# Pollen Dispersal at Arctic Treeline

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# ABSTRACT

## Pollen Dispersal at Arctic Treeline

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Pollen dispersal of *Picea mariana* was studied in reference to abscission direction and long-distance pollen dispersal near Arctic treeline. This study tests two models for pollen dispersal: an advection-diffusion model described by Okubo and Levin (1989) and a proposed model where modifications were made to Okubo and Levin (1989). Pollen was passively collected up to 1300 m (2002) and 1500 m (2003) away from a *P. mariana* area source. I obtained mixed results; none of the three correlations between predicted and observed were significant for the Okubo and Levin (1989) model, whereas two of three trials were correlated significantly for the proposed model. The main problem with the proposed model appears to be underprediction of deposition when the source is nearby, likely due to problems with an angular argument describing the location of a *Picea* tree within the pollen source. Further, I experimentally determined that there was a bias toward abscission by downdrafts. This result could also explain the underprediction.

List of figures, tables, and equations

# 1 Literature review

## 1.1 History of the study of pollination

Long before studies of pollen dispersal, the mere occurrence of male and female parts in plants as sexual organs was in question. Although fertilization was assumed by Theophrastus as early as c. 373-287 BC and some prehistoric artwork shows date palm pollination as early as c.800 BC, by the Middle Ages male and female organs were viewed as organs of plants with little or no association with sexuality (Knox, 1978). Conventionally, female flowers or female dioecious individuals were viewed as fruit-bearing, and males barren.

Acceptance of the sexuality of these organs in plants began in the 17th century with the realization that male parts were required for seed set. In 1676 an English botanist named Nehemiah Grew speculated in his *Anatomy of Plants* that stamens were necessary for fertilization (Knox, 1978).

Intrigued by this idea, several studies were performed. Rudolph Jacob Camerarius, a physics professor in Germany, found that plants failed to set seed when either anthers (using the castor oil plant, *Ricinus communis*, mulberry, mercury, and spinach) or stigmas (using maize) were removed. Further demonstrating the necessity for some substance produced in the anthers, in 1717 Richard Bradley in *New Improvements of Planting* discussed an experiment where seed set only occurred when pollen from male catkins was dusted onto females (knox, 1978). He also discussed the occurrence of a hybrid produced in this manner by Thomas Fairchild, and considered the future of selective plant breeding. By the mid-1800s, sexuality in plants was accepted. The last step in understanding the basics of plant reproduction was also made in this century, this time as a cooperative effort between various scientists, where proof of the existence of alternation of generations in plants was established (Knox, 1978).

Initially, most early studies explored the apparent mutualism between insects and flowering plants. Later, botanists examined important features of plant reproduction such as the fusion of the pollen nucleus with the embryo-sac of the ovule (observed by Strasburger in the middle 18th Century) and meiosis (Knox 1978).

Today, four general topics of pollen dispersal studies can be found in the literature: (1) those on orchard contamination by wild pollen (Di-Giovanni et al. 1995; Di-Giovanni and Kevan, 1991, 1993; Sorensen and Webber, 1997; Caron and Leblanc 1992); (2) studies examining the receptivity of ovulate cones (Allison, 1990; Caron and Powell, 1989; Niklas, 1985; Niklas and Paw, 1982; Roussy and Kevan, 2000; Sorensen and Webber, 1997); (3) studies of pollen dispersal at short distances (4) and long-distance pollen dispersal (see section 2.1.2 below for full description). While the dispersal capacity is clearly great, nonetheless we have no fully-delineated empirical curve showing dispersal out to large distances. Further, we have no empirical validation of a model at large distances.

The importance of palynology in science is undeniable. It is relevant in the medical field because of allergies, in crop management and as a tool for studying past vegetation. It is also studied in the context of ecosystems and nutrient cycling; since the interiors of pollen grains decompose rapidly in aerobic environments and are protein-rich, the pollen cloud is an important nutrient input for the forest (Doskey & Ugoagwu 1989).

This study describes pollen dispersal of *P. mariana*. As such, for each section, emphasis will be given to this species. Below is a review of pollen production and development, pollen dispersal, and fertilization of the ovule.

## 1.2 Pollen in the life cycle of a plant

### 1.2.1 Pollen development

A pollen grain is a resistant capsule that contains the male gametophyte. Pollen is multicellular, produced by meiosis, and contains ½ the genetic makeup of the parent plant (i.e. sporophyte) (Di-Giovanni & Kevan 1991). Its development can be summarized in two steps: first, tissue morphology is determined and pollen mother cells undergo meiosis and second, the tissues develop, and sac dehiscence occurs.

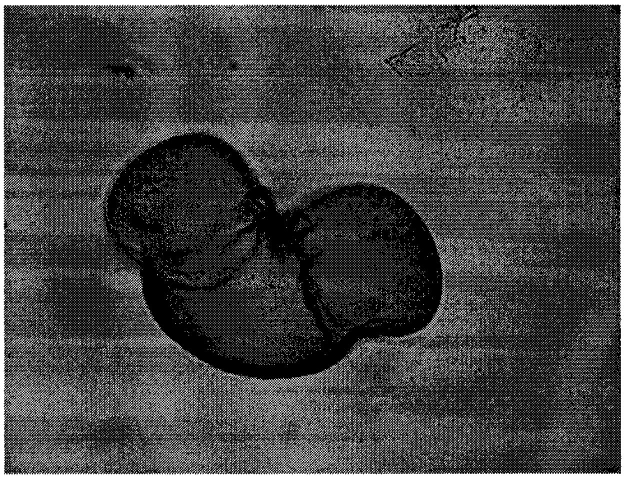
Any given year, a number of bud primordia become sexual rather than vegetative. In turn, for reasons that are not clear, a proportion of these sexual primordia are male rather than female. One year then elapses as the pollen mother cells become dormant (Owens & Blake 1983). Development of the mother cells recommences the following spring on a schedule that can be easily predicted from degree day sums (Owens & Molder, 1979). Following mitosis in the cone axis, pollen mother cells undergo incomplete mitosis (no cell divisions), creating binucleate cells. Meiosis subsequently continues for two weeks, forming microspore tetrads (i.e. pollen grains). At this point, the male cones grow at a noticeable rate concurrent with further development of the grains, such as bladder expansion, pattern formation and thickening of the exine, starch accumulation, intine (inner-layer) development and mitosis, producing a 5-celled grain (Owens & Molder, 1979). At this point in June (approximately 1-2 months after the end of dormancy of the pollen mother cells), pollination is ready to begin (Owens & Molder, 1979).

A pollen grain is the microgametophyte of gymnosperms or angiosperms. Although their size may reach up to 300um, *P. mariana* pollen grains are, on average, 70-85 µm. The shape of a pollen grain is dependent on two main factors, the number and position of apertures. The number of apertures determines the generalized shape of the grain (0 or many apertures creates a round grain, 3 apertures creates a triangular-shape, 4 apertures creates a square, and so on). *P. mariana* pollen grains have 2 small air bladders (i.e. grains are vesiculate) with the vesicles being small in relation to the actual grain (Proctor et al., 1996) (see Figure 1).

Figure 1. Picture of spruce pollen grain.

Average size: 70-85 µm. Note air bladders. Source:

http://www.ess.slu.se/Lindbladh/gammal_och_aktuell_forskning.htm



### 1.2.2 Pollination

Pollination is the movement of pollen from male sexual parts to the receptive surface of a female part with the eventual goal of fertilization. It is achieved via water, wind, or animals. I begin with a description of the characteristics of anemophilous (wind-dispersed) species, followed by a description of the field methods commonly used to study pollen dispersal.

Next, Faegri and van de Pijl (1979) define the process of pollination in three phases: 1. Pollen release 2. Placement of pollen (dispersal), and 3. Germination (deposition). Each step is described in detail below with reference to the variables that affect each phase.

#### 1.2.2.1 Anemophily

Anemophily is the process of pollination by wind. As such, many of the distinguishing features of anemophilous species are those that attempt to compensate for the seemingly random process of wind pollination.

In gymnosperms, these characteristics include cone position and number, stand characteristics, timing of dehiscence onset, and subsequent grain release. Anemophilous species position their reproductive organs (male and female cones) at the tips of branches, where branches and needles create minimal obstruction to wind pollination. Caron and Powell (1989) found that the onset of sexual maturity of cones for young open-grown *P. mariana* trees begins with female cones, the male function not beginning until about 3 years later.

Subsequently, until the age of 14, the number of female cones surpasses the number of male cones. These numbers are subsequently reversed, when the male cone production surpasses the female, peaking at age 18, when an average ratio of 6.6:1 for male vs. female cones occurs.

Female cones are not passive in the fertilization process. Niklas (1985) suggests that female cones are positioned at specific angles at the tips of branches, to optimize fertilization. In addition, female cones are morphologically adapted to wind pollination; their cone bracts create species-specific eddies which foster the capture of species-specific pollen Niklas (1985).

Further adaptations of anemophilous species also involve pollen grain morphology. Pollen grain number is far higher for species pollinated by wind than those pollinated by animals because anemophilous plants can exert so little control over the flight trajectory. Anemophilous pollen facilitates transport by its light mass (buoyancy) and (for conifers at least) bladders. The argument that air bladders promote dispersal by augmenting buoyancy (Di-Giovanni & Kevan, 1991) is questioned by Pohl (1937, in Proctor et al., 1996), who found that for pine, it is the low density of the grain, and not the air sacs that make it fall so slowly.

Pollen grains must also survive various environmental hazards until they reach the ovule. As such, in addition to being produced in mass quantities, grains have protective coatings. Further, some speculate that bladders may reduce desiccation of grains while in transit, as well as orient the grains when they reach the female cones (Di-Giovanni & Kevan, 1991).

Lastly, wind pollinated conifers are cued to release pollen and to open ovulate cones under specific climatic conditions, to optimize the chances of ovule encounter (see 1.2.2.3 below).

### 1.2.2.2 Field methods for pollen collection

Field methods for capturing pollen or spores during flight have changed little over the years. The first such study, in a sense, was the inadvertent discovery of bacterial deposition by scientists such as Louis Pasteur. Indeed, the first devices used to trap spores, pollen and other microorganisms were simple flasks containing growth media. Following the realization that there were large numbers of organisms and particles in the atmosphere, some of which could harm humans, different devices were developed.

During the “golden age of bacteriology”, Salisbury (1866) studied the connection between air spora and malaria by placing glass sheets above marshes and then looking under the microscope. Over the years, many passive collection devices such as this have been used.

Adhesive surfaces are the most widely use method for pollen collection. Their validity is questioned, however, because they do no mimic the receptive surface of females (Roussy & Kevan, 2000). Other studies that used passive sticky surfaces include Peeters and Totland (1999) who put adhesives on microscope slides. A more complicated passive collector was used by Lee et al. (1996), a Durham (1946) pollen collector, which consists of 2 horizontal disks (23 cm in diameter, and 15cm apart), with a lower disk 9cm from the ground. A standard 2X8 cm glass slide covered with petroleum jelly was placed on the lower disk.

One of the first mechanical devices used to collect airborne particles was a vacuum employed by Pasteur which sucked in a known volume of air, and filtered the particles onto cotton. Similarly, a device named the "aeroconiscope" was invented by Maddox (1870, 1871, in Proctor et al., 1996), and later refined by Cunningham (1873). The aeroconiscope consisted of a funnel facing the wind, with a glass slide at the end, collecting the particles. He found that moist air diminished the number of particles obtained. Hesse (1846) took a 70cm-long tube, 3.5 cm wide, which sucked in a known volume of air. The tube was coated with Koch's nutrient gelatine inside. He found that spores went further down the tube than bacteria. He concluded that, spores are lighter than bacteria, and that bacteria must travel in clumps (Gregory, 1973). In 1876, Pierre Miguel was surveying the microbiology of the air using a glycerin coat on glass slides, and air was sucked to the slide through a 0.5-0.75 mm tube.

There exist also various volumetric collectors of airborne particles. Volumetric measurements of aerobiology in the Alps were made by Miguel (1884 in Gregory 1973, p. 10) by precipitating and counting hourly rain content on sticky slides.

The preferred pollen-collecting method is dependent on the purpose at hand. For allergy-related studies, for example, a volumetric count is desirable as a measure of the amount of pollen in the air that can affect individuals. In the present context, where pollen is collected away from a source in order to predict it's dispersal, the most economic and practical method is one where pollen is collected passively with adhesive collectors.

### 1.2.2.3 Pollen sac (microsporangia) dehiscence and pollen release.

The literature agrees that the most important factor initiating the release of pollen grains from male cones is desiccation (Sarvas 1955, 1962, 1968, Sharp & Chisma 1961, Silen 1962, Ebell & Schmidt 1964) because relative humidity controls dehiscence of the pollen sac (Sanchez-Mesa et al., 2002). Owens and Molder (1979) describe pollen sac dehiscence as resulting from a last elongation of the cone axis due to dehydration; thus causing the pollen sacs to split along an axis with a thinner wall.

Moisture may also play a role once the grains are released from the parent-plant. Cunningham (1873) found that the number of airborne particles in moist air is less than in dry air. This is an advantage to anemophilous plants because optimal climatic conditions that include low relative humidity (instability of the lower atmosphere during clear warm days) are the result of thermally-generated vertical eddies, (Sanchez-Mesa et al., 2002) which aid in long-distance dispersal. Studies also show that pollen release is most likely to occur at midday, when the above-mentioned conditions are most prominent (Sarvas 1952, 1962, 1968, Sharp & Chisma 1961, Silen 1962, Ebell & Schmidt 1964). Sanchez-Mesa et al. (2002) found that wind-dispersed pollen traveled significantly farther when conditions were unstable

Probably, grains are released from the opened pollen sac by a sudden vibration of the branch induced by wind or more directly by the drag of a gust. Which of these two mechanisms is more important for the initial liberation is not understood. Likewise, it is not clear whether a fraction of the grains can be released in the absence of wind (although a mechanical force such as a bird landing on a branch will also cause grains to be released). For subsequent re-entrainment (e.g. of a grain that has been deposited on a leaf), drag on the grain is the motive force. The grain is held on a surface by adhesive, inertial, and electrostatic forces. In addition, larger surfaces hold particles more strongly than smaller ones (larger boundary layer), which is beneficial to gymnosperms such as *P. mariana* because of the small surface areas of their needles and cones. Studies of the wind speed required to move a particle from a surface have found that gale-force winds are required to re-entrain small particles. Further, Aylor (1978) has demonstrated a lag between the re-establishment of the boundary layer and the preceding wind gust. Therefore, even with the duration of only one thousandth of a second, a modest gust is sufficient to cause re-entrainment of a grain or, perhaps, pollen grain release from a parent-tree. Since conifer leaves have less surface area (and so less boundary layer) than most angiosperm leaves, smaller gusts are sufficient to release pollen grains. Also, these cones and needles promote vertical eddies which may help in pollen release.

