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The release of genetically modified grasses. Part 2: the influence of wind direction on pollen dispersal

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Abstract In part 1 an experiment was described for determining the extent of pollen dispersal from a *Lolium* source. The results were used to test Bateman's pollen dispersal equations, which were found to be not particularly useful for describing variation in pollen deposition with distance. An improvement is suggested here which takes the influence of wind direction into account. For 11 of the 12 datasets the new equations fit significantly better than the original ones. Mean wind directions were used to produce 15 data subsets for testing Bateman's equations for dispersal downwind of a pollen source. These equations fitted only 4 of the data subsets, all of which were collected from traps facing towards the pollen source. The usefulness of the model equations in estimating the importance of turbulence is brought into question. It is shown that models incorporating only distance and wind direction do not accurately describe pollen deposition. The amount of pollen deposited does not always decrease smoothly with increasing distance from the source. The variation in the amount of pollen deposited is probably influenced by several factors, including wind speed and turbulence.

Key words Pollen dispersal · Wind direction · *Lolium perenne*

Introduction

The first measurements of pollen dispersal in ryegrass were made to determine appropriate isolation distances for seed crops (Griffiths 1950). Then the concern was to prevent incoming pollen from contaminating ryegrass seed stocks. Since these early studies pollen dispersal has often attracted the interest of population biologists (Jain and Bradshaw 1965; Bos et al. 1986; Gliddon, et al. 1987), while recent resurgence of interest in pollen-flow studies has been a result of concerns over the release of genetically modified plants (Giddings 1992; Raybould and Gray 1993). We are now concerned that outgoing pollen does not contaminate agricultural and natural environments (Crawley et al. 1993; Ellstrand, 1992, Kareiva 1993; Raybould and Gray 1993, Regal 1988). The present paper examines modifications to existing pollen-dispersal equations that are intended to improve our ability to predict the outcome of such dispersals.

Materials and methods

For experimental details see 'Part 1' in the series. Here we present only additional mathematical and statistical details.

Dispersal equations

The equations given in part 1 (Giddings et al. 1997) to describe variation in pollen deposition with distance were modified to allow for wind direction. It is assumed that, at a given distance, pollen deposition varies with compass direction, θ, in accordance with a normal distribution about a mean direction, w, towards which the wind is blowing, and standard deviation s. Effects of distance and direction were combined by raising distance equations (1–3) (1) to a power of the normal distribution function $f(\theta) = \alpha + \beta\phi(\theta : w, s)$, thus:

$$p = a\,\mathrm{e}^{(-bD - \log D)(\alpha + \beta\phi\,(\theta:\, w, s))} \tag{1w}$$

ignoring turbulence,

$$p = a\,\mathrm{e}^{(-bD^{1-m} - (1+m)\log D)(\alpha + \beta\phi(\theta:\, w, s))} \tag{2w}$$

allowing for turbulence, and

$$p = a\mathrm{e}^{(-bD^{d} - c\,\log D)(\alpha + \beta\phi\,(\theta:\, w, s))} \tag{3w}$$

