Part 1

# Techniques for dispersal studies

# Chapter 1

# Measuring and modelling seed dispersal of terrestrial plants

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## Introduction

In this review we will focus on seed dispersal as an empirically verified function that could be coupled with other life history arguments to simulate spatially explicit population dynamics at any scale of interest. Our interest, therefore, is on the problems of observing and then expressing the dispersal curve. A review of techniques in the study of seed dispersal and recruitment is timely because it has become clear that there are two outstanding problems, and both are related to present limitations in field methods: (i) the shape of the dispersal curve near the maternal source as a function of source geometry and dispersal capacity, and (ii) the magnitude of seed deposition as a function of source strength (seeds per metre squared within the source) at very large distances.

We begin by defining these two scales of interest more concretely, and then offer a formal definition of a dispersal curve. Next, we summarize what is known about seed dispersal curves in relation to dispersal vectors for ideal situations where the seed or recruit can be attributed to a source without ambiguity. We then deal with models (primarily empirical; mechanistic models are dealt with cursorily), not merely because of their utility in spatially explicit simulators, but because of their recent importance as a tool for 'disentangling' overlapping dispersal curves. Finally, we will examine vector-specific methods for determining dispersal curves, analyse their merits and drawbacks, and, for the more tractable problems, make some recommendations for improvements.

## Scales of interest

At one extreme, we know from the palynological literature that most trees, shrubs and herbs have (in the higher latitudes at least) migrated at a velocity ($V$) on the order of 200 m year$^{-1}$ (MacDonald 1993). It is likely that the potential velocity is greater than this but migration rates were constrained by the rate at which the climate regime (affecting reproduction and growth rates) itself was moving latitudinally (e.g. MacDonald *et al.* 1993). The scalar for this minimal migrational velocity

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can be written as $Vt_g$ where $t_g$ is the characteristic generation time (in years). For annuals ($t_g = 1$ if they cannot produce more than one generation in a growing season), $Vt_g$ is about 200 m. For trees, the age at which they can produce a large (we leave this undefined) crop is a function of the species-specific growth rate (not age). Unconstrained by any serious data set, let us assume this generation time is on the order of 20 years for trees, and therefore the scaled distance is $Vt_g = 4$ km. This great difference in the value of the scalar for herbs versus trees has obvious implications for field logistics. We note in passing that the scalar for migrational distance is also of interest in metapopulation studies given landscape fragmentation (Hanski 1999; Cain *et al.* 2000).

The shortest distance of interest is more difficult to define. A population that can seize vacant space from dying competitors or conspecifics will tend to persist across a few disturbance cycles, thus easing the required immigration within a metapopulation (Bolker & Pacala 1999). Let us arbitrarily assert that population persistence requires that some fraction of the crop achieves a dispersal distance ($x$) greater than $0.5H$ (where $H$ is the plant height). Thus, we argue that population persistence requires that vectors disperse a large fraction (again, undefined) of the crop to a distance greater than about 0.1 m for a small herb such as *Taraxacum officinale* or 12 m for a tree.

In summary, short-term and long-term population persistence requires that the species available for study today have simultaneously satisfied the requirement that dispersal curves span about three orders of magnitude. Below, we examine how individual species have achieved this range using one vector (rarely) or more typically a large number of vectors.

## Defining the dispersal curve

A point source is an individual plant where the lateral spread among the preabscission seeds is small compared to the median distance travelled. Obviously, widely spread clonal plants are not point sources. We define the dispersal curve as the number of seeds deposited at distance $x$ from a point source bearing $Q$ seeds:

$$Q_x = Q f(x) \tag{1.1}$$

Here $f(x)$ is the dispersal term. Alternatively, one might be more interested in the density of seeds at $x$ ($Q_{Dx}$), and this density curve is merely

$$Q_{Dx} = Q_x / 2\pi x \tag{1.2}$$

For an area source (a very large array of point sources) the curve is given by

$$Q_{Dx} = (Q N_D / 2) f(x, y) \tag{1.3}$$

where $Q$ is now the averaged seed production of a conspecific point source, $N_D$ is the density of these point sources, $x = 0$ is defined as the edge of the area source, and $f(x,y)$ is an empirical function that accounts for the position of the point source in Cartesian space.

Any of these three equations can be changed into a recruitment curve by multiplying $Q$ by the mean survivorship averaged across the area of interest if this survivorship is expected to be roughly independent of distance. In what follows, we will casually let $Q_x$ and $Q_{Dx}$ refer to recruitment as well as seed curves.