The horizontal wind speed, $U_1$ required for a grain to be entrained from a surface is based on:

$$U_1 = 2r^2 \rho g \tan\theta \div 9u \qquad (1)$$

where $r$ = particle radius, $\rho$ = particle density, $g$ = gravitational acceleration constant (981cm/sec$^2$), $u$ = viscosity of air (1.8X10-4 g/cm/sec for air at 18°C), and $\theta$ =angle between particle radius perpendicular to the surface of the particle's furthest point of contact with the surface from that radius. Clearly then, in the case of *P. mariana* pollen, their small size ($r$) and low density ($\rho$) due to air bladders (or the grain itself, see Pohl, 1937) promote pollen release and re-entrainment (Grace & Collins, 1976).

### 1.2.2.4 Parameters for pollen dispersal

Once released from the parent plant, the shape of the dispersal curve (pollen number vs. distance from tree) is a function of the source and meteorological characteristics. Of the latter, the most important are horizontal wind speed ($U$), vertical wind speed ($W$), terminal velocity ($f$), and release height ($Za$). Each is described in turn, and related to its effect on dispersal distance.

#### *1.2.2.4.1 Horizontal wind speed ($U$)*

The two most important effects of horizontal wind on the dispersal profile are the distance traveled by particles and the width of the plume created. Insofar as the wind speed remains higher than the settling velocity, grains can travel indefinitely (see section 2.1.2 below on dispersal distances), provided there are no obstacles (see Section 1.2.2.5) or destructive agents (see Section 1.2.2.6) along the way.

Once pollen grains are released from a parent plant, their concentration in the air decreases with distance from the source. More precisely, the horizontal surface plane occupied by grains decreases in grain density with distance from the source at a rate that is inversely proportional to the square of this distance:

$$G \propto \frac{1}{d^2} \qquad (2)$$

where G= Number of grains on a horizontal plane (Jackson & Lyford, 1999).. Except in very unstable conditions, decreasing horizontal wind speed leads to an increase in azimuthal variation and a decrease in the variation and magnitude of vertical wind. Since wind slows dramatically within a forest, the pollen is scattered more in forests than in clearings per unit of distance traveled. Further, the more time a grain remains inside a vegetated area, the more likely it is to settle, because vertical eddies are more subdued. Wind patterns within a forest are dependent on three forest characteristics (Brown et al., 1969): roughness of canopy top, resistance to vertical transfer provided by the canopy, and resistance to horizontal transfer provided by various layers of the canopy (Di-Giovanni & Kevan, 1991). As such, the different vegetation gradients at different height layers in the forest are the main physical determinants of horizontal wind patterns in a forest. Horizontal wind speed declines exponentially with height down to the lower trunk space where the wind speed remains constant or even increases a bit (Jarvis et al., 1976, Reifsnyder, 1955, Gregory, 1973). This is because the upper part of the forest includes the main drag-producing elements (leaves, twigs). Wind speeds are of course much greater above the forest or in clearings.

It has always been assumed that pollen capture rate would increase at higher wind speeds because then the grains would have more inertia and thus would be less likely to follow the streamlines as they curved around an obstacle. However, Roussy & Kevan (2000) report no relationship between wind speed and pollen capture efficiency of jack pine in a wind tunnel.

#### *1.2.2.4.2 Vertical wind speed ($W$)*

Because pollen grains have such a low terminal velocity, the vertical wind speed is much more important than horizontal speed in determining dispersal distance.

The frequency of rapid and irregular alterations in vertical wind direction, or vertical turbulence, leads to an increase in the variance of dispersal distances; i.e. both the near and far tails of the dispersal curve are augmented by downdrafts and updrafts, respectively. One source of vertical turbulence is thermally induced and is positively related to atmospheric instability. In an unstable environment such as a clear hot afternoon, the air's temperature decreases more rapidly than the adiabatic lapse rate. Therefore, rising air masses will continue to rise as a result of their being warmer than their surroundings. The buoyancy effects cause overturning and high turbulence, gusting, and in general, frequent changes in wind speed and direction. This type of turbulence is greatest in the afternoon when, as previously mentioned, sac dehiscence is also most likely.

A second type of vertical turbulence is proportional to the horizontal speed. As the wind moves over a rough surface, vertical eddies result. A third type of vertical turbulence is due to lee-side vortices around objects such as twigs and leaves. Thus, vertical turbulence is greater in the canopy, despite the fact that horizontal winds are lower there than above the canopy (Di-Giovanni & Kevan, 1991). But vertical winds are potentially greatest of all in large openings due to the thermal effects mentioned earlier.

Pollen released initially in a clearing will tend to rise above a dense forest canopy and loop down a distance of 8-10 tree heights (Edmonds, 1971). For a more open forest, the particles will tend to simply move laterally into it.

Once inside the canopy, vertical diffusion within the canopy is hindered by vegetation density. Eventually, however, the great majority of the grains slowly arrive at the ground. Pollen grains released within the canopy can, similarly, escape upward through a gap in the forest, but will most likely remain within the forest, eventually landing on the ground. However, Raynor et al (1975) and Di-Giovanni and Kevan (1991) released pollen grains into a forest (from a clearing), and found that a considerable number were found above the canopy within a short distance from the parent tree. They proposed that this may be the result of particles being released in a low-density forest.

### *1.2.2.4.3 Terminal velocity ( $f$ )*

Terminal velocity is defined as the speed at which particles fall due to gravitational forces alone in still air. The main factors affecting terminal velocity are particle mass, density, size and shape, and moisture content. Terminal velocity for such small objects as pollen grains can be approximated by Stoke's law:

$$f = 2r^2 g(p_o - p) \div 9u \qquad (3)$$

where $r$ =particle radius (cm), $g$ = the gravitational acceleration (m/s$^2$), $p_o$ = particle density (g/cm$^3$), $p$ =fluid density (1.27 X10$^{-3}$ g/cm$^3$ for air), and $u$ = fluid viscosity (1.8X10$^{-4}$ g/cm/sec for air at 18°C).

Although smaller grains have a smaller terminal velocity and thus, intuitively, will travel farther, there is a lower limit to the size a pollen grain may have and still be able to land on a stigma or pollen drop. This is because smaller particles have smaller inertia, and will be therefore more difficult to capture (Whitehead, 1983). Pollen grains must be small enough to be easily entrained by wind, but not so small as to elude capture.

Table 1 shows the results from different studies which calculated the terminal velocity for *P. mariana* pollen. Much of the variation is due perhaps to differences in moisture content of the grains.

The effect of *P. mariana*'s air bladders on terminal velocity has been questioned. Intuitively, air bladders should decrease terminal velocity, and thereby increase dispersal distance (and perhaps, efficiency). However, Di-

Giovanni and Kevan (1991) report contrary evidence: bladders may actually increase terminal velocity or not have any effect at all, because the large size of the grains may swamp any effect of the bladders.

### *1.2.2.4.4 Release height* ($Za$)

Models of pollen dispersal that use a ground-level source (even those that use equations to convert from ground level to higher elevations) predict much shorter dispersal distances than those predicting emissions from above-ground.

Release height is the height at which pollen grains are being released from the parent-tree. Personal observation indicates that, for *P. mariana,* this value is between ⅔ and ¾ the height of the tree.

The skip distance (interval on the ground between the base of the source and the first captured grains) increases with the release height. Likewise, all things being equal, the maximum density of grains at the ground will be lower and located farther from a tall source than a short source.

All of the above mentioned variables dictate the distance ($X$) that pollen grains will take to reach the ground (ignoring any interception by adhesive surfaces and assuming $W$ (the vertical wind velocity) is 0)):

$$X = Uh \div f \qquad (4)$$

Table 1. Terminal velocity values for *P. mariana* pollen grains reported in different studies. From Jackson and Lyford, 1999. Variation in values may be explained by relative humidity of the air at the time of recording.

| **Study** | **Year** | **Terminal velocity (cm/s)** |
|---|---|---|
| Niklas | 1984 | 2.7 |
| Di-Giovanni & Kevan | 1996 | 3.19 |
| Eisenhut | 1961 | 5.2 |
| Eisenhut | 1961 | 5.5 |
| Eisenhut | 1961 | 6 |
| Dyakowska & Zurzycki | 1959 | 6.8 |

### 1.2.2.5 Pollen deposition

Deposition is the transfer of an airborne particle to a solid surface and is governed by what is called the depositional velocity: the ratio $f/U$ (Sanchez-Mesa et al., 2002). The greater this ratio, the more grains will be deposited (sedimentation). As such, sedimentation onto vegetative surfaces increases with lower wind speeds and is most prominent in the trunk space of a forest (Aylor, 1978).

More specifically, adding grain concentration in the air, the deposition rate (grains/$m^2$/s) (flux) is:

$$Flux = VdC(z) \qquad (5)$$

where $Flux = grains/m^2/s$, $Vd =$ deposition velocity (m/s), $C$ = grain concentration ($m^{-3}$) at height $Z$ (m) (Chamberlain, 1975).

At impaction, particles are carried onto the surface of an object by inertia instead of being entrained around it by the air stream. Therefore, impaction occurs at higher wind speeds than sedimentation. Impaction rates are increased by the "shelter factor", where one shoot shelters another, an occurrence that is therefore more prominent in dense forests (Jarvis et al., 1976). Some particles may be deposited onto the lower surfaces of leaves when turbulence works against gravity (Gregory, 1973 and Aylor, 1978). Because of the high probability of subsequent entrainment, impaction on vegetative surfaces is deemed insignificant, except on sticky surfaces (Raynor et al. 1975, Aylor 1975, Chamberlain & Chadwick 1972, Chamberlain and Little 1981).

Some forces create electrostatic and thermal deposition, causing the grains to adhere to surfaces, and thereby ending their dispersal. Little is known about this process, and even less about the number of grains that experience these effects (Di-Giovanni & Kevan, 1993).

Last, precipitation scrubbing ("washout") is the deposition of particles due to precipitation: the grains become a part of drops that fall with a much greater terminal velocity. This need not be due to rain: a fog is sufficient.

There are only anecdotal studies of the process whereby grains can sometimes bounce off objects and then resume their journey. Hesse (1981) states that anemophilous pollen grains are typically non-sticky, so they ought to be susceptible to rebounding and thus resume flight.

#### 1.2.2.6 Pollen viability once it is dispersed

Once a pollen grain is released from a parent tree its capacity to fertilize a female is not only dependent on its ability to reach an ovule, but also on its ability to survive the dispersal process. Gregory (1973) describes the dispersal process as a slow delayed decay period for airborne particles.

Little is known about pollen viability once it leaves the parent-tree. As anemophilous species are adapted to dispersal in the atmosphere, most do not suffer much during short-distance dispersal. It is long-distance transport that may cause grains to suffer from dispersal. Reports on the effects of light, relative humidity and temperature show that these variables can have adverse effects on pollen grain viability.

Pollen grains can decay quickly when exposed to wavelengths shorter than visible light, or ultraviolet light. This problem is therefore made worse in northern locations, where there is 24hours of sunlight during pollination. Most ultraviolet radiation is absorbed before it reaches ground level. As such, pollen grains travelling at high altitudes, unprotected by clouds, are most susceptible to this type of decay.

Both humidity and temperature can have adverse effects on pollen viability. Some argue that certain concentrations of solutes in rain and washout may damage grains through osmosis. However, Allen and Sziklai (1962) argue that pollen in raindrops is still viable. Desiccation can also be a problem, especially since pollen is released on dry hot days.

#### 1.2.2.7 Fertilization

Just like male cones, *P. mariana* female cones are initiated the year before pollination especially when the late spring weather is warm and dry (Eis & Inkster, 1972 and Rudolph & Yeatman, 1982, Boyer 1981). Thus, a year where male cone production is high will also result in a high production of female cones.

The ultimate goal of pollination, fertilization, is aided by a number of characteristics that are related to the female cones and promote fertilization. Indeed, female cones are initiated at locations that promote pollen receipt.

Niklas (1985) and Niklas and Paw (1982) both state that female cone morphology of conifers in general is conducive to fertilization. Niklas (1985) reports that the bracts of female cones promote species-specific eddies around them, and a grain traveling in the vicinity of this eddy will be drawn within the cone bracts, thereby promoting fertilization. This specificity is related to the pollen grain's density and size, which creates eddies that are optimal for the species in question. Indeed, Niklas and Paw (1982) and Niklas (1985) showed that pollen grains of conifers are most likely to fertilize their own species.

Neighbor distance (i.e. tree density) and pollen production has been correlated with seed set and the proportion of ovules fertilized by Allison (1990) for *Taxus canadensis.* They found that neighbor distance and pollen production explained 86% of the variation in pollination success. Seed set correlated significantly with pollen production and neighbor distance.

### 1.2.2.8 Inbreeding

I have found no direct information on the consequences of inbreeding in *P. mariana.* All gymnosperms suffer inbreeding depression when they self-pollinate (except maybe *Pinus resinosa*, see Mergen et al., 1965). Inbreeding depression may result in reduced seed set, reduced germination ability and viability, growth malformations, and delays in flowering (Mergen et al., 1965). Specifically, inbreeding depression in *Picea glauca* results in a reduced seed and cone production, seed germination ability, seedling vigor, and increased mortality (Mergen et al., 1965). Since pollen release occurs when the female cones are fully receptive, the potential for self-pollination in conifers may be great (Owens and Molder, 1979).

