ENGELMANN SPRUCE AND SUBALPINE FIR SEED DISPERSAL IN THE ESSF WET COLD SUBZONE

By

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Abstract

Conventional silviculture practices used on lower elevation stands have failed to adequately restock stands within the Engelmann spruce/subalpine fir zone (Butt 1990, Farnden 1994). The supply of viable seed is critical for successful natural regeneration (Rowe *et al.* 1970). This study was conducted at the Sicamous Creek site in the ESSF zone of interior British Columbia over the winter of 1997-1998. Four harvest treatments (Individual Tree Selection (ITS), 0.1 ha cut, 1 ha and 10 ha clearcuts) were analyzed in terms of the seed dispersed by the Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) trees remaining after harvest. The spruce seed populations in the ITS and 0.1 ha treatments were not statistically different from the uncut spruce seed population; however, the quantity of fir seed was reduced significantly. Within the 10 ha and 1 ha clearcuts the relative composition of Engelmann spruce to subalpine fir seed increased to a ratio of over 5 to 1 from 1.7 to 1 in the uncut stands. This compositional change suggests spruce seed is more amenable to wind dispersal than fir seed. The south edge supplied the most seed into the clearings, while the north edge contributed the least. The amount of seed deposited closest to an edge was positively correlated to the frequency of its respective prevailing winds; however, the magnitude of the relationship declined as the clearing decreased in area.

A mechanistic seed dispersal model (DISPERSE) was developed to estimate the spatial distribution of seed in a clearing. The spatial distribution of spruce and fir seed were simulated for the wind directions and velocities recorded at the Sicamous Creek site, in conjunction with the corresponding tree heights and aerodynamics inherent to the seeds. DISPERSE estimated the spatial distribution of seed in the 10 ha clearing accurately; however, its predictions did not adequately characterize the decline of seed densities with distance from the edge in the 1 ha clearing.

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1.0 Introduction

Until the mid 1980's, forestry operations in British Columbia were concentrated in lower elevations (<1000m) (Farnden 1994). It has since become economically feasible to harvest trees located at higher elevations such as the Engelmann spruce/subalpine fir biogeoclimatic zone (ESSF). The ESSF ranges from a minimum altitude of 1000m to 2000m (Meidinger and Pojar 1991).

As the name of the ESSF biogeoclimatic zone suggests, the predominant tree species are Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*). Often Engelmann spruce interbreeds with white spruce (*Picea glauca*) in this zone and it is difficult to differentiate between the pure and the hybrid spruce species. Hybrid spruce is commonly called interior spruce. High elevation spruce (1400m-1600m) found at Sicamous Creek study site are considered to be Engelmann spruce (Coates *et al.* 1994). Lower elevation stands consist primarily of pure spruce or a mix of spruce and fir. At higher elevations, stands are predominantly fir. Lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*) can also occur as seral species (Farnden 1994). At the upper elevations, the ESSF is characterized by open parkland with trees clumped and interspersed with meadow, heath and grasslands (Still *et al.* 1994).

Conventional silviculture practices used on lower elevation stands have failed to adequately restock stands within the ESSF zone (Butt 1990, Farnden 1994). The supply of viable seed is critical for successful natural regeneration (Rowe *et al.* 1970). Seed dispersal is a key ecological process and a better understanding would aid forest managers to make informed silviculture decisions that minimize costs. The Sicamous Creek Project (SCP) provided an opportunity to study Engelmann spruce and subalpine fir seed dispersal in relation to four harvest treatments, namely: Individual Tree Selection (ITS), 0.1 ha cut, 1 ha clearcut and 10 ha clearcut. The overall objective of the thesis is to gain a better understanding of the factors influencing seed dispersal as well as to improve the methodology of predicting seed dispersal. The specific objectives of the thesis are to:

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1. review the literature on modeling seed dispersal;

2. analyze the influence that various harvest treatments have upon the supply of Engelmann spruce and subalpine fir seed;

3. assess the relationship between windward winds and seed dispersal; and

4. specify a model to simulate seed dispersal into open areas.

1.1 Engelmann Spruce and Subalpine Fir Seed Supply

The inability of Engelmann spruce and subalpine fir to consistently produce seed is a major deterrent to successful natural regeneration. The section discusses the ability of Engelmann spruce and subalpine fir to produce seed and the extrinsic (environmental) and intrinsic (internal) factors that influence spruce and fir seed production.

Coates et $al.$ (1991) indicate that seed production is influenced by size, age and density of trees. Engelmann spruce begin to produce seed between the ages of 15 and 40 years (Alexander and Sheppard 1990). Alexander (1987) concluded that spruce trees between the ages of 150 – 300 years with a dbh greater than 15cm are the primary seed suppliers. Subalpine fir seed production begins once a tree reaches 20 years of age; however, maximum seed yield does not occur until fir trees are between 150-200 years old (U.S. Department of Agriculture 1974). Klinka et al. (2000) rank Engelmann spruce and subalpine fir as moderate seed producers; however, Alexander et al. (1984) suggests that when the two species are mixed in a stand that Engelmann spruce produce relatively more seed. Using long-term conifer data, Greene and Johnson (1994) developed Equation 1.1 to estimate annual seed production of a single tree. According to Equation 1.1, seed production is correlated positively with mean basal area (T); however, seed production diminishes as seed mass (q) increases. The density of seeds at a particular site can be solved by multiplying the annual seed production of a source tree (S) with the mean density of source trees in a stand.

$$S = 3067T^{0.92}q^{-0.58} \qquad\qquad \textbf{1.1}$$

where;

S = annual seed production (seeds/m²)
T = mean basal area of source tree (m²)
q = individual seed mass (grams)

At the study site T and q were 0.0890 m² and 0.0034 grams, respectively for Engelmann spruce and 0.0453 m² and 0.0132 for subalpine fir. Equation 1.1 estimates that a spruce and fir source tree will produce 8950 and 2190 seeds, respectively. There is a higher frequency of subalpine fir trees (0.0425 tree/m2) at the study site compared to Engelmann spruce (0.0079 tree/m2), resulting in an estimation of 90 fir seeds/m² and 71 spruce seeds/m². The actual recorded seed production at Sicamous Creek in 1997/1998 was 395 spruce seed/m² and 236 fir seeds/m², exceeding their seed densities estimated with Equation 1.1.

Based on seed fall recorded over a 10-year period, Alexander et al. (1982) determined that 41% of the total spruce seed fall was viable. Alexander et al. (1984) indicated that on average 34% of subalpine fir seed are viable (Alexander et al 1984). For the 1997-1998 dispersal season at Sicamous Creek, 20% of Engelmann spruce seeds and 22% subalpine fir seeds were viable[1]. According to Alexander and Nobel (1976), Engelmann spruce and subalpine fir would be characterized as having heavy and good seed crop years (refer to Table 1.1).

Table 1.1. Ranking of annual seed production of Engelmann spruce (Alexander and Noble 1976)

Number of Viable seeds/m²	Seed Crop Rating
0-3	Failure
4-12	Poor
13-25	Fair
26-62	Good
63-125	Heavy
>125	Bumper

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[1] Personal communication with Alan Vyse (Research Forester) on April. 19, 1999

The variability of Engelmann spruce and subalpine fir seed production is not captured within Equation 1.1. The annual seed production for Engelmann spruce and subalpine fir is extremely variable. In B.C., peak spruce seed yields occur once every 4-12 years (B.C. Ministry of Forests 1990; Konishi 1985). Alexander and Noble's (1976) study identified good to bumper Engelmann spruce seed crops occur every 2-5 years. Subalpine fir averages a good seed crop every 3 years (Franklin et $al.$ 1974, LeBarron and Jemison 1953, US Department of Agriculture 1974). Due to the variability of seed production in the ESSF, Alexander (1987) concluded that adequate seed density necessary to naturally restock a stand is not a realistic expectation each year.

The climatic conditions at higher elevation can reduce the spruce and fir seed supply. Zasada and Gregory (1969) indicate that the shorter and cooler growing season at high elevation sites result in an inadequate supply of resources necessary to produce large spruce seed crops. Good seed years have been shown to correspond with warm and dry conditions during floral bud initiation the previous year. Frosts, which are more frequent at higher elevation sites, during floral bud development, significantly reduce the size of spruce and fir seed crops (Zasada 1971, U.S. Department of Agriculture1974). Studies have indicated that at the alpine timberline, trees often are unable to produce a viable seed crop (Baig 1972, Elliot 1979).

The success of a seed crop depends the proportion of cross pollination. The extent of cross pollination is dependent upon the wind and stand conditions during pollination. Engelmann spruce and subalpine fir can self-pollinate; however, it causes an increase in the frequency of empty seeds as well as genetically inferior seeds (Coates et $al.$ 1991).

The physiological condition of a tree is a critical factor influencing seed supply. Cone maturation consumes a considerable quantity of nutrients, which are not available for the next year's vegetative buds. The direct competition for nutrients results in a bumper crop rarely succeeding a bumper crop (Coates et $al.$ 1991). Bumper crops have been known to result from an environmental stress (such as frost, insect and disease) increases the sexual reproduction within a tree.

Prior to a dispersal season, insects and squirrels can reduce Engelmann spruce and subalpine fir seed supply. Schmid *et al.* (1981) reported that 28% of the Engelmann spruce seed population in the ESSF was lost to insects, especially the spruce seed worm (*Cydia = Laspeyresia youngana* Kearfott) over a four year period. Red squirrels (*Tamiasciurus hudsonicus*) commonly consume seed prior to dispersal (Alexander 1987). During bumper seed years, the impact of squirrels on the seed population is relatively slight; however, during low yielding years squirrels can significantly reduce the seed population as well as consume vegetative buds, reducing next year's seed crop (Zasada *et al.* 1978, Zasada and Gregory 1969).

Following seed dispersal, small mammals are the cause of most Engelmann spruce and subalpine fir seed loss. The primary seed consumers are deer mice (*Peromyscus maniculatus*), red voles (*Clerthrionomys gapperi* Vigors), montane voles (*Microtus montanus* Peale) and chipmunks (*Eutamias minimus* Bachman) (Alexander 1974). The seed population is impacted significantly during peak rodent populations occurring during medium to poor seed years (Rowe 1955).

1.2 Seed Dispersal

Seed dispersal patterns are dependent on the spatial location of the seed sources. According to Barrett (1966) and Ronco (1970) clearcut with diameters exceeding 200 – 400m will be poorly stocked by natural regeneration. Dispersal constraints such as tree height, seed morphology, wind direction and velocity limit the range that seed moves from its source (Greene and Johnson 1996).

Engelmann spruce and subalpine fir cones are located in the upper portion of the crown. Their seeds mature by mid-August and begin to be dispersed by mid-September (U.S. Department of Agriculture 1974). Engelmann spruce cones begin to open in September and most seeds are shed by mid-October; however, some seeds are dispersed later in fall and throughout the winter (Alexander 1987). Subalpine fir disintegrates when

they are ripe. Scales and bracts fall away with the large winged seeds leaving only the central spike like axis. For subalpine fir dissemination begins in September and has competed by the end of October (U.S. Department of Agriculture 1974).

