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ORIGINAL PAPER

Pollen dispersal in sugar beet production fields

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Abstract Pollen-mediated gene flow has important implications for biodiversity conservation and for breeders and farmers' activities. In sugar beet production fields, a few sugar beet bolters can produce pollen as well as be fertilized by wild and weed beet. Since the crop, the wild beets, and the weed beets are the same species and intercross freely, the question of pollen flow is an important issue to determine the potential dispersal of transgenes from field to field and to wild habitats. We report here an experiment to describe pollen dispersal from a small herbicide-resistant sugar beet source towards male sterile target plants located along radiating lines up to 1,200 m away. Individual dispersal functions were inferred from statistical analyses and compared. Pollen limitation, as expected in root-production fields, was confirmed at all the distances from the pollen source. The number of resistant seeds produced by bait plants best fitted a fat-tailed probability distribution curve of pollen grains (power–law) dependent on the distance from the pollen source. A literature survey confirmed that power–law function could fit in most cases. The *b* coefficient was lower than 2. The number of fertilized flowers by background (herbicide-susceptible) pollen grains was uniform across the whole field. Airborne pollen had a fertilization impact equivalent to that of one adjacent bolter. The individual dispersal function from different pollen sources can be integrated to provide the pollen cloud composition for a given target plant, thus allowing modeling of gene flow in a field, inter-fields in a small region, and also in seed-production area. Long-distance pollen flow is not negligible and could play an important role in rapid transgene dispersal from crop to wild and weed beets in the landscape. The removing of any bolting, herbicide-resistant sugar beet should be compulsory to prevent the occurrence of herbicide-resistant weed beet, thus preventing gene flow to wild populations and preserving the sustainable utility of the resistant varieties. Whether such a goal is attainable remains an open question and certainly would be worth a large scale experimental study.

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Introduction

Gene flow between cultivated plants and their wild relatives has been identified as a major concern for several transgenic crops because of the risk of inducing genetic changes in wild relatives in the fields and in wild habitats (Stewart et al. 2003) and because of the potential economic consequences of gene transfer between cultivated fields.

The possible creation of "super weeds" through gene flow from transgenic crops to wild relatives is a major concern for farmers. In European sugar beet (*Beta vulgaris* L.) production fields, weed beet is already known to be a major problem, impossible to eradicate by chemical means, because it is the same species as the crop (Longden et al. 1975; Soukup and Holec 2004). The use of genetically modified, herbicide-resistant sugar beet to make weed control cheaper and more efficient is an opportunity to destroy weed beet, but gene flow between the crop and the weed would jeopardize this strategy. Weed beets acquiring transgenes encoding pest and disease resistance would become more damaging in sugar beet fields (Bartsch et al. 2001) and, perhaps, in other uncompetitive crops such as peas. Besides crop areas, the immigration of such transgenes to wild sea beet (*B. vulgaris* ssp. *maritima*) could modify the interaction of this naturally evolving form of beet with its specific plant community (Sukopp et al. 2005). Indeed, wild sea beet was recently reported to be an actual recipient of gene flow from beet fields (Bartsch et al. 1999; Viard et al. 2004; Cureton et al. 2006). Finally, gene flow is also a threat to seed production, because wild beet populations growing adjacent to seed-production areas could introgress transgenes and then pollinate the seed mother plants, thus introducing unwanted transgenes in certified seed (Lavigne et al. 2002; Alibert et al. 2005).

Since sugar beet is a biennial crop grown for its root, it is not expected to flower during the first year of growth and, therefore, root-production areas are assumed to be exempt from such problems. However, a few bolting plants were repeatedly reported in root-production fields, either induced by low temperature during spring growth (vernalization), or due to the presence of a bolting gene in a small percentage of the certified seeds sown. This bolting gene is known to originate from wild beet populations through pollen contamination of the seed-production fields (Hornsey and Arnold 1979; Longden et al. 1975; Boudry et al. 1993; Fauchère et al. 2003). *B. vulgaris* is an obligate outbreeder with a complex self-incompatibility system (Maletsky and Weisman 1978) and its pollen is easily transported by wind, and probably by insects too (Down and Lavis 1930; Archimowitsch 1949, Free et al. 1975). Sugar, fodder, sea and weed beets all intercross freely (Ford-Lloyd and Hawkes 1986). It was therefore necessary to assess the pollen dispersal of sugar beet in root-production fields to estimate its potential for crossing with surrounding weed beets and wild relatives, and to estimate how transgenes are dispersed from field to field, and from fields to wild habitats in the root-production areas.