The timing at which inbreeding affects plants differs between species. Mergen et al. (1965) reported increased seed and cone production in *Picea glauca* and improved seed viability in *Picea omorkia* when they self-pollinate, but they subsequently observed reduced viability when seedlings reached 1 year old. However, most cases of inbreeding depression manifest themselves earlier in the seedling's development. Some studies propose that the mortality of selfed seeds is due to either an accumulation of lethal homozygous alleles in the embryo (Mergen et al., 1965) or physiological incompatibility between the embryo and the gametophyte tissue.

Empty seeds, however, may not be solely the result of inbreeding. Sarvas (1962) found that the percentage of empty seeds may be related to pollen availability rather than to selfing.

In a study where hand pollination was applied (and therefore pollen availability was not limited) to *P. glauca*, Mergen et al (1965) attempted to identify the timing at which self-pollination affects the plant. They report that a genetic incompatibility is more likely than a physiological one based on the fact that the embryos were able to develop for a period of time before aborting. Of the surviving embryos, no significant differences were found in rate of cone elongation, final cone length, germination rate, and survival between selfed and non-selfed individuals. Significant differences were found in seedling height at 6 weeks, but this difference disappeared by the end of the growing season.

The literature agrees that selfing is detrimental for most plant species, but the similarities appear to end at this point. Each species reacts differently to selfing, with different physiological characteristics, and timing of the effects.

One way that conifers can limit selfing is by spatial segregation of the genders. Unless there are strong updrafts at the time of pollen release then self-pollination ought to be greatly reduced by the fact that conifers place their male cones under the female. Females are typically in the upper third of a crown while males are in the middle third.

## **2** Modeling pollen dispersal

It is obvious that there is a higher concentration of pollen near a source, and a decrease in the amount of pollen that is inversely proportional to the distance from the source. One only has to see how allergy sufferers will avoid the source of their allergens during hay fever season to confirm this. It is not, however, obvious what path pollen grains may take beyond this source. There are two types of underlying process which are important in modeling particle dispersal by wind: physical parameters (predominantly wind patterns, described above) and biological parameters (parameters that are directly related to tree morphology, i.e. terminal velocity and release height) (Di-Giovanni & Kevan, 1991). The parameters that affect this path are invariably simple and straightforward, but their interaction with each other is what makes pollen dispersal more difficult to predict.

## 2.1 Biological parameters

Biological parameters used in pollen dispersal models include source strength, terminal velocity, and release height. The source strength describes the number of grains produced within a given area, usually in grains/m$^2$. The release height and terminal velocity were discussed previously

### 2.1.1 Source strength

Source strength will ultimately affect the number of grains found at a given location. It will depend on tree density, male cone production, and the number of grains produced per cone. As previously mentioned, production of male cones only commences when the tree is about 10 years old (+/- 2-3 years) (Caron & Powell 1989). Following this, cone production exhibits a somewhat predictable pattern of yearly high and low cone production (Caron & Powell 1989).

The amount of pollen produced by a tree depends on the quantity of resources it has to allocate to reproduction. This in turn depends on health, which is related to site location. Topography, climate and proximity to others are used to describe site quality (Di-Giovanni & Kevan,1991)

### 2.1.2 Dispersal distances

The literature includes a number of anecdotal reports for short and long-distance pollen transport. Studies of pollen dispersal at short distances include: Di-Giovanni and Kevan (1993) who studied dispersal at less than 1 km, while Lee at al. (1996) looked within the source only, and Caron and Leblanc (1992) looked at dispersal up to 500 m.

Long-distance pollen dispersal studies often present anecdotal results. For example, Van De Water and Levetin (2001) deduced that *Juniper ashei* pollen can disperse up to 200 km.

## 2.2 Model description

### 2.2.1 The Okubo and Levin (1989) model

The pollen dispersal model applied here is based on that of Okubo and Levin (1989) which has never been tested, and is the only published closed-form solution for particulate dispersal in turbulent flow. It is based on a single tree idealized as an elevated point source. While individual grains may rise or fall with vertical winds, nonetheless the mean downward velocity will be given by the terminal velocity of the grains. This essentially produces a dispersal curve where no grains fall directly below the tree (although this “skip distance” is typically less than a meter), a modal deposit is found a short distance away from the tree, and the remaining grains are spread across a very large area due to their very low terminal velocity (

Figure 2). In this model no allowance is made for adhesion to sticky objects such a spider webs or stigmas nor for washout by rain or fog. That is, it is assumed that the flight is terminated only by impaction on the ground.

Equation 6 shows the dispersal equation proposed by Okubo and Levin (1989):

$$Q(x) = \frac{Qf}{Z_a \bar{u} \Gamma(1+(f/w^*)} \left\{ \frac{Z_a{}^2 \bar{u}}{2(1+\alpha)\bar{A}} \right\}^{1+(f/w^*)} x^{-(f/w^*)-1} \exp\left\{ \frac{Z_a{}^2 \bar{u}}{2(1+\alpha)\bar{A}x} \right\} \qquad (6)$$

where Q(x) is the number of grains/annulus at location x, Q is the number of grains produced/m$^2$ within the primary pollen source, $f$ is the terminal velocity, $Z_a$ is the release height, $\Gamma$ is a function which allows decimals to be factorials, $\bar{u}$ is the average mean wind speed from $Za$ to $Z$ =0, $\alpha$ is the exponent on $Z$ in a power law relationship between the horizontal wind speed and height above the vegetation, $\bar{A}$ is a measure of vertical turbulence, as given by:

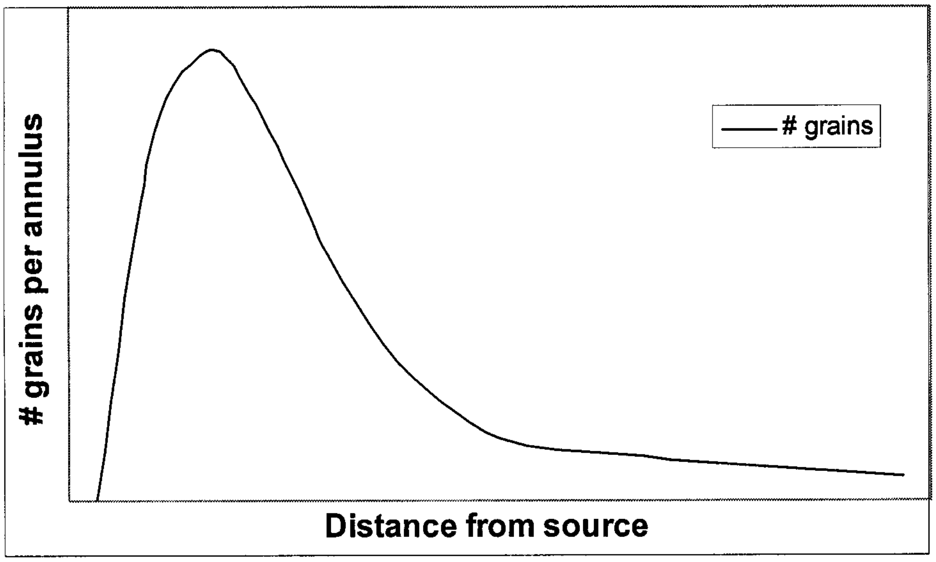
$$\bar{A} = ku^* f / 2 \qquad (7)$$

where k =0.41 is Von Karmen constant (a dimensionless number), and $u^*$ is the friction velocity, and $w^*$ is the vertical mixing velocity, as given by:

$$w^* = 2(1+\alpha) f / z_a \qquad (8)$$

Figure 2. Dispersal curve from a point source, as predicted by Okubo and Levin (1989).

Distance from source here is in arbitrary units. Distance “0” represents the center on the point source.


# grains per annulus
Distance from source
# grains

This model is exceedingly simple to used, requiring as input only the terminal velocity, release height, and the mean horizontal wind speed from release height to the ground (this in turn requires some argument about the decline in wind speed with height). The magnitude of the vertical turbulence is merely a function of the horizontal wind speed and thus need not be specified. This is because it only deals with mechanically-induced vertical turbulence (due to shearing of the air as it travels over rough surfaces), and any thermal effects are ignored.

I have made a number of changes to the Okubo and Levin model. Since Okubo and Levin's model runs for a point source (i.e. one tree at a time), it is not applicable for a stand of trees. In order to predict pollen dispersal for a stand one must run the point-source model repeatedly (i.e. once for every tree) in order to predict dispersal to a collector in Cartesian space. Further, when dealing with a stand of trees, the angle of the trajectory of a grain to a 2-dimensional passive collector must be considered (This is not an issue if collection is made by a revolving device such as a Roto-rod that sweeps out a volume of air.). A third problem is that Okubo and Levin (1989) predict the pollen catch at the ground. This is difficult to accomplish in the field due to debris accumulation on adhesive surfaces, and is not representative of the ovulate cones above ground, and so I needed to modify the model to estimate the catch by an elevated collector. These modifications are dealt with in the Methods section below.

Finally, the original model required only a single input value for the horizontal winds. But clearly there is a great deal of variation in horizontal wind, and so I will introduce a log-normal distribution of wind speeds, running the model repeatedly for a sequential number of wind speed values drawn from this distribution. .

## **3** Objectives

The objectives of this study are, broadly, to make the first empirical test of the Okubo-Levin model. In particular, for black spruce near arctic treeline, I will: 1) quantify the initial direction of pollen grain release once they have left the male cone, (2) Test the ability of Okubo and Levin's (1989) model to predict the observed pollen density along the transect; and (3) test the modified version of the Okubo and Levin's (1989) model against observed values.

# **4** Methods

## 4.1 Study area

This study was conducted in Inuvik NWT, which was built on the East channel of the Mackenzie Delta in 1953 as a result of frequent flooding events in the nearby community of Aklavik. A government town, Inuvik achieved village status in 1967 and became an official town in 1970. Although the population size was recorded at 3451 inhabitants in a 2000 census, the population of Inuvik has fluctuated considerably since its establishment, due to the discovery of oil and gas buried in air pockets of the underlying sedimentary rocks (http://www.ccea.org/ecozones/tp/land.html). Today, the community is equally composed of southerners, Gwich'in, and Inuvialuit people. Located at 68° 18' 19" N and 133° 29' 14" W, Inuvik is located 97km south of the Arctic Ocean, just 5 km south of treeline, approximately 10 km west of the tundra, and at an elevation of 68.30 m (Figure 3).

Figure 3. Map of Canada, showing location of Inuvik.

Source:
http://atlas.gc.ca/site/english/maps/reference/outlinecanada/canada01/referencemap_image_view


CANADA

## Climate and weather

Inuvik is located in the subarctic, and is subject to long cold winters and short cool summers, in part due to the Richardson Mountains to the west, which prevent warm moist air from reaching the area (http://www.grc.k12.nf.ca/climatecanada/inuvik.htm). The average annual temperature at the Inuvik airport is -8.8°C. The average July temperature is 14.2°C, and in January is -27.6°C. Mean annual precipitation is 248.4mm, with 167.9mm of this (67.6%) in the form of snow. (Canadian Oxford World Atlas, 4th ed., 1998). Water melting from permafrost in the summer months is the major water source for plants, since rain amounts are sufficiently small to classify the Inuvik area as a desert.

## Landscape

20,000 years ago, Inuvik was covered by the Laurentide ice sheet. The ice sheet began melting some 10,000 years ago, and was completely melted 5,000 years ago, depositing sand, gravel, and boulders that shape part of the landscape we see today. Underlying these are various layers of sedimentary rocks composed of limestone, shale, sandstone, and conglomerates of varying ages. Such deposits have resulted in shallow, acidic soils which are poorly developed.

The ecosystem is a taiga plains ecozone, or northern forest. Soils are underlain by permafrost and subject to winter freeze and summer thaw. Much of the landscape consists of thermokarst lakes and small streams. Rolling hills and flatlands dominate the landscape. (Western Arctic Handbook Committee, 2002).

## Biota

The tree species in the Inuvik region are *Picea mariana*, *Picea glauca*, *Betula papyrifera*, *Pinus banksiana, Populus tremuloides*, and *Larix laricina*. The physical characteristics of these trees are highly dependent on the depth and other characteristics of the active layer. Trees are stunted and grow a copious amount of lateral roots. They are often bent over due to the heaving of the ground, the short growing season, and the low nitrogen availability within a thin active layer.

The low density of trees in the area (*P. mariana* cover 44% of the landscape) (Post, 1996; Lee et al., 1999) allows for a large amount of the ground surface to be covered by tundra-like vegetation. Shrubs include *Salix spp.*, *Alnus crispa*, *Betula nana*, *Andromeda polifolia*, *Empetrum nigrum*, *Juniperus communis*, *Ledum groenlandicum, Vaccinium vitis-idaea*, *Rosa acicularis*. Wildflowers include *Pinguicula vulgaris*, *Rubus chaemaemorus*, *Plantago major*, *Achillea millefolium*, *Chamerion angustifolium*, *Castilleja raupii*, *Dryas integrifolia*, *Saxifraga tricuspidata*, *Potentilla anserina*, grasses, sedges, mosses and lichens, ferns and horsetails.

Figure 4. Typical vegetated landscape in Inuvik area.