Engelmann spruce and subalpine fir seeds are dispersed primarily by wind. As a result the release height of seed and the terminal velocity of seed limit the range that seed is dispersed from its source (Greene and Johnson 1996).   The cones in either species are found at the top of the crown with the average release height estimated to be 0.75 the height of the tree. At the Sicamous study site, Engelmann spruce and subalpine fir were the same height (29m) and therefore their release points were similar. Engelmann spruce seed have a lower terminal velocity (0.61 m/s) compared to subalpine fir (0.8m/s), enabling spruce seed to be airborne longer and thus dispersed further downwind.

The wind direction is a critical component influencing the quantity of seed at the edge of a clearing. Seed dispersal studies have concluded that the windward edge is the primary seed source for a cleared opening (Alexander 1987). Alexander and Edminster (1983) indicated that the seed densities along the windward edge were approximately 70% of the seed densities in uncut stands. Greene and Johnson (1996) assume that the seed density along the edge relative to the uncut stand is related directly to the frequency of windward winds. It follows that the leeward edge contributes less seed to a clearing as the predominant windward winds blow seed back into the forested edge.

The wind direction is a critical component influencing the spatial distribution of seed in a clearing. In a cleared opening about 40% of the Engelmann spruce and 50% of the subalpine fir is found within 31 meters from the windward edge (U.S. Department of Agriculture 1974). The density of seed decreases at a decreasing rate, until that point where seed begins to be contributed from the leeward edge.

A number of mathematical models have been used to represent the decline in seed density as distance from the edge increases. Figure 1.1 illustrates dispersal curves for Engelmann spruce seed estimated from three studies (Roe 1967; Alexander and

Edminster 1983; McCaughey and Schmidt 1987). The studies were standardized to 100 seed/m^2 on the edge. As distance from the source increases, the density of seed decreases at a decreasing rate where less than 40 seed/m^2 are dispersed beyond 50m from the edge and fewer than 13 seeds/m^2 are found 200m from the edge. The tailing off suggests that significant quantities of seed were dispersed during periods of high winds (U.S. Department of Agriculture 1974).
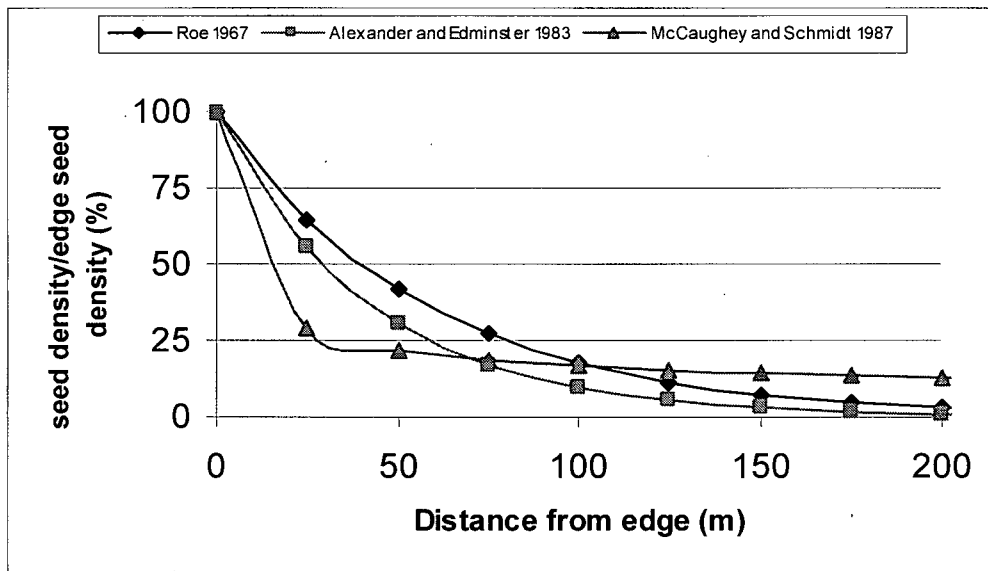
Figure 1.1. Estimates of Engelmann spruce seed from leeward edge

Seeds can be blown over the snow if they abscise following snowfall. Greene *et al.* (1999) site dispersal studies on white spruce and balsam fir which indicate that 30%-50% of their seeds abscise on the snow. Snow can cover the Sicamous Creek study site by late September and therefore secondary dispersal over the snow can increase the distance seed travels from an edge to be greater than a few hundred meters.

1.3 Thesis Outline

The thesis consists of six chapters. The following chapters are: a literature review on modeling seed dispersal, the statistical design of the seed dispersal study within the Sicamous Creek project, an analysis of the seed data, the framework of a spatial seed

dispersal model (DISPERSE) followed by its recalibration and validation, and finally the summary and conclusions of the study.

2.0 Models of Tree Seed Dispersal

Seed dispersal is a fundamental component in understanding the ecology of forests and trees and their response to environmental variability. In this chapter, seed dispersal is assessed in terms of statistical and mechanistic models specified to predict dispersal patterns. Statistical models are based on inferences drawn from seed collected at predetermined positions at various distances away from the seed source. Mechanistic models attempt to account for the physical and biological factors underpinning seed dispersal.

2.1 Statistical Models

Seed dispersal studies often have involved placing seed traps in various configurations in cleared areas to study the relationship between seed density (seeds/m^2) and distance from the nearest edge. Regressing seed density (N_x) found at specific distances from the edge on distance (x) is the basis of statistical models. Statistical models are used generally to predict spatial seed dispersal; however, hypotheses addressing the differences between seed density in terms of one location compared to another, or one species relative to another can also be tested.

Scatter plots of seed trap data show that seed density is related inversely to distance from the nearest source and that seed density decays at a decreasing rate with distance. Past studies have represented this nonlinear relationship in terms of an exponential decay model (Frampton *et al.* 1942, Kiyoshawa and Shiyomi 1972) or an inverse power law model (Gregory 1968). The exponential decay and inverse power law models are specified in Equations 2.1 and 2.2.

Equation 2.1 shows the exponential decay model that reflects seed density (N_x) associated with dispersal distance (x) from the closest source. The parameters B_0 and B_1, indicate the density of seed at the edge and the decay in seed density with distance from source, respectively. The true seed population parameters B_0 and B_1 are estimated by

linear regression from a sample of seed collected at predetermined distances away from an edge. A plot of seed density and the distance seed travels is a nonlinear relationship; however, taking the natural log of the seed density data points linearizes equation 2.1. Transforming distance and seed density by natural logs prior to executing ordinary least squares linearizes the dispersal data with the inverse power function (Equation 2.2).

$$N_x = B_0 \exp^{-B_1 x + \in} \qquad\qquad \textbf{2.1}$$

where:

N_x = seed density at points x meters from the edge (seeds/m^2)
x = distance from edge (m)
B_0 = density of seed at edge (seeds/m^2)
B_1 = rate of decline in seed density with respect to distance from edge
$\in$ = error $N(0, \sigma^2)$

$$N_x = \ell_0 x^{-\ell_1} \eta \qquad\qquad \textbf{2.2}$$

where:

ℓ_0 = density of seed one meter from the edge (seeds/m^2)
ℓ_1 = rate of decline in seed density with respect to distance from edge
η = lognormally distributed error

The difference between the two models is whether seed density and distance have a log-linear (exponential decay) or a log-log (inverse power law) relationship. On mathematical grounds the exponential decay model is preferable, as the quantity of seed estimated on the edge is a finite number source (B_0), while the seed estimate from the inverse power model at the edge ($x = 0$) does not exist. Comparisons in terms of statistical superiority do not indicate a clear preference for either model. Gregory (1968) found that for 124 dispersal curves estimated from dispersal data on air-borne spores or pollen, 65 had a higher correlation coefficient (r^2) when estimated by the negative exponential model and 59 by the inverse power law model (Fitt and McCarthing 1986).

The statistical seed dispersal models are one-dimensional and assume that seed obtained by a trap was dispersed from the closest edge. With only one independent variable, the three remaining edges are not considered possible seed sources. Therefore, any contribution of seed from these edges will bias the parameter estimates. For example, if an equal amount of seed is added to each trap by the three remaining edges then the source factor (B_0 or ℓ_0) will be inflated. Alternately, the decay rate (B_1 or ℓ_1) will be underestimated, if seed originating from the other edges add more seed to the traps further from the closest measured edge.

The distances between the closest edge and seed traps are only accurate measurements of the distance seed travels if all windward winds intersect the edge at right angles. A predominant wind at 45^0 to the edge requires seed to travel over 40 percent further than the distance closest to the edge. If the closest distance to the traps is calibrated to be the distance the seed was carried, then the estimated decay parameter (B_1) will have greater decay than the true decay rate. For example, if the estimated model were used to predict seed dispersal under similar conditions, except that the leeward winds were perpendicular to the edge, the forecasted seed concentrations in the clearing would be too low.

Overall, statistical models are simple, with only two parameters that fit the spatial dispersal of seeds reasonably well. The seed dispersal component of this study uses the negative exponential decay model. The exponential model was specified to test for any differences in the seed dispersed from the north, east, south and west edges as well as differences between locations. Statistical models do not provide a clear understanding of the underlying mechanisms (e.g. aerodynamics of the seed, wind speed, tree height) that are primarily responsible for seed dispersal. Variables reflecting a cause and effect relationship are not accounted for in statistical models, and therefore their findings can not be generalized to conditions at other sites, species or dispersal seasons. The mechanistic models developed by Greene and Johnson (1989 and 1996) and Okubu and Levin (1989) attempt to account for the factors responsible for seed dispersal and result in models that are neither site, species, nor time dependent.

2.2 Mechanistic Models

Mechanistic models predict seed dispersal by specifying equations that account for the influence of the underlying factors responsible for seed dispersal. Greene and Johnson (1989 and 1996) developed point and area source mechanistic models to predict seed dispersal. This section will describe the foundation of the point and area source models followed by a discussion on the models.

2.2.1 Point Source Models

Greene and Johnson (1989) defined a point source as a tree with little vertical and lateral variation in the detachment position of seed. A forest of trees bordering an open area acts as an area source. A point source model predicts dispersal from a particular tree, whereas an area source model predicts dispersal from an entire edge into the opening. Quantity of seed at the source, seed release height, terminal velocity of seed and wind velocity are the primary factors considered to influence seed rain into an open area.