With lesser or greater difficulty, these equations can be changed to express density dependence or azimuthal bias in dispersal. Empirical demonstrations of azimuthal bias can be found in Harris (1969) (bias induced by the abscission response to the relative humidity of air masses), Yumoto (1999) (birds preferentially defecating into gaps) and McDonnel and Stiles (1983) (birds' defecation biased by structural elements of the vegetation).

### Empirical dispersal curves ($Q_x$)

In this section we divide seed dispersal vectors into those that can merely satisfy the requirement for local dispersal and those that can also satisfy the migrational requirement. We further dichotomize vectors as primary (the initial postabscission event) or secondary (i.e. involving subsequent re-entrainment). These dispersal agents are listed in Table 1.1.

### Local distance vectors

These include ants (secondary), small flightless mammals (primary or secondary), wind (primary but for seeds with very large terminal velocities) and ballistic (primary). These generally produce right-skewed $Q_x$ curves (we know of two exceptions for ballistic), and most place the modal density of the $Q_{Dx}$ curve at the point source (Figs 1.1 and 1.2). A large fraction of the crop is transported well beyond 50% of a plant height from the source. While distances for herbs (Fig. 1.1) are much less than for trees (Fig. 1.2), note that an ant dispersing seeds 1 m from a 0.3 m tall herb is, using the scalar $x/H$, equivalent to a rodent transporting tree ($H = 25$ m) seeds about 75 m. Maximum reported distances are several plant heights for ants, caching rodents, ballistic and species with large terminal velocities (Table 1.1; maxima for herbs are also tabulated in Willson 1993). Even for herbs with short generation times, however, these distances are too small to satisfy the migrational scale ($Vt_g$).

### Long-distance vectors

These include wind as both a primary (plumes, wings or seeds less than about 0.02 mg) and secondary (on low-friction surfaces such as snow, ice or sand) vector, defecating large terrestrial or arboreal mammals (primary or secondary), defecating birds (primary), caching birds (primary or secondary), and epizoochory by both primary (the seed is attached to the animal via hooks or an adhesive substance) and secondary (a very small seed, say <10 mg, is attached to an animal in a fleck of mud) means.

At the migrational scale our assertion of the adequacy of these vectors is based completely on anecdotes or models. There are anecdotal reports for distances of many kilometres achieved by *Nucifraga* (Vander Wall & Balda 1977) and other caching birds, but of course we have no estimate of the proportion of the crop in-

**Table 1.1**   Seed dispersal vectors by mode: primary (p) or secondary (s). Our categorization is based on similarities in vector-specific field methods *and* in similarities in mechanistic modelling. Vectors are typified by logarithmic seed size (mg) classes (<0.05 is very small; 0.05–5 is small; 5–50 is large; >500 is very large) where rare exceptions are ignored. Maximum distances (Max. $x$) observed are only for full dispersal curves (from a source of any shape or size), not anecdotal reports. The empirical argument that a seed size <0.05 mg will have terminal velocities as low as many plumed or winged seeds is based on Cremer (1977), Woodall (1982) and Jongejans and Schippers (1999). (Based on Cremer 1966; Howe & Smallwood 1982; Willson 1993; Greene & Johnson 1995; Yumoto 1999.)

| Vector and mode | Common vegetation and strata | Seed size range (mg) | Max. $x$ (m) |
|---|---|---|---|
| Ants (s) | Short plants; sclerophyllous vegetation and forest understories | 0.05–5 | 8 |
| Small terrestrial vertebrates (p or s) | No limits on height; no typical vegetation | >0.05 | 60 |
| Ballistic (p) | Mainly shorter plants; no typical vegetation | 0.05–50 | Herbs: 12 Trees: 30 |
| Wind (large terminal velocity) (p) | Wide range of plant sizes; no typical vegetation | >0.05 | Herbs: 5 Trees: 120 |
| Wind (plumes or wings or very small size) (p) | All plant heights; mainly canopy-stratum plants | <50 | Herbs: 150 Trees: 1600 |
| Wind (s) | Low-friction substrates: sand, snow, ice; high-latitude vegetation and deserts | <50 | 100 m |
| Caching birds (p or s) | Mainly mid-latitude trees | >50 | – |
| Defecating large animals (flying, arboreal or terrestrial) (p or s) | No limit to plant size or vegetation type | >0.05 | 700 |
| Epizoochory (hooks, barbs, adhesive material) (p) | Small plants; grasslands and disturbed sites | 0.05–5 | Herbs: 300 Trees: – |
| Epizoochory (seeds in mud) (s) | Small plants: grasslands and hydric sites | <5 | – |

volved in this far tail. For epizoochory, essentially nothing is known at any scale with the lone exception of Yumoto (1999; but the sample size is quite small). For wind (secondary) entraining seeds on snow or sand there is no observed dispersal curve extending beyond 100 m (Greene & Johnson 1997; Vander Wall & Joyner 1998).

