Refining, testing and evaluating spatially explicit models for wind dispersed plants

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Abstract

Refining, testing and evaluating spatially explicit models for wind dispersed plants

Catherine Calogeropoulos, Ph.D.

Concordia University, 2005.

Dispersal is the process by which plants expand their range and explore new habitats. When local habitats become inhospitable, dispersal ability becomes the key mechanism allowing species to evade extinction. Despite the efforts in obtaining empirical dispersal curves and developing sophisticated spatial models, the main issue that remains unresolved is that of scale. Although predictions at the local scale are better than those aiming to describe dispersal at greater distances, they remain too unrealistic to be used in subsequent models that govern growth, mortality and resource exploitation. My first chapter aims to improve predictions at the local scale by refining the parameters of a spatially explicit model. I determined the effect of substituting basal area for cone production as a proxy for seed output. The results showed that the r^2 from the regression of predicted versus observed densities increased by 5% for seeds and 15% for seedling simulations. Next, I determined the effects of allowing the horizontal wind speeds to vary. The results showed that correlations of observed vs. predicted recruitment are a function of the assumed meteorological conditions used to drive them. My second chapter tested the ability of inverse modeling to predict recruitment both at the stand level and beyond. Using the maternally derived DNA from seed coats of the North American tree species *Pinus strobus*, I compared the most common approach (inverse modeling) with the newer but far more time-consuming method of using microsatellite markers. I showed that inverse modeling grossly underestimates seed dispersal potential in this species and thus caution against its continued use. With the aim to improve spatial models, this thesis would not be complete without an examination of the role of wind on seed abscission –the precursor to dispersal. Previous attempts to link the probability of abscission with meteorological phenomena were set within averaging times that exceeded the time frame of seed abscission (<1 second) by at least 15 times. Using 1-minute averaging times, I showed that seed release, for the wind dispersed tropical tree *Ceiba aesculifolia*, is proportional to the square of the horizontal wind speeds. Furthermore, the data showed that this relationship is highly time sensitive where a correlation is no longer evident at averaging times exceeding 25-minute intervals. This thesis is concluded by showing that updrafts are much more effective at causing seed release than all other wind directions (i.e. downdrafts and horizontal). What it can not show, however, is the frequency of upward abscission events within a forest environment and how these results can be implemented within spatially explicit models that predict the dispersal potential of seeds traveling horizontally or vertically. Indeed, this can be addressed in future work.

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General Introduction

The concept of the metapopulation was formulated with the objective of uncovering the mechanisms responsible for the spatio-temporal complexity of plant and animal populations (Levins 1969). Over the past two decades, metapopulation dynamics have been of increasing interest in ecology. This trend is primarily because of habitat loss (Hanski 1998) in addition to threats on global biodiversity driven by climate change through the spreading of invasive species (Kot et al. 1996; Higgins et al. 1996; Smith et al. 2000) and range shifts under an already highly fragmented landscape (Honnay et al. 2002; Kareiva and Wennergren 1995; Pitelka 1997).

A metapopulation is defined as a network of populations that are geographically or temporally separated, but linked together through a balance of local extinction and recolonization. The resilience of a metapopulation depends on the local and regional patch dynamics (i.e. the local vs. the network of patches). The dynamics of interest at the local scale include fecundity, mortality and resource availability (e.g. nutrition, mates). The key process operating at the regional scale is the migration rate of individuals, their predators (Prakash and de Roos 2002) and competitors (Namba and Hashimoto 2004) between the occupied and unoccupied patches of the metapopulation. Together the intra- and inter-patch dynamics determine the rate at which species randomly walk toward extinction.

Migration, or dispersal in the case of plants, connects the spatially disjunct patches of a metapopulation. Unlike most animals, plants are sessile organisms whose local patch dynamics are easily investigated—at least at short time scales. The regional population dynamics, however, require data on dispersal potential and therein lies the challenge.

Plant diaspores can be dispersed by abiotic or animal vectors. Abiotic vectors consist of wind (anemochory) and water (hydrochory), or some propulsive mechanism within the fruit. Animal agents are varied but their dispersal mechanism can be dichotomized as ingestion (endozoochory or caching) or external adhesion/clutching (ectozoochory). Globally, the three most common vectors are these latter two plus wind (van der Pijl 1969). Modeling the dispersal potential of seeds ingested (Murray 1988; Hickey et al. 1999) or carried externally by animals (Kiviniemi and Telenius 1998) requires data on the animals' rates of movement (foraging at a short time scale but migration at a somewhat larger time scale) and passage times of seeds through alimentary tracts or duration before the seed falls off the fur or feathers. Modeling the trajectory of wind dispersed seeds has different but equally challenging data requirements (reviewed below). Despite the challenges, research in dispersal (broadly defined; not just of seeds) has risen 30-fold over the past 3 decades (Nathan 2003) with over 10 reviews written on seed dispersal alone (e.g. Cain et al. 2000; Nathan and Muller-Landau 2000; Greene and Calogeropoulos 2001; Wang and Smith 2002; Nathan et al. 2003) .

The focus of my thesis is to refine, evaluate and validate the current methods used to describe and model the dispersal of seeds by wind. I examine the performance of our present spatially explicit models using a field data set from northern Québec (Chapter 1), compare the results from inverse modeling techniques with the more trustworthy data from molecular techniques (Chapter 2), and conclude by examining the role of wind in seed abscission –the precursor to dispersal (Chapter 3).

The empirical approach to seed dispersal

Until about 1985, seed dispersal research was highly descriptive. Initially, emphasis was on categorizing dispersal types based on obvious structural characteristics: e.g. wings (wind dispersal) or nutritious pericarp (endozoochory) (Ridley 1930; van der Pijl 1969; Venable and Levin 1983; Gautier-Hion et al. 1985). By the 1950s we began to see the first people empirically describing dispersal curves (deposited seed density vs. distance). These dispersal curves were from isolated trees in open fields (Woodall 1982; Forb et al. 1983; Zasada and Lovig 1983) or from seeding edges dispersing into open areas (Pickford 1929; Garmans 1951; Isaac 1953; Cremer 1966; Gashwiler 1969; Mair 1971; Franklin and Smith 1974). Invariably, the distances described were quite short – typically less than 10 m for herbs or 100 m for trees.

The contiguous distribution of plants in space has made it exceedingly difficult, especially in the species-poor regions outside the tropics, to find a reproductively mature tree more than 300 m from another reproductively mature conspecifics tree. Consequently, there were far fewer studies that investigated dispersal from solitary trees within an intact forest (Rudis et al. 1978; Augspurger and Hogan 1983; Augspurger 1983). Those data sets, however, suffer from insufficient sampling intensity and are biased toward describing short distance dispersal. Finally there are no delineated dispersal curves from a group of conspecific trees within the same forest. The problem was, and remains, that trapping seeds or examining seedlings within intact forests leads to problems in disentangling overlapping dispersal curves. Ultimately, one has a recruit and does not know which maternal parent sponsored it.

There is little doubt that the next array of empirical dispersal curves to appear in the literature will be obtained through molecular markers. Techniques developed in molecular biology now enable us to side-step the problem of overlapping dispersal curves by assigning maternity to all seeds retrieved within a forest with multiple seed sources.

The new empirical approach: molecular markers

At present, the markers most capable of identifying parentage are microsatellites. Microsatellites are composed of highly repeated tandem sequences of di- tri- or tetra-nucleotides. Changes in allelic states (i.e. mutations) are caused by polymerase slippage during DNA replication, resulting in insertions and/or deletions of these tandem nucleotide sequences (Schlotterer and Tautz 1992). This high mutation rate ($\approx 10^{-2} - 10^{-5}$ per haploid genome per generation) (Dallas 1992; Weber and Wong 1993; Dib et al. 1996), gives rise to the wide range of scorable alleles per locus (2-50 alleles) that allows for parent-offspring identification.

In addition to being highly polymorphic, microsatellites are ideal molecular markers for dispersal research because they are: (1) neutral markers (i.e. not under selective pressures), (2) codominant (i.e. homozygous and heterozygous pairs are distinguishable) and (3) easily scorable (i.e. the number of base pairs per allele per locus are easily determined). All these attributes make them far superior to other available markers (e.g. allozymes, restriction fragment length polymorphism (RFLP), randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP) and minisatellites).

Microsatellites have greatly improved dispersal research but this benefit has been restricted to pollen-mediated dispersal studies (e.g. Dow and Ashley 1998; Chase et al.

1996). Seed dispersal has been neglected because of the difficulty in isolating the maternal origin when both parental units are unknown. This limitation was lifted by genotyping the maternally derived seed tissue (Godoy and Jordano 2001). This technique is used in chapter 2 to fully delineate the dispersal curve and test the current inverse modeling approach (described below).

The modeling approach

Despite the promise held by molecular markers, even an exhaustive list of species with fully delineated dispersal curves can not shed light on the driving mechanisms behind seed dispersal. The ultimate goal in dispersal ecology is to obtain a model that describes the potential for dispersal between species and across environments and can be, ultimately, implemented within metapopulation models.

The expression of any dispersal curve includes an estimate on (1) fecundity (α) and (2) the dispersal function ($f(x)$). Below, I introduce the three most common dispersal functions used in the literature and within my thesis. Each model below takes a different approach to modeling recruitment but treats fecundity similarly. For simplicity, I denote all fecundity estimates as α.

Fecundity (α)

Seed production is invariably related to tree diameter. The relationship is generally expressed as: $Q = aB^b$, where Q and B are seed production and basal area, respectively (Greene and Johnson 1994; Clark et al. 1994). Typically the exponent (b) fitted on the relationship is about 1. Although generally accepted, and used, the omission of the variation that surrounds the slope causes an underprediction of at least some of the variation in seed deposition on the ground. The extent at which this expression limits the predictive potential of dispersal models is tested in Chapter 1.

The dispersal function (*f*(x))

2-parameter Weibull

The Weibull is a statistical function. It owns its popularity to its ability to adopt various forms through the parameterization of one, two or three of its shape parameters. This statistical function is commonly used, usually in a three-parameter form, in modeling survival data in biological systems (e.g. Gavrilov and Gavrilova, 2001) and for modeling failure rates in a host of other fields (e.g. engineering). Since 1994 the 2-parameter Weibull function (eq. 1) found a place in dispersal ecology when it was introduced by Ribbens et al. (1994):

$$\alpha * [(\exp\text{-}Dx^{\theta})/n] \qquad (1)$$

where, x is the distance from the source plant. D and θ are the shape parameters that govern the shape of the curve. To give some idea of the flexibility of this function, when the shape parameter θ equals 2.0, we obtain the "right" half of a Gaussian curve. At $\theta = 1$ the Weibull becomes a negative exponential. The value most frequently used, $\theta = 3$ (Ribbens et al, 1994; Lepage et al 2000), predicts a much flattened dispersal curve that declines suddenly at some distance set by the scale parameter, D. Finally, n is the normalizer which converts the equation into a probability distribution: i.e. the summation of equation (1) (but lacking 1/n outside the exponential term) multiplied by $2\pi x$ would give us n rather than 1.0. The first limitation of this function is its thin tail—it can not be used (or modified) for dispersal at the landscape level (metapopulations); substantial numbers of seeds cannot travel say 100 m from a tree without using a very low value of

θ, but there is no evidence for such dramatically concave curves in the empirical literature (Greene and Calogeropoulos 2001). A second major constraint is its inability to be adapted for modeling dispersal in other environments (e.g. clearcuts) simply because it can not incorporate variable wind conditions or forest canopy heights.