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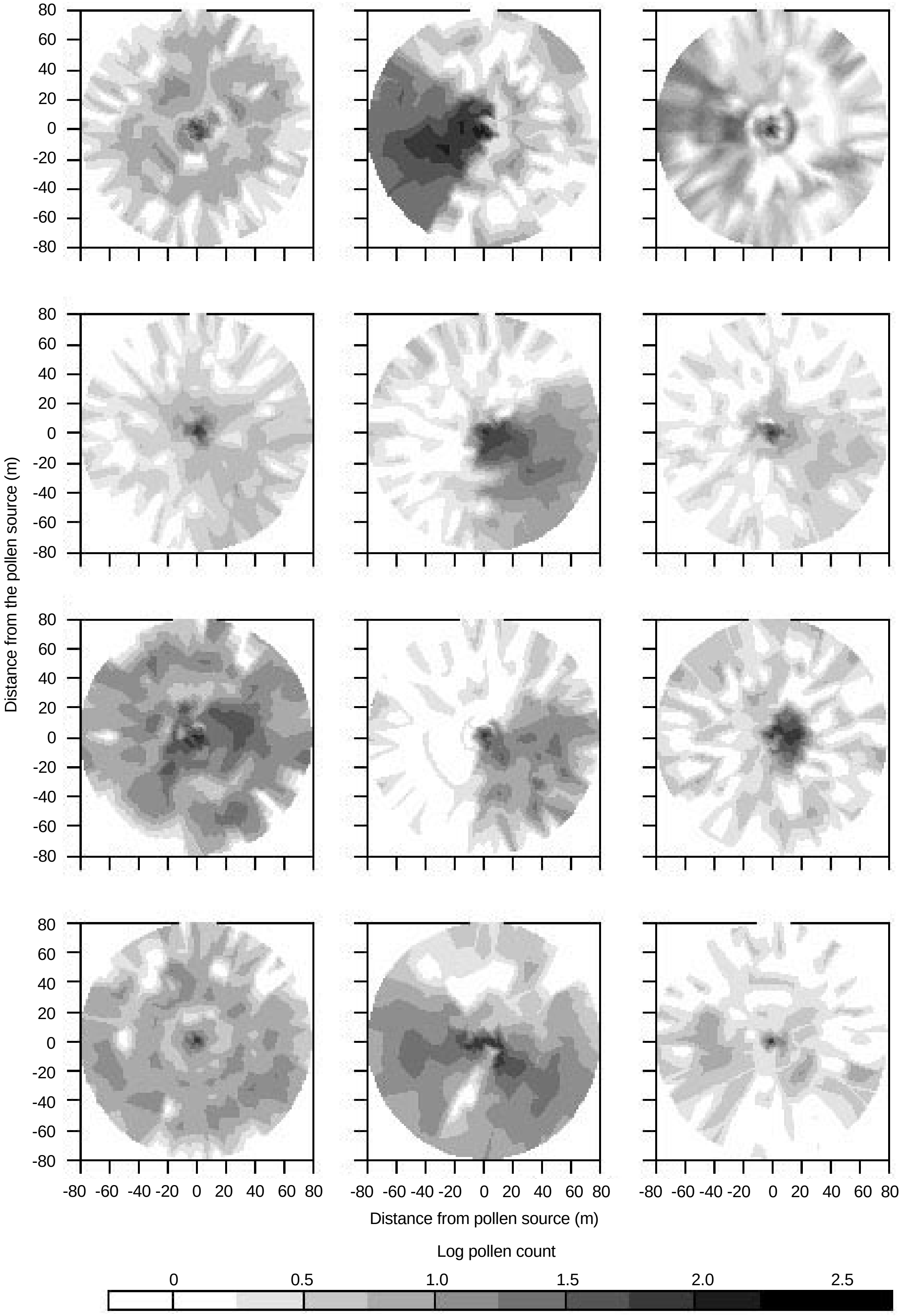

Fig. 1 Maps of pollen deposition (log scale) from a central *Lolium source* (x and y in metres) to skywards (*left*), forwards-facing (centre) and reverse-facing traps (*right*). The rows, from top to bottom, show early, mid 1, mid 2 and late anthesis

Table 1 F-tests of the adequacy of Eqs. 1w, 2w and 3w in describing variation in pollen trapped with distance from the source are in columns 3–5. The F values in column 2 show whether there are significant differences between the simplest fitting equation and that equation when parameter b is fixed to zero. The F values shown in bold are significant, indicating a difference between the equations. The last column shows the residual deviances which give a χ^2 for the goodness-of-fit of equation 3w

