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Modelling the spread of pollen from *Lolium perenne*. The implications for the release of wind-pollinated transgenics

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Abstract The dispersal of pollen from a *Lolium perenne* source has previously been described using various Gaussian plume models which take distance and wind direction into account. One of these models is used here to calculate, using integration, possible pollen deposition onto small conspecific populations a kilometer from the source. The percentage of immigrant pollen is compared for six different sets of parameter values previously estimated from pollen-dispersal experiments. The source size is then scaled up to simulate what might happen if transgenic ryegrass was grown on a large scale. In this case it is seen that small conspecific populations might, in some conditions, be swamped by immigrant pollen, even if they are not directly downwind of the source. The implications of this are discussed in terms of assessing and managing the risks of releasing wind-pollinated transgenic crops.

Key words Pollen dispersal · *Lolium perenne* · Modelling · Transgenics

Introduction

There is currently concern that escaped transgenics, or transgenic-wild hybrids, might become weeds of agriculture or natural ecosystems, with the potential for habitat modification and harm to non-target organisms, including direct competitive exclusion. Where transgenic crops are grown close to wild relatives, e.g. forage crops and trees, rare genetic resources might be threatened by genetic assimilation or outbreeding depression.

Hybrids of conventionally bred crops and weeds have sometimes become aggressive weeds. Johnson grass

(*Sorghum halapense*), for example, is one of the worlds worst weeds (Holm et al. 1977). Its hybridisation with cultivated *Sorghum bicolor* resulted in the evolution of especially invasive weed biotypes (Arriola and Ellstrand 1996). Plants such as forages and turf grasses, which have undergone little domestication and often have wild relatives growing nearby, are particularly at risk from hybridisation (Arriola and Ellstrand 1996, Giddings et al. 1997a). Introgressed transgenes for pest resistance or salt tolerance, for example, might increase the aggressiveness and range of such weeds and have a consequent economic and ecological impact (Ellstrand and Hoffman 1990).

Transgene transfer to wild or feral species would only occur if the species and transgenic are cross-compatible and flower simultaneously. In Europe this could include forages, such as *Lolium perenne* which is cross-compatible with wild *Lolium* and *Festuca* species (Raybould and Gray 1993; Giddings et al. 1997a), and sugar beet (*Beta vulgaris*) which will cross with *Beta maritima*, the wild sea beet, and adventitious or weed-type beets (Boudry et al. 1993; Bartsch and Schmidt 1997). Genes might also be passed from oilseed rape to feral populations or to the species *Brassica rapa* and *Brassica juncea* (Timmons et al. 1995; Metz et al. 1997).

Modelling can help us understand how the establishment and spread of transgenes in wild and feral populations is affected by such factors as pollen flow, the population turnover rate, selective advantage and genetic drift. Giddings et al. (1997b) developed models that described pollen dispersal from a *Lolium perenne* source to traps arranged in concentric circles around it. In this paper one of those models is used predict what might have happened if the pollen had been dispersed onto a small conspecific population a kilometer away from the source.

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Modelling pollen dispersal

There are many studies of pollen dispersal (e.g. Bing et al. 1996; Lavigne et al. 1996; Giddings et al. 1997a, 1b; Nurminiemi et al.

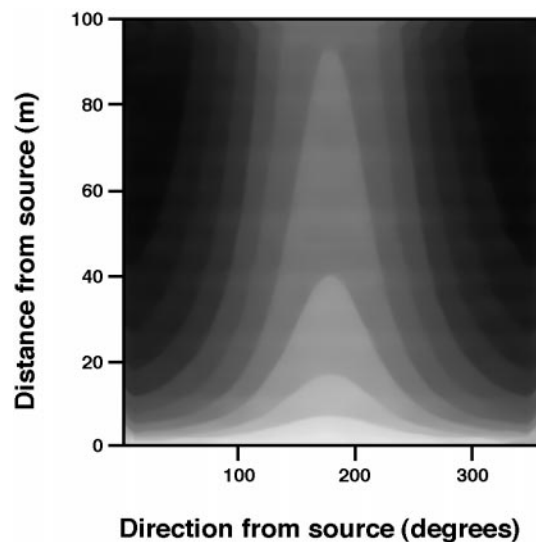


Fig. 1 A Gaussian plume model of wind mediated pollen dispersal in the form given in equation 1*w*. Shading intensity indicates the amount of pollen deposited, the paler the colour the higher the pollen deposition

1998). Some indicate that dispersal can occur over distances of hundreds or even thousands of meters (e.g. Ellstrand and Hoffman 1990; Klinger et al. 1991; VanRaamsdonk and Schouten 1997).