2D*t*

The 2D*t* is the second statistical model I included (Chapter 2) (*sensu* Clark et al. 1999). It is a two-dimensional version of Student's *t* distribution,

$$\alpha * p/ [\pi u(1+(x^2/u)^{p+1}] \qquad (2)$$

where p and u are shape and scaling parameters, respectively and x is the distance from the source plant. As p gets large the distribution becomes Gaussian. The parameter u gives the potential for long distance events to occur. Increasing u fattens the tail of the dispersal curve. Relative to all other models (in my thesis and beyond) it has the greatest potential of predicting long distance dispersal events.

Lognormal

The lognormal (*sensu* Greene and Johnson 1989) (described at length in Chapter 1) is the most commonly used mechanistic model in the literature (e.g. Tanaka et al.1998, Stewart et al. 1998, Tackenberg 2003) and the only one I include.

$$\alpha * [(2\pi)^{1.5}\sigma_{\ln x}x^2]^{-1} \exp [-(0.5/\sigma^2_{\ln x}) (\ln(x/x_{0.5}))^2] \qquad (3)$$

where, x is the distance from the source plant, $x_{0.5}$ is the median dispersal distance and $\sigma_{\ln x}$ is the standard deviation of the logarithms of the distances traveled. The appeal of this function over others is its ability to include the stochastic nature of meteorological conditions, especially of horizontal winds. The shape parameter, $x_{0.5}$, is directly proportional to horizontal wind speed. This attribute is critical when attempting to link meteorological condition to a species dispersal potential (Chapter 1). The scaling parameter $\sigma_{\ln x}$, determines the mode of the dispersal curve.

The main disadvantage of the model is that vertical winds are inadequately considered. Greene and Johnson (1996) suggested sequentially adding the effect of vertical winds by recalculating eq. 3 repeatedly to include the effect of different vertical winds. The main problems then become (1) the model is no longer simple, and (2) it cannot deal with the fraction of the seeds whose terminal velocity is less than a very strong updraft. The modeling approach therefore falsely assumes closure, by including only updrafts that do not exceed a seed's terminal velocity. While closed-form solutions that seriously include vertical turbulence exist (Okubo and Levin 1989; Soons et al. 2004), they are far too complicated to be parameterized as part of an inverse modeling exercise.

The inverse modeling approach

The dispersal functions just described model seed dispersal through the classic forward approach to problem solving. Beginning with a predefined set of conditions (e.g. fecundity, location, etc.), predictions are made on the density of seeds deposited at various distances. Inverse modeling begins with a set of results and produces estimates on the set of conditions that maximize the probability of obtaining a similar set of observations. Thus, as the name implies, inverse modeling is the backward approach to problem solving. The method, introduced to dispersal ecology by Ribbens et al. (1994) and subsequently used by others (Clark et al. 1999; Lepage et al. 2000), is regarded as a powerful methodology for modeling seed dispersal in intact forests. But, this solution to the empirical dilemma of overlapping dispersal curves has yet to be properly tested because such a test requires that we can know unambiguously which seeds came from which plants in a stand with overlapping dispersal curves. My second chapter tests the capacity of inverse modeling to delineate dispersal curves. I test this theory using the newer approach of molecular markers. Using the seed coat of *Pinus strobus* seeds obtained from Mont St-Hilaire, Quebec, I obtain a full delineated dispersal curve to compare with the predicted curves derived via inverse modeling.

The purpose of my thesis is to improve upon our current ability to predict seed dispersal. This would not be complete without a deeper understanding of the role of wind on seed abscission. In the literature, the dispersal potential of the wind once the seed is in motion has received a great deal more attention than the effect of wind on abscission. Establishing the link between the abscission probability and ambient wind speed requires quantitative data on a number of meteorological parameters as well as a censusing technique for the seeds, and all these measures must be made at the shortest averaging time (sampling interval) possible. The limit has been set by the difficulty of making rapid censuses over sustained periods. Greene and Johnson (1992) bypassed the latter issue by dealing with a species (*Acer saccharinum*) that completed its abscission schedule in only a few days, but at best they could sample the seed population in a time no less than 15 minutes. This time scale is far too gross relative to the time scale of abscission (less than a second); all other studies have used time scales of 24 hours or even weeks. In chapter 3, I solve the censusing issue by filming the abscission process in the wind-dispersed tropical tree, *Ceiba aesculifolia*; while simultaneously collecting high-frequency meteorological data. I tested the effects of averaging times on predicting abscission probabilities and also examine the role of vertical turbulence in seed abscission probability.

Chapter 1. Refining tree recruitment models

Introduction

Recently, the field of ecology has seen a shift from research seeking to describe patterns and generalities to a science seeking to develop simulation models that express these underlying processes. These simulations couple life history arguments (e.g. recruitment, subsequent growth, competition and death) as subroutines. A spatially-explicit tree recruitment subroutine (e.g. Lepage et al. 2000) is of the form:

$$F_{Dx,y} = \lambda B S_{x,y} f(x) \qquad (1)$$

where $F_{Dx,y}$ is the density of seedlings in Cartesian space, B is the basal area (m^2) of the source tree with the coefficient λ scaling the relationship between basal area and seed production, $S_{x,y}$ is the expected survivorship during the establishment phase (a function primarily of seedbeds and granivory), and $f(x)$ is the dispersal term. It is assumed that the exponent on B (omitted here for simplicity) is about 1.0 (Greene and Johnson 1994; Clark et al. 1994) but the literature is far too sparse to warrant confidence.

The recruitment subroutine subsequently passes the established seedling density on to subroutines governing growth, light, and thinning-induced mortality (e.g. Pacala et al. 1996). However, a problem that has not been remarked upon involves the coefficient of variation in seedling density. Competition for light declines with distance between competitors and yet existing recruitment subroutines (eq. 1) tend to homogenize density at small scales (i.e. predict a monoculture). For example, Ribbens et al. (1994) predict a relatively uniform distribution of recruits of *Acer saccharum* with a coefficient of variation (CV) of 0.33 despite the clumped distribution of the observed recruitment

(CV=0.91). Clearly, with two or more competing species in a system, it matters greatly in the subsequent dynamics if all species are found everywhere versus a more clumped distribution where, most cogently, the inferior competitor can occasionally establish in areas (say a few m^2 in extent) that contain no recruits from more competitive species.

Two of the important sources of homogenization arising in present approaches to eq. 1 involve the terms λB (the source strength term) and $f(x)$ (the dispersal term). There are a number of problems with the source strength term (e.g. the assumption that light receipt is unimportant and thus a small tree at the edge of a gap would produce fewer seeds than a large subcanopy stem within an intact stand). Here, we merely point out that although basal area may well be our single best predictor of seed production for a species (cf. Greene and Johnson 1994), nonetheless, the proportion of variation explained is typically only on the order of 0.5 (e.g. Greene and Johnson 1999; Greene et al. 2002). Our first objective is to show that accounting for this unexplained variation in seed production will indeed increase the expected CV of predicted seed or seedling density in a non-trivial manner, and, further, lead to a higher correlation for observed vs. predicted recruit density.

Our second objective is to examine the effect of the dispersal term ($f(x)$) on the predicted CV. There are three possible sources enhancing the homogenization of the predicted recruitment. The first factor is the assumption that wind direction can be ignored: that is, an annulus around a tree is expected to have a constant density of seeds. Of course, however, wind speed azimuthal distributions are never random or uniform. Further, a number of studies have shown that seed abscission by conifers and hardwoods is much more likely when relative humidity is low; in turn, relative humidity typically shows an azimuthal bias (e.g. Harris 1969; Nathan et al. 2001). Not surprisingly, therefore, a few studies have shown that dispersal curves do indeed show strong azimuthal preferences (e.g. Tanaka et al. 1998; Stoyan and Wagner 2001).

A second dispersal-related factor promoting homogenization is the use of *f*(x) as a continuous function. In reality, most abscission events occur in a few brief episodes when relative humidity is low and wind speeds are high. For example, with a 15 minute averaging time, 2% of the dispersal season (defined arbitrarily as the time from the first to the 99th percentile of the cumulative distribution for abscission) accounted for 57% of all abscised seeds in *Acer saccharinum* (Greene and Johnson 1992) and 52% in *Taraxacum officinale* (Greene, unpublished data). Thus, rather than a smooth continuous function, actual one-dimensional dispersal curves should be much more poorly behaved.

The third factor is the choice of *f*(x) itself. To take an extreme example, Ribbens et al. (1994) and Lepage et al. (2000) used an exponential function with distance taken to the power three. This results in a dispersal curve (density versus distance) that is virtually flat out to about the mean dispersal distance, and then subsequently declines quite rapidly. Now, if the mean distance between source trees is less than the mean dispersal distance (quite likely given that recruit sample size considerations will encourage one to work with a high density of conspecific trees), then we predict a very small CV (e.g. Ribbens et al. 1994).

Strangely, given the growing prominence of stand dynamics simulators with spatially-explicit recruitment subroutines, the issue of the underprediction of the observed CV has not been examined. In this paper we look only at the effects of λB and *f*(x), holding the role of seedbeds (a prime determinant of juvenile survivorship in eq. 1) relatively constant by examining only mineral soil seedbeds.

Methods

Study area

The southern boreal forest study site was located in western Quebec in the Abitibi Temiscamingue region (79° W, 48° N) on the south shore of Lac Duparquet. Soils are post-glacial lacustrine clays. The forest originated from a 1916 fire about 100 ha in size. Bergeron and Charron (1994) provide a detailed description of the long-term dynamics at this site via stand reconstruction. The forest is presently dominated by aspen (*Populus tremuloides*) with a large amount of post-1916 conifer understory comprised primarily of balsam fir (*Abies balsamea*) with small numbers of white spruce (*Picea glauca*) and eastern white cedar (*Thuja occidentalis*). The site was chosen because it is bisected by a 530 m long, 3 m wide bladed path created in 1992 by a mining company. This path, initially mineral soil, is now covered by a thick deposit of leaf litter from the adjacent aspen and colonizing herbs. Ring counts on samples (n=30) of fir seedlings found on the path showed that more than 90% of the recruitment occurred in the period 1993-1996 when there was presumably a great deal of exposed mineral soil remaining. Further, the majority of these aged seedlings were from the two years 1994 and 1996, corresponding to measured mast years (1993 and 1995 respectively) in the study of Raymond (1998) 500 km to the east of our site.