Given the empirical void at great distances, it is not surprising that there is no agreement on whether some vectors are more effective at achieving such distances than are others. Willson (1993) argued that wind (primary) is more effective at modest distances than animals (all vectors grouped), whereas Hewitt (1999) made
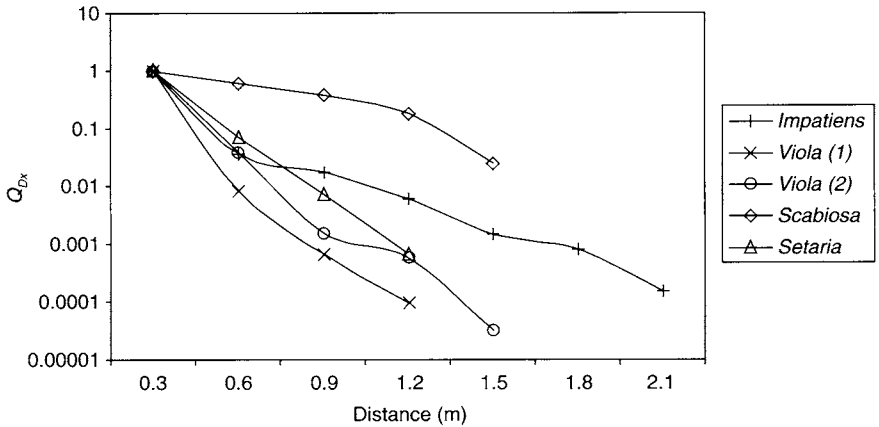
**Figure 1.1** Local dispersal for herbaceous point sources dispersing ballistically (*Impatiens*, Schmitt *et al.* 1985), by ants (*Viola* 2, Ohkawara & Higashi 1994; *Viola* 1, Anderson 1988) and by wind (seeds with a high terminal velocity) (*Scabiosa*, Verkaar *et al.* 1983; *Setaria*, Ernst *et al.* 1992).
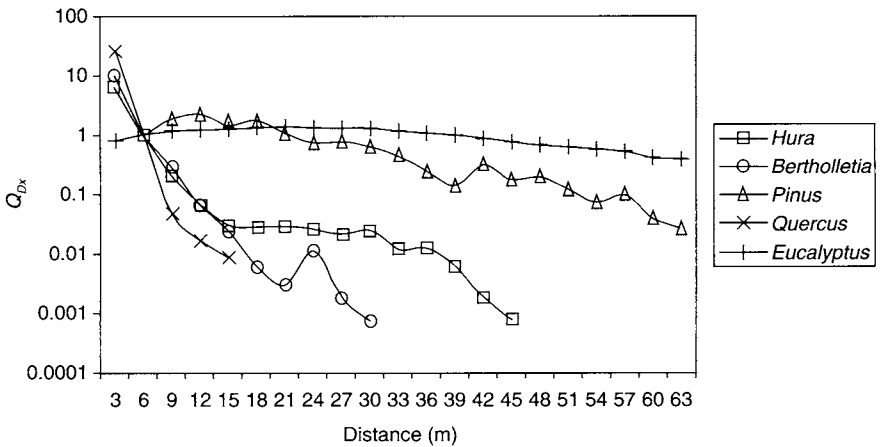


**Figure 1.2** Local dispersal for tree point sources dispersing ballistically (*Hura*, Swaine & Beers 1977), by rodents (*Bertholletia*, Peres & Baider 1997; *Pinus*, Vander Wall 1993; *Quercus*, Sork 1984) and by wind (seeds with a high terminal velocity) (*Eucalyptus*, Cremer 1966). Note that the *Eucalyptus* is an 80 m tall tree.

the opposite argument for colonization of *Pinus* plantations by hardwood species. Wilkinson (1997) asserted that birds must be the unacknowledged long-distance vectors for even winged or plumed seeds because it was (somehow) clear that the wind was incapable of moving seeds many kilometres. Given that our best data sets

at the scale of 1 km are at present provided by wind-dispersed species, this specula-
tion seems odd.