2.2.1.1 Ballistic Model

Pasquill and Smith (1983) proposed a ballistic function (Equation 2.3) that incorporates the mean wind velocity, release height and terminal velocity of seed to predict the horizontal distance seed is deposited away from its parent (point source). The length of time required for a seed to fall is given by the release height of seed (Z_e), divided by its terminal velocity (V_f). The horizontal distance traveled in this time is given by the mean wind speed (u) multiplied by the falling time. The ballistic function is deterministic and predicts that for a given wind speed all seed from a point source will fall to the ground at a specific distance from the origin.

$$x = Z_e u / V_f \qquad\qquad\qquad \textbf{2.3}$$

where:

x = distance from source (m)
Z_e = release height of seed (m)
V_f = terminal velocity (m/s)
u = mean wind speed between Z to the ground (m/s)

2.2.1.2 Horizontal Wind Variability

Green and Johnson (1989) incorporated the variability in wind speeds to explain the downwind deposition of seeds from a point source. Over a dispersal season, the wind speed varies minute by minute and hour by hour. At a given height (Z), Luna and Church (1974) reported that the frequency distribution of average hourly wind velocity is skewed toward the higher wind speeds, but is distributed normally when the average hourly velocities are transformed logarithmically. Greene and Johnson (1989) specified a lognormal probability density function to represent the distribution of winds during the dispersal season (Equation 2.4).

$$p(u) = \frac{1}{u \sigma_u \sqrt{2\pi}} \exp\left\{-\left[\frac{\ln(u/u_g)}{\sqrt{2}\sigma_u}\right]^2\right\} \qquad\qquad \textbf{2.4}$$

where:

$p(u)$ = probability density of wind at a specific speed (u)
u = a specific wind speed
u_g = geometric mean of wind during dispersal season
σ_u = standard deviation of the ln(u) during dispersal season

Q defines the quantity of seed released from a point source. To account for a change in seed density due to a change in wind speed ($\frac{dQ}{du}$), Q is inserted in the numerator of Equation 2.4 (Equation 2.5).

$$\frac{dQ}{du} = \frac{Q}{u\sigma_u\sqrt{2\pi}} \exp\left\{-\left[\frac{\ln(u/u_g)}{\sqrt{2}\sigma_u}\right]^2\right\}$$ **2.5**

The final step is to determine the relationship between the change in quantity of seed and the distance from source ($\frac{dQ}{dx}$). Referring to Equation 2.3, the change in u with x, ($\frac{du}{dx}$), is equivalent to V_f/Z_e. Applying the chain rule $\frac{dQ}{dx}$ (Equation 2.6), is equal to $\frac{dQ}{du}$ (Equation 2.5) multiplied by V_f/Z_e.

$$\frac{dQ}{dx} = \frac{dQ}{du}\frac{du}{dx} = \frac{V_f Q}{Z_e u\sigma_u\sqrt{2\pi}} \exp\left[-\left(\frac{\ln(u/u_g)}{\sqrt{2}\sigma_u}\right)^2\right]$$ **2.6**

Substituting $\frac{xV_f}{Z_e}$ (Equation 2.3) for the given wind speed (u) results in Equation 2.7, which estimates the frequency of seed at specific distance from a point source. The density of seeds at a given distance (N_x) can be calculated by dividing Equation 2.7 by $2\pi x$.

$$\frac{dQ}{dx} = \frac{Q}{x\sigma_u\sqrt{2\pi}} \exp\left\{-\left[\frac{\ln(xV_f/Z_e u_g)}{\sqrt{2}\sigma_u}\right]^2\right\}$$ **2.7**

Equation 2.7 depicts the relationship between quantity of seed and distance from a point source to be skewed due to the lognormal distribution of winds. This skewed relationship has been exhibited in previous studies (e.g. Augspurger and Hogan 1983, Augspurger and Franson 1987, Gladstone 1979).

Table 2.1 and Figure 2.1 are used to represent the effects of the dispersal parameters (u_g and σ_u) on the downwind distribution of seeds. Population A is used as a base, to illustrate the effects of changing u_g and σ_u for populations B and C, respectively. Population A has a slight positive skew with the mode at approximately 50m. Population

B uses the same parameter values as A except u_g is increased to 3.15m/s from 2.5 m/s.

The resultant seed population for B has a greater positive skew, with the mode shifted away from the point source to 70m. A relative increase in the release height of seed (Z_e), or decrease in terminal velocity of seed (V_f), would have the same influence on the downwind distribution of seeds. Populations A and C have identical dispersal parameters, except the variation of winds during dispersal for C (σ_u=0.825) is larger than A (σ_u=0.55). The increased variation causes the mode to be shifted closer to the seed source and the downwind distribution of seed densities has a greater positive skew.

Table 2.1. Point source dispersal parameter values for populations A, B and C

Dispersal Parameters	Populations		
	A	B	C
Seed Release Height (m)	22	22	22
Terminal Velocity (m/s)	0.8	0.8	0.8
Geometric Mean of Wind (m/s)	2.5	3.15	2.5
Std. Deviation of Winds (m/s)	0.55	0.55	0.825
Number of Seeds per Tree	10000	10000	10000
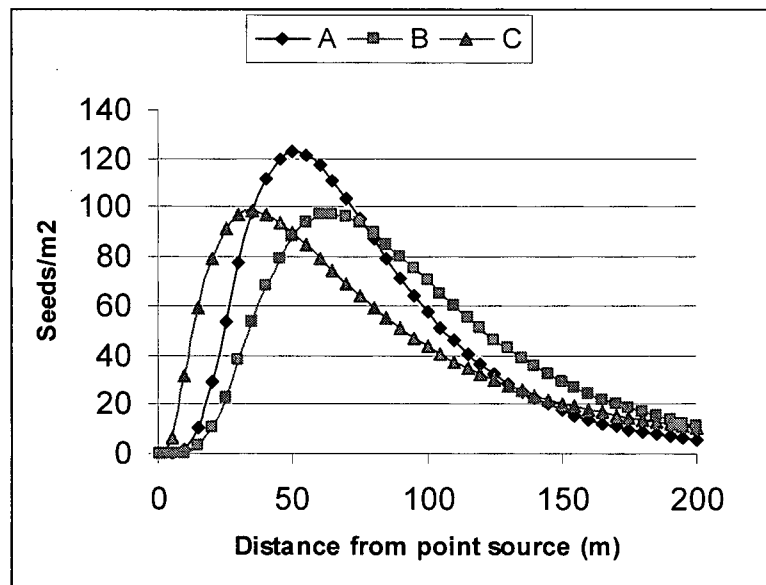
Figure 2.1. Point source dispersal curves for seed populations A, B and C with differing wind velocities and wind variability (parameters defined in Table 2.1)

2.2.1.3 Variability in Seed Descent

Descent variability of seed changes its downwind distribution. Greene and Johnson (1996) attributed descent variability to variance in the terminal velocities of seed, as well as to any variance in vertical winds. Any change in forces that influence the time it takes for seed to fall is viewed as independent of the horizontal wind variance (σ_u^2). Greene and Johnson (1989) assumed that the vertical and horizontal variances were independent. It follows that variation in the velocity that seeds descend (σ_z^2) could be accounted for by adding it to the horizontal variance. The combined variance would replace σ_u^2 in Equation 2.7 and the result is a distribution of seed densities with a greater positive skew and a mode closer to the point source. Population C in Figure 2.1 illustrates the seed dispersal relationship with increased variability.

Okubu and Levin (1989) defined Equation 2.8 to account for vertical variation (σ_z^2) in the rate seeds settle to the ground. Following the arguments by Pasquill and Smith (1983), the variation in the rate that seed falls (σ_z^2) increases with the time it is airborne. In Equation 2.8, A is the vertical diffusivity of seed with $\frac{x}{u}$ representing the length of time seed is airborne. Okubu and Levin (1989) depict vertical diffusion to increase linearly at a rate of 2A.

$$\sigma_z^2 = 2A\frac{x}{u} \qquad\qquad \textbf{2.8}$$

As A increases, the vertical variation increases causing the distribution of seed along the x plane to become positively skewed, with the mode shifting to the left of the mean. For heavy seeds, where the terminal velocity (V_f) exceeds 1m/s the influence of vertical diffusion is relatively small and the modal and mean dispersal distance are similar and can be solved using the ballistic equation (Equation 2.3). As the terminal velocity decreases, data from seed dispersal studies indicates that the ballistic equation

overestimates the modal distance. Okubu and Levin (1989) concluded that vertical diffusion was the factor shifting the mode in the direction of the seed source. The respective mean terminal velocities of Engelmann spruce and subalpine fir are 0.61 m/s and 0.8 m/s (Greene and Johnson 1996, Greene pers. com. 1999). Given these terminal velocities, the findings of Okubu and Levin (1989) would suggest that the spatial distribution of Engelmann spruce and subalpine fir seed would be skewed away from the point source.

Point source models cannot be applied to the dispersal of seeds across a forested edge into a clearing because they are limited to an isolated tree in an open area. A collection of point sources could represent an area source, but the influence that the edge has on horizontal and vertical wind profiles in the opening must be accounted for. Point source models provide the principal underpinnings for an area source model; however, they cannot be used directly to predict seed dispersal from the edge of a clearing.

2.2.3 Area Source Model

Greene and Johnson (1996) defined an area source to be an aggregation of point sources uniformly distributed with depth (D) and length (Y) (Figure 2.2). Each point source is defined by B (number of trees/m^2) and Q (number of seeds/tree). Referring to Figure 2.3, Greene and Johnson (1996) simulated seed dispersal from each originating point within the area source to estimate the spatial distribution of seed along $x_\perp$, a line perpendicular to the edge. Since wind velocity within the canopy and the cleared opening is influenced by the forested area source, the distance that seed is airborne within the canopy (x_D) and the cleared opening (x_p) are modeled independently by the point source model. A single tree does not influence wind in the point source model; however, a stand of trees acts as a force of friction on wind, reducing its velocity within a clearing. This section begins by defining how Greene and Johnson (1996) estimated the influence of the forested edge on the vertical and horizontal wind profiles in a clearing, as well as within the canopy. The section concludes with the derivation of a synthetic area source model estimated from the point source simulations.

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Figure 2.2. Illustration of an area source of seeds depicted as a group of uniformly distributed point sources (Greene and Johnson 1996).

2.2.3.1 Vertical Wind Profile

Greene and Johnson (1996) used a power-law function to estimate the wind velocity at any given vertical position between the ground and the any given height (Z_i).

$$\frac{u_z}{u_r} = (\frac{Z_i}{Z_r})^m \qquad \qquad \textbf{2.9}$$

where:

u_z = horizontal wind velocity (m/s) at height Z
m = power function exponent
u_r = horizontal wind speed (m/s) at reference height
Z_r = anemometer height (m) at reference station (normally 10 m)
Z_i = height above the ground (m)

Equation 2.9 indicates that the ratio of the wind velocity (u_z), to the wind velocity at a reference vertical position (u_r) and is related to the ratio of the two heights (Z_i and Z_r) taken to an exponent (m). A study by Pasquill and Smith (1983) estimated the value of 0.14 for m. It follows that the wind speed increases at a decreasing rate as the height above the ground increases.