Studies of pollen dispersal of sugar beet initially were carried out in the middle of the twentieth century in order to maximize the seed production of male sterile plants, pollinated by interspaced rows of pollen donor (Stewart and Campbell 1952), and to set up isolation distances between nurseries to produce commercial seed with the rate of genetic impurity (i.e. hybrids between two varieties) under a given threshold (e.g. Bateman 1947). A direct approach consisted in checking experimentally the frequency of cross-pollination in rows of sugar beet flowering at various distances from a pollen donor conferring a dominant trait. This generally was investigated over short distances, 15–30 m (Bateman 1947; Stewart and Campbell 1952; Scott and Longden 1970; Dark 1971). Only one study provided data up to 600 m away from the pollen source (Archimowitsch 1949). A physical approach, assuming that the frequency of cross-pollination was a function of the density of pollen in the air above a target plant, consisted in scoring the amount of pollen at various distances from the source (Meier and Artschwager 1938; Jensen and Bøgh 1942; Chamberlain 1967; Dark 1971). However, the correlation between effective plant fertilization and daily dose of pollen grains was not clear (Scott 1970).

More recently, these studies gained renewed importance because public concern about the impact of genetically modified plants imposed seed admixture thresholds for crop certified seeds (Lavigne et al. 2002; Alibert et al. 2005) and more accurate knowledge about the possible gene flow to wild sea beets (Bartsch et al. 1999; Viard et al. 2004; Andersen et al. 2005; Cureton et al. 2006). Several independent experiments were set up to practically determine the realized pollen flow (Table 1). They were hardly comparable because the experimental designs varied widely. These variations included the plant material (male sterile, weed beet, sea beet, related wild *Beta* species) in pure or mixed stands, the size and location of pollen donors, and the presence of isolation barriers (Brants et al. 1992; Madsen 1994; Vigouroux et al. 1999; Vigouroux 2000; Saeglitz et al. 2000; Alibert et al. 2005). Flower fertilization of bait plants up to 1,000 m away from the pollen source was confirmed. In all cases, there was a rapid decline in the crossing frequency as the distance increased, which could be described by a leptokurtic function, either a power–law or a negative exponential model.

However, beyond these general descriptions of the observed patterns of dispersal, the necessity to forecast efficient pollen dispersal in various spatiotemporal configurations of an agro-ecosystem through a simulation model of gene flow (Sester et al. 2008) requires a robust estimation of the dispersal curve. Several studies proposed the individual dispersal function (IDF, or dispersal kernel) as a good candidate (Lavigne et al. 1998; Austerlitz et al. 2004; Klein et al. 2006; Fénart et al. 2007). This function is a 2D-probability function defining the probability that a pollen grain emitted at a reference point (0, 0) will fall still alive at any point (x, y). Estimating thoroughly the whole

Table 1 Literature review of studies on pollen flow in sugar beet

Authors	Methods	Range of distances	Maximum dispersal	Regression $y = ax^b$		
				a	b ± 95% CL	R^2 (n)
Alibert et al. (2005)	SPF + MS	10–200	2.1% at 200 m	36.6	−0.69 ± 0.30[1]	0.99 (4)
Archimowitsch (1949)	SPF	30–606	0.3% at 606 m	294	−1.01 ± 0.22[1]	0.99 (4)
Bateman (1947)	SPF	0.2–23	0.07% at 19 m	2.92	−0.87 ± 0.13[1]	0.98 (15)
Brants et al. (1992)	SPF + MS	25–75	8% at 75 m	33.2	−1.48 ± 1.48[1]	nd (3)
Dark (1971)	SPF	0–30	0.1% at 30 m	0.80	−0.49 ± 0.06[1]	0.92 (5)
Dark (1971)	PT	150–1200	1,200 m	15,000	−1.39 ± 0.02[2]	0.98 (7)
Darmency et al. (2007)	SPF + MS	6–300	1.3% at 280 m	65.7	−0.72 ± 0.60[3]	0.48 (17)
Jensen and Bøgh (1942)	PT	50–800	800 m	1147	−0.81 ± 0.09[2]	0.99 (8)
Madsen (1994)	SPF	9–75	0.31% at 75 m	16.4	−0.89 ± 0.17[1]	0.99 (4)
Saeglitz et al. (2000)	SPF + MS	10–300	40% at 200 m	351	−0.94 ± 0.24[1]	0.99 (5)
Scott and Longden (1970)[4]	PT	1–8	8 m	0.65	−0.62 ± 0.06[2]	0.99 (4)
Stewart and Campbell (1952)	SPF + MS	1–15	10% at 15 m	83.4	−0.75 ± 0.11[1]	0.96 (12)
Vigouroux et al. (1999)	SPF + MS	3–15	1.2% at 15 m	60.8	−1.73 ± 0.46[1]	0.99 (5)