As shown in Fig. 1.1, the site is bordered on one side by the 1717 forest. In the 1717 forest, the tall canopy fir was removed in the early 1980s by a budworm epidemic.

These older stands are now dominated by cedar with some white spruce and aspen. Thus, only the subcanopy fir can presently act as seed sources.

Data Collection

For 40 m to either side of the path, within the lakeside and 1717 forest (Fig. 1.1), we measured the basal area and Cartesian coordinants of every conifer stem taller than 3 m (n =384). In 1998, the number of ovulate cones for every fir stem on our site was counted with binoculars (n = 9294 cones). Only the visible portion of the canopy was counted for cones. The values were then multiplied by 1.5 to account for the nonvisible portion. Franklin (1968) argued that this method gives a reasonable estimate of the number of cones per tree. An estimate of 25 filled seeds per cone for fir was obtained from a companion study (Greene et al. 2002) using some recently cut stems about 30 km from the study site.

In 1998 along the 530-m length of the path within the 1916 forest, we counted the number of fir seedlings every 10 m in 1 m radius circular plots (n = 305). As mentioned previously, these were mainly from the years 1994 and 1996. In the spring of 1999 we counted the number of filled fir seeds (derived from the enumerated 1998 cone crop) in these same plots (n = 792). The mean hourly wind speeds (60-second averaging time, one recording each hour) were obtained from Environment Canada (reporting station at La Sarre, Que., about 50 km from Lake Duparquet) for the months of September and October between 1992 and 1999.

The data collected were used to generate dispersal curves from each tree within our sampled area. The summed contribution of seeds or seedlings was then used to generate the expected density of recruits every 10 m along the path.

Modeling

To reach our objectives, we adopted the lognormal dispersal function (Stewart et al. 1998; Greene et al. 1999; Tanaka et al. 1998). The lognormal has the advantage of being mechanistic, and can therefore easily be parameterized to account for the physical properties of the dispersing units and stochastic meteorological variables. When this $f(x)$ is multiplied by the number of seeds (or seedlings) produced per tree (Q) we have:

$$Q_{Dx} = [Q/(2\pi)^{1.5}\sigma_{\ln x}x^2] \exp(-(0.5/\sigma^2_{\ln x})(\ln(x/x_{0.5}))^2) \qquad (2)$$

where Q_{Dx} is seeds/m^2 at the distance x from a point on the path, $x_{0.5}$ is the median dispersal distance and $\sigma_{\ln x}$ is the standard deviation of the logarithms of the distances traveled.

In eq. 2 the median distance ($x_{.5}$) traveled by a seed is given by

$$x_{0.5} = \bar{u}_g \ \bar{z}_a / \bar{f} \qquad (3)$$

where $\bar{z}_a$ is the mean height (meters) at the time of abscission ($\bar{z}_a = 0.90 * z_h$, where z_h is the mean height of fir trees from this forest (7.47m)), $\bar{f}$ is the mean terminal velocity (m/sec = 0.85 for balsam fir according to Greene and Johnson, 2000), and $\bar{u}_g$ is the median horizontal wind speed (m/sec) averaged from z_a to the ground. The study site chosen for this modeling exercise was dominated by *Populus tremuloides*, a deciduous tree species. Previous modeling exercises using eq. 2 had been done in conifer-dominated forests. As such, leaf abscission and its effects on the drag experienced at the top of the canopy during the seed dispersal period have not been formally evaluated. Changing the wind speeds ($\bar{u}_g$) will directly influence the median distance at which seeds are deposited. For example, if we take the mean and standard deviation of the natural logarithms of the winds during the 1998 dispersal season, and assume dispersal to occur in a full canopy forest, then $\bar{u}_g = 0.116u_r$ m/sec (calculated using the protocol from Greene and Johnson 1996), where u_r is the measured median wind speed at 10 m at the meteorological reporting station in LaSarre in 1998. Conversely in a leafless canopy this horizontal wind speed is $0.358u_r$ m/sec.

The standard deviation of the logarithms of distances traveled ($\sigma_{\ln x}$) can be estimated (Greene et al, 1999) as

$$\sigma_{\ln x} = [(\sigma_w^2/f^2) + i_u^2]^{0.5} \qquad (4)$$

where σ_w is the standard deviation of the vertical wind speeds (we use the abscission-adjusted default value of Greene and Johnson (2000), σ_w=0.76), i_u is the horizontal turbulence (to be measured empirically using the airport data at La Sarre).

In the case of the 1998 seed crop of fir, our basal area measurements allow us to estimate Q in eq. 2 with the empirical value,

$$Q = (S_D / B_D)\, B(i) \qquad (5)$$

where S_D is the observed density of seeds (#/m^2) across the 530 m long bladed path, B_D is the mean basal area per area from the 1916 study site and B(i) is the basal area (m^2) measurements recorded for *i*th individual tree. For simulations involving seedlings, S_D in eq. 5 was replaced with F_D (the density of seedlings per m^2 across the path). Finally, for modeling seed and seedling dispersal using cone counts (as a predictor for productive output of individual trees), B_D and B(i) were replaced with Q_{CD} (density of cones/m^2 in the forest transect) and $Q_C(i)$ (number of cones on the *i*th individual tree) respectively. The estimated source strength here allows us to implicitly include the effect of mortality subsequent to abscission.

Modifications to the micrometeorological model

We used the empirical relative humidity data obtained from Environment Canada (reporting station at La Sarre, Quebec, about 50 km from Lac Duparquet) to examine the effect of this factor on the expected CV of seeds and seedlings. While we know there is a strong bias for abscission during low relative humidity (reviewed in Greene et al. 1999), there is no mechanical model we can appeal to. Arbitrarily then, we divided days into greater than or less than 50% relative humidity, and assumed that all seeds abscised only when the relative humidity was less than 50%. This generated a frequency distribution of eight azimuths, and seeds could only disperse along these azimuths with a frequency dictated by this distribution of low relative humidity. In short, we have, for each tree, applied the weighted one-dimensional model (eq. 2) eight times (eight azimuths). Our initial hypothesis for this exercise is that the bias due to relative humidity will be mild given that the overlapping curves will tend to cancel out any bias in dispersion from individual trees. We attempt it nonetheless so as to determine to what degree the omission of this element decreases fine scale variation.

A final source of fine scale variation is that of differential survivorship along the path. The present model does not account for seedbed-induced mortality differences, but can be explicitly modeled (e.g. Lepage et al. 2000). In our case, however, given that the seedbed from this site was held constant, we can ignore this source of variation as negligible.

Results and Discussion

The correlation between the 1998 cone density (cones/m^2) and basal area per area along the half kilometer path was significant ($r^2 = 0.47$; $p<0.001$), with the exponent and intercept of the power law regression calculated as 1.38 and 49.7, respectively. This exponent is significantly higher (t-test; $p<0.05$) than the implicit expectation of 1.0 (eq. 1). The sparse literature on seed production in relation to tree size indicates that the exponent varies anywhere from about 0.5 to 1.5 (Greene and Johnson 1994;1999; Greene et al. 2002). A small amount of the unexplained variation is due to differential light receipt (Greene et al. 2002) as some fir stems find themselves far from or near to gaps. Substituting basal area for cone production in the model led to a decline in the r^2 for the predicted distribution of seeds and seedlings, as well as to a large decline in the predicted CV (Table 1.1).

The median and the standard deviation of the natural logarithms of the horizontal wind speeds at the LaSarre reporting station were measured as 3.5m/sec and 0.34 m/sec, respectively, for the 1998 dispersal season. Thus, the median dispersal distance (from eq. 3) for full- and leafless-canopy forests for our study site was estimated as 3.2 and 9.9 m respectively. For the combined crop years 1993 and 1995 (responsible for virtually all the seedlings on the path), the median wind speed at the reporting station was very similar (3.3 m/sec) and thus the two extreme median distances traveled are likewise similar (3.5m (full leaf) and 10.7m (leafless)). The standard deviation of the natural logarithms of the horizontal wind speeds was 0.44 m/sec.

Figure 1.2 shows the results of the regression analyses (predicted on observed deposited seed densities) using a range of $x_{0.5}$ values based on either cones or its proxy, basal area. The results are shown for median distances ranging from 3 to 20m where all of the regressions performed were significant ($p<0.001$). The best r^2 for the 1999 deposited seed densities was for a median distance of 7 m (using cones) and 8 m (using basal area). That is, on average it would appear that the 1998 seeds mainly abscised when about half of the aspen leaves have been removed. This would be roughly early October in our region.

For this range of median dispersal distances the simulations using cone data yielded higher coefficients of determination than our basal area measurements (Figure 1.2). This is not surprising given that basal area explains less than half the variation in cone production.

Prediction was better for the seedlings than the 1999 deposited seeds (Table 1.1). This may be because the seedling data includes two mast years (1993, 1995: Raymond, 1998) and, thus, may average out outliers from either year. As with seeds, the model with cones outperforms the model with basal area: the r^2 increases by about 15% (Fig. 1.3) for the seedlings. The most likely median distance (best r^2) is, however, slightly higher than when we modeled the 1998 seed dispersal, corresponding to the end of the aspen leaf abscission period (say, early November), where the r^2 peaks at 11m for cones and 10 m for basal area.

Most high latitude tree species abscise their seeds in the autumn over a period of a few months, typically September to early December for 90% of the seeds. Most hardwoods abscise their seeds somewhat earlier (September to early November). We cannot know the precise seed abscission schedules for the three mast years (1998, and the two years sponsoring most of the seedlings: 1993 and 1995), but seems likely, based on our results, that this may occur during the last half of the leaf abscission schedule. Indeed, future modeling in deciduous forest should attempt to include on-site empirical evidence on the timing on leaf and seed abscission.

A comparison between the observed and predicted coefficients of variation has not been previously attempted in the literature. The observed CV for our cone density measurements (total cones per 10 m section of the half-kilometer path) was 1.27 versus 0.56 for basal area/area. The observed CV values for seed and seedling densities across the path were 1.5 and 0.96 respectively. The predicted CV (corresponding to the highest r^2) using cones was 0.91 for seedlings and 1.08 for seeds (Table 1.1). By contrast, using basal area the CV values were predicted to be 0.64 for seedlings or 0.70 for seeds. Basal area is therefore not only a modest predictor of seed production (relative to using cones) but it is far less variable. Necessarily then, recruitment models as conventionally formulated (e.g. Clark et al. 1994; LePage et al. 2000) with basal area used as a proxy for female function will greatly underestimate the real CV of seeds or seedlings. A simple way to "restore" the variation for subsequent dynamics simulations would be to draw seed production values from a regression of seeds on basal area that predicts only about half the variance. In summary, using basal area rather than cones leads to a lower correlation and a much lower predicted CV.