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2.2.3.2 Horizontal Wind Profile in the Clearing

Figure 2.3 illustrates the relationship between horizontal wind velocities measured at various distances leeward of an edge (u_{xp}) and a reference wind velocity (u_r). Both u_{xp} and u_r are measured at the same height. Nageli (1953) concluded that the forest edge provides friction on the horizontal wind flow at the edge. As the leeward distance increases, the horizontal wind speed approaches the reference wind speed. Equation 2.10 accounts for the friction an edge has on the horizontal wind velocity at a specific distance (x_p) downwind from the edge (Green and Johnson 1996).

$$\frac{u_{x_p}}{u_r} = k(\frac{x_p}{Z_h})^{0.186}$$
2.10

where:

x_p = leeward distance between the forest edge to a point in the open area (m)
Z_h = height of the stand (m)
u_r = reference horizontal wind velocity (m/s)
u_{xp} = horizontal wind velocity (m/s) measured at x_p meters downwind from the area
        source (recorded at the same height as u_r)
k   = constant equal to 0.508 for a forest with full canopy

The ratio of the horizontal winds ($u_{xp} : u_r$) taken x_p meters downwind from the edge, depends upon the tree height. Taller trees along the forest edge cause wind velocity in the opening to be reduced further downwind. For a leafless canopy, the constant (k) is increased to account for the reduced friction on wind by the edge. Greene and Johnson (1996) estimated a value of 0.88 to represent k for a leafless canopy. According to Equation 2.10, wind speeds on the leeward side of the edge increase at a decreasing rate with distance from the edge and reach the reference velocity when the distance is 38 times the height of the surrounding trees.
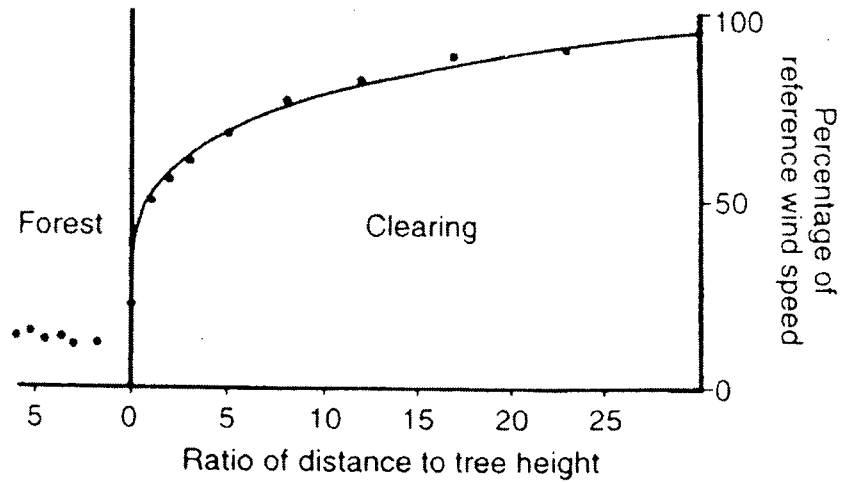
Figure 2.3. Horizontal wind speed as a function of leeward distance from the edge with a full canopy (Greene and Johnson 1996).

Greene and Johnson (1996) estimate the mean wind velocity at any point (x) within the clearing by integrating Equations 2.9 and 2.10 (Equation 2.11). In Equation 2.11, Z_i is replaced by $\dfrac{Z_a}{2}$, representing the mean vertical height between the point of release and the ground.

$$u_{xpz} = u_r a (\frac{x_p}{Z_h})^{0.186} (\frac{Z_a}{2})^m Z_r^{-m}$$ **2.11**

where:

u_{xpz} = horizontal wind velocity (m/s) x_p meters from the edge averaged
        between Z_a and the ground
a = a constant equal to 0.38 for a full leaf canopy and 0.65 if it is leafless
Z_a = average release height (m) for seed (assumed to equal 0.75 Z_h for conifers)

2.2.3.3 Wind within the Canopy

Nageli (1953) concluded that the wind velocity within the canopy was 11-14% compared to its reference wind speed. Assuming that the horizontal velocity within the canopy (u_s) is constant, Greene and Johnson (1996) developed Equation 2.12 to estimate u_S.

$$u_s = bu_r(\frac{Z_h}{Z_r})^m \qquad\qquad \textbf{2.12}$$

where:

u_s = horizontal wind velocity in the forested stand
u_r = horizontal wind velocity at the reference station
b = constant accounting for friction attributed to the treed area (0.116 and 0.21 for full and leafless canopy, respectively)
Z_r = anemometer height at a reference station (m)

Equation 2.13 estimates the exit height that seeds leave an edge (Z_e) from point sources within the forested area. Referring to Figure 2.2, x_D is the distance seed travels within the canopy to reach the edge of a clearing. The time that seed is airborne in the canopy before it reaches the edge of the clearing is determined by $\frac{x_D}{u_s}$. Time multiplied by the terminal velocity of seed (V_f), provides the vertical distance the seed falls while traveling through the canopy. The total distance seed falls is subtracted from the average height that seeds are released from the point source (Z_a). Therefore, seeds originating from point sources along the edge are assumed to be released at Z_a, while seeds from point sources within the forest depend upon the variables in Equation 2.13 to determine their exit height (Z_e).

$$Z_e = Z_a - (\frac{x_D}{u_s})V_f \qquad\qquad \textbf{2.13}$$

Referring to Figure 2.2, Greene and Johnson (1996) simulated seed dispersal at various points along x_p from points (Y_i, D_j) within a forested area. The expected seed

deposit at x_p was divided by $2\pi(x_p + x_D)$ to convert into a seed density relationship at various points along x_p. Following the simulation from each point source, the seed densities at various points along a perpendicular line from the edge ($x_\perp$) were determined. Greene and Johnson (1996) identified that this level of modeling complexity is not required and developed a modified negative exponential decay function to estimate seed dispersal from an area source.

2.2.3.4 Synthetic Area Source Model

The synthetic area source model is based on a modified negative exponential function that is scaled using a non-dimensional dispersal parameter T (Equation 2.14).

$$N_x = N_0 \exp(-\tau T^\phi)$$ **2.14**

where;

N_x = the density of seed at distance x from the edge (seeds/m^2)
N_0 = the density of seed at the edge (seeds/m^2)
τ = a parameter accounting for the decline in seed density from an area source
T = a dimensionless variable incorporating distance (x), terminal velocity (V_f), wind velocity (u) and seed exit height (Z_e)
ϕ = a parameter accounting for the initial steep decline of seed densities from area source

Rearranging the variables in the ballistic equation solves for the T variable (Equation 2.15). For an area source the seed exit height (Z_e) and terminal velocity (V_f) are assumed constant, while wind velocity in the clearing (u) increases with distance from the treed area and height off the ground.

$$T = \frac{xV_f}{Z_e u}$$ **2.15**

Wind velocity (u) in the T variable is replaced by u_{xpz} to account of the vertical and horizontal wind profiles within a clearing,. Equation 2.16 represents the new T variable following the substitution of x for x_p and Z_a for Z_e.

$$T = \frac{x^{0.814}(2Z_r / Z_a)^m V_f Z_h^{0.186}}{Z_a u_r a} \qquad\qquad \textbf{2.16}$$

Greene and Johnson (1996) calibrated a synthetic area source model from the spatial distribution of seed densities along $X_\perp$ estimated by the point source simulations. Nonlinear regression methods were utilized to minimize the residual sum of squares between $\dfrac{N_x}{N_0}$ and T and the respective parameter values for τ and ϕ of –2.64 and 0.72 for a full canopy and –2.31 and 0.85 for a leafless canopy were estimated.

Greene and Johnson (1996) validated the area source model with 59 observations from 11 seed dispersal studies, which included nine different species. Since none of the studies provided information on wind velocity and tree height, these variables were assumed. Therefore, only distance (x) and terminal velocity (V_f) were unique for each experimental observation. When parameter values for τ and ϕ were estimated for each data set, 3 parameter sets were statistically different than -2.64 and 0.72. However, when the data from all the studies were pooled together, the parameters for the full canopy model were within acceptable estimates.

The T variable can be defined in terms of distance from the edge and a constant c (Equation 2.17) given similar dispersal conditions in terms of wind velocity, tree height and the terminal velocity of seed. The parameter c equals $\dfrac{5.55V_f}{Z_h^{0.954} u_r}$ when the exit height is $0.75Z_h$, Z_r equals 10m and a is equal to the constant for a full canopy, 0.38.

$$T = cx^{0.814} \qquad\qquad \textbf{2.17}$$

The resultant decay function for an area source model (Equation 2.18) is similar to the exponential decay function ($N_x = B_0 \exp^{-B_1 x + \epsilon}$), where B_1 is represented by

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$-2.64(c)^{0.72}$; however, the decay function of the area source model has distance taken to the exponent 0.59.

$$N_x = N_0(\exp^{-2.64(c)^{0.72}x^{0.59}})$$ **2.18**

The advantage of the synthetic area source model is the decay coefficient $(-2.64(c)^{0.72})$ changes for specific site and species conditions. The parameter c would increase if either Z_h or u_r are smaller or V_f is larger, and results in a greater decline of seed density with distance from the edge. A statistically determined decay parameter (B_l) in the exponential decay function would be hypothesized to be relatively larger for seed with larger terminal velocities or sites with lower winds or shorter trees; however, experimental conditions may not exist for all the other factors to remain constant.

Greene and Johnson (1996) assumed that approximately half the seed in the uncut stands would be available for dispersal into the clearing, if half of the winds are windward to an edge and carry seed into the cleared opening. In Equation 2.19, B and Q are multiplied together to estimate the mean seed density in the uncut stand. To account for the frequency of windward winds BQ is multiplied by 0.5.

$$N_x = 0.5BQ\exp(-\tau T^{\phi})$$ **2.19**

where $T < 2.5$;

2.2.3.5 Shortcomings of Area Source model

For statistical evaluation of parameters τ and ϕ, the variable T differed between experimental data sets in terms of a species' terminal velocity (V_f), tree height (Z_h) and distance from the edge (x) that seeds were collected. For each study, u_r was replaced by the median wind velocity accounting for nonrandom abscission $(u_{gr*} = 7.87\text{m/s})$. Non-random abscission assumes that a critical wind velocity is necessary to abscise seed from a cone. Greene and Johnson (1992) solved for $u_{gr*} = 7.87$ m/s while studying the dispersal characteristics of silver maple (*Acer saccharinum*) seed; however, these

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findings could be species dependent. At the Sicamous Creek study site, only two out of 1255 wind hours exceeded an hourly average wind speed of 7.87 m/s. It should be noted that at Sicamous Creek the distribution of wind speeds within an hour were not provided and it is likely that more than two wind hours contained gusts exceeding 7.87m/s. However, a nonrandom abscission velocity of 7.87m/s should not be generalized to all other seed dispersal studies. For the eleven experiments, if u_{gr*} is not 7.87 m/s, then the parameter estimates for τ and ϕ would be biased. For example, if abscission were random and the North American average wind speed of 4.3 m/s ($\bar{u}_g$) was used to determine T, T would increase, resulting in a larger parameter value for τ than the –2.64 estimated for a full canopy.

The observed seed densities simulated in the open area from a point source assumes a lognormal distribution of winds with a standard deviation of 0.55. Neither the standard error nor the probability density function was changed when the mean wind velocity was increased from u_r to u_{gr*}. The lognormal distribution of winds represented in Equation 2.4 is unlikely to be the correct probability density function for u_{gr*}. Assuming the same lognormal distribution and standard error without any evidence or theoretical basis results in dispersal errors by the point source model.

Greene and Johnson (1996) assumed that the horizontal and vertical variability of wind is constant between sites and/or species. Okubu and Levin (1989) argued that vertical variability increases the longer a seed is airborne and therefore is linked to a species' terminal velocity. Variability is not explicitly factored into the area source model. If horizontal and/or vertical variance were underestimated, the point source simulation would under predict seed closer to the edge and over predict seed further from the source. It follows that the estimates of τ and ϕ from the synthetic model may be too small.

The drag effect of an edge on the horizontal wind profile was estimated from readings taken between the edge and a transect hundreds of meters downwind (Nageli 1953). Greene and Johnson (1996) indicated that Equation 2.10 does not account for the

reduction in wind velocity in relatively smaller openings. Equation 2.14 underestimates the friction by an edge on windward winds, causing the area source model (Equation 2.19) to overestimate the density of seeds dispersed away from the edge.

Multiplying the area source seed density by 0.5 (Equation 2.19) assumes 50% of winds are windward of each edge. Franklin and Smith (1974) concluded that the number of seeds dispersed from one edge to another differs by up to threefold and is positively correlated with the frequency of the prevailing windward winds. Hence, the area source model is limited because it does not account for variation in the frequency of windward winds.