In Fig. 1.3 we show the only long-distance point source dispersal curves for animal
vectors (two defecating terrestrial bird species and a large arboreal mammal). As
before, the $Q_x$ curves are right skewed. We are not, of course, able to say if there is a
characteristic $Q_{Dx}$ curve shape.

## Models, source geometry and the empirical curves of wind-dispersed trees

The contagious distribution of conspecific sources means that, almost invariably,
dispersal curves overlap. There are two classes of models: (i) simple dispersal terms
with one or more parameters that are fitted to a data set, or (ii) mechanistic terms
whose parameters can be estimated independently of an empirical dispersal curve.
We begin with the former class, showing their performance at various scales, and
then we use one of them (the 2Dt) to demonstrate the effect of source geometry on
the shape of the dispersal curve. Mechanistic models are treated here only briefly as
an alternative although one might presume they will eventually be of more interest
as this discipline tires of curve-fitting and begins to seek generality.

### Empirically fitted models

Figure 1.4a and Table 1.2 show some commonly used functions in their $Q_{Dx}$ forms
with the median distance ($x_m$) set at 40 m and $Q$ (seed crop size) at 1000 seeds. We
have also added the simplest intuitive argument: a rectilinear model that has seed
density ($Q_{Dx}$) declining linearly with distance. The log-normal and 2Dt forms are
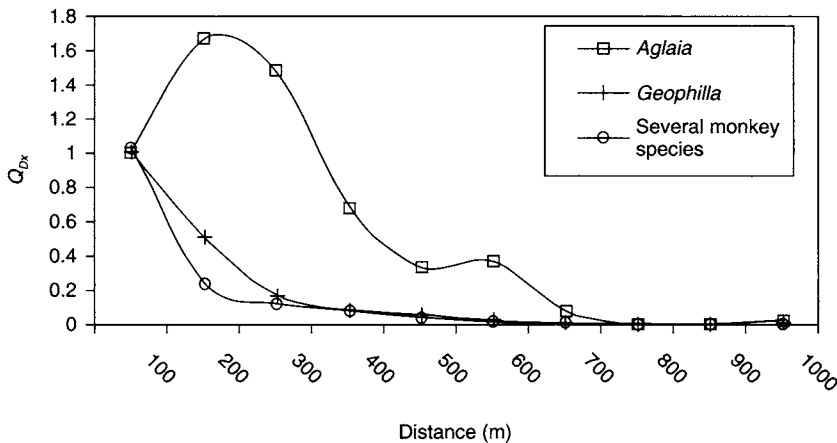


**Figure 1.3** Long-distance seed dispersal of trees via defecation by a large terrestrial bird
(*Aglaia*, Mack 1995), a flightless bird (*Geophilla*, Yumoto 1999) and monkeys (Stevenson
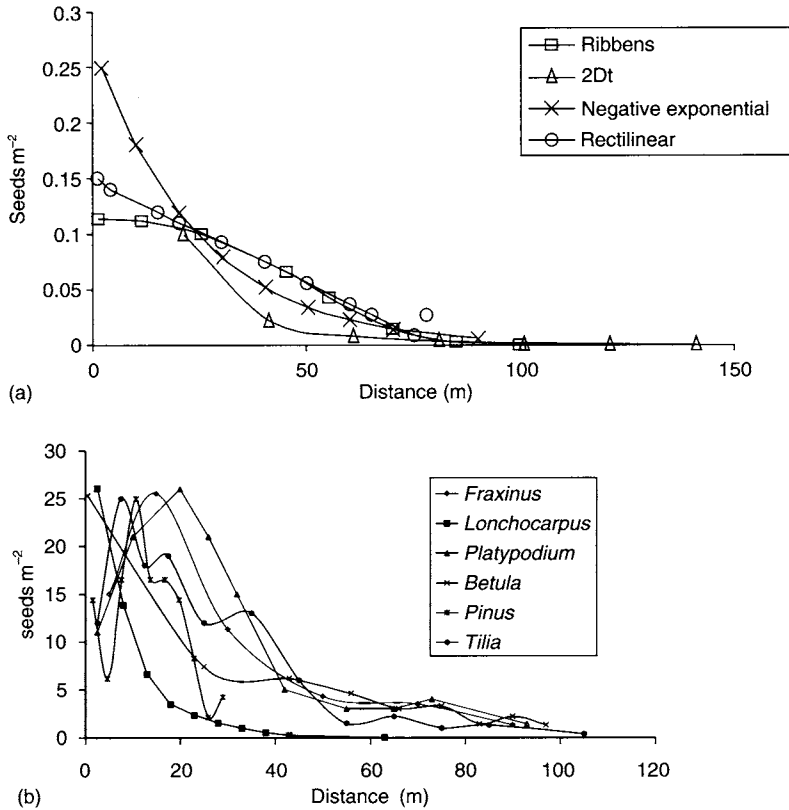2000).