Regression equation to which test applies:		$b = 0$	1w	2w	3w	3w
Regression equation whose residual was used to test goodness-of-fit:			2w	3	3	χ^2
Degrees of freedom for F test:	Single normal:	1 321	1 320	5 323	5 323	320
	Double normal:	1 1318 or 1 320	1 317	8 323	8 323	317
Trap orientation	Time					
Forward	Early	0.85	3E- 05	**58.93**	**58.94**	1055.26
Forward	Mid1	**33.99**	3.31	**69.49**	**69.71**	2256.47
Forward	Mid2	**19.24**	0.93	**70.14**	**70.18**	2715.16
Forward	Late	3.05	0.79	**30.05**	**30.05**	1246.69
Upwards	Early	**6.57**	0.88	**30.48**	**30.48**	841.20
Upwards	Mid1	**8.23**	1.66	**7.50**	**7.51**	1947.16
Upwards	Mid2			1.22	1.24	1029.70
Upwards	Late	**18.23**	**9.99**	**3.82**	**3.82**	1026.00
Reverse	Early	1.17	2.96	**16.71**	**17.86**	904.88
Reverse	Mid1	0.29	0.87	**13.92**	**13.92**	1372.01
Reverse	Mid2	**35.28**	0.01	**18.35**	**18.59**	2103.79
Reverse	Late	**29.51**	**5.96**	**11.15**	**11.15**	597.52

as a generalization of Eq. 2w allowing a test for the symmetry of parameter m. In equation 3w α has been arbitarily fixed to 1 to eliminate aliasing between b, c, α and β.

In some cases it was necessary to assume two distinct wind directions, w_1 and w_2, associated with a change in wind direction during the trapping period. In such cases a double normal distribution was fitted, with distribution function $f(\theta) = \alpha + \beta_1\phi(\theta: w_1, s_1) + \beta_2\phi(\theta: w_2, s_2)$.

Bateman modified the dispersal equations to account for gene flow downwind of a point source (Bateman 1947). When turbulence is assumed to have an effect on dispersal the equation is given by

$$p = a\,\mathrm{e}^{(-bD^{-m} - 2m \log D)} \tag{4}$$

This becomes

$$p = a\mathrm{e}^{-bD} \tag{5}$$

when turbulence is ignored.

Procedure for curve fitting

Two sets of analyses were undertaken. In the first set all data were analysed using the direction modified Eqs. 1w–3w. The need to allow for wind direction was tested by an F-test of the improvement of fit obtained by fitting the directional rather than the non-directional form of the general line plus exponential model (Eq. 3w above vs Eq. 3 of part 1). The adequacy of Bateman's equations after allowing for direction was tested by comparing the fits of the simpler Eqs. 1w and 2w respectively with 2w and 3w. Since Eqs. 2w and 3w have the same number of parameters there is no formal test for the difference between them.

ANOVAS for the downwind datasets were used to provide a test for the goodness-of-fit of the downwind dispersal equations, as in part 1.

Results

Modelling the effects of wind direction

Some of the datasets presented in part 1 show obvious biases in dispersal according to wind direction (Fig. 1). For 11 of the 12 datasets there was significant improvements in fit when direction was taken into account (Table 1, Fig. 2). Late in anthesis a double, rather than a single, normal distribution was necessary to describe directional variation for dispersal (Fig. 2). However, although the fits are better than for Bateman's equations tested in part 1, they still do not fit the data well, as indicated by the significant χ^2 for the goodness-of-fit of Eq. 3w (Table 1).

Although it is not possible formally to test for differences between the fits of Eqs. 2w and 3w, it is clear from Table 1 that the fits are not different from one another. In all but 2 cases – data from upwards-and reverse-facing traps during late anthesis – Eq. 1w gives as good a fit to the data as 2w.

From Figs. 1 and 2 it is obvious that mean wind direction (w) is similar within times but changes over time; Tables 2–5 indicate that it is consistent between equations, as are the standard deviations of wind direction.