The Greene and Johnson's (1996) area source model simulates seed disperse perpendicular from an edge. Perpendicular seed dispersal from two adjacent edges in a clearcut causes simulated seed densities to overlap in the corner. As a result, the area source model overestimates seed densities in the corner of a clearing. A correction factor must be applied to the area source model to account for the double counting of seed in a clearing's corner.

The area source function ($N_x = 0.5BQ\exp(-\tau T^\phi)$) was incorporated into a simulation model (DISPERSE). DISPERSE was validated using the Engelmann spruce and subalpine fir seed data collected at the Sicamous Creek study site for 1997-1998 (Chapter 5.0). Prior to validation, τ and ϕ were adjusted to reflect random abscission and the actual distance (x_p) seed traveled downwind of an edge. The dispersal function within DISPERSE explicitly incorporates wind direction and its frequency. Dispersing seed downwind prevents the overestimation of seed density in the corners, which is attributed to perpendicular dispersal. As well, the frequency of windward winds replaces the constant 0.5 assumed by Greene and Johnson (1996). These adjustments to DISPERSE were made to more accurately represent conditions during dispersal.

3.0 Design of Seed Dispersal Study within Sicamous Creek Project

The SCP is located in the Engelmann spruce/subalpine fir wet cold subzone and situated south of the north fork of Sicamous Creek, and north of Mount Mara, near the town of Sicamous. The study site is located on a north aspect between the elevations of 1530m and 1820m. The stand consists of Engelmann spruce and subalpine fir primarily between 100-150 years with tree up to 350 years. The site receives 1200mm – 1400mm of precipitation annually, with approximately 60% falling as snow and an average annual temperature between 0.7^0C to 1.1^0C. The volume of the stand is approximately 243 m^3/ha, with 35% of the volume Engelmann spruce and the remaining 65% subalpine fir (Vyse 1997).

The broad objective of the SCP was to gain a better understanding of the ecology of high elevation stands in southern British Columbia. Specifically, the project was designed to study the response of the ESSF to removing trees, as well as the effect of subsequent site preparation on regeneration (Vyse 1997). The information obtained will enable operational foresters to design improved silviculture regimes to meet specific goals for stands in the ESSF.

The area was harvested in the winter of 1994-95. The SCP consists of four harvest treatments and a control (no harvest). Each harvest treatment was undertaken in a 30 ha experimental unit and removed one third of the timber volume. The harvest treatments were:

1) Control: where no trees were removed (uncut)
2) Individual Tree Selection (ITS): approximately 33% of the volume was removed from the 30 ha experimental units with every fifth tree being removed (fallers choice) as well as marked skid trail.
3) 0.1 ha cut (0.1 ha): all trees were removed from sixty areas of approximately 30m by 30m. The centers of adjacent 0.1 openings are 60 m apart and linked by skid trails.

4) Small Clearcut (1 ha clearcut): all trees were removed from nine areas approximately 100m by 100m. The centers of adjacent 1 ha openings are 200m apart and linked by skid trails.

5) Large Clearcut (10 ha clearcut): all trees were removed from an area approximately 330m by 330m.
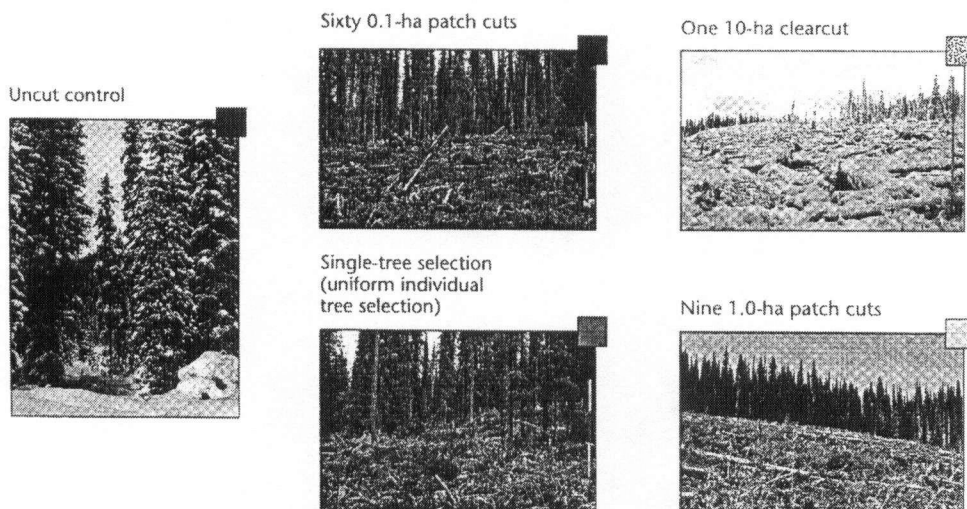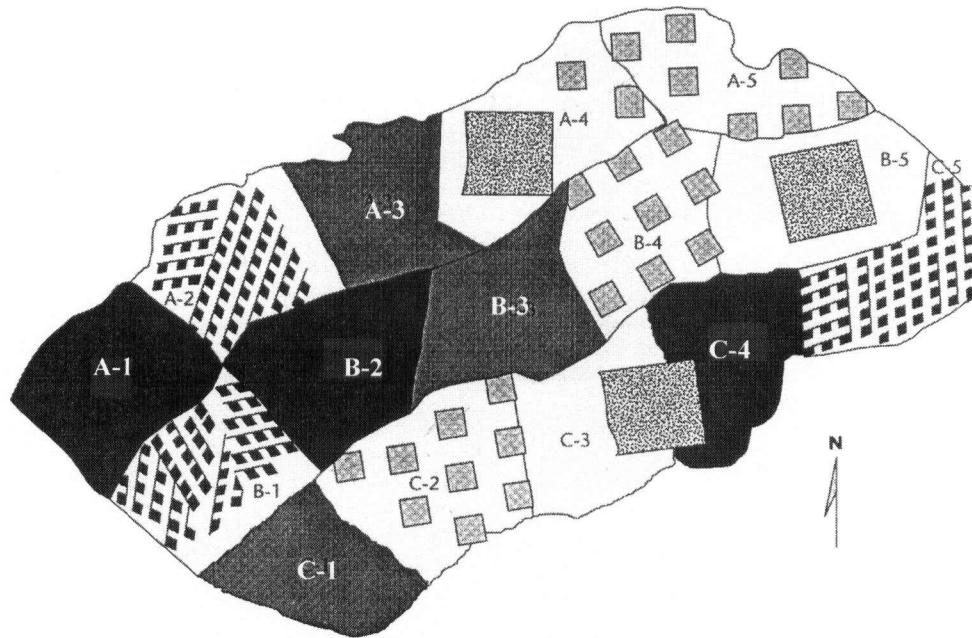
Figure 3.1. Five harvest treatments in SCP (Vyse 1997)

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The SCP has a randomized block design with 15 experimental units, each consisting of 30 ha. The experimental units are stratified according to altitude. Group A is at the base of the slope, Group B is at mid slope and Group C is found at the highest elevation. Groups A, B, and C each include all five treatments, where each treatment was randomly assigned to an experimental unit. Figure 3.1 shows the arrangement of groups and treatments. Currently, a wide range of studies are ongoing to analyze the influence of harvest treatments upon wind profile, early germination and advanced regeneration of spruce and fir, snow accumulation, small mammal populations, logging costs and other related subjects. This seed dispersal study will utilize wind and seed data collected in the 1997-1998 dispersal season.

3.1 Design of the Seed Dispersal Experiment within SCP

Seed traps (tripod and box traps) were deployed by mid-August, prior to the 1997 dispersal season (Kraft 1997, Vyse 1997). The majority of the traps were collected the following spring in late June; however, a sample of the tripod traps in the uncut and 0.1ha treatments were sampled on Oct.20, 1997. The following section provides a description of how seed and wind data were acquired.

3.1.1 Trap Design

Tripod traps featured a $0.25m^2$ collecting surface and were constructed according to the guidelines set by Hughes *et al.* (1987). They have a galvanized wire frame and are secured to the ground by wire legs pushed into the soil (Figure 3.2a). Litter is collected in polyethylene bags attached to the wire frame to form an inverted cone. The litter is funneled down the inverted cone and is easily removed from the trap. The porous polyethylene bag allows for the water to be drained from the trap. The tripod trap is stable; when weight is applied on the trap, the wire legs bend until the trap rests on the ground, as weight is removed the trap lifts off the ground. It can be placed on steep slopes because of the flexible wire legs. A tripod trap is easily made, durable and inexpensive.

The box traps have a 0.64m² collecting surface with a square wood frame and window cloth on the bottom. They have a removable wood frame top covered with 1cm mesh hardware cloth (Figure 3.2b). The sturdy structure of the box trap protects it against intense pressure from snow during the winter allowing it to be used up to 10 years in succession. The window cloth at the base of the box trap and the tight fitting lid deter rodents from entering the trap.

a) Tripod Trap
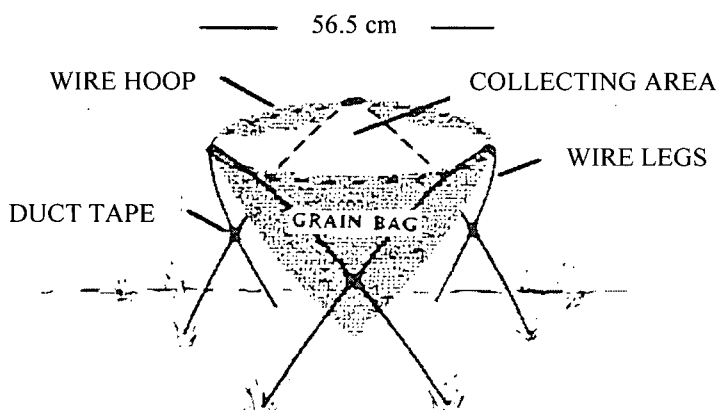
b) Box Trap
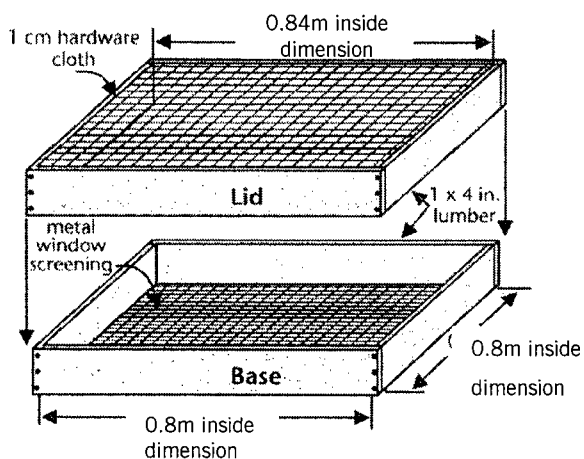
Figure 3.2. Illustration of (a) tripod trap (Hughes *et al.* 1987) and (b) box trap (Leadnom *et al.* 1997)

3.1.2 Trap Layout For Each Treatment

In each uncut treatment, tripod traps were laid out systematically in six parallel rows exactly opposite each other, with 30 meters between adjacent traps (Figure 3.3). There were six traps per row placed at 0, 30, 60, 90, 120 and 150m along each row, for a total of 36 tripod traps per experimental unit. Ten box traps were placed in each experimental unit. The box traps were oriented in a straight line with a trap every 50m. There were three uncut treatments for a total of 108 tripod traps and 30 box traps. Ten box traps were placed in each ITS experimental unit in the same configuration as in the uncut stand, for a total of 30 box traps (Figure 3.3b). There were no tripod traps deployed in the ITS treatment.

a) Tripod Trap Orientation   b) Box Trap Orientation
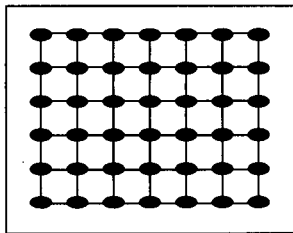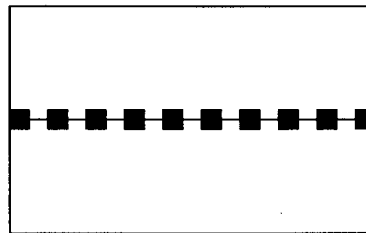
30 m between traps   50 m between traps

Figure 3.3. Orientation of tripod traps (a) and box traps (b) in uncut treatment

Tripod traps were placed in the center of 20 of the 60, 0.1 ha openings in each experimental unit. They were approximately 15 meters from each edge (Figure 3.4). Box traps were placed in one 0.1 ha opening per experimental unit. Box traps were oriented in two parallel transects, from the middle of the west edge to the middle of the east edge. The pairs of traps were 5 meters apart and found at 0, 15 and 30m from the west edge (Figure 3.5b). There were 60 tripod traps and 18 box traps for the three experimental units receiving the 0.1 ha treatment.