Note spindly appearance of Black spruce, and low vegetation density.
Source: http://www.grrb.nt.ca/images/blackspruce.jpg

## 4.2 Direction of pollen release

In order to observe and quantify the direction of pollen grain release once they leave the parent-tree (objective 1), *P. mariana* pollen was collected vertically above, below, and horizontally on either side, around a cluster of male cones. Pollen was collected using adhesive tape exposed on plastic nursery tags (see Figure 5). These adhesive collectors allowed the experimental set-up to be prepared ahead of time, are very cost-effective and easily manipulated. Two tags, each bearing 10 holes (6mm diameter each), for each of the four collection directions, were mounted on a wooden stick, and stapled onto a frame atop the stick. The adhesive surface faced the cone cluster, and tags were approximately 15-20 cm from the cone cluster. The study was performed for 4 daytime periods in June 2003 (exact times not recorded). Pollen counts were made and recorded for each direction, for a total sample size of 20 holes per side, and 4 replicates.

## 4.3 Pollen dispersal;

Pollen dispersal was recorded during two different field seasons. For each collection period, pollen was collected every 100 m from a *P. mariana* pollen source, using adhesive surfaces. Adhesive surfaces were positioned so as to face the predominant wind direction (i.e. north). For both years, tree density for all *Picea* patches was recorded from a line transect, where the distance to the nearest tree was measured. The data was converted to density by: 0.534 / Ave. distance$^2$.

All weather data (temperature, relative humidity, wind speed and direction) were taken at the Inuvik airport (approximately 80km from 2002 transect, and 15km from 2003 transect). Wind speed values collected at the airport were subsequently converted to expected wind speed values at collector heights (see equations 9, 10, and 11 below).

Pollen counts were made using a microscope at 100X magnification. Although *Picea mari*ana and *Picea glauca pollen* are not morphologically distinct, this was not a problem as there was no significant number of *Picea glauca* found in the local area. Thus, all *Picea* pollen was treated as that of *Picea mariana*.

Each field season is described further below.

### 4.3.1 2002 Set-up

*P. mariana* pollen was collected on June 26th 2002 from 3 to 6 PM. The site was located within a 1999 burn at Lynx Creek, approximately 80km south of Inuvik (Figure 6). This location was chosen because of its large surface area (total burned area 172 000 ha, see Figure 6) without any cone-producing *P. mariana* trees. The transect extended 1.3 km away from the primary *Picea* source.

The burned area had begun regenerating, and included mostly of sedges, grasses, mosses, and *Chamerion angustifolium*, which were no higher than 1.5m. In addition, most of the burned trees were still standing at the time of pollen collection (Figure 7).

Pollen was collected using adhesive surfaces made by boring approximately 20 holes (6mm diameter) into 1-meter long wooden stakes (approximately 0.5cm thick), and covered with adhesive tape. The stakes were positioned horizontally, 0.5m from the ground, with the adhesive surface facing the predominant wind direction (i.e. north). The number of replicates per site was dependent on the distance from the source: for collection sites 0 to 500m, 4 collection sticks were used; for collection sites 600 to 1000m 6 collectors were used; and for collection sites 1100 to 1800m 8 collectors were used. For each collection site, a small amount of vegetation was cleared which might interfere locally with the collection.

In order to begin and end the collection period simultaneously on all pollen traps, 10 people worked on site, and were coordinated with radios. This assured that the collection period for each collection site was as similar as possible.

Figure 5. Picture of collector tags used in 2003.

Ten holes (6mm diameter) were punched into each tag. Tags were used in 2003 vertical release direction experiment and in dispersal experiment in 2003.

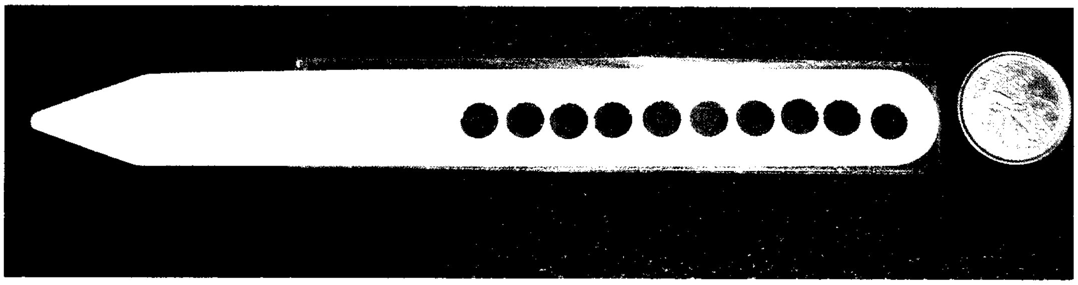


Figure 6. Aerial view of location of 2002 transect at Lynx Creek.

(Top figure) Dempster highway is shown at bottom-right of picture.

Figure 7 Picture of typical landscape on 2002 transect.

(Bottom figure) Person in the background is approximately 1.5m tall. Burned trees remained standing, and some unburned trees were located along the transect. Of the latter, unburned trees that had male cones along the transect were recorded and accounted for as patches in the model. Vegetation included willows, sedges and mosses.

### 4.3.2 2003 Set-up

In 2003, pollen was collected along a 1.5km transect across from Campbell Lake, approximately 10km south of Inuvik. The collection period lasted 5 days and 5 nights, from June 26th to June 30th. During this period, the tags (Figure 5) were routinely replaced with fresh ones, resulting in 10 series of different collection periods. The transect extended from a *P, mariana* source of density 0.3 trees/$m^2$, and an average height of 2.87 m. The area extending from the source contained *Betula nana*, some *Alnus crispa*, *salix spp.*, *Ledum groenlandicum*, and various sedges and mosses, which reached 2.0m in height at some locations.

At each collection site there were 20 collector tags stapled onto a wood stake, each stake placed 0.5m from the ground.

This method was preferred to that used in 2002 because of it's practicality (tags were small and much more manageable) and effectiveness. The tags are approximately 0.5mm in depth and the holes could therefore be much more uniform on the plastic than that on the wooden stakes as in 2002. Unlike during the 2002 collection, only 2 people were available on site to change the tags as required. Each person was therefore responsible for changing the tags on ½ the transect: it took approximately 5 minutes to move from one collection site to the next.

For both years, the collectors were placed at a specific height (as opposed to at ground level, as Okubo and Levin (1989) predict) for 2 reasons. First, the adhesive surfaces would collect less debris if placed above the shrub layer. Second, since female cones are located above ground, the placement of the collectors was an attempt to mimic reality.

Figure 8. Map of 2003 transect.

Star shows location of transect, black square shows location of Inuvik, and black circle shows location of Inuvik airport (where climate data was recorded). Source: www.nwtresearch.com/simply/images/deltafig1.jpg

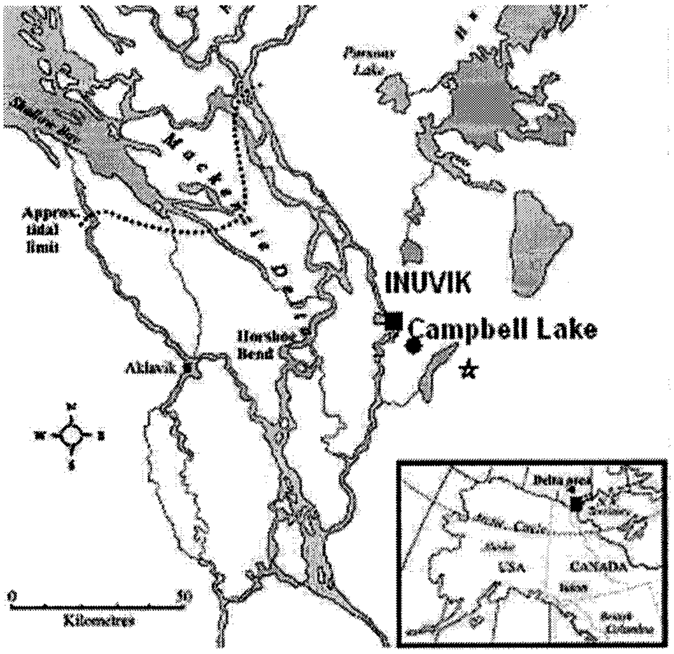

Shallow Bay
Mackenzie Delta
Parsons Lake
Approx. tidal limit
INUVIK
Campbell Lake
Horshoe Bend
Aklavik
N
W
E
S
0
50
Kilometres
Delta area
N.W. Territories
Arctic Circle
Alaska
USA
CANADA
Yukon
British Columbia

Figure 9. Picture of 2003 set-up.

Wooden stakes held 20 plastic tags with 10 holes each at each collection site. Although picture shows anemometer (at the right of the tags) and a rotorod (at the left), neither was used in this study

## 4.4 The model

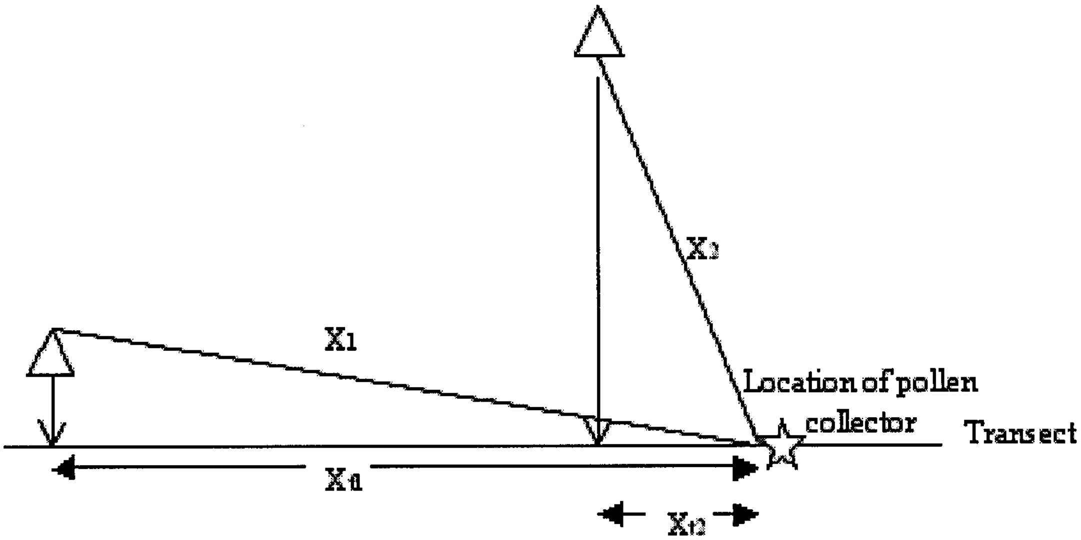
I have made several modifications to the model proposed by Okubo and Levin (1989) using QBasic software. First, pollen flight will be modeled as a collection of point sources in order to mimic a collection of contiguous trees. This will produce a dispersal curve (density vs. distance with $x=0$ now defined as the edge of the forest) quite different in shape and magnitude from the individual point source curves that comprise it. That is, this model is essentially the summation of overlapping point-source curves; the resulting dispersal curve for our model will have its peak at the edge of the forest due to this overlap.

The model would take too long to run if it dealt with every tree. Thus, I do not sum the contributions of individual trees but rather of squared blocks of trees, each block modeled with the Okubo-Levin model as a single tree located in the block center. To save time, these blocks become progressively larger as we examine more sources farther to the west and the north.

I am using a 2-dimensional collector with adhesive on one side ad oriented perpendicular to the transect (i.e. parallel to the forest edge). Therefore, I need to account for the fact that as the angle between the source tree and the collector steepens, the collector will receive less pollen than predicted by the original model. Let $x_p$ be the straight-line distance from tree to collector (and thus $x_p$ is the hypotenuse of a triangle). The base of that triangle (a section of the transect) is x. Employing a simple trigonometric argument (see Figure 10), the expected catch is reduced by the factor $x_p/x$. Thus, at one extreme a tree emitting pollen grains that fly parallel to the transect (perpendicular to the collector) will deposit all its grains on the adhesive: i.e. the expected grains density is multiplied by $x_p/x$ (=1). But deposition declines as the angle becomes more oblique (i.e. $x_p/x$ keeps getting smaller) until finally, when the wind direction is parallel to the collectors (perpendicular to the transect), there is no deposition at all. Note that this angle argument assumes that the density of grains collected is a function of the angle of approach of the grain, whether it is a result of the position of the original source, or the wind direction. Note also that this argument is not necessarily true, because of small-scale eddies: locally, the grain's trajectory can be quite different than the line drawn from its present position back to the source tree. Finally, the model does not account for sources outside of the 180° plane facing the traps as it is assumed that no back eddies can bring grains back toward the adhesive surface.

Figure 10. Depiction of angular argument.

A multiplier consisting of Xt/X is included in modified pollen dispersal model in order to allow for different locations of pollen sources. In this case, the wind is coming from the left-hand side of the figure, onto the adhesive surface of the trap, which is facing the left-hand side of the figure. As such, a tree located at an acute angle from the trap ($X_2$), will deposit $X_{t2}/X_2$ times less pollen than a tree located perpendicular to the trap ($X_1$).