Another feature to note in Table 1.1 is that the predicted CV declines as function of increasing median dispersal distances. This is not surprising: as the median distance increases, the seed rain (or seedling distribution) becomes more homogenous across the area.

When we modified the simple micrometeorological model to account for azimuthal bias due to low relative humidity, prediction did not improve (Table 1.1). Only at very short distances did we observe an increase in r^2. Figure 1.4 depicts the proportions of low and high relative humidity autumnal days. As expected, given the latitude, winds are primarily from the west, southwest, and northwest. Autumnal winds from the west and south are modestly drier than other azimuths. The effect may have been subdued because of overlapping dispersal curves where any bias due to azimuth or wind speed for a single tree is somewhat cancelled out by the same bias applied to neighboring trees. For coastal or montane environments where azimuthal biases in relative humidity are much more pronounced (e.g. Harris 1969), adequate modeling of seed dispersal will have to include this source of variation. But in most cases, azimuthal bias will not be an issue.

In conclusion, we have shown that the choice of median wind speed will alter the predictive capacity of the micrometeorological model. For deciduous forests the choice of the appropriate value will depend on the timing of the leaf abscission schedule as well as the seed abscission schedule. Furthermore, we have shown that the choice of parameter for expressing seed production (i.e. cones or the proxy basal area) will also affect the precision in the modeling. Cones invariably have more fine scale variation than basal area and thus using cones, as the predictor, will allow the coefficient of variation to increase. Future work can include forests stands with a more pronounced azimuthal bias (e.g. montane or coastal environments) so as to determine the effects of wind direction and relative humidity.

Table 1.1 Coefficients of determination (r^2) and coefficients of variation (CV) for simulations involving seed and seedling dispersion using (1) the simple micrometeorological model and (2) the model with azimuthal bias due to relative humidity.

	cones-seedlings				cones-seeds		BA-seedlings				BA-seeds	
$x_{0.5}$	r^2_1	r^2_2	cv_1	cv_2	r^2_1	r^2_2	r^2_1	r^2_2	cv_1	cv_2	r^2_1	r^2_2
3	0.33	0.31	1.76	1.58	0.36	0.46	0.3	0.25	1.09	1.05	0.29	0.36
4	0.41	0.38	1.46	1.4	0.43	0.48	0.35	0.3	0.92	0.94	0.35	0.39
5	0.48	0.44	1.28	1.26	0.47	0.48	0.39	0.34	0.87	0.86	0.39	0.41
6	0.53	0.49	1.16	1.17	0.48	0.48	0.41	0.38	0.79	0.8	0.42	0.42
7	0.57	0.52	1.08	1.09	0.49	0.47	0.43	0.4	0.74	0.75	0.43	0.42
8	0.59	0.55	1.02	1.04	0.48	0.46	0.44	0.42	0.7	0.71	0.44	0.42
9	0.61	0.57	0.97	0.99	0.47	0.45	0.45	0.42	0.67	0.68	0.43	0.41
10	0.61	0.58	0.94	0.95	0.45	0.43	0.45	0.43	0.64	0.66	0.43	0.4
11	0.62	0.59	0.91	0.92	0.44	0.42	0.45	0.43	0.62	0.64	0.42	0.39
12	0.62	0.6	0.89	0.89	0.43	0.41	0.44	0.43	0.61	0.62	0.41	0.38
13	0.61	0.6	0.87	0.87	0.41	0.4	0.44	0.42	0.59	0.61	0.4	0.37
14	0.61	0.6	0.85	0.85	0.4	0.39	0.43	0.42	0.58	0.59	0.39	0.36
15	0.6	0.6	0.83	0.83	0.39	0.38	0.42	0.41	0.57	0.58	0.38	0.35
16	0.6	0.59	0.82	0.81	0.38	0.37	0.41	0.4	0.56	0.57	0.37	0.34
17	0.59	0.59	0.8	0.8	0.37	0.36	0.41	0.4	0.55	0.56	0.36	0.33
18	0.59	0.58	0.79	0.79	0.36	0.35	0.4	0.39	0.54	0.56	0.35	0.32
19	0.58	0.58	0.78	0.77	0.36	0.34	0.39	0.38	0.54	0.55	0.34	0.32
20	0.57	0.57	0.77	0.76	0.35	0.33	0.38	0.37	0.53	0.54	0.33	0.31

Note: Results are presented for cone and basal area simulations

Figure 1.1 Schematic diagram of the location of the 1717 forest edge, lake edge and source trees (*A. balsamea*) within the 1916 forest. (Shaded band represents the 530m mineral soil path)

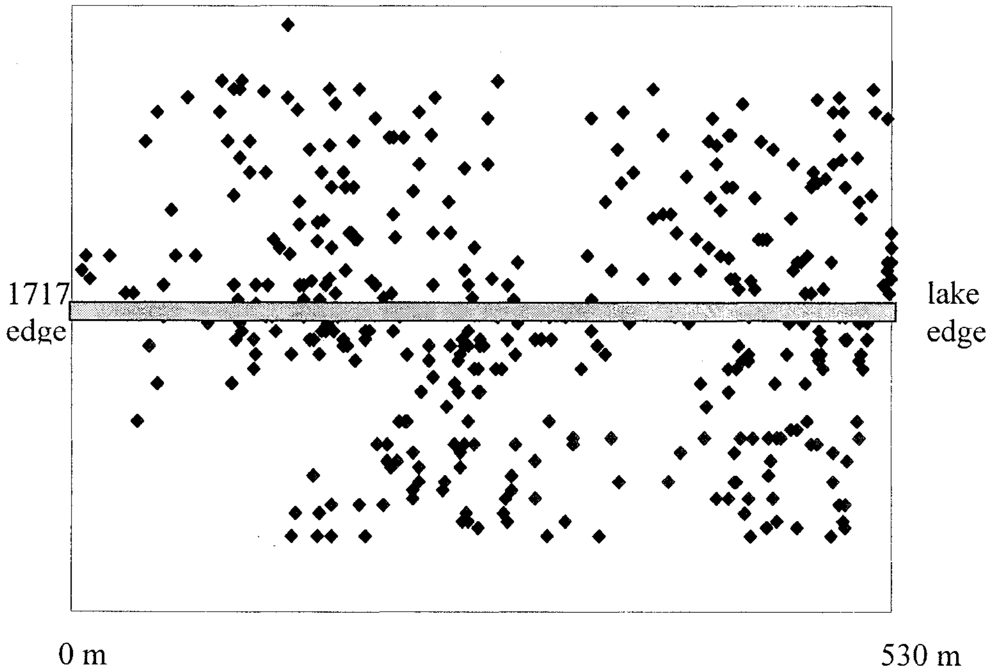

1717 edge
lake edge
0 m
530 m

Figure 1.2 R^2 (for regressions of predicted vs. observed densities) versus the median seed dispersal distance using cones (solid circles) or basal area (open circles) in the model.

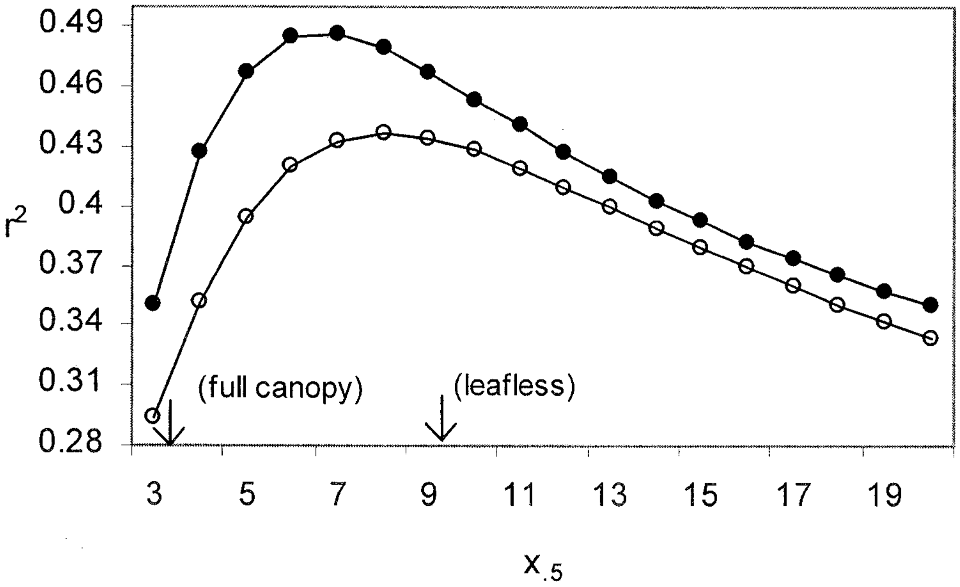

0.49
0.46
0.43
0.4
0.37
0.34
0.31
0.28
r²
(full canopy)
(leafless)
3
5
7
9
11
13
15
17
19
x.5

Figure 1.3 R^2 (for regressions of predicted vs. observed densities) versus the median seedling dispersal distance using cones (solid circles) or basal area (open circles) in the model.