The studies estimated pollen dispersal by using pollen trap (PT) or hybrid seed production by groups of fertile (SPF) and male sterile plants (SPF + MS) along lines radiating from a pollen source. The maximum dispersal was the highest rate at the farthest distance to which pollen or hybrids were found in the study. Pollen dispersal distribution according to the distance x from the pollen source was fitted by a negative power regression $y = ax^b$ using the mean values of the records at n given distances (n in brackets)

CL confidence limits at $P = 0.95$, *nd* not determined

[1] In % of pollen counts at 0 m

[2] In % of total seed set

[3] In number of total seed set

[4] The authors proposed log $p = 1.84 - 0.077x$

shape of the IDF is necessary because (1) the tail of the function determines the long-distance pollen income, and (2) the shape of the curve close to the origin determines the local protection by dilution of incoming pollen (Lavigne et al. 2008). The distribution of sugar beet bolters is patchy among fields and their density depends on the bolting sensitivity specific to each of the sugar beet varieties (Perarnaud et al. 2001; Fauchère et al. 2003). The field distribution of establishing weed beets is also patchy among fields as the farming system and the industriousness of farmers to control weed beets are widely variable within a region. It will be even more patchy when herbicide-resistant varieties will be used because they allow complete weed control where they are grown (at least as long as the weed beets have not integrated the transgene), whereas conventional varieties do not allow such a complete weed control. It is patchy again within each field as it reflects the seed rain of the progeny of one previous plant per patch. Using the IDF seems therefore a relevant way of accounting for this particular spatial arrangement of plants emitting pollen and of comparing long-distance airborne pollen dispersal against local pollen.

The question of the intensity of the background pollen pool over a root beet field is of particular importance. First, it has been demonstrated for corn that airborne pollen can travel at high altitudes in the atmosphere, keeping the ability to germinate up to 1,200 m above ground level (Brunet et al. 2008). This mode of transport could lead to a homogeneous pollen rain, almost independent of pollen source positions, over large areas (dozens of km). For beet fields in root-production areas, this phenomenon could be of major importance since pollen sources are numerous and widespread, but each produces only a small amount of pollen because few plants bolt. Indeed, Fénart et al. (2007) showed that a large fraction of effective pollen in a given field could originate from other fields, even situated several hundred meters away. Similarly, seed producers are quite aware of this phenomenon and send teams of technicians to look for and destroy any beet within a 1-km radius of the multiplication field (Tyldesley 1978; Lavigne et al. 2002). In addition, models using fat-tailed IDF have shown that the cumulated pollen contributions from all fields in the agricultural landscape (i.e. the background pollen pool) could be a more significant source of (trans)gene flow inside a target field than only the closest field (Lavigne et al. 2008).

Here we report the results from a pollen dispersal experiment that was conducted in a root-production field of beet by measuring seed set of male sterile plants sown at distances up to 1,200 m from a controlled source of genetically-modified herbicide-resistant sugar beet pollen. Our goals were to (1) quantify the pollen limitation at different distances from the source, (2) calibrate an individual dispersal function that could be used in simulation models, and (3) evaluate the amount of pollination events due to the long-distance, background pollen pool.

Materials and methods

Plants and experimental design

An experiment to measure pollen flow was set in a 25-ha field of conventional sugar beet field near Châlons, Champagne (France) (GM trial agreement B/FR/99.01.17). The only pollen source in the field consisted of a 2 × 2 m^2 containing 50 bolting plants of an experimental germplasm homozygous for the transgene *bar* conferring resistance to the herbicide Liberty® (provided by KWS). One vernalized root of male sterile beet was planted on each of eight radiating lines from the pollen source, at each of 24 distances: 0, 0.5, 1, 2, 3, 5, 6, 7, 9, 11, 13, 15, 20, 25, 30, 50, 75, 100, 125, 150, 175, 200, 225 and 250 m (Fig. 1). Three lines were continued in adjacent sugar beet fields with plants up to 600 m, and one up to 1,172 m away from the pollen source. The experiment was visited twice a week in order to remove all spontaneous sugar beet bolters and check simultaneous flowering of the pollen donor and the male sterile plants. Plants were covered with paper bags in mid-September, at the beginning of seed maturation, in order to collect all shedding fruit. A total of 204 plants were harvested, then threshed. Since the male sterile line was monogerm, every fruit represents one flower, and the fruit had potentially one or zero seed.