Figures 3.5 a and b illustrate the locations of the tripod and box traps placed in the 1 ha clearcuts. There are nine 1 ha clearcuts for each experimental unit. Five of the nine 1

ha openings had tripod traps which were oriented in two transects, one along a W-E direction and the other along a N-S direction. Each transect (W-E and N-S) passed through the middle of their respective edges, with traps placed at 16.5, 33, 50, 67 and 83.5m from the West (North) edge. Therefore, there were 5 traps along each transect, with the center trap being shared by both the W-E and N-S transects (Figure 3.5a). In the remaining four 1 ha clearcuts, the tripod traps were placed along W-E and N-S transects; however, traps were only placed at 16.5 meters from each edge.
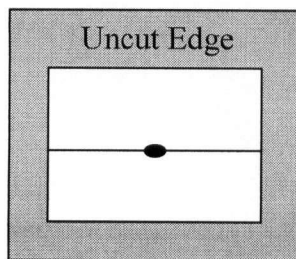
a) Tripod Trap Orientation   b) Box Trap Orientation
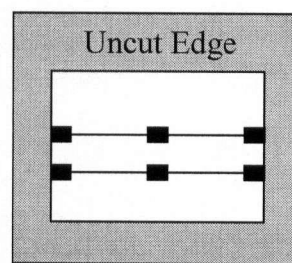
Figure 3.4. Orientation of tripod traps (a) and box traps (b) in 0.1 ha treatment

Box traps were placed in one 1 ha clearcut per experimental unit. Traps were placed along two parallel W-E transects, 5m apart (Figure 3.5b). The transects passed through the middle of the west and east edges. Traps were located along each transect at 0, 15, 30, 50, 70, 85 and 100m away from the west edge. Each 1 ha clearcut treatment had 61 tripod traps and 14 box traps per experimental unit, resulting in 183 tripod traps and 42 box traps in the three experimental units.

Tripod and box traps placed in the 10 ha clearcuts followed the same orientation as the 1 ha clearcuts. Spacing between tripod traps was at 0, 15, 30, 60, 90, 165, 240, 270, 300, 315 and 330m from the West (North) edges (Figure 3.6a). Box traps had the same orientation as the 1 ha clearcuts, with two parallel transects going W-E. At each of these points along the transect, two box traps were positioned 2.5 meters on either side of the transect. Box traps were placed in the same location as the tripod traps; however, there were no box traps at 240m from the west edge (Figure 3.6b). There were a total of 21

tripod traps and 20 box traps per experimental unit, with a total of 63 and 60, respectively, for the three 10 ha clearcut treatments.

a) Tripod Trap Orientation
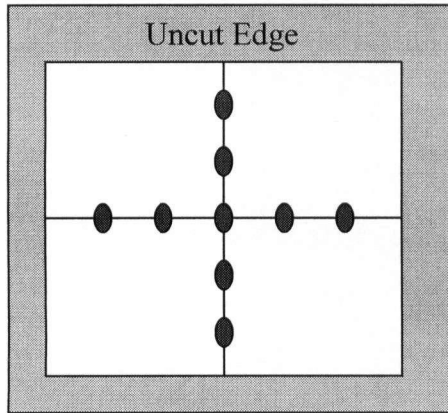
b) Box Trap Orientation
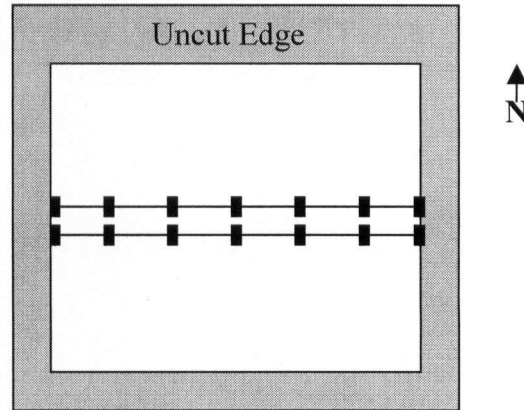
Figure 3.5. Orientation of tripod traps (a) and box traps (b) in 1 ha clearcuts

a) Tripod Trap Orientation
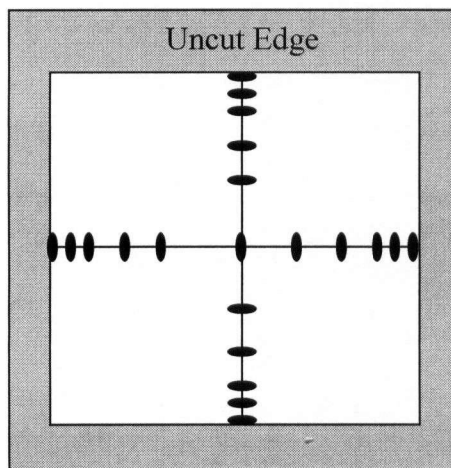
b) Box Trap and tripod trap Orientation
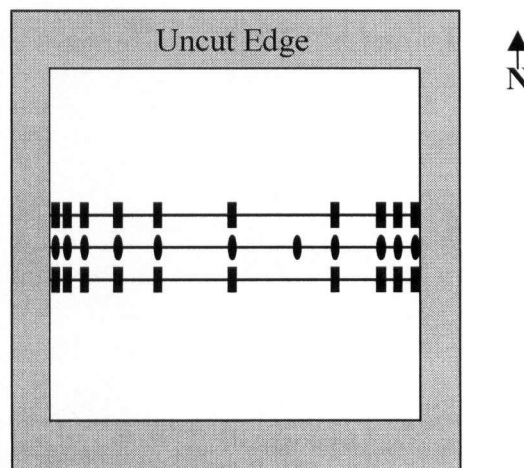
Figure 3.6. Orientation of tripod traps (a) and box traps (b) in 10 ha clearcuts

3.1.3 Wind Data

Novak *et al.* (1997, unpublished) monitored the direction and hourly wind speed in the B5 10 ha clearcut. Wind data were measured with an anemometer located six meters above ground in the center of this clearcut. Every hour from Sept.1 – Oct.30, the date, time, hourly mean wind velocity and hourly mean wind azimuth were recorded. Freezing conditions prevented the acquisition of wind data beyond October.

The wind data were grouped into four categories (N, E, S and W) based on the direction of the prevailing wind. Due north was assigned 0^0 or 360^0 and all winds within 45^0 of due north ($315^0 - 45^0$) were categorized as northerly prevailing winds. Moving clockwise, the easterly prevailing winds fell between 45^0 and 135^0, the southerly winds ranged between 135^0 and 225^0 and the westerly winds were between 225^0 and 315^0.

3.2 Statistical Methods

This section elaborates on statistical techniques used to:
1. compare spruce and fir seed acquisition by trap design;
2. analyze spruce and fir seed populations for the uncut, ITS and 0.1 ha treatments; and
3. analyze spruce and fir seed dispersed closest to the four edges in the 10 ha and 1 ha clearcuts.

3.2.1 Trap Comparison

Seeds gathered along the W-E transect in the 10 ha clearcuts were used for the trap type comparison (Figure 3.6b). Due to the differences in the collecting surface area for each trap type, seed densities were transformed to seeds/m^2 prior to comparison. At each location along the transect, the mean was taken of the two box trap seed density values. Comparison of the trap types was done by regressing the tripod seed density (N_x) on the average of the two box trap seed densities at the same distance along the transect ($X_\perp$)

from the west edge. A slope equaling one and an intercept equaling zero signifies that seed densities collected by the tripod and box trap are statistically equivalent. Any significant difference in either coefficient represents a lack of equality between trap types in terms of seed collection. In the preliminary analysis it was observed that the absolute variation was increasing when more seeds were collected by the box traps. Therefore, after converting seed densities to seeds/m^2, the seed densities for each trap type were transformed logarithmically to account for the increasing residual. For both species, at least one trap had no seeds. One seed was added to every trap's seed density (seeds/m^2) to eliminate the zeros prior to the log transformation (Dunn and Clark 1974, Snedecor and Cochran 1989, Sokal and Rohen 1995). A two tailed t-test ($\alpha = 0.05$) was conducted on each species to determine if the intercept and slope coefficient differed significantly from zero and one, respectively.

3.2.2 Uncut, ITS and 0.1 ha treatments

A lack of normality of the seed populations for both species excluded using analysis of variance. The seed populations were described visually using the cumulative distribution function (cdf) (Snedecor and Cochran 1989), and empirically by comparing the median values and using the non-parametric Kruskal – Wallis test (Conover 1980). The Kruskal – Wallis test statistic is based upon ranking the observations in the sample and evaluating whether the treatment populations are identical, or if one or more of the treatments tend to yield larger observations.

The tripod seed data from the uncut stand were used to characterize the spatial patterns of Engelmann spruce and subalpine fir seed densities. Thirty-six tripod traps were placed in a 6 by 6 configuration that delineated a 2.25 ha area (Figure 3.2a). Seed densities from each trap were ranked in ascending order and grouped into one of three categories so that each category contained 12 observations. Group I represented the 12 lowest seed densities followed by groups, II and III. Once a seed density has been assigned to a category, it was plotted into one of 36 cells according to the location where it was collected. Each cell, depending upon its location in the grid had two, three or four

adjacent cells. If two adjacent cells were categorized to have the same seed density, they were grouped together and the inclusive area was assumed to have the same seed density. A random distribution of seed densities in the 6 by 6 grid would have fewer large aggregation of adjacent cells in the same group. The distribution of spruce and fir seed densities were qualitatively assessed to determine if groupings I, II and III were randomly distributed within the 6 by 6 grid.

Sites A to C represent an increase in elevation. Zasada and Gregory (1969) indicated that Engelmann spruce seed production tends to diminish at higher elevations. Pre-harvest cruise data at the Sicamous Creek site indicated that Engelmann spruce declines from 45% of the tree population at 1550m to 18% at 1750m. Subalpine fir frequently dominates the forest canopy at high elevations (Coupe *et al.* 1991). For the uncut, ITS and 0.1 ha treatments, the influence of elevation on the Engelmann spruce and subalpine fir seed populations was tested in terms of differences between sites. For each harvest treatment, the cdf plot and Kruskal-Wallis test were conducted to determine if any site consistently had more or less seeds for each treatment.