X2
X1
Location of pollen collector
Transect
Xt1
Xt2

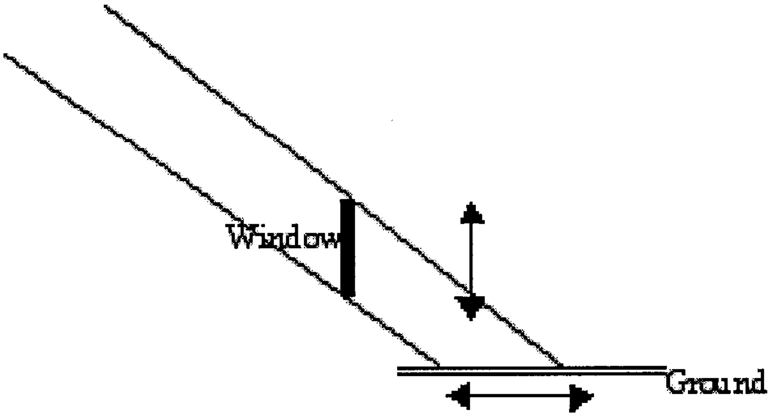
Another modification was made from Okubo and Levin's (1989) model because it predicts the number of grains on the ground, while the present study collected grains at 50 cm (Z=0.5) from the ground. As such, the resulting effect is that in Okubo and Levin's version, the total capture is unaffected by the horizontal wind ($U$) or terminal velocity ($f$). However, this is not true in the present case where I expect that I will collect far more pollen grains at 0.5m height than would have been deposited on the ground at that location because I am collecting the pollen that would have traveled much further than that position along the transect. The $\overline{U}_{(z=o.5)}/f$ ratio will determine the length of the potentially intercepted ground and thus I will multiply the predicted Okubo-Levin catch by that ratio. To develop some intuition, consider that when $\overline{U}_{(z=o.5)}$ equals $f$, the length of the intercepted ground (well beyond the collection point) is equal to the diameter of the "window" (i.e. diameter of adhesive surface capturing pollen) and thus I multiply the expected result by 1.0. In the case where $\overline{U}_{(z=o.5)}$ is much larger than $f$, the length of the ground intercept increases accordingly, and thus the expected amount must be multiplied by a much larger number

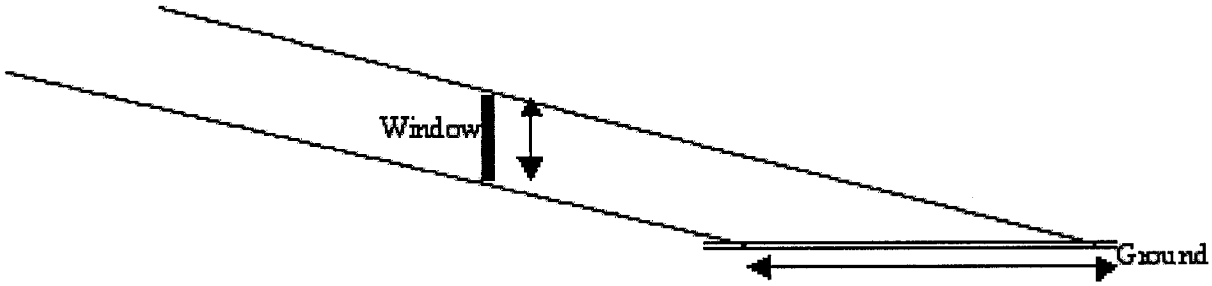
Figure 11. Diagram of ground intercept when $\overline{U}_{(z=o.5)} = f$.

(Top figure) Double-sided arrows show that window diameter = ground cover. In this case, the angle of the wind intercepting the pollen trap is 45°, and the length of the ground that would have been intercepted is equal to that intercepted by the pollen trap ("window").

Figure 12 Diagram of ground intercepted when $\overline{U}_{(z=o.5)} >> f$.

(Bottom figure) Double-sided arrows show that window diameter << ground cover. In this case, the amount of pollen grains captured by the traps will be higher than that predicted by the model by $\overline{U}_{(z=o.5)} / f$ times.


Window
Ground


Window
Ground

The value used for $\overline{U}$ at 0.5m (height at which pollen was collected) was obtained from reference wind speeds at the Inuvik airport (z=10). This was necessary because climatic variables were not taken on site. Based on equations 9 through 11 (below), I converted the data collected at the meteorological station ($\overline{U}_r$) to our collector heights ($\overline{U}_{(z=o.5)}$).

The approach to calculating local wind speeds from a reference value follows Greene and Johnson (1996). As with their study, I began by assuming a power law profile well above the tundra vegetation canopy as well as at the airport reference station. I use the tundra height rather than the tree height because the spindly black spruce in this area seldom form a closed canopy and are thus better regarded as emergents above the continuous shrub canopy. The data collected at the reference station height ($Z_r$ =10m) here linked to the collection site by Equation 9:

$$U_{(z)} = \ln((z-d) \div z_o)0.317(z_h{}^{alpha})U_r \qquad (9)$$

where $U_{(z)}$ is the horizontal wind speed at height z (the *same* wind speed above both the airport and above the tundra if we link them at the suitably high altitude of two times the canopy height), d is the zero plane displacement height (assumed to be 2/3 of $Z_h$ (canopy height)), $z_o$ is the roughness length, assumed to be $0.105z_h$, alpha = 0.14, which relates $U_z$ to z at the reference station, and $U_r$

is the horizontal wind speed at the reference (i.e. meteorological station (Greene & Johnson, 1996).

Equation 9 above links the reference station data to the top of the canopy layer. Equation 10 below describes the wind in the top half of the canopy layer. A negative exponential decline in horizontal wind speeds is assumed:

$$U_{(z)} = U_{zh}(\exp(-c(1-(z \div zh)))) \qquad (10)$$

where c is the coefficient that governs the rate of decline of U in the canopy (higher c value for a dense forest) (Greene & Johnson, 1996).

I do not expect the wind to continue declining at an exponential rate in the lower half of the canopy. Therefore, I assume an invariant wind for the lower half, based on the wind value obtained at $z=z_h/2$ (Equation 11):

$$U(z) = Uzh(\exp(-c \div 2)) \qquad (11)$$

The model proposed applies these three equations for horizontal wind speeds, then averages the horizontal wind from $Za$ (release height) to $Z=0$ (ground). This averaged wind speed is then used in the Okubo-Levin model (The reader is reminded that this same approach can be used to estimate the wind speed at 0.5m, the collection height).

A final modification was made to the model. Okubo and Levin (1989) inputs only the mean horizontal speed whereas clearly there is a great deal of variation around that value. I have allowed for a lognormal distribution of horizontal wind speeds, and thus I have a program that must sum the results of a large number of runs for the Okubo and Levin model (one run for each horizontal speed drawn from the lognormal distribution).

The resulting equation from the modifications is thus:

$$Q_{(dx)} = \frac{Q_x X_t (\overline{U}_{(z=0.5)}}{2\pi X^2 f} \qquad (12)$$

The source strength (grains produced/m$^2$ within the source) was difficult to estimate because the area involved is at the regional scale. I did it as follows. First, tree density was recorded (see above) near the transect. The average number of pollen grains produced per male cone was previously estimated in an earlier study to be 46,200,000 pollen grains per tree (± 62,900,000)(Resch, 2002). An attempt was subsequently made to correlate the number of male cones produced per tree, based on tree size, in order to predict grains/m$^2$. Two additional variables were used in estimating source strength: a vegetation reducer, and a time reducer. The vegetation reducer was based on Post (1996) and Lee et al. (1999) who stated that black spruce-dominated forests represent 44% of land cover in the Inuvik region (far lower of course than in the densely treed areas where I was sampling). That is, at great distances from the transect I will reduce the expected pollen output by 56%. The time reducer consisted in reducing the amount of pollen released by the fraction of the entire pollination season during pollen was collected for this study.

The significance of each model type will be tested using a correlation of observed with the predicted deposition values. Further, when the correlation is significant, using a t-test, I will test whether the slope is significantly different from 1.0, and the intercept significantly different from 0.

# **5** RESULTS

## 5.1 Vertical pollen release

Figure 13 depicts the results of four trials intended to test for no bias toward either updrafts or downdrafts during pollen release. In 2 trials (Trial 1 and trial 3, see Figure 15), the majority of pollen grains abscised laterally, with a preference for the prevailing wind direction. In trials 2 and 4, however, 42% and 48% of grains abscised in the downwards direction, respectively. Upwards movement was consistently lower than downward movement in all four trials. Table 2 shows the actual number of pollen grains collected for each trial.

2 $\chi^2$ tests were performed on the data. A significant difference between the 4 sides was found (df=3, p<0.001). Likewise, there was a significant difference between the 2 vertical sides (up and down) (df=3, p<0.05).

Figure 13. Results for 4 trials on vertical movement of grains.

Each bar represents the percentage of grains being released in one of 4 directions. The “top” direction consistently received the least amount of grains, while the largest percentage of grains went either to the side, or vertically downwards, depending on the trial. For all trials, one horizontal side consistently received a larger percentage of grains.

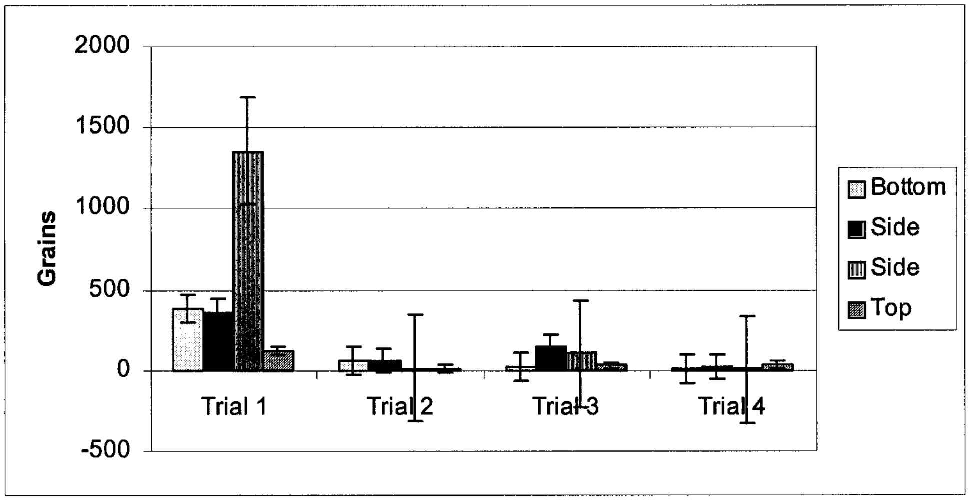

2000
1500
1000
500
0
-500
Grains
Trial 1
Trial 2
Trial 3
Trial 4
Bottom
Side
Side
Top

Table 2. Pollen grain counts for vertical dehiscence .

| | Trial 1 | Trial 2 | Trial 3 | Trial 4 |
|---|---|---|---|---|
| **Bottom** | 379 | 58 | 23 | 8 |
| **Side** | 363 | 57 | 147 | 25 |
| **Side** | 1356 | 15 | 107 | 7 |
| **Top** | 118 | 9 | 29 | 37 |

## 5.2 Pollen dispersal

### 5.2.1 Model inputs for source pollen production

Recall that the modified model predicts the number of grains falling to the ground, and that this amount is related by $\overline{U}_{(z=0.5)}/f$ to the amount collected at 50 cm from the ground. Using equations 1, 2, and 3 above, I calculate the average $\overline{U}_{(z=0.5)}/f$ ratio to be = 7.8 m/s. Therefore, all of the observed data was divided by 7.8.

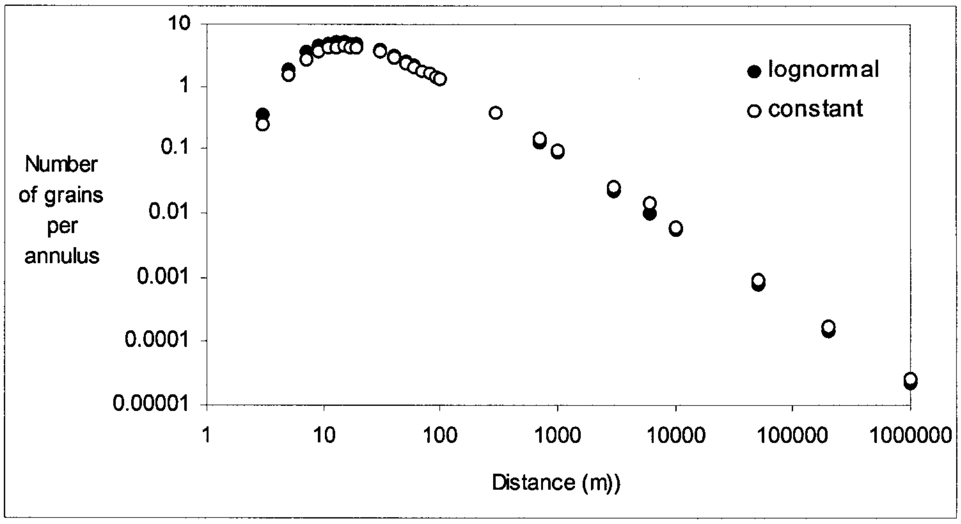
Figure 14 and Figure 15 show the results of allowing variation in the horizontal wind speeds; in particular, here, as per convention, I used a lognormal distribution of horizontal winds. The model ran by sequentially using 200 horizontal wind speed values chosen from a lognormal distribution and weighted by their probability. When the terminal velocity is tiny (as in Figure 14) the addition of a distribution of horizontal wind speeds adds little to the predicted distance variation because vertical turbulence dominates. Here, the terminal velocity is 0.05 m/sec, a value typical of conifer pollen. By contrast, when the terminal velocity is large (Figure 15), horizontal winds can play a larger role, and so the added realism is called for. In this figure, the terminal velocity is 1.0 m/sec, a value typical of winged seeds.

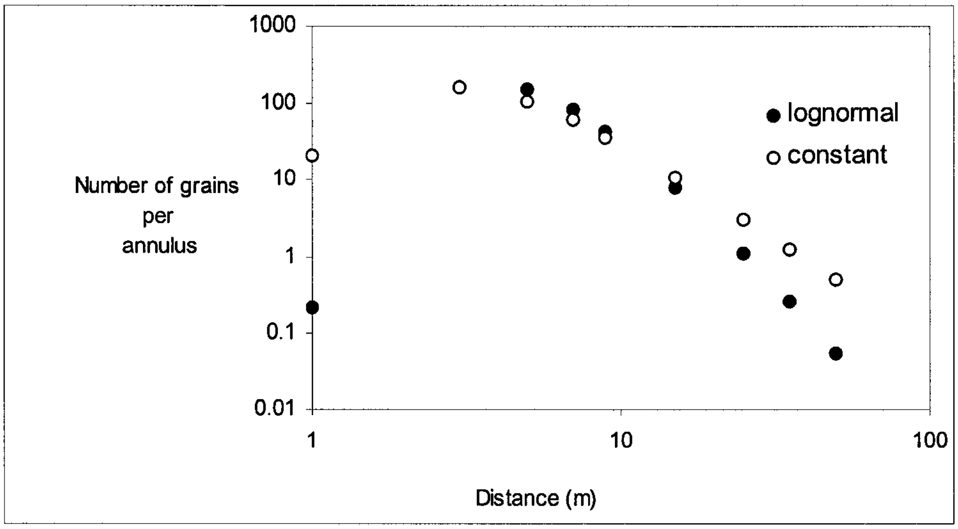
Figure 14. Predicted dispersal curve with $f$ =0.05 m/s.