Two types of models sometimes used for describing pollen dispersal from a source are inverse-power and negative-exponential models (Manasse 1992; Giddings et al. 1997a; VanRaamsdonk and Schouten 1997). Studies of wind dispersal from a *L. perenne* source indicate that better fits to data can be achieved by including terms to describe the effects of wind direction (Giddings et al. 1997b), in what VanRaamsdonk and Schouten (1997) describe as a Gaussian plume model (Fig. 1; Giddings et al. 1997b). Even so, data often shows a lack of overall fit to models in which deposi-

Table 1 Parameter estimates for equation 1*w* from six pollen dispersal data sets to which more complex models with more parameters did not give significantly improved fits (from Giddings et al. 1997b)

Dataset	<i>w</i>	<i>s</i>	<i>a</i>	α	β
1	114.53	62.24	103.00	1.39	-52.72
2	125.79	41.71	143.40	1.18	-29.07
3	258.04	40.68	143.40	1.18	-27.11
4	1.21	122.78	127.80	0.94	-8.79
5	109.11	32.34	335.40	1.40	-9.94
6	63.10	87.20	355.90	1.362	-24.27

Table 2 Percentage of pollen deposition on a 2-m radius recipient population derived from a donor population 1-km away, according to the model of pollen dispersal given by equation 1*w*

Dataset	After scaling-up the size of the donor population		
	Recipient population downwind of donor	Recipient population downwind of donor	Recipient population centered 90° from ω
1	3.520	99.55	51.12
2	0.506	99.55	16.65
3	0.373	95.50	15.40
4	0.013	41.50	35.52
5	0.008	29.74	4.90
6	0.030	62.08	28.79

tion decreases smoothly with distance, and it is assumed that wind speed and turbulence also have significant effects that would be complex to model (Giddings et al. 1997b).

Despite these problems it is interesting to calculate possible pollen deposition from the models fitted to some of the data (Giddings et al. 1997b). The simplest model for deposition (*p*) including wind direction was given by:

$$p = ae^{-\log D[\alpha + \beta\phi(\theta; w, s)]}, \quad \text{where } \phi(\theta; w, s) = \frac{1}{\sqrt{2\pi}s} e^{-\left[\frac{(x-w)^2}{2s^2}\right]} \quad (\text{equation 1}w)$$

D and *x* are the distance and direction from the source, *w* and *s* the mean and standard deviation of wind direction and *a* is a coefficient indicating maximum deposition. There were six data sets for which more complex models with more parameters did not give significantly improved fits. The parameter estimates in these six cases have been previously reported (Giddings et al. 1997b), but are given in Table 1 for completeness.

Method

The expression for *p* was integrated over *D* and *x*. Immigrant pollen was then calculated as a percentage of the total pollen deposited on a region, for each set of parameter values given in Table 1. Deposition was assumed to be from a source population of 2-m radius (like the source on which the data is based) to a similar-sized "recipient" population 1 km downwind. The assumption is made that there are only these two populations contributing pollen to the recipient population. The Mathcad programme devised to make these calculations is shown in appendix 1.

The donor population was then scaled up to fill an area of 320 m×320 m (just over 10 hectares, or about 25 acres) as a series of 2-m radius circles (i.e. about 79% filled with ryegrass, which is about 8 hectares, or just under 20 acres). Pollen deposition onto the recipient population was worked out from each circular "sub-population" and the results summed to find the total deposition. The programme in appendix 1 was modified so that distances between subpopulations and the recipient population were calculated using the relationships of Pythagoras; angles using those of trigonometry. The procedure was repeated assuming the recipient population to be centered at 90° from the mean wind direction (*w*).

Results

Some $7.96 \times 10^{-3} = 3.52\%$ of the pollen deposited on the downwind "recipient" population was from the donor "transgenic" population (Table 2). This increased to 29.74–99.64% when the source size was scaled up to $(320 \text{ m})^2$, or 4–51.12% for a recipient population at right angles to the mean wind direction (Table 2).

Discussion

These results demonstrate the difficulty involved in predicting what transgene dispersal to wild and feral populations will be. However, it does show that when transgenics are grown on a field scale, their pollen could, in some circumstances, swamp that of small conspecific populations. Most of the pollen landing on plants of downwind populations could be from the transgenic. There could also be substantial pollen dispersal even to populations a kilometer away, and not necessarily directly downwind. One does have to bear in mind though that the models say nothing about other factors that determine transgene spread. In particular, whether pollination results in fertilisation and seed formation will depend on such things as pollen longevity, the extent of cross-compatibility and how synchronized flowering is between the two populations. Thereafter the spread of transgenes will depend on other factors, such as the scale of recruitment from seed and the fitness and evolution of any hybrids that result. Furthermore pollen from a transgenic may not all carry transgenes if the plants are heterozygous, or mixed with non-transgenics of the same or another species.