**Figure 1.4** (a) Four empirical models of dispersal from a point source in their $Q_{Dx}$ form. In this scenario, $Q$ (seeds per plant) equals 1000 and the median distance ($x_m$) travelled is 40 m. All parameter values are as in Table 1.2. The predicted curve of the log-normal is so similar to that of the 2Dt that we omit it. Note that the 2Dt would predict a density of 0.78 at $x=0$ (not shown for clarity). Scaled as median distance, we examine the range 0–2.5 $x_m$. (b) Empirical results for solitary wind-dispersed (primary) trees within forests. The empirical curves are from Wagner (1997: *Fraxinus excelsior*), Augspurger and Hogan (1983: *Lonchocarpus pentaphyllus*), Augspurger (1983b: *Platypodium elegans*; deposition reduced by 100), Rudis *et al.* (1978: *Pinus strobus*) and *Tilia americana* (D.F. Greene, unpubl. data).

additionally constrained (based on the empirical evidence below) to have a deposited density at 1 km that is 2% of the density well inside an area source.

Because of the crucial role of recruitment in postharvest stocking success in forestry, there is, compared to herbs and shrubs, a wealth of studies on the dispersion of seeds or germinants of trees within forests and adjacent clearings. Figure 1.4b depicts observed curves of mid-latitude and tropical wind-dispersed tree species where: (i) we have a reasonable density of sampling points, (ii) the authors explicitly state that there are no other nearby conspecifics, and (iii) the tree is not in a clearing or at a forest edge. (Our 40 m median in Fig. 1.4a is based loosely on Fig. 1.4b.) In four of five cases, the mode of the $Q_{Dx}$ curve is clearly displaced well away from the base of

**Table 1.2**  Empirical models and parameters. $x_m$ (median distance travelled) is set at 40 m and $Q$ (seed production) at 1000 seeds. The log-normal and 2Dt are given the additional constraint that the density of deposition at 1 km must be 2% of the density well within an area source. The sources for the functions include Willson (1993), Ribbens et al. (1994), Clark et al. (1999) and Greene and Johnson (2000). For the rectilinear model (introduced here) the single parameter is the maximum distance travelled ($x_{max}$).

| Model | Dispersal term for seeds m$^{-2}$ at distance $x$ | Parameter values |
|---|---|---|
| Gaussian | $a\exp(-ax^2)/\pi$ | $a = 0.000425$ |
| Ribbens | $1.1d^{0.67}\exp(-dx^3)/\pi$ | $d = 0.0000057$ |
| Rectilinear | $3(x_{max}-x)/\pi x_{max}^3$ | $x_{max} = 80$ |
| Negative exponential | $g^2\exp(-gx)/2\pi$ | $g = 0.0415$ |
| 2Dt | $p/[\pi u(1 + (x^2/u)^{p+1})]$ | $p = 0.25; u = 110$ |
| Log-normal | $[(2\pi)^{1.5}\sigma_{ln}x^2]^{-1}\exp[-(0.5/\sigma_{ln}^2)(\ln(x/x_m))^2]$ | $\sigma_{ln} = 2.4; x_m = 40$ |

the tree. Clark et al. (1999) argued that the modal density should be beneath the tree because the tree is not truly a point source (i.e. there is variation in release height as well as in lateral position within the crown) but we consider that this justification for locally convex models is not correct. While the log-normal (as an empirical argument or a mechanistic model) can place the modal density at a distance greater than 0, the $\sigma_{ln}$ value we have chosen (Table 1.2) for the proper fit at great distances is so large that it places the modal deposit virtually at 0. Thus all these models (especially the 2Dt and log-normal) fail to capture the shape of the $Q_{Dx}$ curve for wind-dispersed trees at this scale. Likewise, they would do poorly as a universal argument for the defecation curves in Fig. 1.3.