Examination of Tables 2–4 reveals that b is often close to zero. There are 5 datasets for which equations can be fitted with $b = 0$, with no loss in the goodness-of-fit (Tables 1 and 5). This indicates that the amount of pollen deposited is extremely small in comparison to the size of the pollen cloud. In 3 cases b is significantly negative (data from reverse-facing traps during mid 2 anthesis and from upwards- and reverse-facing traps during late anthesis). This implies that there is eventually an increase in pollen deposition with distance. Although this may be a real effect within the dataset collected, more pollen collected at 80 m than at 60 m, for example, it is not expected to be a true characteristic of dispersal over greater distances.

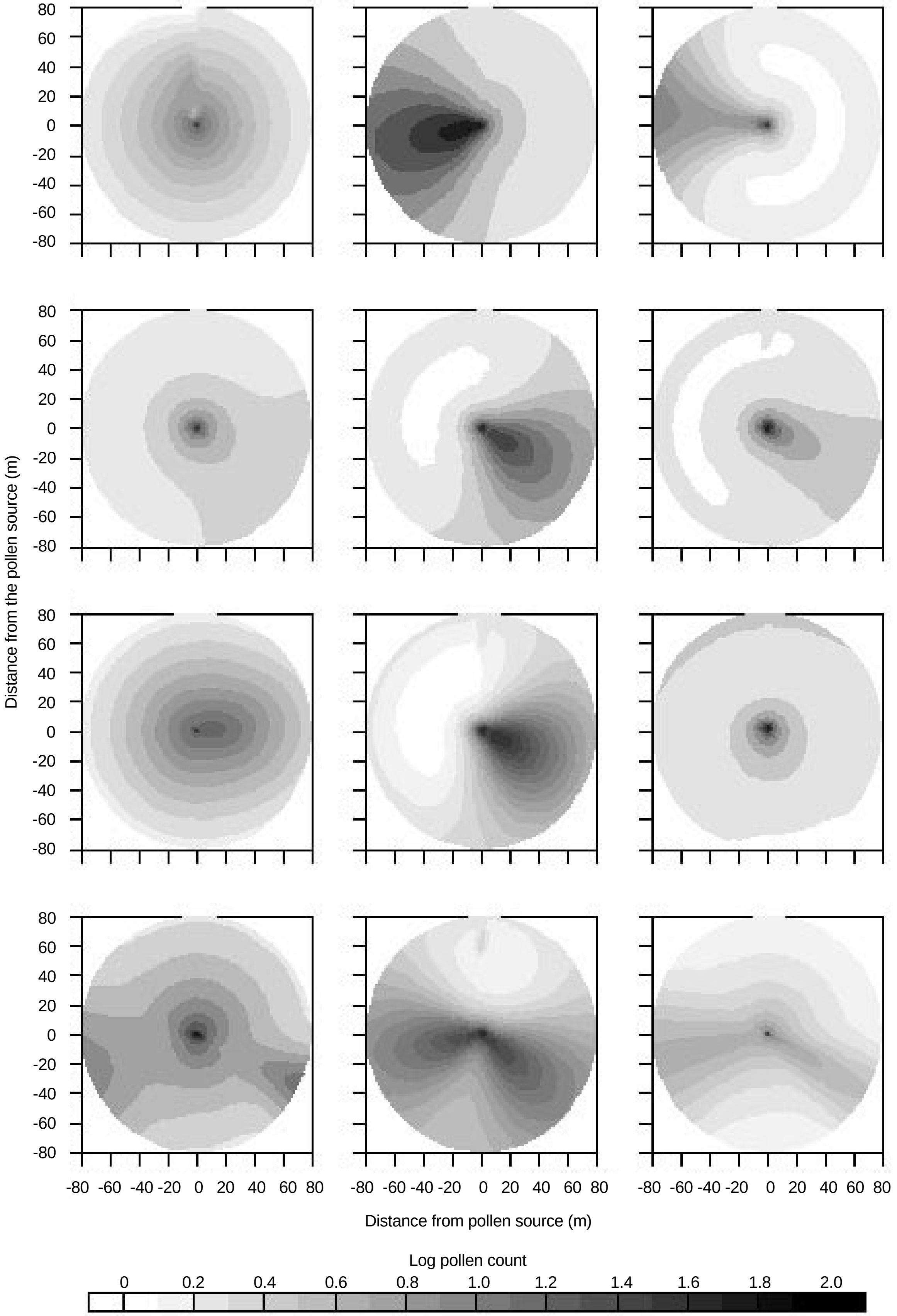
Distance from the pollen source (m)
80
60
40
20
0
-20
-40
-60
-80
-80 -60 -40 -20 0 20 40 60 80
Distance from pollen source (m)
Log pollen count
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0