Alexander (1987) indicated that the majority of Engelmann spruce and subalpine fir seeds are dispersed by late October. A sample of the traps in the uncut stands was collected in the fall (October 20th) and the remaining traps were sampled the following spring. The cdf plot and Kruskal-Wallis test were conducted to determine if the fall and spring spruce and fir seed populations differed significantly.

Qualitative (cdf plot) and quantitative (Kruskal-Wallis test) comparisons of the ITS and patch cut with the uncut treatment (control) were conducted to determine the effect of each treatment on the Engelmann spruce and subalpine fir seed populations.

3.2.3 10 ha and 1 ha clearcut treatments

For the 10 ha and 1 ha clearcut openings, a negative exponential relationship was estimated to represent the decay of seed density with distance away from the closest

edge. This relationship was generated by regressing the natural log of the seed density by its corresponding distance from the edge (Equation 3.1). As with the trap comparison, seed densities were transformed to seeds/m^2 and then one was added to each seed density to eliminate zeros prior to the log transformation. Equation 3.1 relates seed density to the source factor (b_0), which reflects seed production and the winds unique to respective edge, and the exponential decay of seed with distance from the edge (b_1).

$$\ln(N_x) = b_0 + b_1 x + \in \qquad\qquad \textbf{3.1}$$

where:

N_x = the density of seeds at distance x (seeds/m^2)
x = perpendicular distance from the closest edge (m)

Dummy variables (A and B) were incorporated into the negative exponential decay model to account for location effects of sites A and B on b_0 and b_1 (Equation 3.2). In Equation 3.2, b_0 and b_1 represent the source factor and exponential decay of seed, respectively, for site C. Variables A and B have a value of 1 for data collected from their respective site and a value of 0 for data collected at the remaining two sites. Parameters b_{1A} and b_{1B} represent differences in the exponential rate of decay for site A and B, respectively, compared to site C. The first step of the analysis was to determine if the decay relationship differed between sites. If either b_{1A} or b_{1B} were significant (α=0.05) then the decay relationship differed between sites and the seed data collected from the respective site was analyzed separately using the exponential decay function. Those sites with similar decay parameters were pooled together. Parameters b_{0A} and b_{0B} represent a difference in the source factor for sites A and B, respectively, compared to site C. Covariance analysis was conducted to determine if b_{0A} or b_{0B} were significant (α=0.05) (Snedecor and Cochran 1989). If either were significant, a source factor representing seed from the respective site was included into the resultant dispersal equation. If no significant difference was found, a common source factor was estimated for the resultant dispersal equation.

$$\ln(N_x) = b_0 + b_{oA}A + b_{0B}B + b_1x + b_{1A}xA + b_{1B}xB + \varepsilon \qquad \textbf{3.2}$$

where:

N_x = the density of seeds at distance x (seeds/m^2)
x = perpendicular distance from edge (m)
b_0 = source factor at site C
b_1 = exponential decay rate at site C
b_{0i} = difference in source factor for site i as compared to site C
b_{1i} = difference in exponential decay rate for site i as compared to site C

Franklin and Smith (1974) concluded that seed dispersed from an edge was positively correlated with the frequency of the respective prevailing wind. The final component of the analysis qualitatively and quantitatively assessed whether more or less seed was dispersed closer to one edge. The quantity of seed dispersed from an edge (N, E, S and W) was estimated by integrating its respective dispersal function. Assuming that seed production was constant for each edge, the seed supplied from each edge was qualitatively assessed in terms of whether the quantity of seed closest to an edge was correlated positively to the frequency of their respective prevailing wind.

The seed share model (Equation 3.3) consists of regressing the proportion of seeds deposited closest to an edge (%ES(SF)$_{kj}$), on the frequency of the respective prevailing wind direction (W$_j$). In the 10 ha clearing, seed traps were located at 0m, 15m, 30m, 60m, 90m from each edge. For example, Equation 3.4 determined the proportion of spruce seed at 15m from an edge relative to the total amount of spruce seed collected at 15m from all four edges.

$$\%ES(SF)_{kj} = b_0 + b_1W_j \qquad \textbf{3.3}$$

where:

%ES(SF)$_{kj}$ = percent of Engelmann spruce (subalpine fir) seed deposited closest to the jth edge and the kth distance from the closest edge, where k = 0, 15, 30, 60 and 90m (10 ha clearcut) or k = 16.5 and 33m (1 ha clearcut)
W$_j$ = percent of wind from jth direction, where j = N, E, S and W

$$\%ES_{15j} = \frac{ES_{15j}}{\sum\limits_{j=1}^{4} ES_{15j}}$$

3.4

where:

$\%ES_{15,j}$ = percent of Engelmann spruce seed supplied from the jth edge relative the total supply of seed by all four edges at 15m

$ES_{15,j}$ = number of Engelmann spruce seeds at 15 meters from the jth edge

The seed share model (Equation 3.3) assumes the supply of seed in a trap originates from the closest edge. The model indicates whether a significant relationship exists between the frequency of a prevailing wind and the share of seed collected closest to its respective edge. A perfect correlation between the relative frequency of prevailing winds and the proportion of seed supplied from its respective edge has an intercept (b_0) of zero and a slope (b_1) of one. A 1:1 relationship implies that the prevailing wind direction is the sole factor underpinning the dispersal of seed downwind into the open area.

4.0 Analysis of Engelmann Spruce and Subalpine Fir Seed Data

This chapter analyzes seed and wind data collected at the Sicamous Creek site. The objectives of the chapter are to determine if:

1) the design of the tripod and box traps influenced the quantity of Engelmann spruce and subalpine fir seed collected;

2) the density of spruce and fir seed was distributed randomly in the uncut stands;

3) the seed dispersed by late October was equivalent to seed collected in the following spring;

4) the spruce and fir seed density was consistently different between sites A, B and C;

5) the ITS and 0.1ha treatments had the same spruce and fir seed supply as the uncut stands;

6) the spatial distribution of seed was related to distance from edge for the 10ha and 1ha clearcuts;

7) the geographic orientation of the edge was related to the seed density closest to the edge; and

8) the seed dispersed closest to an edge in the clearcut was related to wind azimuth.

The analysis is presented in three sections. For each section Engelmann spruce and subalpine fir are analyzed independently, followed by a summary and discussion. The first section compares Engelmann spruce and subalpine fir seed collected by the two trap designs. The second section analyzes spruce and fir seed populations for the uncut, ITS and 0.1 ha treatments. The section begins with a spatial analysis of seed densities in the uncut stands followed by determining the effects of site and season on seed supply. Treatments are also compared to the uncut stand (control). The third component analyzes the seed densities with distance from the closest edge for the 10 ha and 1 ha clearcut treatments. The influence of site and geographic orientation of the edge in relation to the

cleared openings are evaluated in terms of seed density. The frequency of prevailing winds are also evaluated in the context of the quantity of spruce and fir seed collected closest to the windward edges.

4.1 Box Trap and Tripod Trap Comparison

The Engelmann spruce data sets collected by box traps and tripod traps were not equivalent. Figure 4.1 shows that the tripod traps retained more spruce seed than the box traps at low seed densities. Traps further from the seed source collected fewer seeds. When the traps were closer to the edge, the seed densities increased and both traps collected similar quantities of spruce seed. At higher seed densities, the regression line for Engelmann spruce converged with the diagonal line ($B_0 = 0$ and $B_1 = 1$) representing the 1:1 relationship between tripod and box trap seed collection. The intercept (1.89) and slope coefficients (0.62) for the spruce trap regression were significantly different than 0 (P<0.001) and 1 (P=0.003), which would be expected if equivalent amounts of seed were collected by the traps. Since differences in the Engelmann spruce data sets were related to trap design, the spruce tripod and box trap data sets were analyzed separately.
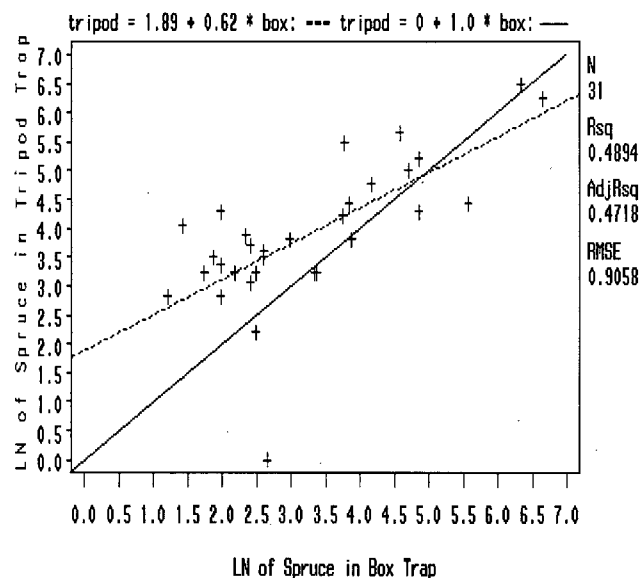
Figure 4.1. Regression relationship between the quantity of Engelmann spruce seed collected in tripod traps and box traps.

When the subalpine fir seeds were collected at comparable distances from the seed source, the numbers recorded in either trap design were similar (Figure 4.2). The intercept (-0.27) and slope (1.03) coefficients were not significantly different than 0 (P = 0.51) and 1 (P=0.874), respectively. Therefore, the fir seed data sets from the box and tripod traps were combined to increase the number of observations in the statistical analysis.
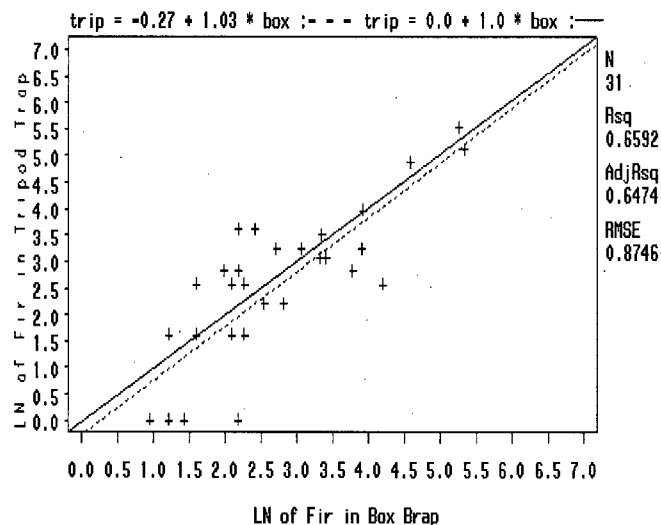
Figure 4.2. Regression relationship between the quantity of subalpine fir seeds collected in tripod and box traps.

The design of the trap, as well as the procedures in which the seed were collected are possible causes for differences in spruce seed acquisition. The cone shaped tripod trap funneled the seed to the bottom of the trap and had less exposure to wind. The winds within the clearing may have blown lighter spruce seed off of the wire grid on top of the box trap prior to settling into the box trap. As well, the shallower box trap will fill up with snow earlier than the tripod trap and seed that falls on the surface of the snow could have been blown away before they were covered by snow. Removal of seed from the tripod traps is easy to accomplish due to the aggregation of seeds and litter at the bottom of the funnel. Seed and litter must be swept together prior to collection in the box trap. The larger subalpine fir seeds are more visible and easily identified in the litter. The spruce seeds, being smaller, may have been missed during this procedure.