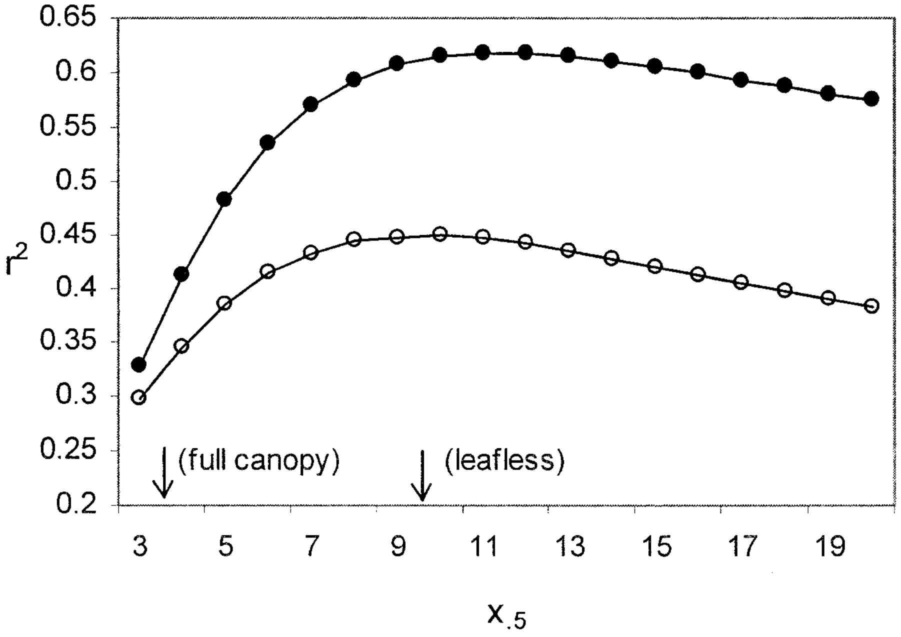
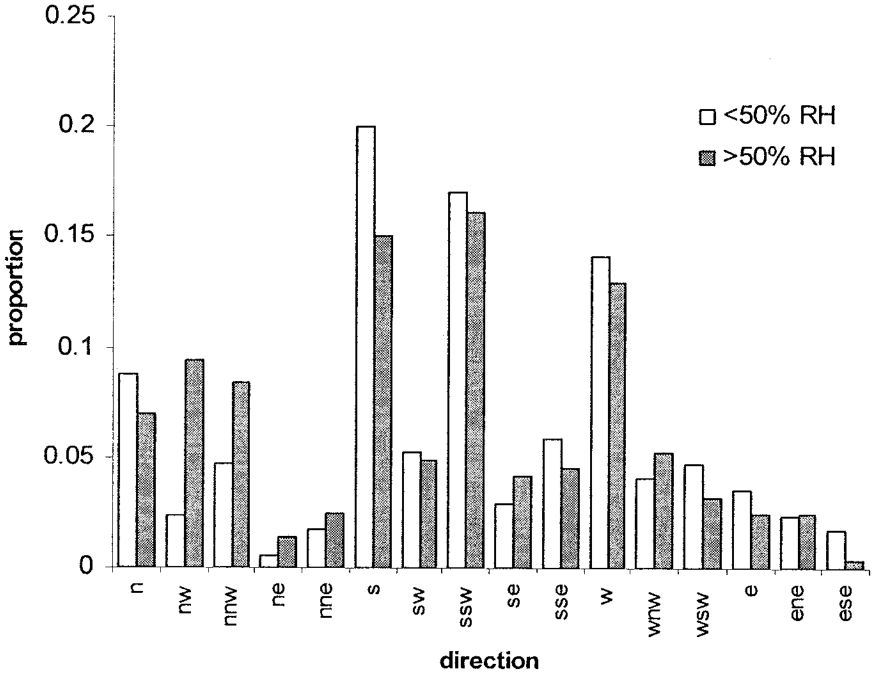

0.65
0.6
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0.2
r^2
(full canopy)
(leafless)
3
5
7
9
11
13
15
17
19
$x_{.5}$

Figure 1.4 Prevailing azimuths during periods of low and high relative humidity (RH).


0.25
0.2
0.15
0.1
0.05
0
proportion
□ <50% RH
▨ >50% RH
n
nw
nnw
ne
nne
s
sw
ssw
se
sse
w
wnw
wsw
e
ene
ese
direction

Chapter 2. Using molecular methods to test inverse modeling estimates of plant dispersal

Introduction

Ultimately the dispersal curve (number of seeds at distance x from a source plant) is a coupling of two terms: (1) a dispersal function that distributes across space (2) the seeds produced by the source plant (termed the *source strength*). While one can make estimates of the total seed number on a plant, there is no simple way to delineate the far tail of the dispersal function. If we work with a single plant or experimentally released seeds, the number of seeds *per area* quickly becomes small with increasing distance from the source, and so investigators may prematurely conclude that little dispersal occurs beyond the distance where zero densities proliferate. However, observed post-Holocene migrational velocities make clear that an appreciable amount of the average seed crop must be traveling a very great distance (Greene and Johnson 1995). Even for near dispersal, the empirical problem is muddied by the often contiguous distribution of conspecific trees: how do we understand the dispersal from a single tree when we cannot attribute a seed or seedling to any particular maternal parent?

In the last decade two approaches have been developed for interpreting overlapping dispersal curves from many conspecific source plants: inverse modeling (Ribbens et al. 1994) and molecular markers (Godoy and Jordano 2001). The inverse modeling approach is simple. Parameter values for both the dispersal and source strength functions are iteratively optimized as the congruence of the observed number of seeds (or seedlings) within each trap or quadrat (in Cartesian space) with the predicted number. This method is currently the most commonly used in plant ecology, offering a solution to the empirical dilemma of overlapping dispersal curves. But despite its widespread use, there has not been any rigorous testing of the approach, primarily reflecting a lack of alternative methods of attributing parentage.

The use of molecular markers for studying seed dispersal has just begun. To date, there have been a few studies using microsatellite markers for pollen dispersal (e.g. Chase et al. 1996; Dow and Ashley 1998). Also, the maternally-derived seed endocarp tissue has been used to infer maternity and delineate the dispersal profile for the animal-dispersed tree, *Prunus mahaleb* (Godoy and Jordano 2001). It should be noted that no study to date has made an attempt to alter the empirical distance data to account for differences in the density of the source tree. The main disadvantage of this approach is the time-consuming laboratory analysis. But clearly, if nothing else, this is the method to use to provide a yardstick for judging the accuracy of the dispersal curves derived through inverse modeling.

The goal of this paper is to use molecular data obtained from seed coat DNA of the tree species, *Pinus strobus* (the wind-dispersed white pine) to test the inverse modeling approach. In addition, we introduce a simple, yet necessary, measure to adjust the observed dispersal distances derived from the molecular approach to correct for the bias in the population density of trees that may or may not be present within any given distance class. For tests of the inverse modeling, we used the three most common two-parameter dispersal functions in the forest ecology literature: the 2Dt (Clark et al. 1999), two-parameter Weibull (Ribbens et al. 1994) and lognormal (Greene and Johnson 1989).

Methods

Study Site

The study was conducted at the Gault Nature Reserve on Mont St-Hilaire, located 35 kilometers southeast of Montreal (45° 32' N, 73° 09'W). This reserve is an old-growth mixed northern hardwood-coniferous forest. The dominant tree species are *Acer saccharum* and *Fagus grandifolia*. *Pinus strobus*, *P. resinosa* and *Tsuga canadensis* constitute the typically minor coniferous component.

Data collection

A 4 ha area rich in pines was surveyed and the spatial coordinates and diameter at 1.4 m height of all white pine source trees (n=96) were recorded. Twenty-five 1 m^2 seed traps with 1 m high walls were arrayed within a 1 ha area centered on the 4 ha area during the second week of September 2002, just as cones were beginning to open at the start of the abscission season. The sewn cloth traps were topped with metallic mesh to exclude seed-eating rodents and were emptied monthly from September to November 2002 and one final time in April 2003. Examination of the traps in April revealed that no rodent had chewed through the cloth; i.e. we can ignore seed predation. Tissue samples were from needles or cambium if needles were not within reach.

DNA extraction, amplification and genotyping

The mega-gametophyte and embryo were carefully separated from seed coats by making longitudinal cuts across the seeds and the interior was removed. DNA extraction for needle tissue samples involved crushing, with a rolling pin, the material inside a plastic bag with 3ml of Extraction Buffer. The cambium tissue samples were crushed, using a mortar and pestle, in liquid nitrogen and followed a previously published extraction procedure (Dayanandan et al. 1997). DNA was extractioned from seed coats by using the QIAGEN DNeasy® Plant Mini Kit.

Maternity was determined by comparing the multi-locus genotype of each seed with all potential candidates using the microsatellite markers of *Pinus strobus* developed by Echt et al. (1996). The loci selected were: RPS 12, 20, 39, 50, and 118b. We made slight modifications to the forward and reverse primers from Etch et al. (1996) for labeling purposes. We added a tail to all forward primers so that universal labelled primers could be used for labelling PCR products to be detected on an ABI 310 Genetic Analyzer. The universal labelled primers were M13FAM, M13HEX and M13TET each with a 19-nucleotide tail sequence (CAC GAC GTT GTA AAA CGA C). Furthermore, to minimize stutter bands, we modified the reverse primers by adding a small DNA sequence (GTTTCTT) (Brownstein et al.1996). We used an Applied Biosystems GeneAmp PCR System 9700 for DNA amplification using the previously published protocols of Echt et al. (1996). The amplified DNA was then genotyped across all 5 loci with an ABI 310 Genetic Analyzer.

Only seeds whose maternity could be assigned conclusively were used to create the dispersal profile. The seeds that did not match any of the genotyped source trees were assumed to have arrived from outside the perimeter of the study area. Any seeds with incomplete genotypes, or with several potential mothers within the first 60m of the dispersal profile were omitted.

Inverse modeling

The inverse modeling approach is based on maximizing the likelihood probability under an assumed Poisson distribution of seeds per trap. The parameters for both the dispersal and source strength terms (two in each case) are solved for by optimizing the congruence of the observed with the predicted number of seeds per trap. Data include the Cartesian coordinates of the source trees (n=96) and traps (n=25) within the 4 ha area.

The seed production term was aD^b, where D is tree diameter, and a and b are constants that scale the relationship and must be solved for. Given the low amount of variation in size for this shade-intolerant species, not surprisingly the exponent b approached 0 and can be ignored in what follows.

Data analysis for the genotyped seeds

We adjusted our dispersal observations to account for the aggregated distribution of white pine trees using the following argument:

$$Q_x = (w2\pi x N_{sx}/AN_{tx}) \qquad (1)$$

where Q_x is the adjusted number of seeds dispersing to an annulus of width w whose midpoint is x. N_{sx} is the total number of seeds in the traps at x, A is the area of a trap, and N_{tx} is the number of potential source trees at distance x from the traps. Note that a source tree can be counted n times if it is equidistant from n traps. Equation (1) is a general argument that should be applied in the future to all raw curves based on genetic analyses. This expression was used for each of the 12 classes (at 5m intervals) along the first 60 m of the dispersal curve. We calculated the fraction dispersing beyond 60 m as:

$$Q_{x>60m} = Q_T - \Sigma \{Q_{x(0\text{-}5m)} + \ldots + Q_{x(55\text{-}60m)}\} \qquad (2)$$

where, Q_T is the estimated mean seed production per tree. Tree seed production was estimated as:

$$Q_T = (N_{sD} / (N_{tD}) \qquad (3)$$

where N_{sD} is the density of all seeds from the traps we could successfully genotype, and N_{tD} is density of trees. The total number of seeds in equation (3) included those whose maternal origin was outside the genotyped perimeter under the assumption that our population lost an equivalent fraction of seeds dispersing outside the surveyed area.