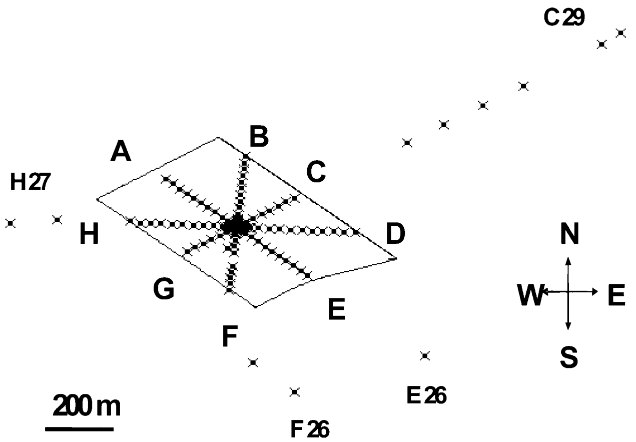

Fig. 1 Experimental design (GPS data). The *rectangle* represents the limits of the 25 ha sugar beet field. The locations of target male sterile plants are indicated by *crosses*, C24–C29 in another adjacent sugar beet field, E26, F25, F26, H26 and H27 in waste places

Measurements

The fruit were washed for 24 h in clear water, and then gently dried at room temperature. They were sown in trays filled with vermiculite and placed in the greenhouse (16 h day at 22°C; 8 h dark at 18°C). The number of fruit collected (NF) and the number of germinating seeds (GS) were recorded for each plant. Then, in order to check that the collected seeds actually originated from pollen from the GM controlled source, the young 2–4 leaf seedlings were sprayed with Liberty® (provided by Bayer Crop Science, 200 g l^{-1} a.i.) at dose 5.3 l ha^{-1} using an automatic sprayer delivering 300 l ha^{-1}. The numbers of plants alive and dead were recorded. A second spray was performed a few weeks later to score the resistance to herbicide of the plants germinated, if any, after the first spray. The number of resistant seeds (GRS) and the number of susceptible seeds (GSS) among the germinating seeds were then recorded for each plant.

Statistical analyses

To investigate the effect of distance on pollen dispersal, we used two families of dispersal kernels differing in the shape of the tail (Klein et al. 2006). The exponential power family with the scale parameter, a and the shape parameter, b is defined as:

$$f(a,b,r) = \frac{b}{2\pi a^2 \Gamma(2/b)} \exp\left[-\left(\frac{r}{a}\right)^b\right], \qquad (1)$$

where Γ is the classic gamma function (see e.g. Abramowitz and Stegun 1964). This family contains the bivariate Gaussian kernel ($b = 2$) and the bivariate exponential kernel ($b = 1$). It leads to fat-tailed kernels for $b < 1$.

The power–law family with the scale parameter, a and the shape parameter, b is defined as:

$$f(a,b,r) = \left(1+\frac{r}{a}\right)^{-b}. \qquad (2)$$

All the kernels from this family are fat-tailed, fatter-tailed as b decreases, and fatter-tailed than any exponential power function. The usual normalizing constant [e.g. $(b-2)(b-1)/2\pi a^2$, see e.g. Klein et al. 2006] was suppressed from the expression of the power–law kernel to allow the exploration of fatter tails ($b < 2$), requiring however to cut the function after an arbitrary distance threshold in order that the function could be a PDF.

Following Devaux et al. (2007), compound kernels were also tested. They consisted of exponential kernels for distances below 10 m and power–law kernels for greater distances, connected at $r = 10$ m to insure a continuous function. We fitted these kernels to the data using simultaneously the GRS and GSS measures and accounting for the fruit production and the pollen limiting effect. To do this, we assumed that a plant at a distance, r from the source produces an average of germinating seeds (GS) equal to

$$E[\mathrm{GS}|\mathrm{NF}] = Q(r) = \mathrm{NF}\min(q_0 f(a,b,r) + q_{\mathrm{ext}}, q_{\mathrm{sat}}),$$

where NF is the number of fruits, q_0, q_{ext} are the amount of efficient pollen grains per ovule, respectively, emitted by the source and present in the background pollen cloud, and q_{sat} is the proportion of ovules that could provide seeds if the pollen was not limiting.

This means that the amount of pollen coming from the background pollen pool (independent of r) and from the source plot would produce $\mathrm{NF}(q_{\mathrm{ext}} + q_0 f(a,b,r))$ seeds. But if this number is higher than the number of available ovules (i.e. pollen is non-limiting), then the plant produces only NF q_{sat} germinating seeds.

We also assumed that, conditionally on the number of germinating seeds GS, the proportion of seeds not carrying the resistance gene is on average

$$E\left[\frac{\mathrm{GSS}}{\mathrm{GS}}|\mathrm{GS}\right] = P(r) = \frac{q_{\mathrm{ext}}}{q_0 f(a,b,r) + q_{\mathrm{ext}}}.$$

This means that pollen from the source plot and background pollen have the same competitive ability whatever the density of pollen over a plant.

Finally, we assumed that the actual number GS follows a Poisson distribution with average $E[\mathrm{GS}|\mathrm{NF}]$ and that, conditionally on GS, the actual number GSS follows a binomial distribution with parameters GS and $E[\mathrm{GSS}/\mathrm{GS}|\mathrm{GS}]$.