Two other source geometries of interest are line sources and patch sources (Fig. 1.5). Using the 2Dt model, we express a line source as a single linear array one plant (occupying a $10 \times 10$ m cell) deep, and $x = 0$ at the edge of the source. Likewise we show in Fig. 1.4 what we will term a *patch source* which is defined, necessarily vaguely, as a collection of conspecifics much smaller than an area source. Here we depict the 2Dt model for a patch source $80 \times 40$ m (32 individuals). For the line source the edge deposit is around 25% of the product $QN_D$ (where $N_D$ is the point source density as plants per metre squared), and for the patch source it is around 35%. Note that both source shapes produce a flatter curve than would a point source. (This effect would be even more dramatic if our co-ordinant system placed $x = 0$ in the middle of the line or patch source). Intrepretation of dispersal curves must take account of source geometry. For example, Johnson (1988) argued that *Fraxinus americana* was a better disperser than *Acer saccharum* because the empirical $Q_{Dx}$ curve for the former (a line source along a fence row) was flatter than that of the latter (a single tree source) when plotted on a semilog graph. His many biomechanical speculations
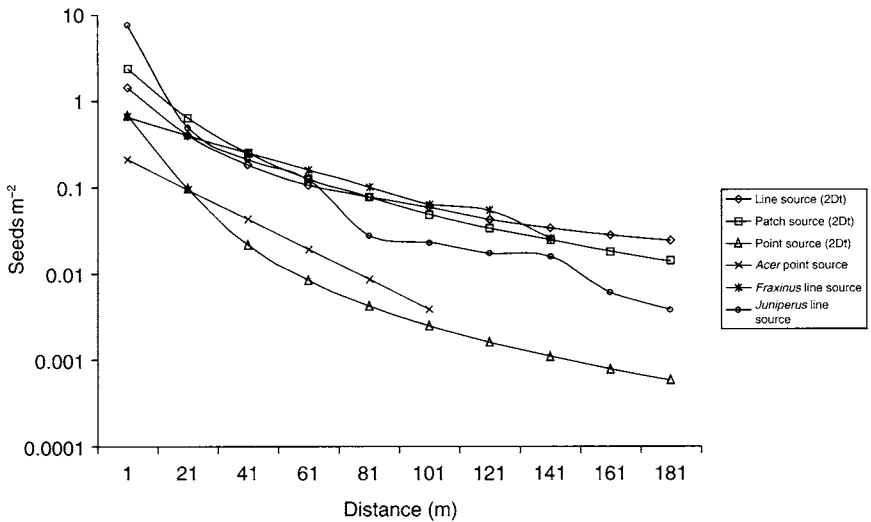
**Figure 1.5** The 2Dt model as a line source or small patch source with the same point source parameter values as in Table 1.2. The line source is 4 km long, and has a width of one point source per $10 \times 10$ m, and this can be scaled as $0.25 \times 100\, x_m$. The patch source is $80 \times 40$ m (scaled $2 \times 1\, x_m$). We also show two empirical curves for *Fraxinus americana* (line source) and *Acer saccharum* (point source) from Johnson (1988) that are made identical to the simulated density at $x = 20$ m. For comparison, a line source of *Juniperus virginiana*, a bird-defecated species, is also shown.

notwithstanding, it is clear from Fig. 1.5 that no such intuitive interpretation was warranted.

Where the empirical models differ most is at larger spatial scales. In Fig. 1.6 we show the expected curves (again, for each point source, $Q = 1000$ seeds; $x_m = 40$ m) for an area source (an array of individual conspecific sources of extent $\gg x_m^2$). In this case, the plants were uniformly distributed across a rectangle $4 \times 2$ km abutting an area with no conspecific sources; $x = 0$ marks the edge of the area source with increasing $x$ as we sample further from the source. With a spacing ($S$) of 1 plant per $10 \times 10$ m contiguous cell (and the seeds located at a single point in the middle of that cell), we have a deposited seed density of 10 seeds m$^{-2}$ ($10 = QN_D$ where $N_D$, as in equation (1.3), is the individual source density ($1/S^2$)) well within the area source. This density declines slowly to 5 m$^{-2}$, i.e. half of $QN_D$, at $x = 0$. It subsequently declines more rapidly from $x = 0$ to $x = 200$. Only the log-normal and 2Dt permit appreciable dispersal at this scale.

Empirical studies of greater distances than 200 m for wind-dispersed trees abutting clearings are rare; the few available examples are shown in Fig. 1.7. The flattening hinted at in Fig. 1.6 is confirmed; at larger distances there is a remarkable reduction in the rate of decline of seed deposition. Of the models presented in Table