Results

We collected 149 seeds from the seed traps, successfully genotyped the seed coats of 80, and estimated mean seed production (using eq. 3; see methods) as 1,366 seeds/tree. We determined the maternity (origin) for 61 seeds but the remaining 19 did not have a matching genotype from within the genotyped tree population (n=96) and must have come outside our 4 ha area. Of the 61 seeds whose maternity we determined, 2 came from a distance greater than 60 m within the nested 4 ha plot. Therefore, the molecular data lead to the estimate that 26% ((19+2)/80) of the seeds from the average tree traveled >60 m while our adjusted estimate (using eq. 2; see methods) increased this fraction to 50%. By contrast, predictions for the first half of the dispersal profile (0-60 m) were not affected as strongly by the transformation (Fig. 2.1).

We ran 2 separate simulations to estimate parameters for the three dispersal functions. The first inverse modeling exercise included only the seeds that were successfully genotyped (80 seeds) to allow a direct comparison with the adjusted dispersal distances. We see that the 2Dt and Weibull functions were able, roughly, to express the central tendency (mode or mean: Table 2.1) for the distribution of seeds per annulus at 15-20 m away from an average tree, but were unable to account for the 26 to 50% traveling more than 60 m (Fig. 2.1). The lognormal performed poorly, placing almost all seeds in a torus at about 110 m.

Previous tests of the inverse approach (using the two-parameter Weibull dispersal function) included simulations in replicate forests and omitting trap data for those species without replicate data sets (Ribbens et al. 1994). In both cases a statistically significant correlation with the observed data was maintained, with no change in the mean dispersal distance. The consistency of the dispersal curve was used (Ribbens et al. 1994) as evidence in support of the inverse modeling approach. To test the reproducibility with our data, our second simulation included all seeds collected during the season (n=149; Table 2.1). The lognormal now placed the mode very near the source, underpredicting the modal distance from Figure 2.1 by 3 times. The Weibull and 2Dt parameter estimates remained relatively unaffected by the addition of seeds. What we highlight here is that despite the consistency (Weibull and 2Dt) none of the models predict more than a tiny fraction of a percent of the seed crop will travel beyond 60 m (Fig. 2.2). (We still expect about 26 to 50% to exceed this distance based on the analysis with 80 seeds).

Discussion

The adjusted dispersal curve in Figure 2.1 is, to our knowledge, the first to be transformed to reflect the dispersal potential of each distance class investigated. We have shown that an appreciable fraction (26-50%) of the crop dispersed beyond 60 m. Although this distance hardly approximates long distance dispersal, it should be clear that inverse modeling is an untrustworthy approach to estimating the fraction of a crop that exceeds some modest distance, let alone allocating that fraction at various distances. Further, even if we are interested in near dispersal, inverse modeling cannot be trusted to get the magnitude of the deposit right: in this example far too much of the crop is allocated to nearby dispersal.

Why does inverse modeling perform so poorly? One reason is the problem of estimating the relative source strength of individual trees. Although tree diameter may well be the single best predictor of seed production within a species, it is still relatively poor (Calogeropoulos et al. 2003) with the r^2 values in allometric regressions of seed or fruit number on diameter for individual trees are typically in the range 0.5 to 0.3. Indeed, intra-annual variation in crop size within a population remains poorly understood. A second problem is that a non-trivial fraction of the seeds collide with the trunks of consepecifics (Greene et al. 2004) (or, in the case of birds and bats carrying seeds internally, can be defecated from the branches of conspecifics). The deposited seed or subsequent seedling is interpreted as having traveled a very short distance from the base of *that* tree. A third reason for problems is that the dispersal capacity estimates are always constrained by the lack of documented sources outside the sampled area. The tiny sampled area is explicitly an isolated island. These second and third arguments are likely explanations for under prediction by inverse modeling; we think it will turn out to be a general flaw. It seems to us that, until significant improvements are made to the inverse approach to better reflect the dispersal potential of plant populations, there is no choice but to switch to molecular markers.

Table 2.1. Observed (using microsatellites) and inverse modeling estimates of the median and modal dispersal distance based on (1) the 80 seeds genotyped and (2) the complete seed population (n=149).

		Lognormal		2D*t*		Weibull	
	Observed	1	2	1	2	1	2
median	46	112	3	20	15	10	10
mode	18	110	6	12	13	15	15

Figure 2.1. The predicted dispersal curves generated from inverse modeling using the 2Dt, Weibull and lognormal dispersal functions vs. the observed raw and adjusted empirical dispersal curves (n=80 seeds) for *Pinus strobus* on Mont- St-Hilaire, Québec.

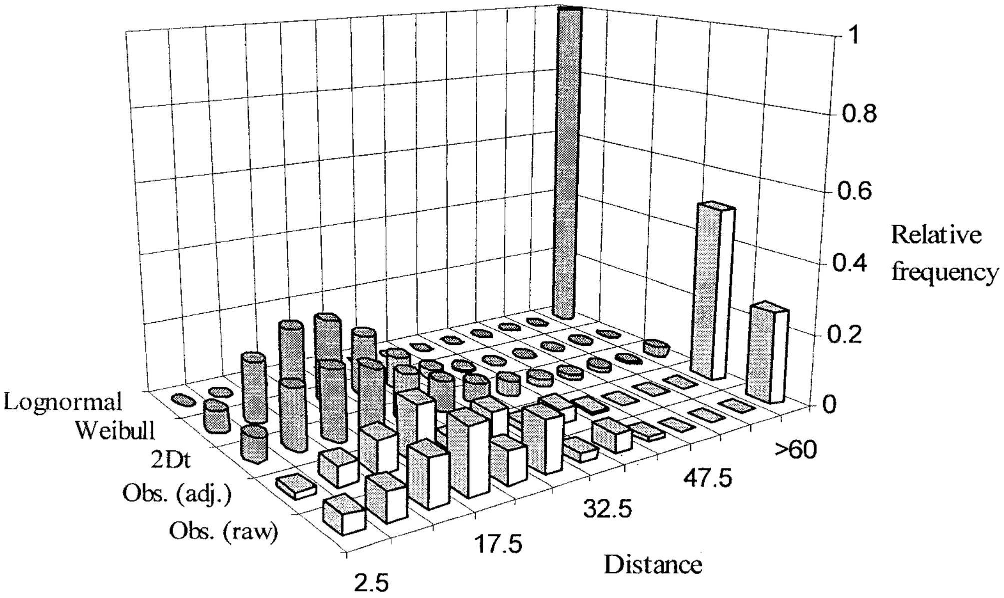
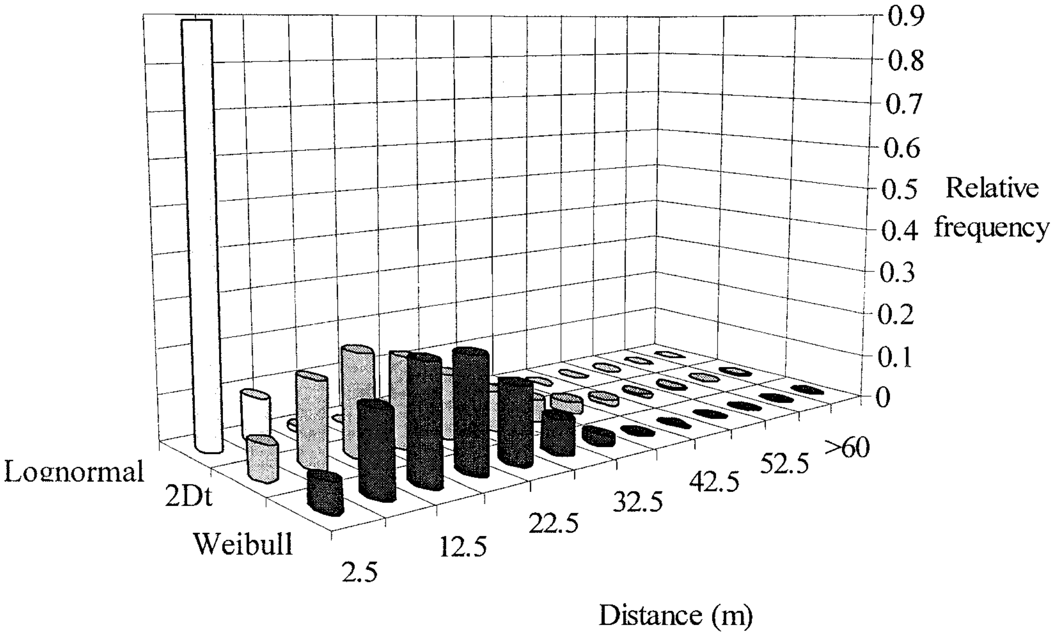

1
0.8
0.6
0.4
0.2
0
Relative frequency
Lognormal
Weibull
2Dt
Obs. (adj.)
Obs. (raw)
2.5
17.5
32.5
47.5
>60
Distance

Figure 2.2. The predicted dispersal curves generated from inverse modeling using the 2Dt, Weibull and lognormal dispersal functions based on the total population of trapped seeds (n=149 seeds).


0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Relative frequency
Lognormal
2Dt
Weibull
2.5
12.5
22.5
32.5
42.5
52.5
>60
Distance (m)

Chapter 3. The relationship between ambient winds and seed abscission potential

Introduction

The distance traveled by a dispersing seed is proportional to the height of abscission, the horizontal winds speeds and inversely proportional to a seed's terminal velocity (*f*) (Augspurger and Franson 1987, Greene and Johnson 1989). It is expected that variations in release heights within a population would have only negligible effects on the distances traveled. While we can expect some modest intraspecific variation in terminal velocities (coefficient of variation typically around 0.13*f* (Greene and Johnson 1992), Augspurger and Franson (1987) showed that wind speeds during the time of release can outweigh any reasonable variation in terminal velocities.

Evidence of seeds abscising at higher than average wind speeds is common in the literature (Mair 1971; Ford et al. 1983; Verkaar et al. 1983; Zasada and Lovig 1983; Morse and Schmitt 1985; Johnson 1988; Augspurger and Franson 1987; Jongejans and Schippers 1999), but coupling those observations with meteorological data within the same time frame (<1second) has been a major challenge. For example, Greene and Johnson (1992) reported the mean wind speeds and the corresponding abscission probabilities for *Acer saccharinum* over 15-minute intervals. While their data set extends over 3 dispersal seasons, the resolution of their meteorological data remains at least 15 times too high to predict a relationship that occurs within fractions of a seconds. Nevertheless, they modeled the relationship as a power-law function ($y=ax^b$) where abscission rates are proportional to the square of the horizontal wind turbulence (i.e. $b=2$).

The major methodological problem has not been anemometry but rather the difficulty of censusing abscission rates within short time intervals. Consequently, the relationship between wind speeds and a species' dispersal potential, rather than the abscission potential, has been more intensively studied. In particular, we know nothing about the probability of abscission in relation to updrafts even though rising winds, either as convective thermal uprisings in open grasslands (Tackenberg et al. 2003; Soons et al. 2004) or in the form of mechanical turbulence (Nathan et al. 2002), have been consensually identified as critical in long distance dispersal.