Table 2 Parameter estimates for Eq. 3w

Dataset	*w*	*s*	*a*	*b*	*c*	*d*	*β*
Forward, early	114.61	62.27	107.80	−0.0010	1.449	1.350	−37.386
Forward, mid1	121.01	59.21	399.60	0.2800	0.819	0.607	−35.860
Forward, mid2	256.54	52.48	193.40	0.6467	0.169	0.463	−37.592
Forward, late	126.04	42.11	128.50	0.0683	0.967	0.623	−25.620
	258.30	40.76					−23.720
Upwards, early	74.53	57.76	167.60	0.1350	0.876	0.597	−20.510
Upwards, mid1	84.25	25.66	127.70	0.0006	0.595	1.566	−6.309
Upwards, mid2	9.47	119.37	134.10	−0.0482	1.044	0.522	−8.650
Upwards, late	122.90	21.20	128.90	−0.4600	1.620	0.477	−4.200
	239.20	30.70					−4.080
Reverse, early	108.78	31.91	348.60	−5.0E-8	1.441	3.710	−6.880
Reverse, mid1	64.50	86.90	344.30	0.0292	1.274	0.640	−17.990
Reverse, mid2	273.54	32.87	68.09	−0.0246	1.327	1.017	−14.088
Reverse, late	119.79	19.53	99.12	−1.1540	2.668	0.406	−5.380
	256.27	32.95					−9.720

Table 3 Parameter estimates for Eq. 2w

Dataset	*w*	*s*	*a*	*b*	*α*	*β*	*m*
Forward, early	114.60	62.27	108.00	−0.0035	1.463	−54.660	0.000
Forward, mid1	121.00	59.47	409.80	0.0930	0.912	−32.690	0.203
Forward, mid2	256.58	52.60	191.70	0.5583	0.412	−15.556	0.407
Forward, late	126.04	42.11	128.50	0.0972	0.703	−18.000	0.377
	258.33	40.76				−16.660	
Upwards, early	74.64	57.52	167.40	0.0476	0.830	−16.930	0.200
Upwards, mid1	84.25	25.66	129.70	0.0007	1.202	−7.585	−0.506
Upwards, mid2	6.29	122.09	134.00	−0.0298	0.740	−6.600	0.372
Upwards, late	123.00	21.24	128.90	−0.4317	1.061	−4.413	0.523
	239.20	30.74				−4.328	
Reverse, early	108.80	32.04	349.10	−0.0001	3.261	−24.920	−0.599
Reverse, mid1	64.50	86.90	344.30	0.0311	0.937	−16.860	0.359
Reverse, mid2	273.53	32.87	68.09	−0.0183	1.350	−19.020	−0.017
Reverse, late	119.79	19.54	99.04	−0.6942	1.678	−9.036	0.595
	256.30	32.92				−16.300	