Under these assumptions, we maximized the log-likelihood of the observations to find the values of q_0, q_{ext}, q_{sat}, a and b that provide the best fit of the model to the data. The log-likelihood is given by

$$\begin{aligned}\log L(q_0, q_{\mathrm{ext}}, q_{\mathrm{sat}}, a, b) = \mathrm{cst} + \sum_{\theta,r} -Q(r) + \mathrm{GS}_{\theta,r}\log Q(r)\\ + \mathrm{GSS}_{\theta,\mathrm{r}}\log P(r)\\ + \mathrm{GRS}_{\theta,r}\log(1-P(r)),\end{aligned}$$

where the summation is achieved over all radiating lines θ and all sampling distances r and where $\mathrm{GS}_{\theta,\mathrm{r}}$, $\mathrm{GSS}_{\theta,\mathrm{r}}$ and $\mathrm{GRS}_{\theta,\mathrm{r}}$ are the observations at the sampling point (θ, r). $\mathrm{cst} = -\log(\mathrm{GS}_{\theta,r}!) + \log\left(C^{\mathrm{GSS}_{\theta,r}}_{\mathrm{GS}_{\theta,r}}\right)$ is a constant regarding the estimated parameters.

Results

Fruit and seed production

Pollen donor and male sterile plants flowered at the same time. Fruit number per plant ranged from 117 to 13,417, with a mean value of 4,760 ± 330 (± confidence limits at 95%). However, 8 out of the 204 male sterile plants had a markedly low number of fruit, from 117 to 680. And since every flower produces a fruit, whether fertilized or not, these eight plants must have experienced noticeable trouble for their growth and reproduction to have so few flowers compared to the others. Therefore, we discarded them from the statistical analysis. They included plants located from 13 to 200 m from the pollen source as well as the three farthest plants from 864 to 1,172 m.

Limitation of pollen amount with distance

The germination rate varied greatly between plants, from 0.4 to 64%. It depended on the distance of the mother plant from the pollen source (Fig. 2a). Both genetic and environmentally induced variations of seed dormancy were unlikely, because all the fruits were obtained under the same conditions from the same germplasms and at the same time. Therefore, it is likely that the differences in the percentage of non-germinating seeds were due to difference in the intensity of flower fertilization that is the dilution of pollen according to the distance from the pollen source. A plateau at 40% was observed near the pollen source, from 0 to 3 m, then the germination rate decreased to 10% at 20 m and 1% at 300 m away from the pollen source. The plateau could have indicated that the abundant pollen close to the pollen source saturated all the available ovules. However, fitting the data with the equations described above indicated an absence of pollen saturation (i.e. for the power–law function, q_{sat} could not be estimated because useless). The fitted model thus predicted a continuous decrease of the proportion of germinating seeds (Fig. 2a; GS/NF = $f(r)$, $R^2 = 0.82$), so that the pollen could be considered as limiting over the whole field.

Background pollen cloud

The herbicide treatment revealed the presence of susceptible seedlings that must be subtracted in order to consider only the actual pollen flow from the controlled pollen source. The number of seedlings destroyed by the herbicide per male sterile plant ranged from 0 to 387 with an average of 56 ± 8 seeds. Except the individual plant variation, the rate of susceptible seed per fruit (GSS/NF) was constant over all the distances, ca 0.012 ± 0.001 (Fig. 2b), which indicated a homogeneous pollination efficiency of background pollen. This indicated in particular that there was no competition between the pollen source and the background pollen, which fitted the conclusion drawn from the germination data and confirmed that the pollen was limiting from 0 m to the longest distance. Consequently, the number of ovules fertilized by either the background pollen