A solution to this logistical problem, to be adopted here, is to film abscission events while acquiring high-frequency meteorological data. The objectives of this study are (1) to establish a functional relationship that links the likelihood of abscission with high-frequency wind data, (2) to determine the effects of increasing the averaging time on this relationship and (3) to examine the abscission potential of vertical vs. horizontal winds.

Methods

Study species

We studied the relationship between seed abscission and the ambient wind conditions of the neotropical wind-dispersed species, *Ceiba aesculifolia*. This species, with a geographical range spanning from Mexico to the northern part of Costa Rica (Cascante-Marin 1997), includes individuals that can reach 20 m with typical diameters of 20–50 cm. Fruit development in *C. aesculifolia* is a two-year process with the bat-pollinated flowers blooming during the mid to late dry season (April - June). Fruits develop at the onset of the wet season and reach maturity before the start of the next dry season (December). Seed abscission begins in January, ending around April.

Unripe fruits are green, turning brown at maturity as the hard exocarp dries. At maturity the exocarp splits along four longitudinal dehiscence zones, exposing the underlying matted kapok fibers surrounding the seeds (Cascante-Marin 1997). The five separated exocarp sections (corresponding to the original five locules of the ovary) fall off as the mat of wet kapok fibers begins to dry. This drying process is greatly hastened by low relative humidity and especially direct exposure to the sun. The kapok fibers begin to push away from one another as they dry. A typical abscission event carries one seed surrounded by a roughly spherical bundle of curling fibers. Individual fibers are about 30 mm long but only about 30 microns in diameter. The bundle is sufficiently dense that it acts as solid body, impenetrable by the wind. The diaspore has a terminal velocity of about 0.95 m/sec (Greene and Quesada 2005). Prior to reaching a constant rate of descend, diaspores initially free fall at about 0.3 m/sec (Greene unpublished data).

Filming

In late February 2003, we selected 17 unripe (green) fruits from trees in the forests within 50 km of Chamela, in Jalisco Mexico. At maturity, fruits were suspended on the roof of a two-story house along a 1.2m wide by 2m high wooden frame. The frame held a maximum of 3 fruits at any one time, separated from each other by 25 cm to avoid collisions with one another by oscillating fruits. All fruits were suspended 1.6m above the roof. All abscission events (N=1,057, □x = 62 seeds/fruit) were captured on 2 video cameras placed 1m apart from each other on 1.3m high tripods. Both cameras were 1.7m away from the suspended fruits at approximately a 45° angle from the center of the suspension frame.

Replicating our experiment across space was not logistically possible. We therefore replicated across a temporal scale with 17 fruits over 4 days. Our experiment began at 8:00 hrs on March 15th, 2003 when three fruits were suspended along the wooden frame. Fruits were replaced immediately following abscission of the last seed. No fruits were suspended after 16:00 hrs, and filming was stopped after 19:00 hrs. Any fruit that did not completely abscise all its seeds within one day, was left suspended overnight, and recording of abscission resumed the following day. These fruits were not filmed but the night time meteorological conditions were recorded. Our experiment ended on March 19th, 2003 (excluding March 17th when no fruits were suspended).

Meteorological data

An anemometer (RM-Young 05103 Wind monitor, Campbell Scientific, USA), connected to a datalogger (CR10X model, Campbell Scientific, USA), was positioned 1.5 meters away from, and at the same height as, the suspended fruits. The datalogger was programmed to record the mean horizontal wind speeds ($\bar{u}$) and the maximum wind speeds ($\bar{u}_{max}$) at one-minute intervals (averaged across a 1-second interval). The time (hour, minutes and seconds) on both cameras was synchronized with that of the datalogger. We also obtained the minimum and maximum air temperatures during the four days of investigation from the meteorological station at the biological research station of UNAM located approximately 10km from our site.

Simulated wind experiment

Using 19 additional fruits, we tested the differential abscission potential of differing wind directions using an electrically powered fan. To greatly reduce the influence of ambient winds, this experiment was conducted in an empty swimming pool on the same property as the filming on the roof. The hub of the fan was positioned 40 cm either directly above, directly below or to the side of a drying fruit to simulate updrafts, downdrafts or horizontal winds, respectively. We subjected each fruit to a steady air flow lasting until all seeds were abscised or 5 min had elapsed. There were three possible fan settings with the lowest corresponding to a speed of about 2.7 m sec^{-1} at the constant distance used from hub to fruit. For each fruit, we would begin with a randomly-chosen speed (low, medium, high) and direction. If any seeds remained after 5 min we then switched to a different speed but maintained the same direction.

Data analyses

Abscission rates for any averaging time (constant sampling interval) were calculated as the ratio of the sum of all seeds abscising during the interval to the number of seeds available at the start of the interval, with this ratio then divided by the length of the interval (min). Our simulated wind experiments subjected each fruit to episodic wind conditions lasting a few minutes or less. We calculated the resulting abscission rates in the same way as above.

To determine the effects of time-averaged data on the relationship of wind speed with abscission rates (using power law regressions: $y = ax^b$), we calculated the mean wind speeds ($\bar{u}$) starting at 45-minute intervals down to 1-minute intervals. The number of fruits suspended on each day served as our replicates.

Results

The peak abscission period for all days investigated was between 10:00 hrs and 16:00 hrs, when 88% of the abscission events were recorded. Only 3.1% and 8.2% of the abscission events occurred in the morning (8:00-10:00 hrs) and during late afternoon/early evening hours (16:00-19:00 hrs), respectively. No abscission events were noted for fruits that remained suspended overnight (between 19:00-10:00 hrs) when $\bar{u}$ was only 0.35 m sec^{-1}. Thus, in what follows all our results reported are limited to those taken during the peak abscission period (10:00 – 16:00 hrs) and only for fruits whose kapok fibers appeared to be fully expanded as of 10:00 hrs.

There was a significant difference ($F=363$; $df=3$; $p<0.0001$) among days in the ambient wind speeds recorded (Table 3.1). A post-hoc Tukey test revealed that the horizontal wind speeds significantly dropped during days 3 & 4 of the experiment relative to days 1 & 2 ($p<0.003$) (Table 3.1). Counterintuitively, the mean abscission rates were lowest when the horizontal wind speeds were highest (days 1 and 2). This difference, however, was not significant ($\chi^2_{0.05,3}=0.0061$) because of the tremendous variation in abscission rates measured along 1-minute intervals. Despite the low sample sizes on days 1 and 2, the associated standard error remained low relative to days 3 & 4.

A major difference between the two periods was in the strength of vertical turbulence. Days 1 and 2 had only about 5% of the seeds uplifted but the last two days averaged 35% of the crop being uplifted. Given the strong differences in the results for the first and second half of the filming, we made separate analyses for each period.

Combining the data from days 1 and 2, we have 720 minutes of film data with corresponding meteorological conditions and 200 abscission events. All regressions calculated at averaging times between 45 and 25-minutes intervals had non-significant correlations between abscission rates and horizontal wind speeds. At averaging times less than 25 minutes we begin to see evidence of a positive correlation (Table 3.2), with 13 of these 25 regression slopes significantly different from zero. For these 13 significant correlations, the exponent on the power law relationship is significantly different only from the expected value of 2 at 16- and 1-minute averaging times.

The intercepts (α) were not affected by varying averaging times (Table 3.2), but the exponents (*b*) were significantly time sensitive (Figure 3.1). Using only slopes significantly different from 0, figure 1 shows that increasing averaging times significantly affects the value of the predicted slopes ($r^2=0.38$; $p= 0.02$).

Our second set of power-law regressions includes data only from days 3 and 4. All regressions beyond 15-minute averaging time intervals were not statistically significant. We plotted the slopes generated from 15, 10, 5, 2 and 1-minute averaging times (Figure 3.2). With the exception of 1-minute averaging times, none of the slopes were significantly different from zero.

Our final experiment examined the abscision potential in relation to vertical and horizontal winds. A one-way ANOVA performed on the arsine transformed abscission rates from the simulated wind experiment, showed a significant difference between wind vectors ($F=6.3$; $df=2$; $p=0.007$) (Table 3.3). Relative to downdrafts and horizontal winds, updrafts were much more effective in causing seed abscission (Tukey test; $p<0.019$). The same trend was observed with our roof experiment with a significant bias toward updrafts (t-test; $t=-3.89$; $df=34$; $p<0.0001$) (Table3.3) relative to the lumped abscision rates of horizontal and downward wind vectors.

Discussion

Despite the variation in ambient wind speeds observed among days, and the corresponding abscission rates, there was a clear indication of a peak abscission period occurring around mid-day. This pattern seems to be the same for most wind-dispersed species regardless of latitude (Kohlerman, 1950; Greene and Johnson 1992; Harris, 1969). There are at least two meteorological phenomena that influence abscission rates. The first is the horizontal wind speed and second the ambient relative humidity (Godman, 1953; Jemison and Korstian 1944). We can not speculate on what influence the relative humidity levels may have had on the sudden jump in abscission rates on days 3 and 4 when the horizontal wind speeds dropped significantly. We showed however that the maximum air temperature (occurring during peak abscission) fell by at least 3° and 6° on days 3 and 4, respectively. The presence, however, of strong vertical winds as indicated by the 28 % increase in uplifted seeds is a more likely explanation for the increase in abscission rates.

Using our data set from days 1 and 2 we saw a clear relationship between $\bar{u}$ and mean abscission rates beginning to form as the averaging interval (of the ambient wind speeds and abscission rates) fell below a 25-minute interval. Although our sample size was quite small, the advantage of more data (under a similar set of meteorological conditions) could be narrower confidence intervals and more significant correlations beyond 25-minute averaging times. However, Tackenberg et al. (2003) showed that even with a very large sample size a significant relationship can not be predicted when the averaging interval is 24 hours ($p=0.7$).

With two exceptions, all slopes from Table 3.2 are not significantly different from 2. The first exception, at 16-minute averaging times, can be ignored given that the relationship becomes increasingly blurred as a function of higher averaging times. The other exception is at a 1-minute interval where the slope is significantly less than 2, but this is also not significantly different from zero and therefore must be ignored. The data then support contention that the slope is proportional to the square of the horizontal wind speeds.

Over one-third of the seeds abscising on the third and forth day dispersed vertically up. Not surprisingly then, figure 3.2 indicates a complete lack in correlation between the horizontal wind speeds and abscission rates. Unfortunately, we can not speculate on the velocity of these vertical gusts and therefore a relationship between these vertical wind speeds and corresponding abscission rates can not be established.