Table 4 Parameter estimates for Eq. 1w

Dataset	*w*	*s*	*a*	*b*	*α*	*β*
Forward, early	114.60	62.27	108.00	−0.0035	1.463	−54.660
Forward, mid1	121.01	59.14	410.40	0.0249	1.193	−42.360
Forward, mid2	256.59	52.54	194.30	0.0267	0.873	−32.799
Forward, late	125.98	42.04	130.90	0.0069	1.072	−27.290
	258.25	40.77				−25.310
Upwards, early	74.56	57.40	168.30	0.0133	1.048	−21.290
Upwards, mid1	83.93	25.39	127.80	0.0161	0.557	−3.508
Upwards, mid2	6.00	121.00	131.20	−0.0017	0.967	−8.700
Reverse, early	108.92	32.08	343.70	−0.0026	1.441	−10.010
Reverse, mid1	63.37	87.10	350.40	0.0015	1.337	−23.940
Reverse, mid2	273.53	32.88	68.19	−0.0202	1.334	−18.780

There is a wide variety in the value of parameter *m*, including 3 negative values (Table 3). In no case does its value fall within the previously published range of 0.62 to 0.88. Ranking the data-sets with respect to the value of *m* reveals no consistency with respect to time or trap orientation. Together these observations support the suggestion that *m* is not a reliable estimate of the importance of turbulence and may be influenced by other factors not measured in the experiment, such as wind strength or air moisture content. In the majority of cases the good fit of 1w suggests that *m* is not measuring anything that has a major effect on dispersal.

Fig. 2 Maps of fitted Eq. 3w showing pollen deposition (log scale) from a central *Lolium* source (x and y in metres) to skywards (*left*), forwards-facing (*centre*) and reverse-facing traps (*right*). The rows, from *top to bottom*, show early, mid 1, mid 2 and late anthesis

Table 5 Parameter estimates for Eq. 1w when $b = 0$

Dataset	w	s	a	α	β
Forward, early	114.53	62.24	103.00	1.394	−52.720
Forward, late	125.79	41.71	143.40	1.180	−29.070
	258.04	40.68			−27.110
Upwards, mid 2	1.21	122.78	127.80	0.941	−8.791
Reverse, early	109.11	32.34	335.40	1.398	−9.940
Reverse, mid 1	63.10	87.20	355.90	1.362	−24.270

Table 6 F-tests of the adequacy of Eqs. 5 and 6 in describing variation in pollen trapped with distance downwind of a source. Tests for Eq. 6 are not given where the fit for Eq. 5 is significantly worse than fitting distance as a factor

Regression equation to which goodness-of-fit test:		5		4	
Regression equation or ANOVA whose residual:		4		ANOVA	
Trap orientation	Time interval		*df*		*df*
Forward	Early	**0.221194** **0.6348**	1, 110	1.964725 > 0.05	8, 102
Forward	Mid1	16.2137 0.0001	1, 104	**1.218953** > **0.05**	8, 96
Forward	Mid2	**3.942156** **0.0502**	1,96	0.999208 > 0.05	10, 86
Forward	Late	**1.788854** **0.185**	1,76	0.681716 > 0.05	8, 68
Forward	Late			2.210685 < 0.05	7, 59
Upper	Early			6.808458 < 0.001	10, 94
Upper	Mid 1			10.48739 < 0.001	7, 36
Upper	Mid 2			8.776425 < 0.001	10, 203
Upper	Late			13.41492 < 0.001	7, 32
Upper	Late			15.89973 < 0.001	10, 47
Reverse	Early			9.276204 < 0.001	8, 48
Reverse	Mid 1			16.7069 < 0.001	10, 144
Reverse	mid 2			7.207941 < 0.001	8, 50
Reverse	Late			3.534845 < 0.01	7, 30
Reverse	Late			4.637131 < 0.001	7, 49

Equations for downwind of a pollen source

Fifteen data subsets were derived as the data within one standard deviation of the mean wind direction and used to test Bateman's equations for dispersal downwind of a source. Two separate data subsets were derived for each of the sets of late anthesis. A good (statistical) fit was obtained for 4 of the 15 data subsets (Table 6 and Fig. 3), all of them to data collected from forwards-facing traps.