(Top graph) Graph of number of grains with increasing distance from a point source using the Okubo-Levin model with a constant horizontal wind speed vs. the same model with lognormal distribution of horizontal wind speeds.

Figure 15. Predicted dispersal curve with $f$ =1.0 m/s.

(Bottom graph) As in Figure 26 but with a terminal velocity of 1.0 m/sec.


10
1
0.1
0.01
0.001
0.0001
0.00001
Number of grains per annulus
1
10
100
1000
10000
100000
1000000
Distance (m))
● lognormal
○ constant


1000
100
10
1
0.1
0.01
Number of grains per annulus
1
10
100
Distance (m)
● lognormal
○ constant

Source density was defined as pollen grains/m$^2$ present within the source area. First I estimated male cone number (Nc) as a function of basal area (B). For *P. mariana* trees, a log-log regression of number of male cone number on tree basal area (in cm$^2$) yielded:

$$Nc + 1 = 3.03 * B^{0.91} \qquad (13)$$

(n=300, $r^2$=0.164; p<0.05). Based on the mean basal area of 7.4cm$^2$ for the nearby forest in 2002, the average number of male cones per tree was determined to be 18.74. The relationship was used in our estimate for source strength despite the low $r^2$ value ($r^2$=0.164, p<0.05), due to the lack of relevant data in the literature.

The model estimates pollen input from distances as far as Alaska (>1000 km); thus, the pollen production needed to be reduced because at the landscape and regional scales much of the landscape is composed of other tree species or treeless bogs, as well as lakes and rivers. Further, toward the north, one soon reaches arctic treeline. According to Post (1996) and Lee et al. (1999), spruce trees represent 44% of the land cover in the Inuvik region. I will use this as typical for the area extending west toward Alaska, and will assume that there are no sources beyond arctic treeline. The number of pollen grains per m$^2$ (obtained by multiplying the tree density, $N_d$ by the number of pollen grains produced per tree, $p$ ) was thus multiplied by the reducing factor $L$ =1-0.44 = 0.56. For the source area within several km of the transect, and examined from photos taken from a helicopter, $L$ =1. The burn (2002) and the large clearing (2003) through which the transects ran, were not considered source areas. In addition, the expected number of grains produced within the source area was multiplied by the fraction of the pollination season ($t$ = 120 hours) represented by the short collection period ($t_c$ =3 hours in 2002). Thus, the final estimate of the source density, $Q$ (number of grains/m$^2$), within any single block of source trees is:

$$Q = \frac{N_d p L t_c}{t} \qquad (14)$$

Since the average forest is not as dense as this particular location, I used the high tree density ($N_d$=2.33) for near-sources, and the 2003 tree density (Nd=0.265) for farther sources within a few km of the transect (see Section 8.1). Thus, for 2002, Q=252973 grains/m$^2$.

The same formula for $Q$ was used for the 2003 values. As mentioned above, tree density for 2003 was 0.265 trees/m$^2$, average basal area was 9.35 cm$^2$, and number of male cones per tree was estimated via the power law regression as 23.17. The daytime collection period lasted 13 hours, and the night collection period 18 hours. The total pollination period was again estimated to be 120 hours (5 days). Thus, Q=161915 grains/m2 for the 2003 daytime collection, and 224190 grains/m$^2$ for the nighttime collection.

### 5.2.2 Observed dispersal of the pollen crop: comparison of 2 models

#### 5.2.2.1 2002 Results

The primary source for the pollen had a density of 2.33 trees/m$^2$, with an average height of 5.04 m, and an average diameter at the base of 3.07 cm. As observed on site, the temperature dropped by approximately 5°C, and RH increased from approximately 40-80% during pollen collection. The average wind speed for the collection period was 4.6 m/s, and the average wind direction was 315° (based on 360°, 0 and 360 being due north). Given that the collectors all faced north, winds with a direction of 0 or 360 were considered ideal, and between 270 and 90 acceptable, as these would still carry pollen grains into the traps (see angular argument above).

The following sections show the results comparing the Okubo and Levin (1989) model with the modified model. Results are compared using a linear regression between predicted (models) and observed values. If a significant correlation is found, I present also the slope and intercept significance.

##### *5.2.2.1.1 Original Okubo and Levin prediction (1989) for 2002*

The 2002 observed values (grains/m$^2$) were compared to the values predicted by Okubo and Levin (1989). Their model greatly underpredicts the pollen catch throughout the transect. Correlation results are not significant ($r^2$=0.17, p>0.05, n=19).

### *5.2.2.1.2 Modified Okubo and Levin (1989) prediction for 2002*

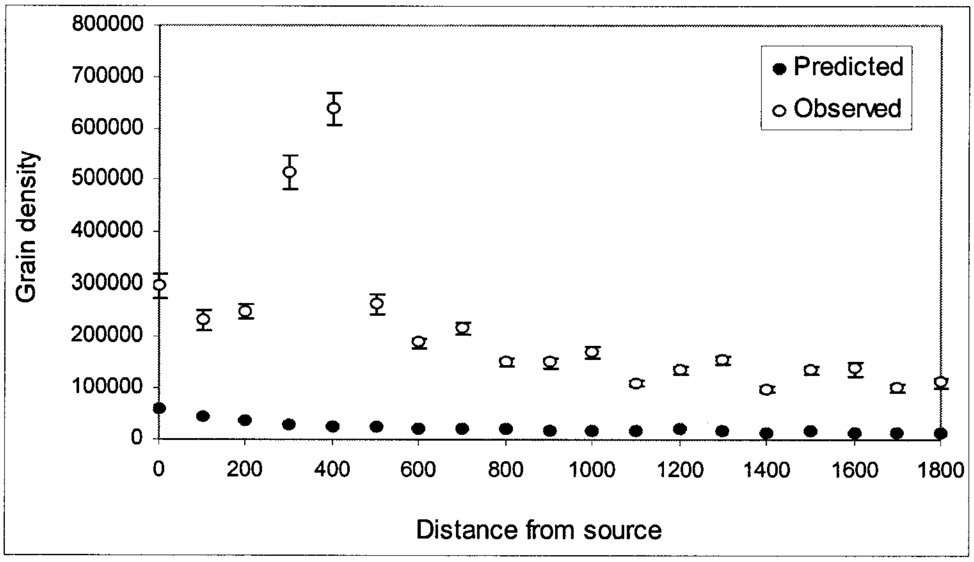
Figure 17 shows the observed and predicted pollen deposition values for the modified version of the model for 2002. Generally, the model modestly overpredicts the number of grains (although it underpredicts at the source edge), but is able to express the observed increase in pollen catch near source trees (at 300, 400, and 500, as well as at 1200 m; see Section 8.1 below). A correlation of the modified model predictions vs. the observed values for 2002 was significant ($r^2=0.53$; $p<0.05$; $N=19$). The intercept was not significantly different from 0 (t-test; $p>0.05$) but the slope was slightly lower than 1.0 (t-test; 95% confidence interval on the slope was 0.31 to 0.89); that is, the model is underestimating the points along the transect where the observed deposition is strong.

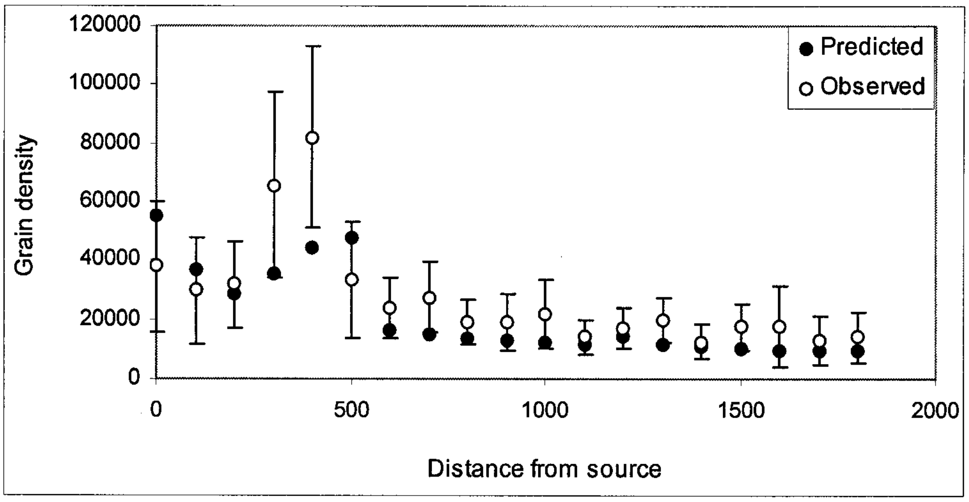
Figure 16: Observed and predicted (Okubo and Levin, 1989) values for pollen dispersal along 2002 transect.

(Top graph) The model badly underpredicts the pollen catch along the entire transect. Although it is not obvious in this figure, the model accurately predicts the peaks where pollen sources are near collectors (i.e. at X=300, 400, 500 and 1300). Regression results are not significant ($r^2$=0.17, p>0.05, n=19).

Figure 17. Observed and predicted (modified model) pollen dispersal values for 2002 pollen collection.

(Bottom graph) The model predicts the increase in pollen catch at 300, 400 and 500 (due to a small area source located within the transect (see section 8.1). In addition, the model predicts the increase in grain density at 1300, where a small patch of spruce trees was located near the transect. Regression results are significant ($r^2$=0.53; p<0.05; N=19).


Grain density
800000
700000
600000
500000
400000
300000
200000
100000
0
0
200
400
600
800
1000
1200
1400
1600
1800
Distance from source
● Predicted
○ Observed


Grain density
120000
100000
80000
60000
40000
20000
0
0
500
1000
1500
2000
Distance from source
● Predicted
○ Observed

#### 5.2.2.2 2003 results

Pollen was collected during the entire 2003 pollination period for black spruce. This occurred between June 26th and July 1st 2003. However, I present here the results of 2 collection periods alone: I chose to present the collection periods where the wind direction was most favorable for comparison with the model, as the model cannot accommodate wind directions that are not towards the adhesive surfaces. The primary *Picea* source had an average density 0.265 trees/m$^2$ with an average height of 2.87 m, and an average diameter at the base of 3.4 cm.

Average wind speed for the daytime collection (June 27th 9AM to 9PM) was 3.6 m/s, and average wind direction was 63°. For the nighttime collection period June 27 9PM to 28 2PM), the average wind speed was 3.4 m/s, and the average wind direction was 88° (predominantly from the East).

##### *5.2.2.2.1 Okubo and Levin (1989) prediction for 2003 daytime*

Figure 18 depicts the results of the original Okubo and Levin (1989) model and the observed pollen deposition values for the 2003 daytime collection period. The model greatly underpredicts the pollen count along the transect. Correlation results from the original model vs. observed for the 2003 daytime collection were not significant ($r^2 = 0.32$, $p<0.05$; N= 13).

##### 5.2.2.2.2 Modified model prediction for 2003 daytime

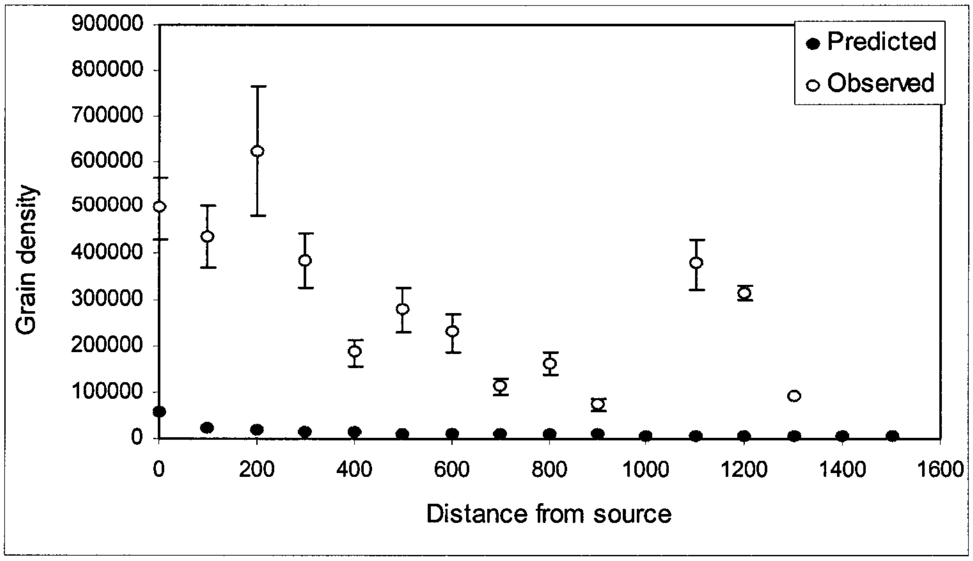
Figure 19 shows the observed and predicted values for the daytime 2003 collection period. The model overpredicts the density of grains at the edge of the source, and underpredicts the contribution of the patch of spruce trees near 950 m along the transect (see Section 8.2). However, both curves follow similar patterns and when correlated against one another, and provide a significant result ($r^2=0.41$; $p<0.05$; N= 16). The intercept was not significantly different from 0, while the slope (0.24) was significantly smaller than 1.0.