When fruits were exposed to continuous air flow, on the roof and in the pool, updrafts were unmistakably more efficient at causing abscission, relative to horizontal winds and downdrafts. Given that our seeds initially free fall at a rate of 0.3m/sec (before reaching a constant rate of descend) we can at least speculate that our updrafts were at least greater than this value. The simulated updrafts, however, may have overestimated abscission potential because the rising air-flow from below splayed the locules open (like an umbrella) exposing the seeds within to the direct action of the air flow. Simulated downdrafts and horizontal winds however never placed the interior of the fruit in direct contact with the air current. The abscission potential of updrafts on the roof experiment (Table 3.3) should more closely resemble those that occur at the surface-layer of a forest canopy but, with a lesser frequency and intensity.

While the relationship of mean wind speed on seed abscission rates is more clearly understood, the relationship between updrafts and abscission remains much less obvious. Although we showed that updrafts are more efficient at causing seed release than all other wind directions, we still need to determine (1) the frequency of updrafts at the surface of a forest canopy that meet the minimum requirement to cause seed release, (2) once abscised (i.e. that last thread connecting the seed to the fruit is broken), if this minimum wind speed is enough to elevate the seeds beyond the canopy and (3) the frequency of updrafts that are capable of sustaining a seed's upward trajectory. Indeed this last factor is the most rare, but would give us a good estimate at the fraction of a seed crop (within a single dispersal season or generation) with the ability to be carried large distances.

Table 3.1. Summary of the meteorological conditions and seed abscission results between 10:00 - 16:00 hrs on four separate days.

Day	N $^{(1)}$	$\bar{u}$ $^{(2)}$	$\bar{u}_{max}$ $^{(3)}$	Minimum temperature (C°)	Maximum temperature (C°)	Σ of abscission events	Σ of seeds available	Mean abscission rate $^{(4)}$	Standard error of mean abscission rate	% of seeds uplifted
1	3	2.14^a	3.62 (± 0.88)	17	31	91	161	0.0018	$5.10X10^{-4}$	4.6
2	3	2.16^a	3.55 (±0.69)	13.5	30	108	117	0.0045	$1.49X10^{-3}$	4.8
3	9	1.13^b	2.78 (±1.08)	18	27	395	512	0.0096	$2.22X10^{-3}$	37
4	5	1.53^c	3.14 (±1.08)	13	25	262	267	0.0077	$2.18X10^{-3}$	33

NOTE: (1) N is the sum of all fruits suspended between 10am and 4pm; (2) $\bar{u}$ is the mean recorded wind speed (m sec^{-1}) averaged over 1-minute intervals between 10am-4pm. Letters assigned denote significant differences among days (ANOVA); (3) $\bar{u}_{max}$ is the mean maximum recorded wind speed over 1-second intervals. Data in parentheses are standard deviations; (4) Mean abscission rates are calculated as: Σ seeds abscising/Σ of seeds available/minutes elapsed since time suspended

Table 3.2. Power-law regression ($y=ax^b$) results for 25 averaging intervals for the relationship of wind speeds on seed abscission. All regressions results are based on abscission rates averaged across 7 wind-speed classes.

Averaging-time (minutes)	N	*b*	Confidence-interval for *b*	*a*	r^2
25	73	3.4	0.37-6.34	0.005	0.63*
24	76	3.65	-0.17-7.47	0.005	0.55
23	78	2.16	-0.8-5.12	0.013	0.41
22	82	4.02	-1.07-9.09	0.003	0.45
21	89	3.14	1.17-5.65	0.005	0.75*
20	92	2.39	0.42-4.37	0.01	0.66*
19	94	2.22	-0.23-4.68	0.01	0.52
18	103	3.66	-0.95-8.27	0.003	0.45
17	108	2.24	-2.77-7.25	0.006	0.21
16	115	4.87	2.29-7.45	0.001	0.82*
15	123	3.14	0.85-5.43	0.004	0.71*
14	130	4.05	0.57-7.50	0.002	0.64*
13	141	1.5	-1.6-4.82	0.013	0.24
12	156	4.53	0.91-8.15	0.001	0.67*
11	168	2.22	0.29-4.15	0.006	0.64*
10	186	1.91	-0.17-3.98	0.007	0.53
9	207	2.97	-0.25-6.19	0.003	0.53
8	233	2.76	-0.03-5.55	0.003	0.56
7	266	2.14	0.47-3.79	0.004	0.69*
6	313	2.11	0.002-4.23	0.004	0.56*
5	373	1.51	0.11-2.90	0.005	0.61*
4	469	2.28	-0.03-4.5	0.002	0.56
3	626	1.76	0.03-3.26	0.002	0.65*
2	939	1.94	0.57-2.05	0.003	0.55*
1	1881	0.26	-1.55-1.97	0.007	0.5

NOTE: *b* and *a* are regression slopes and intercepts, respectively.
* denotes a significant relationship ($p<0.05$)

Table 3.3. Abscission rates resulting from ambient winds or using a fan.

Source	Direction of wind	N fruits	Mean abscission rate	Standard error
fan	down	8	0.011	0.006
	lateral	10	0.028	0.009
	up	7	0.647	0.478
wind	down/lateral	18	0.014	0.005
	up	17	0.094	0.029

Figure 3.1. The relationship between averaging-time and the predicted slope (*b*) from the 13 significant power law regressions of abscission rate on wind speed ($y=ax^b$) for days 1 and 2 only.

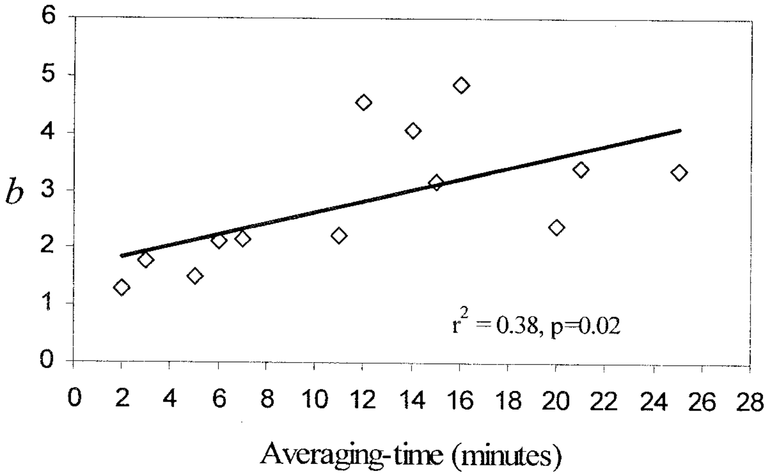
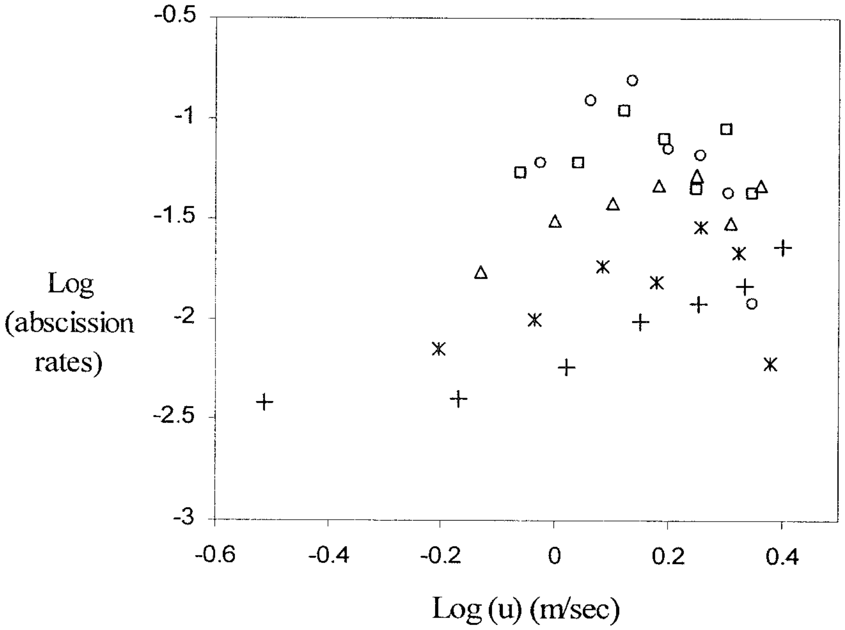

6
5
4
3
2
1
0
b
$r^2 = 0.38$, p=0.02
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Averaging-time (minutes)

Figure 3.2 The relationship between abscission probability vs. the ambient wind speeds across 15 (o), 10 (□), 5(△), 2(∗) and 1(+) minute averaging times for days 3 and 4 only.


-0.5
-1
-1.5
-2
-2.5
-3
Log (abscission rates)
-0.6
-0.4
-0.2
0
0.2
0.4
Log (u) (m/sec)

General Conclusion

The ability to disperse is a critical function in the life history of all organisms ranging from viruses to humans. The quest to describe dispersal curves, with respect to their shape and scale, is therefore a challenge not limited to plant ecologists. As I have shown throughout this thesis, current solutions to mapping seed and seedling dispersion are available. However, these are only approximate solutions that can be applied (with varying success) to model stand dynamics.

For example, in chapter 1 I tested the limits on a refined mechanistic dispersal function. I showed how modeling stand-level recruitment of seeds and seedlings can be improved by using cones to estimate seed production rather than tree basal area. The main conclusion drawn from chapter 1 is that choosing basal area, rather than cone production to infer fecundity, will compromise both the r^2 and the coefficient of variation. Of course, however, without new data, a simple refinement to any existing dispersal model is not enough to allow simulations to be performed at the level of a metapopulation.

The developments made in the area of molecular biology hold great promise in at least obtaining empirical estimates on the frequency of long distance dispersal events. The empirical dispersal curve I obtained in chapter 2 was the first in the literature to originate from multiple seed sources from within an intact forest. It is also the first data set that can be used to evaluate the inverse modeling technique. The conclusions made about inverse modeling are clear: it can not be used to predict dispersal beyond the scale of just 60m –well below the requirements of a metapopulation.

The final contribution of this thesis is aimed toward a better understanding of the mechanisms of seed release. As was shown in Chapter 1, the horizontal wind speeds are critical for describing the dispersion patterns at the local scale. Current research is making it increasingly clear that updrafts are critical determinants for long distance dispersal (Soons et al. 2004; Tackenberg et al. 2003; Nathan et al. 2002). Chapter 3 underscores the importance of obtaining the frequency of updrafts capable of causing seed abscission. This would then allow us to determine the fraction of seeds having the potential to remain uplifted and disperse great distances. Chapter 3 brings us then back to the beginning of this thesis by asking of how to *refine* current models to include the differential abscission potential of varying wind directions.

What I hope to have achieved within this thesis is to highlight the current limitations of the tools available for describing seed dispersal. The main consequence of these limitations will have a direct impact on several other fields within biology, including: population genetics, invasion biology, conservation biology, and in predicting the effects of global climate change on plant populations world wide. Evidently, the quest to understand the dispersal potential of plants, beyond just approximate solutions, is of supreme importance.

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