For all of the 4 data subsets just mentioned the value of m for Eq. 4 is low (Table 7), although only 3 of them are also fitted by Eq. 5 (Tables 6 and 8).

Discussion

For 11 of the 12 datasets the dispersal equations which include terms for wind direction fit significantly better than Bateman's original equations presented in part 1. The importance of wind direction is particularly marked for deposition onto forwards-facing traps. Only 4 of 15 data subsets were fitted to equations for downwind of a source, all were collected from forwards-facing traps.

There is a large variation in the values of parameter m, which fall outside of the previously published range of 0.62 to 0.88 (Sutton, 1932; Taylor, 1915 and 1920).

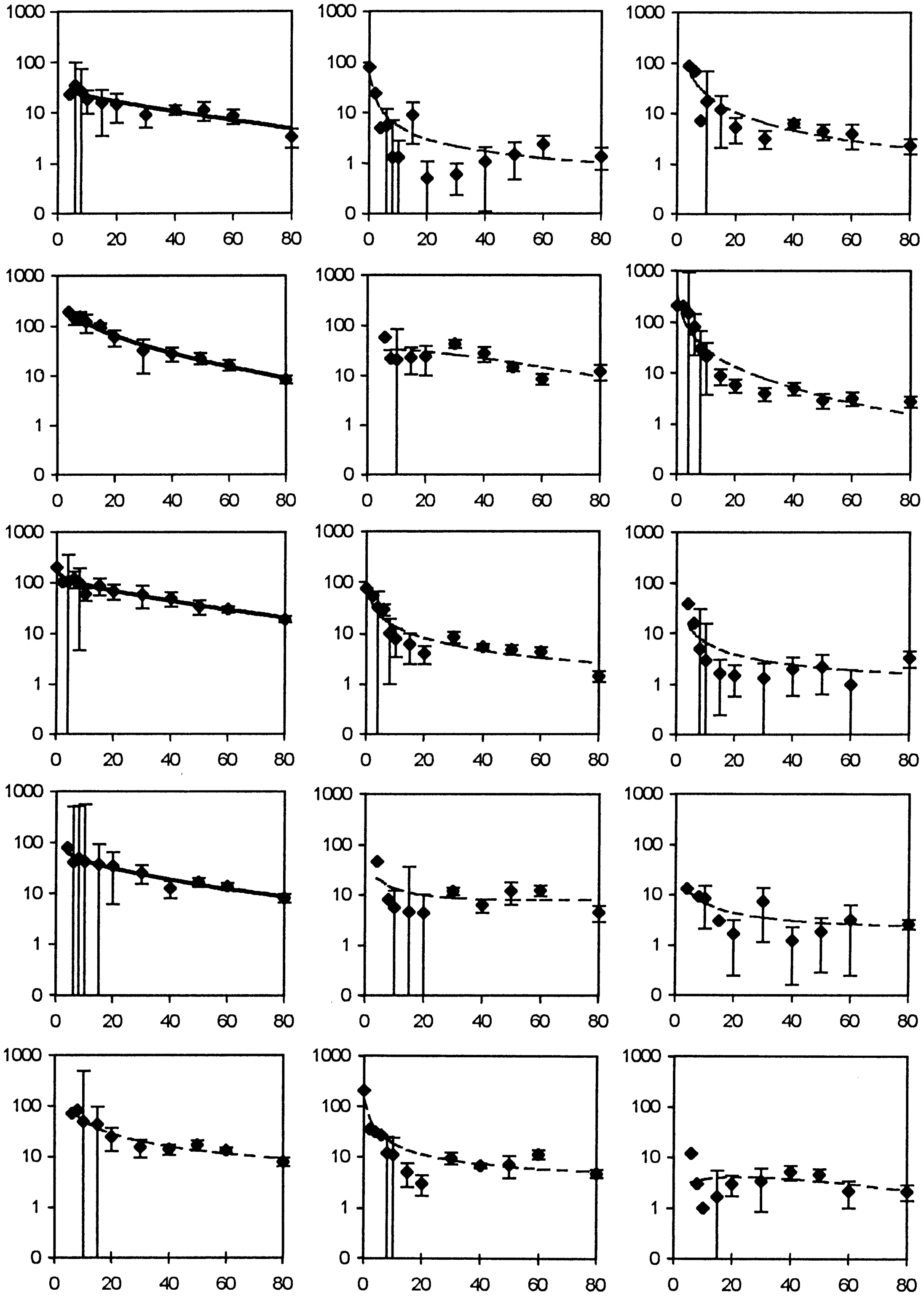

Fig. 3 Data subsets showing pollen deposition downwind of source plotted on a log scale with the 95% confidence limits. Equation 5 is represented by a *solid line* where there is a statistically satisfactory fit and by a *dashed line* where there is not. The rows represent (from *top to bottom*) early, mid 1, mid 2 and late anthesis (2 rows). The columns show data from forwards-, upwards- and reverse-facing traps

Table 7 Parameter estimates for Eq. 5

Dataset	*a*	*b*	*m*
Forward, early	33.68	0.02379	0.049
Forward, mid 1	525.6	0.0706	0.228
Forward, mid 2	161.9	0.02489	0.0736
Forward, late	109.9	0.03044	0.143

Table 8 Parameter estimates for Eq. 4

Dataset	*a*	*b*
Forward early	26.32	0.02206
Forward mid 2	118.7	0.02347
Forward late	55.12	0.02509

This brings into question the usefulness of m as an indicator of the importance of turbulence. The fact that there is no clear relationship between turbulence and deposition onto traps facing away from the source (reverse traps) supports the conclusion that m is not just measuring the effect of turbulence. If it did then we would have expected to find consistently high values of m for data from traps with their reverse side towards the source relative to those for data from traps facing the source. The biological interpretation of m is ambiguous. Perhaps it is estimating the interaction between turbulence and other factors not measured in the experiment. It is often the case that different combinations of parameter values fit the data equally well. This highlights the point that parameters which give the best statistical fits need to be examined to determine whether they give biologically sensible fits.