Where there is any doubt about the consequences of gene dispersal from transgenic crops measures need to be taken to minimize or prevent it. Possibilities include using intensive grazing or harvesting before flowering, or selecting for asynchronous flowering, reduced cross compatibility, or male sterility. Another effective control would be to use transgenes that kill the developing em-

bryo of hybrid seed, a controversial technology recently patented by the US Department of Agriculture and Delta and Pine Land (US patent 5723765, 1998). Given the potential for long-distance dispersal the use of guard rows around transgenic crops to “mop” up pollen seems unlikely to be entirely effective at preventing pollen dispersal away from the crop.

If transgenes are likely to enhance the ability of a crop to establish, survive or reproduce then consideration needs to be given to the likely fitness of volunteers, ferals or transgenic-wild hybrids. Some crops may be so debilitated outside of agriculture that they present little or no risk of becoming weedy. For others increases in fitness may enhance the potential for invasiveness. If this is so then effort needs to be devoted to measuring the finite rate of population change, either directly or as a function of the components of fitness (e.g. see Crawley et al. 1993). Such measurements will need to be done in a range of conditions to match those likely in the release environment over several seasons. The predictive value of the data can be gauged by determining the error due to reduced sampling effort (e.g see Kareiva et al. 1996).

Appendix

Matcad programme for integrating the expression for pollen dispersal (equation 1w) and calculating the percentage deposition on a recipient population. Here both populations are assumed to be of 2-m radius, like that from which the dispersal equation 1 w was derived.

pollen (dist, radius, a, α, β, s):=

a, α, b, ω and s are as in equation 1w, D=dist. radius is that of recipient population

$$\omega \leftarrow 90$$

$$\sigma \leftarrow \text{atan}\left(\frac{\text{radius}}{\text{dist}}\right)$$

σ and φ = maximum deviation of recipient population from mean wind direction (see Fig. 2). σ is in radians φ in degrees.

$$\phi \leftarrow \frac{\sigma \cdot 360}{2 \cdot \pi}$$

$$p \leftarrow \int_{\text{dist}-\text{radius}}^{\text{dist}+\text{radius}} \int_{\omega-\phi}^{\omega+\phi} a \cdot e^{-\log(D) \left[\alpha + \frac{\beta}{\sqrt{2 \cdot \pi \cdot s}} e^{-\frac{(x-\omega)^2}{2 \cdot s^2}} \right]} dx dD$$

$$\text{circle} \leftarrow \pi \cdot \text{radius}^2$$

$$\text{sector} \leftarrow \frac{\pi \cdot \text{radius} \cdot \text{dist} \cdot \phi}{45}$$

$$p1 \leftarrow p \cdot \frac{\text{circle}}{\text{sector}}$$

The integration works out deposition (p) over an area (sector) between the two arcs between ω+φ and ω-φ at dist+radius and dist-radius respectively. The population is assumed to be the circle within this small area, and, for simplicity deposition in this circle (p1) is assumed to be directly in proportion to the two areas.

$$p2 \leftarrow \int_0^{\text{radius}} \int_0^{360} a \cdot e^{-\log(D) \left[\alpha + \frac{\beta}{\sqrt{2 \cdot \pi \cdot s}} e^{-\frac{(x-\omega)^2}{2 \cdot s^2}} \right]} dx dD$$

$$\text{depo} \leftarrow \frac{p1 \cdot 100}{p1 \cdot p2}$$

p2 is the deposition of native pollen within the recipient population. “depo” is the percentage of overall pollen deposition from the donor population.

depo

deposition:= for x ∈ 0.5
 data_x ← pollen(distance, radius, a_x, α_x, β_x, s_x)
 data

This programme applies the preceding procedure to each of the six sets of parameter values estimated for equation 1 w

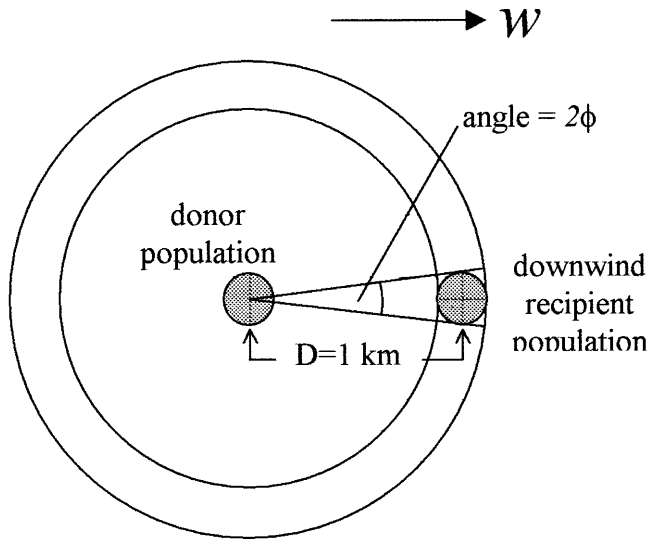


Fig. 2 The relationship between the donor and recipient population modelled in the appendix

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