)
- van den Bosch, F., Frinking, H. D., Metz, J. A. J. & Zadoks, J. C. 1988 Focus expansion in plant disease. 3: two experimental examples. *Phytopathology* **78**, 919–925.
- Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Murphy, E. J., Prince, P. A. & Stanley, H. E. 1996 Lévy flight search patterns of wandering albatrosses. *Nature* **381**, 413–415. (doi:10.1038/381413a0)
- Wilkinson, M. J., Elliot, L. J., Allainguillaume, J., Shaw, M. W., Norris, C., Welters, R., Alexander, M., Sweet, J. & Madson, D. C. 2003 Hybridization between rapeseed and *Brassica rapa* in the UK: a first step towards national-scale risk assessment of GM rapeseed. *Science* **302**, 457–459. (doi:10.1126/science.1088200)