In 3 cases parameter b is negative implying an eventual increase in pollen deposition with distance. Such an effect could be observed due to irregularities recorded at the further distances from the source. A lull in the wind might cause temporary stasis of the pollen cloud and unexpectedly high deposition at a particular distance, for example. Deposition at further distances may be less, but if these are not recorded then the best fitting curve is achieved by assuming an upturn in deposition beyond a certain distance. Such curves should not be used for predictive purposes since extrapolation beyond the 'turning point' is clearly nonsense. In the 2 cases during late anthesis the apparent upturn in deposition may be due to the changing wind direction, with pollen clouds tracking sideways for a while, instead of outwards from the source.

The patchy deposition just described is a feature of several of the datasets, not just those with a negative value for parameter b. It is especially obvious for data from skywards-facing traps, particularly that collected during mid 2 anthesis when the modified equations fitted no better than Bateman's equations. This feature probably accounts for the overall lack of fit, as indicated by the chi-squares in Table 1. It highlights the danger of assuming that deposition decreases smoothly over distance, varying only with direction. It is supposed that pollen clouds are taken high into the atmosphere, moved with the weather and deposited during times of calm. It is conceivable that pollen transported in this way could be moved considerable distances from the source, and so be important in terms of transgene spread. Wind speed and turbulence are expected to be important factors affecting this process. Models involving such additional parameters would be complex and would probably show chaotic dynamics, making prediction difficult. It should be remembered that this paper deals with pollen deposition over periods of a day or two. It remains to be seen whether gene dispersal over the course of a season is as variable, or whether variations are smoothed out over time. This situation is currently being tested and will be reported on in a later paper.

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