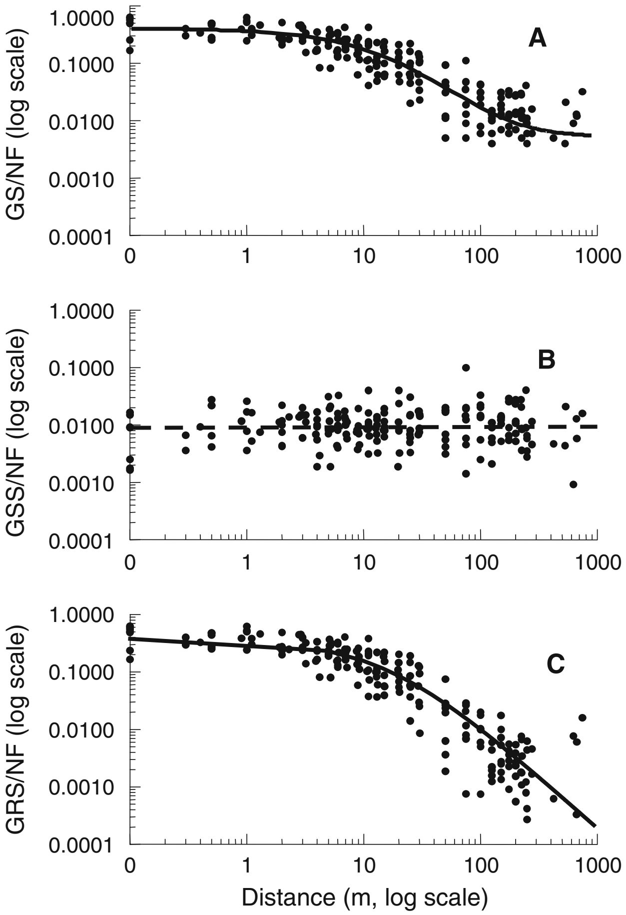

Fig. 2 Numbers of seeds produced per fruit by male sterile plants according to their distance to the pollen source. **a** Proportion of germinating seeds (GS/NF). The *solid line* represents the predicted values with the best model fitted to the data, i.e. power–law dispersal function (Table 2). **b** Proportion of herbicide-susceptible seeds (GSS/NF). The *dotted line* represents the median. **c** Proportion of herbicide-resistant seeds (GRS/NF). The *solid line* represents the predicted values with the best model

or the pollen source was expected to be a direct function of the amount of each type of pollen grain available at the place of each bait plant. Otherwise, in case of saturating pollen with regard to the number of available ovules at a given place, the frequency of realized fertilization close to the pollen source would have been due to pollen competition rather than to a single pollen dispersal function, thus jeopardizing the estimate of the dispersal function.

Dispersion from the central plot

Herbicide-resistant seedlings were produced at all the distances tested, up to 1,172 m away from the pollen source. No significant favored direction was detected ($P = 0.27$, Table 2). This means that the main wind direction, if any during the flowering time, was not a major factor affecting the dispersal pattern. However, differences among transects could exist, but they were badly modeled by the cosine function used (i.e. not a unique favored direction). The distribution of the number of resistant seeds, both in terms of number of fruit and in terms of germinated susceptible seed (GRS/NF or GRS/GSS) showed apparently a plateau from 0 to 3 m, and then a decrease was observed as the distance increased, and finally a tail beyond 200 m away from the pollen source (Fig. 2c). The dispersal function that better fitted the data was the power–law function without anisotropy (Table 2). Pollen from the pollen source fertilized as many ovules as the background pollen at about 80 m from the pollen source but had less effect at farther distances (Fig. 3).

Discussion

Our experiment assessed pollen flow under pollen limiting conditions without competition from local pollen. It mimics well conditions in root-production fields where very few sugar beet bolting plants occur and weed beets are destroyed (by hand pulling or by herbicide in a herbicide-resistant sugar beet field). It allowed to propose a pollen dispersal function and showed evidence of the importance of the background airborne pollen.

Functions of pollen dispersal

The best data fit was obtained using the fat-tailed power–law function without anisotropy (Table 2), i.e. showing a slow decline with long-distance dispersal. Although it was often used in former studies (Gliddon et al. 1999 for a review), the exponential function provided a poorer fit (Table 2). A similar ranking of best fitted equations has been reported in recent studies (Klein et al. 2006; Devaux et al. 2007 for oilseed rape). The exponential power function, although reaching a fit almost similar to the power–law function, led to extreme estimated values of the parameters, and thus was less relevant. The shape parameter estimated for the power function ($b = 1.82$) is particularly low, indicating that this function cannot be extrapolated towards infinity. This would lead to overestimation of long-distance dispersal. Thus, further work is necessary to calibrate a function for distances longer than a few kilometers. A further study would be necessary to investigate the compatibility between the measured intensity of the background pollen pool to the estimated shape of the dispersal function and its tail. This would require having knowledge of beet fields in an extended landscape (e.g. Devaux et al. 2007), several km around the experimental field, which was not available here.

Overall, the dispersal function we found, and particularly the coefficient of the power–law function estimated, is

Table 2 Data analysis using dispersal models (see text for equations)

Model	q_0	q_{ext}	q_{sat}	*a*, scale parameter	*b*, shape parameter	Log *L* (*P* value)
power–law anisotropy	0.40	0.012	–[a]	16.1	1.82	−16,824 ($P = 0.27$)
power–law no anisotropy	**0.40 ± 0.04**	**0.012 ± 0.002**	–[a]	**16.2 ± 7.3**	**1.82 ± 0.46**	**−16,927**
Exponential power short-distance and power–law long-distance	925	0.012	–[a]	55.2	0.73[b] 1.14	−17,152
power–law Fénart et al. (2007)	0.40	0.012	–[a]	30.2	2.96	−17,612 ($P = .0002$)
power–law Sester et al. (2008)	0.53	0.012	–[a]	13.0	2.1	−18,221 ($P < .0001$)
Exponential power	1,780	0.012	0.39	124	0.51	−17,441
Weibull	93	0.013	0.36	131	1.34	−18,256
Exponential	1,086	0.012	–[a]	48.2		−22,312