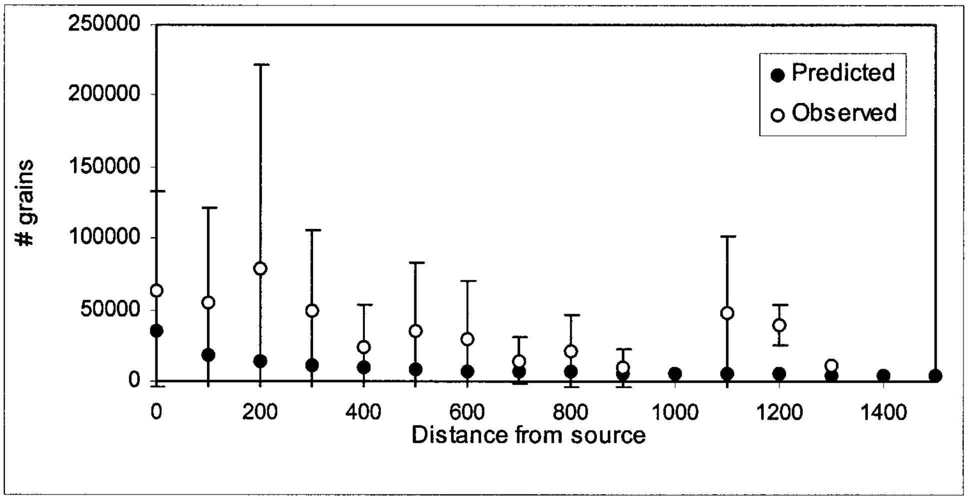
Figure 18. Observed and predicted (Okubo and Levin, 1989) values for 2003 daytime collection.

(Top graph) Model underpredicts pollen counts on the edge of the pollen source, and along the transect. Regression results are significant ($r^2 = 0.32$, $p<0.05$; N= 13).

Figure 19. Observed and predicted (modified model) values for 2003 daytime collection.

(Bottom graph) Model badly underpredicts the number of grains at the edge of the source, and along the transect, although not as badly as Okubo and Levin (1989). Regression results are significant ($r^2=0.41$; $p<0.05$; N= 16).


Grain density
900000
800000
700000
600000
500000
400000
300000
200000
100000
0
0
200
400
600
800
1000
1200
1400
1600
Distance from source
● Predicted
○ Observed


# grains
250000
200000
150000
100000
50000
0
0
200
400
600
800
1000
1200
1400
Distance from source
● Predicted
○ Observed

### *5.2.2.2.3 Okubo and Levin (1989) prediction for 2003 nighttime.*

Figure 20 shows the results of the 2003 nighttime collection, using Okubo and Levin's original model. As before, the model greatly underpredicts pollen catch. The correlation of observed on predicted was not significant ($r^2$=0.01, p>0.05; N= 16).

### 5.2.2.2.4 Modified model prediction for 2003 nighttime.

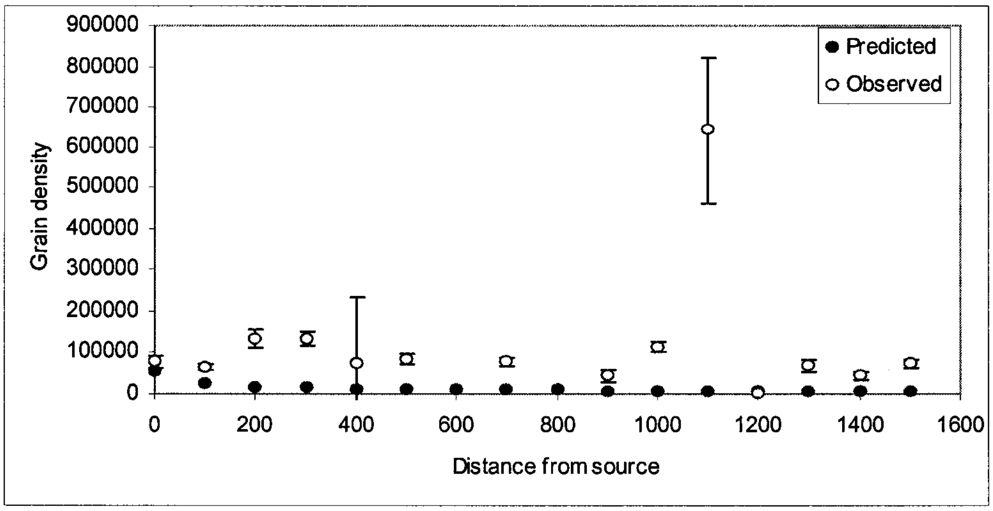
As with the daytime collection, the model overpredicts the amount of pollen grains found at the source edge. As predicted by the wind direction values obtained, which were predominantly easterly, the observed curve is essentially flat, with a pronounced peak where the patch of spruce trees was present, at x=1050. Again, the model greatly minimizes the input from the patch. Correlation results are not significant ($r^2$=0.02, p>0.05, n=12).

Figure 20. Observed and predicted (Okubo and Levin, 1989) values for 2003 nighttime collection period.

(Top graph) Model still underpredicts the pollen catch along the transect, but accurately predicts the pollen catch at the edge of the source. Regression results are not significant ($r^2$=0.01, p>0.05; N= 16)

Figure 21 Observed and predicted (modified model) values for 2003 nighttime collection period.

(Bottom graph) The model overpredicts the amount of pollen grains found at the source edge. The observed dispersal curve is essentially flat, intuitively due to the westerly winds present throughout the collection period. Regression results are not significant ($r^2$=0.02, p>0.05, n=12).


Grain density
900000
800000
700000
600000
500000
400000
300000
200000
100000
0
0
200
400
600
800
1000
1200
1400
1600
Distance from source
● Predicted
○ Observed

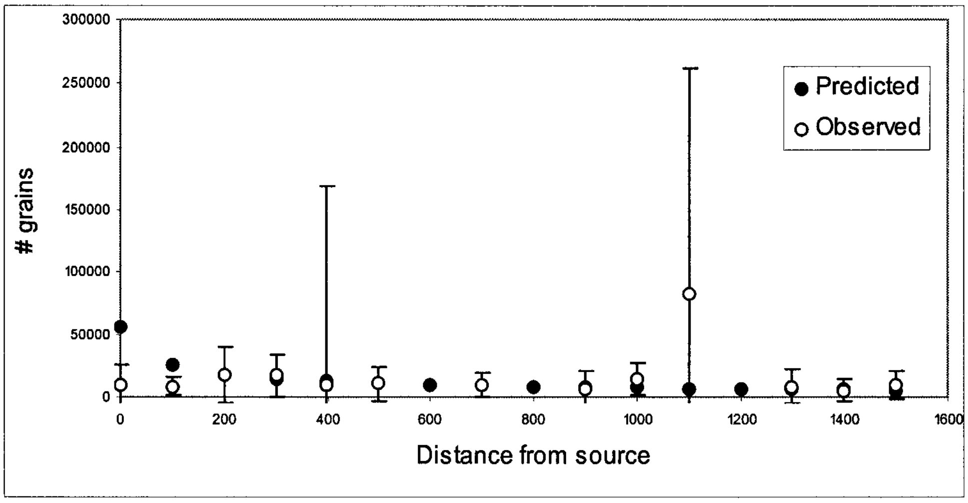

# grains
300000
250000
200000
150000
100000
50000
0
0
200
400
600
800
1000
1200
1400
1600
Distance from source
● Predicted
○ Observed

Table 3. Summary of Correlation results for both models

| **Trial** | **Okubo and Levin (original)** | | **Modified Okubo and Levin (1989) model** | |
|---|---|---|---|---|
| | p-value | $r^2$ | p-value | $r^2$ |
| **2002** | $p>0.05$ | 0.18 | $p<0.05$ | 0.53 |
| **2003 Daytime** | $p>0.05$ | 0.32 | $p<0.05$ | 0.41 |
| **2003 Nighttime** | $p>0.05$ | 0.01 | $p>0.05$ | 0.02 |

### *5.2.2.2.5 Comparison of the 2 modifications made to Okubo and Levin (1989) model*

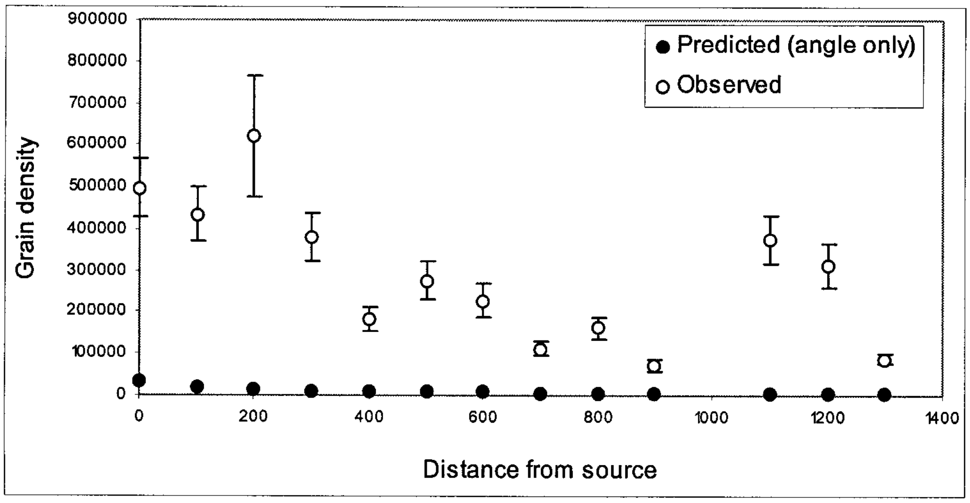
Two modifications made to the Okubo and Levin (1989) model were tested individually against the 2003 daytime values. When the angle argument alone was correlated against the observed values, a significant correlation was obtained ($r^2$=0.37, $p<0.05$, N=16), and this $r^2$ value was much higher than that obtained in the original model ($r^2$=0.32). The slope was significantly different from 1, and the intercept was significantly different from 0.

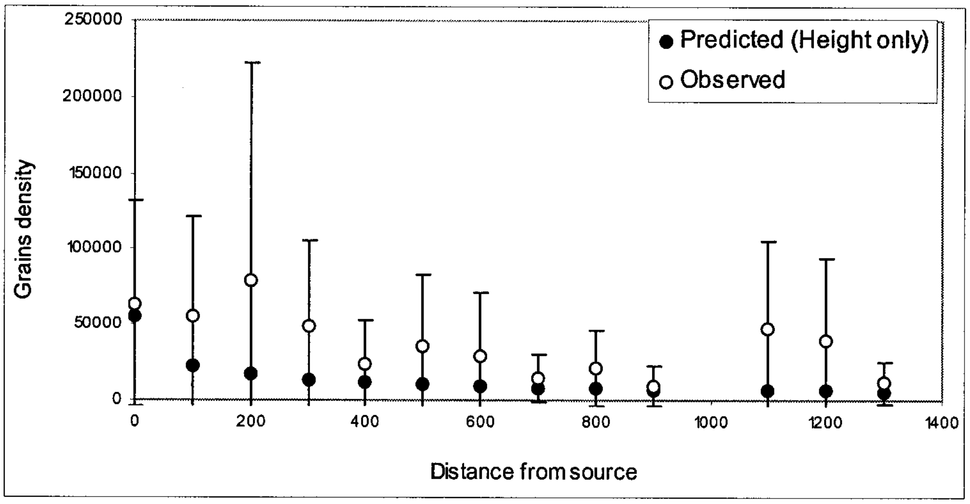
The result of the correlation between the height argument alone and the 2003 daytime observed values was also significant ($r^2$=0.32, $p<0.05$, N=16), but no higher than that for the original model. Similarly, the slope was significantly different from 1, and the intercept was significantly different from 0.

In summary, the angle argument is important in expressing the observed decline along the transect (and thus increases the $r^2$ relative to the original model). The height argument is important because it dramatically raises the predicted values and makes them closer in magnitude to the observed data.

Figure 22. Modified model results with angle argument only. Correlation results are significant ($r^2$=0.37, $p<0.05$, N=16).

Figure 23. Modified model results with height argument only. Correlation results are significant ($r^2$=0.32, $p<0.05$, N=16).


Grain density
900000
800000
700000
600000
500000
400000
300000
200000
100000
0
0
200
400
600
800
1000
1200
1400
Distance from source
● Predicted (angle only)
○ Observed


Grains density
250000
200000
150000
100000
50000
0
0
200
400
600
800
1000
1200
1400
Distance from source
● Predicted (Height only)
○ Observed

# 6 Discussion

## 6.1 Vertical pollen release

The initial direction of pollen release ought to be of some interest but no model explicitly incorporates this. Instead a model such as that of Okubo and Levin (1989) assumes that there is no bias in the vertical. I found significant differences between the four release directions tested. More importantly, there was a significant difference between downdrafts over updrafts. If this finding is a general phenomenon, then this would mean that there will be enhanced deposition near the source tree. Clearly however, I need more data than I have at present (I have only four collection periods) in order to be sure that this bias is real. That is, it is possible that during my collection periods downdrafts were more common than updrafts irrespective of pollen release.

## 6.2 Pollen dispersal

This thesis represents the first attempt to validate the simple advection-diffusion model of Okubo and Levin (1989). It met with mixed success.

Although Okubo and Levin's original model predicts the general "shape" of the dispersal curve from an area source in relation to my observed values, it is clearly greatly underestimating the actual deposition. Most likely the main reason for this is that I am capturing pollen at a height of 0.5m rather than at the ground. Thus, the modified model, which increases the expected deposition (by $\overline{U}_{(z=o.5)}/f$) at a height above the ground, has only a very slight tendency to underestimate the magnitude of the deposition. This modification, though, is not really a change in the way the model predicts the pollen deposition per se, and so I can conclude that Okubo and Levin's model (1989) remains relatively accurate.

Likewise, Okubo and Levin's (1989) original model did not have an argument for the angle at which the grain approaches the collector because they pictured ground-level deposition. For a sampler such as a Roto-rod which actively sweeps pollen from the air, from a 360° angle, no change is needed. But for the passive collectors we used the direction of grain travel necessarily affects the catch. It is noteworthy that my modified model was a significant predictor in 2 of 3 cases, whereas the original model was never significant in any of the three collection periods.

In a very general way, the modified model could predict the observed density of pollen at the forest edge (x=0) for all three trials. That is, the prediction was well within an order of magnitude. Given the tremendous number of assumptions that go into the model (especially estimating the density of source trees farther from the transect, and the assumption that no pollen is captured prior to reaching the collector), it is encouraging that the predicted edge deposits are so close to the observed values.