The values of the parameters estimated from a maximum likelihood approach are reported (higher Log *L* correspond to better fit to the data). Confidence intervals (±2SE estimated from a asymptotic covariance matrix correcting for overdispersion in the data) are provided for the parameters of the preferred model. We also provided *P* value of the likelihood ratio test (corrected for overdispersion in the data) comparing a model with the preferred model (in bold) when they are nested

[a] q_{sat} could not be estimated when the dispersal function alone fits well to the observations at all distance. This depicts to an absence of pollen saturation

[b] The first value refers to the shape of the exponential power component and the second value refers to the shape parameter of the power–law component

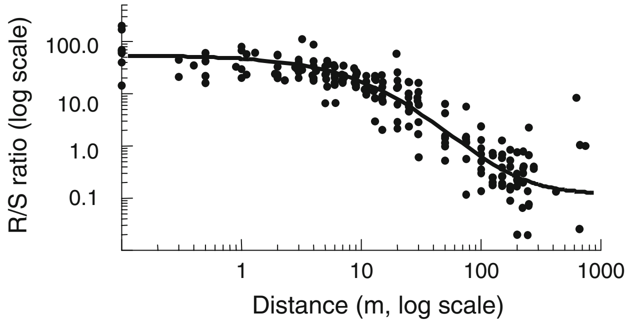

Fig. 3 Pattern of distribution of the GRS/GSS ratio of seeds produced by male sterile plants according to their distance from the pollen source. The *line* represents the predicted values with the best model fitted to the data, i.e. power–law dispersal function (Table 2)

in accordance with previously published studies on sugar beet; for all these studies the data better fitted a power–law distribution and we calculated *b* values always below 2 (Table 1). The average *b* value of the literature data was lower than 1, thus indicating more pollen dispersal over long-distance. This low value could be due to the pollination conditions in the corresponding experiments as they were most often designed to determine the best ratio of pollen donor to male sterile plant to produce an optimum amount of seed in seed-production areas at row-to-row distance. Thus, pollen was far from being limiting, while it was a characteristic (of our experiment) representative of conditions in root-production fields. When the studies were carried out in conditions of root-production fields, as for instance in Darmency et al. (2007), fertile plants such as weed beets were often included in the design, so that the amount of available pollen was certainly larger than in the present study. In addition, the range and the number of distances tested were generally small (Table 1), resulting in irrelevant long-distance prediction. When the number of distances tested was high, i.e. 12–15 scored points, the range was short: 0–15 or 23 m only (Bateman 1947; Stewart and Campbell 1952). In a recent study under genuine field conditions, the best fitted distribution curve inferred from the genetic diversity analyses of weed beet populations several kilometers away was, again, a fat-tailed power–law with $b = 2.96$ (Fénart et al. 2007). This curve would be more adapted to long-distance dispersal, but it had a poor fit to our data (Table 2).

Since the curve was derived from data obtained in conditions of limiting pollen, the equation is valid at nearly the first few cm from the pollen source. The individual dispersal function from different pollen sources can be integrated to provide the pollen cloud composition for a given target plant, whatever the plant density and the distance. For instance, it could be used to design efficient male sterile and pollen donor row arrangement in seed-production areas, both to optimize seed production versus land use and to better protect male sterile flowers from foreign pollen (Lavigne et al. 2002). However, one must remember that in conditions of non-limiting pollen other phenomena, such as competition among the different pollen, occur. Indeed, the pollen of weed beet has often been suggested to be more viable and competitive than that of sugar beet bolters (Darmency et al. 2007), thus probably shifting the fertilization success in favor of the weed pollen.

The choice of a dispersal curve is of critical importance in determining the behavior of weed populations with regard to the herbicide-resistance if transgenic herbicide-resistant sugar beet cultivars were to be used. For local movement among adjacent fields, the best fit obtained with the fat-tailed power–law distribution provides an explanation for the role of pollen immigration from adjacent to moderately distant pollen sources, thus allowing modeling gene flow in the field and interfields in a small region. Earlier model simulations were carried out with preliminary estimates of the dispersal curve, using $a = 13$ and $b = 2.1$ (Sester et al. 2008). These values provide a poor fit (Table 2) and would result in shorter-distance dispersal. We should run new simulations to better predict the speed of geographical spread of resistance genes in an agricultural landscape. In contrast, the ranking of the effects of farming systems on gene dispersal over weed beet populations, as obtained by published simulations, would not be changed. Additionally, airborne pollen migrating from distant areas at this high concentration should be included in the model.