Nonetheless, the modified model does tend to underestimate deposition, especially near source trees. In both of the significant correlations the slope is significantly smaller than 1. In 2002 this was due to the 250m wide band of trees that the transect passed through, while in 2003 the flattening of the slope was mainly due to the patch at 1 km along the transect. The explanation for this problem may lie into the pollen release bias noted earlier. That is, it may be that more pollen than expected is being deposited very close to the individual source trees. In the future, it would certainly be of interest to examine closely the pollen catch around a small, well-isolated patch of trees.

Allowing horizontal wind speed to have a lognormal distribution from Za to Z=0.5, is inconsequential in predicting pollen dispersal. This is due to the small settling velocity for pollen grains, which makes vertical turbulence far more important in determining the magnitude of deposition in both the near and far tails of the dispersal curve. Note, however, that application of the model to seeds (with typically far higher terminal velocity than pollen) will lead to an underestimation of the deposition in the tails if this additional horizontal wind speed variation is not explicitly included. On the other hand, my other two modifications to the model would not be important for seeds. Whether one collects the seeds on the ground or in a trap virtually at the ground surface, one need not worry about either height or the angle of approach of the seed.

One of my three trials did not provide a significant correlation between the predicted (modified model) vs. observed. For the 2003 nighttime collection, the wind was blowing at an acute angle toward the traps, and thus one expects very little decline in deposition with distance. Most of the differences will then be due to microsite variation in the wind speed, something that the model utterly ignores. But for the two trials where one expects a strong observed decline with distance the model made a significant prediction. Thus, it appears that the model is, in some general way at least, expressing the dispersal curve correctly.

A comparison of the two major modifications made to the Okubo and Levin (1989) model revealed that the angle argument alone yields a larger $r^2$ value, but does not predict the magnitude of the curve as well as the height argument. By contrast, the height argument alone yields a smaller $r^2$ value, and a greater magnitude in grain density prediction. These results show that the angle argument may be reducing the predicted pollen catch from a source (either on the edge of the forest, or a patch along the transect) by too much. Further studies on the behavior of this modification are recommended.

This study can be relevant in several areas of biological studies. Knowledge about pollen dispersal can aid in providing estimates on potential tree migration rates, and applied in climate change models. Pollen dispersal models can also provide information to allergy sufferers. Last, knowledge of the patterns of dispersal of pollen grains can aid in crop improvement, by providing insights into reducing the potential for cross-contamination of crops.

We can estimate the probability of fertilization as a function of distance from a forest. Many authors have concluded that rapid, climate-forced migration requires large occasional "jumps" of several km at a time. While such rare seed dispersal events undoubtedly occur, one wonders what the probability of fertilization would be subsequently for such isolated colonists. That is, if the isolated tree subsequently produces few seeds then it cannot contribute greatly to a speeding of the migrational velocity at the range limit. I will use, as before, black spruce at a density of 0.27 trees/m$^2$, each producing 1.5 million grains and each grain falling at a terminal velocity of 0.035m/sec. The reference station horizontal speed is set at a mean of 3.5 m/sec, the canopy in question is tundra shrubs at a height of 1m, and both the male cones and the female cones (the "passive collector") are set at the same height of 2m. The wind speed at 2m height should be 2.68 m/sec and thus the ratio $\overline{U}_{(z=0.5)}/f$ becomes 77 (rather than 8 as when I collected pollen at a much lower height). Finally, the target is the micropylar drop assumed to have a cross-sectional area of about 1mm$^2$ (i.e. one millionth of the area I have been using so far for reporting grains densities). At 1m from the forest, my "isolated" micropyle should receive 5.8 grains. Using a Poisson argument (not quite correct; as shown by Niklas and Paw (1982) the cone scales can preferentially channel the pollen toward the micropyles. Then the probability of pollination (p) becomes p=1-exp(-5.8), which is essentially 1.0. Using this same reasoning, the probability of fertilization would be 0.83 at 100m from the forest, 0.61 at 500m, 0.42 at 1km, and 0.14 at 4km. Thus, ignoring selfing, which will likely contribute to an isolated individual, an isolated tree that has moved well beyond the present range limit will have serious deficiencies in its pollen receipt from another, and should therefore have reduced seed set. This should slow the migration rate appreciably compared to what can happen in a model that simply ignores the issue of pollen receipt.

Much remains to be done in testing the assumptions of my version of the model. For example, in a future experiment, adhesive surfaces should also face away from the expected predominant wind direction. This is shown in the 2003 nighttime trial: neither of the models predicts the dispersal significantly. I suspect that a major reason for this is that, for the entire collection period, the wind was easterly, something that the proposed model cannot deal with to date. In addition to this, one could test the simplifying assumption that significant lee-side deposition does not occur. Also by placing a set of radial transects around a small, very isolated patch, one could test the argument for the effect of an oblique trajectory angle on the probability of capture.

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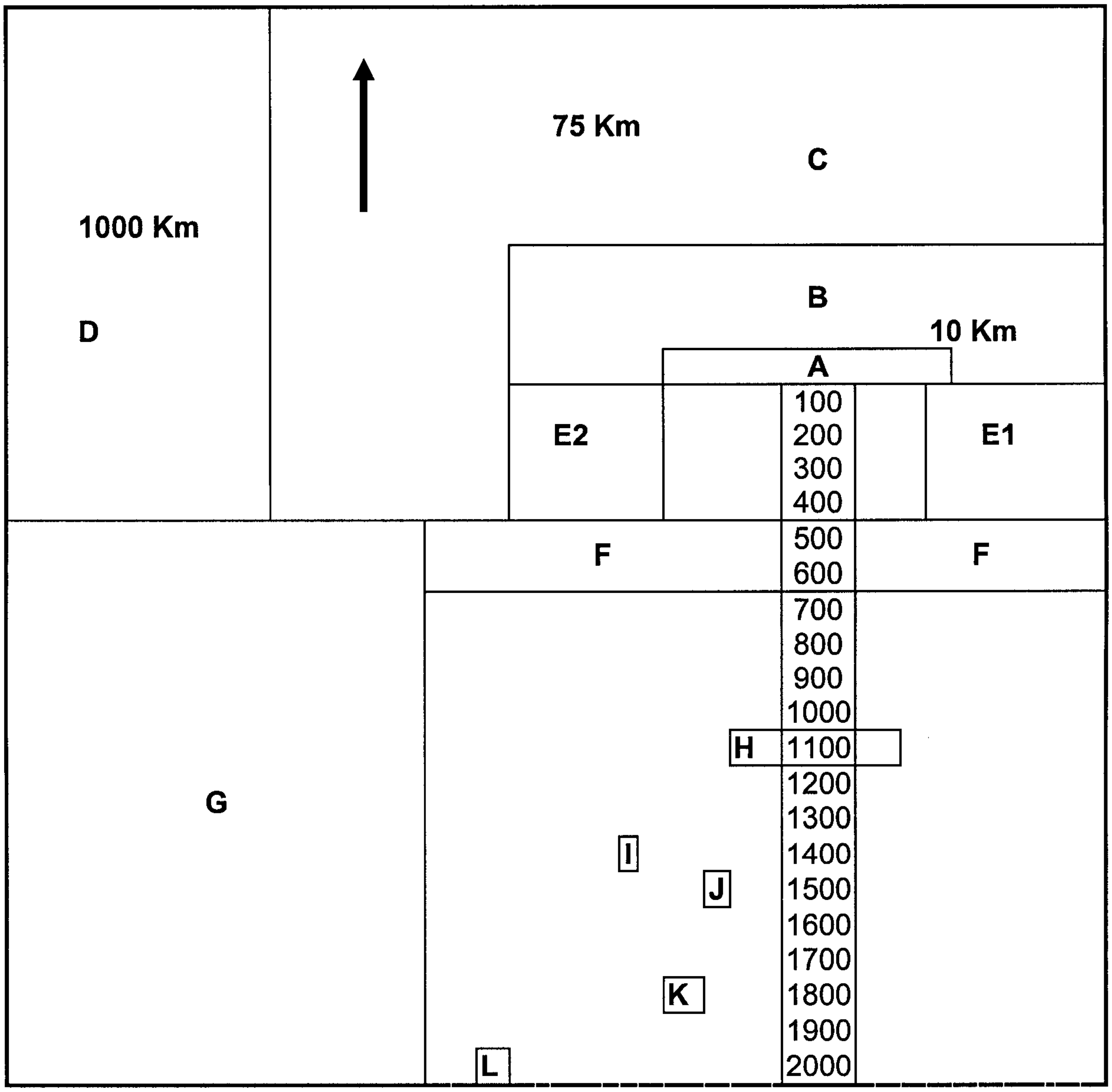
# 8 Appendices

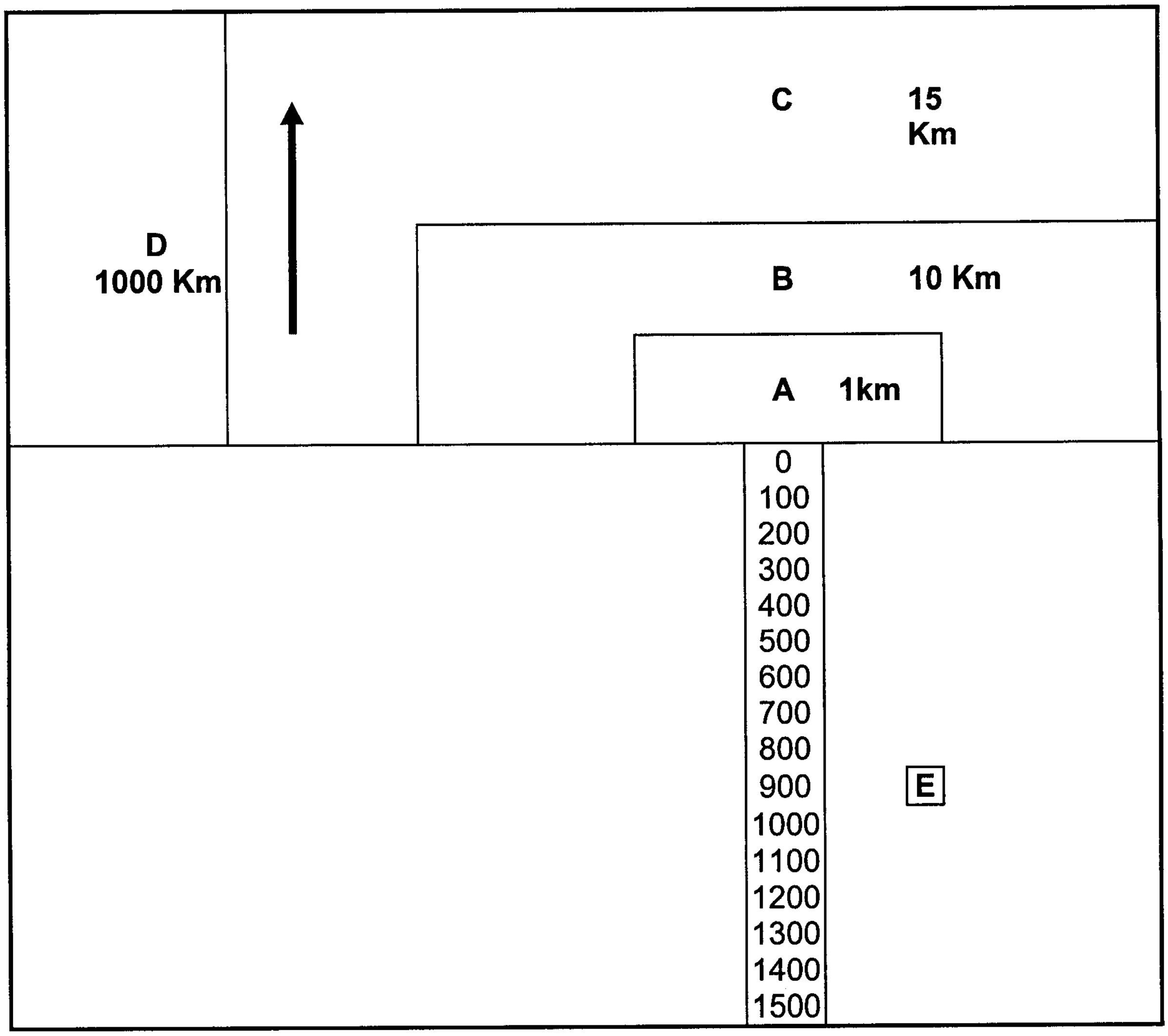
## 8.1 Appendix 1Map of 2002 transect with sections used in model.

Depiction of inputs from the 2002 transect into the model. North arrow shown. Numbers (100 to 2000) represent collection sites every 100 meters along the transect, up to 1300 m away form a significantly large pollen source (from 700 to 2000). In order to input a patch of trees into the model, coordinates must be given in the form of x and y variables. The resulting inputs are represented by each section depicted here (A through L). Therefore, model was run once for section A, once for section B, and so on. Sources extend 10Km in the eastward direction, 85 Km north, and 1000Km west, representing eastern treeline, northern treeline, and Alaska, respectively. Figure is not to scale.


75 Km
C
1000 Km
D
B
10 Km
A
E2
E1
100
200
300
400
F
500
600
F
700
800
900
1000
H
1100
1200
G
1300
I
1400
J
1500
1600
1700
K
1800
1900
L
2000

## 8.2 Appendix 2 Map of 2003 transect.

Depiction of model section inputs for 2003 transect. North arrow shown. Numbers (0 to 1500) represent collection sites every 100 meters along the transect, up to 1500 m away form a significantly large pollen source. Sections A through E each represent one run of the model. Section E represents a small patch of spruce trees along the transect. Sources extend 10Km in the eastward direction, 25 Km north, and 1000Km west, representing eastern treeline, northern treeline, and Alaska, respectively. Figure is not to scale.


C
15
Km
D
1000 Km
B
10 Km
A
1km
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
E