Background pollen cloud

A constant proportion of susceptible seeds per fruit were found over all the distances. Since the 25-ha experimental field was controlled to be bolter-free, and no beet field nor weed beet was present closer than 1,000 m from the experimental field, this result indicated that a non-negligible uniform pollen flow was issued from the background pollen cloud gathering long-distance sources of pollen. It cannot be totally excluded that our technicians may have missed some plants. However, some genetic marking could help rule out this hypothesis. It is worth noting that if this actually occurred, it could occur even more often in real situations (we have taken special care to discard most of the causes of interference upon the studied phenomenon: plant density allowing limiting pollen, bolting synchrony, total bolter control in the field). Here, we will not consider this possibility. Sugar beet pollen is known to be easily transported by wind to such an extent that peculiar care is taken regarding outcrossing due to airborne pollen in certified seed-production areas (Tyldesley 1978). In root-production areas, some sugar beet bolters produce pollen (Fauchère et al. 2003), and weed beets are widespread when farmers do not take special care of them (May 2004). Champagne is a sugar beet growing region, where weed beets are frequently observed to flower, which could account for the high impact of background pollen. In some cases, the infestation density is so high and so competitive with sugar beet that farmers pay up to 40 h of labor per hectar to pull up weed beets by hand, and even so they have to destroy the field when there are 1–10 million weed beets per ha (ITB, personal communication).

In our experiment, the amount of seeds originating from the neighborhood pollen cloud was roughly equivalent to the number of seeds originating from the 50 plants in the central pollen sources at 80 m away from this source, leading to ratios GRS/GSS close to 1 at this distance (Fig. 3). Within the first few meters around the central plot, where pollen availability was only a little limiting, the local source of pollen (resistant plants) provided ~50 times more pollen grains than the background pollen cloud did (Fig. 3). However, with modern sugar beet varieties, the percentage of bolter is now as low as 0.01%, that is one bolter every 1,000 m^2. The pollen contribution of one such plant would be 50 times as low as the pollen source in our experiment, meaning a GRS/GSS ratio below 1 very close to a resistant sugar beet bolter, which suggests a high gene flow from the neighborhood in the region during the experiment. Under these conditions, and assuming that all the (susceptible) weed beets of a future herbicide-resistant transgenic sugar beet field would be destroyed by the herbicide, herbicide-resistant bolters would be half-pollinated by the closest herbicide-resistant bolters and half-pollinated by the background pollen. In addition, bolters of the same sugar beet cultivar display some self-incompatibility alleles in common and a variable frequency of fertility restorer-genes (according to the pollen donor population used to produce the certified seeds), so that bolters could have low pollen fertility and the balance between local to background pollen would be rather at the advantage of the latter. However, the use of the S^f self-fertility allele in breeding programs could change the prediction about the competition between the self-produced and the foreign pollen. The frequency of such allele is not known in weed populations, but an indirect estimate inferred 16–36% of the seeds originating from self-pollination (Fénart et al. 2007). The spread of such allele in weed populations would make these plants less sensitive to pollen flow, thus changing the output of pollen dispersal, which could make necessary to revise the sensitivity analysis of demographic models (Sester et al. 2008).

The GRS/GSS ratio depicts the strength of the foreign pollen versus that of the local pollen. In the case of a farmer adopting a herbicide-resistant variety in a region where weed beet populations occur at low density, the pollen is not limiting, so that a migrating herbicide-resistant pollen could always fertilize an ovule in the neighborhood, as predicted by the fat-tail dispersal function obtained, and even far away from the transgenic field if it is part of airborne pollen. In contrast, the likelihood of such an event would decrease if the weed beet populations were dense or aggregated in patches, because pollen is no more limiting and pollen competition does occur. Questions now arise about how far airborne pollen dispersal could go, how long airborne pollen remains alive, and to what extent a local lack of bolter management in a region can affect weed beet control in a distant region where farmers want to grow herbicide-resistant varieties. This question would be particularly important in the case of sugar beet varieties potentially genetically transformed in the chloroplast (De Marchis et al. 2008), although it is expected that chloroplast genes are not transmitted by pollen (see Shi et al. 2008 for discussion and evaluation in another crop), bolters of these transplastomic varieties could be fertilized by distant bolters or weed beets, so that all their progeny would be definitely resistant. Destruction of such sugar beet bolters must become a compulsory measure to ensure that no seed could be produced with the resistance transgene, as already recommended (Richard-Molard and Gestat de Garambé 1998), thus both preventing gene flow to wild populations and preserving the sustainable utility of the resistant varieties.

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