The loss of one seed has a relatively greater statistical impact when fewer total seeds are collected by either trap. As Figure 4.1 shows, the observations with the lowest number of seed were primarily responsible for concluding that the traps collect differential numbers of Engelmann spruce seed. The traps with fewer seeds were further from the forested edge. In the uncut, ITS and 0.1ha treatments wind is less of a factor. As well, overlooking a few seeds would not cause the seed collected by trap type to differ significantly. However, no tripod and box traps were placed in close proximity in the uncut, ITS and 0.1ha treatments. With only six observation along the edge it would be statistically unreliable to conclude that seed densities collected by both trap types were equal in areas not subject to wind.

4.2 Analysis of Seed Dispersal in Uncut, ITS and 0.1 ha Treatments

This section begins with a spatial analysis of Engelmann spruce and subalpine fir seed data in uncut stands. This is followed by a determination of the influence that site and season have on spruce and fir seed supply. The section concludes with a comparison of the ITS and 0.1 ha treatments with the uncut treatment (control), indicating whether either treatment reduced the spruce and fir seed populations.

4.2.1 Spatial Distribution of Engelmann Spruce and Subalpine Fir Seeds in the Uncut Stands

Seed data collected in the fall from site B were used to spatially represent the distribution of Engelmann spruce and subalpine fir seeds. Half the seed data at sites A and C were collected in fall and the other half in the spring. Due to a possible seasonal influence, A and C data sets could not be used in this analysis (refer to 4.2.3). The median seed density of category III (256 seeds/m^2) is approximately three times larger than category I (90 seeds/m^2) (Table 4.1). Of the 36 cells in Figure 4.3, the 12 cells representing category I are grouped together in the southern portion of the grid while the 12 cells representing category III are grouped in the north. The cells representing

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category II occur throughout the grid with the majority found midway between the north and south boundaries of the 6 by 6 grid. This geographic stratification of spruce seed densities suggests that they are not distributed randomly in the uncut stand at site B. Assuming a constant dbh for spruce trees throughout the grid, Equation 1.1 suggests the pattern of seed densities may reflect the non-random distribution of spruce trees over the grid.

Table 4.1 shows that for subalpine fir the median seed density of category III (296 seeds/m^2) is three times larger than category I (108 seeds/m^2). Referring to Figure 4.4, the spatial distribution of fir seed categories had three groupings of six similar adjacent cells and 11 cells scattered throughout the grid with no adjoining cells with comparable seed density. This spatial pattern of seed densities suggests subalpine fir trees are more randomly distributed at site B, relative to Engelmann spruce.

Table 4.1. Median seed density in the uncut stand (site B) by seed category for Figures 4.3 and 4.4

Seed Category	Median (seeds/m^2)		
	I	II	III
Engelmann spruce	90	132	256
Subalpine fir	108	158	296

⇑
N
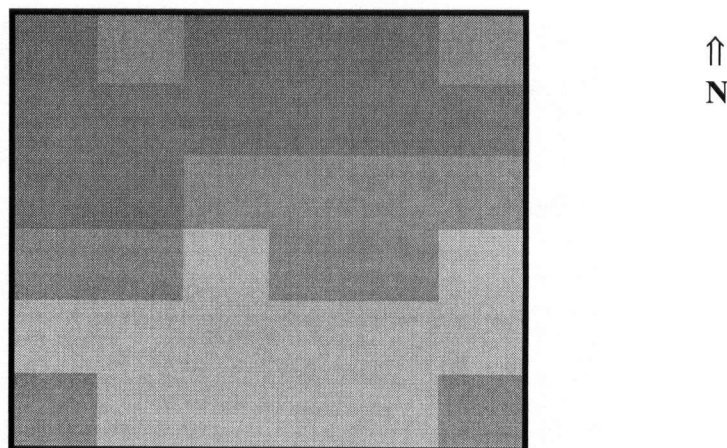
Figure 4.3. The spatial distribution of Engelmann spruce seeds in the uncut stand at site B, where the shade of grey indicates the density of spruce seed.
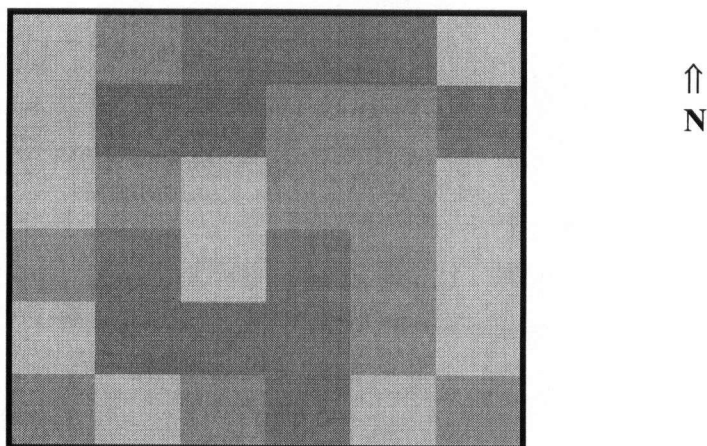
Figure 4.4. The spatial distribution of subalpine fir seeds in the uncut stand at site B, where the shade of grey indicates the density of subalpine fir seed

4.2.2 Location and the Seed Supplies of Engelmann Spruce and Subalpine Fir in the Uncut, ITS and 0.1 ha Treatments

In the uncut stands, the ten box traps placed at sites A, B and C were used to examine location effects on Engelmann spruce seed supply. The median spruce seed density was 441 seeds/m^2, 348 seeds/m^2 and 184 seeds/m^2, respectively (Table 4.2). Despite site C having a relatively smaller median value, the cdf curves overlap for each site and made it impossible to detect any location effect. Figure 4.5a shows the spruce seed density at site A was relatively normal, while sites B and C had a positive skew. The Kruskal-Wallis test did not detect a significant difference among sites in terms of the quantity of spruce seed collected (P=0.322). The cdf and the Kruskal –Wallis test supported the conclusion that the uncut spruce seed population at sites A, B and C were similar.

The box trap data set for the ITS treatment was used to examine location effects on spruce seed density. For each site the cdf showed that the spruce seed populations at site B had a higher relative seed density than sites A or C (Figure 4.5b). Fifty percent of the site B spruce seed population was less than 400 seeds/m^2; however, 100% of site C population as well as 80% of site A population were less than 400 seeds/m^2. Referring to

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Table 4.2, the median seed density at site B (416 seeds/m^2) was more than twice as large as the median values for either site A (205 seeds/m^2) or C (191 seeds/m^2). The Kruskal – Wallis multiple comparison tests showed that sites A and C were similar (P=0.256); however, site B was significantly greater than site A (P=0.004) and C (P<0.001). For the ITS treatment, it is concluded that site B had a relatively greater quantity of Engelmann spruce seed than sites A and C, where the spruce seed populations were similar.

The tripod traps placed in the center of the 0.1 ha openings were sampled in the fall and spring. The tripod traps at sites A and C were sampled in spring, while site B was sampled in the fall. Due to seasonal effects on the spruce seed population (refer to 4.2.3), site B was excluded from the site comparison. Figure 4.5c shows that 95% of the traps at site C had a seed density less than 300 seeds/m^2, where only 50% of traps at site A had fewer seeds at this density. Table 4.2 shows that there was a substantial difference between median values at sites A (300 seeds/m^2) and C (198 seeds/m^2). The Kruskal – Wallis test indicated that there were more spruce seeds present at site A than at site C (P=0.002). Given the supportive visual and empirical evidence, it is concluded that site A had more spruce seed than site C for the 0.1 ha openings.

Table 4.2. Engelmann spruce and subalpine fir median seed density at sites A, B and C, for the uncut, ITS and 0.1 ha treatments.

	Harvest Treatment	Median (seeds/m^2)		
		Site A	Site B	Site C
Engelmann spruce	Uncut	441	348	184
Engelmann spruce	ITS	205	416[*]	191
Engelmann spruce	0.1 ha	300	-	198[*]
Subalpine fir	Uncut	273	325	58[*]
Subalpine fir	ITS	95	92	105
Subalpine fir	0.1 ha	36	-	42

[*] statistically different at the 95% level of confidence (Kruskal-Wallis test)

For a given treatment, the box/tripod observations for sites A, B and C were used to analyze the effect of location on subalpine fir seed supply. Table 4.2 shows similar uncut subalpine fir median seed densities for site A (273 seeds/m^2) and site B (325 seeds/m^2); however, the seed density appears to be significantly lower at location C (58 seeds/m^2).

The cumulative distribution at each site indicates that relatively lower seed densities were more frequent at site C than sites A and B (Figure 4.6a). All traps found at site C had seed densities less than 300 seeds/m^2; however, only half of the traps at sites A and B had less than 300 seeds/m^2. The Kruskal – Wallis multiple comparison tests between sites indicated that the subalpine fir seed supply at sites A and B were similar (P=0.848); however, there were relatively fewer seeds at site C as compared to sites A (P<0.001) and B (P<0.001). It is concluded that subalpine fir seed population at sites A and B were similar; however, site C had significantly less seed.

For the ITS treatment, the median subalpine fir seed densities at sites A, B and C appeared similar with median values of 95, 92 and 105 seeds/m^2, respectively (Table 4.2). The cdf for each site indicated a similar range (25 – 225 seeds/m^2) as well as shape (Figure 4.6b). The Kruskal – Wallis test did not detect significant differences (P=0.668). For the ITS treatment the fir seed supply does not differ between sites.

For 0.1 ha openings, site B was excluded from the site comparisons due to a seasonal effect on subalpine fir seed supply (refer to 4.2.3). The cdf for sites A and C overlap each other with seed densities ranging between 0 seeds/m^2 and 200 seeds/m^2 (Figure 4.6c). The median seed densities for site A (36 seeds/m^2) and C (42 seeds/m^2) were similar (Table 4.2). The Kruskal – Wallis test indicated the fir seed populations at sites A and C were similar (P=0.828). The visual and empirical evidence supports the conclusion that the subalpine fir seed populations at sites A and C were comparable.

The rankings of sites A, B and C for each treatment are provided in Table 4.3. A higher ranking indicates significantly more seed at a site. For Engelmann spruce and subalpine fir, site C consistently had either lower or equivalent seed supply relative to sites A and B. This is contrasted to site B that had either more or an equivalent number of seeds as sites A and C for all treatments.

a)
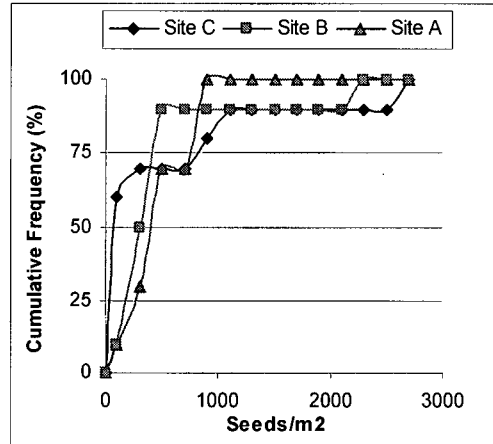
b)
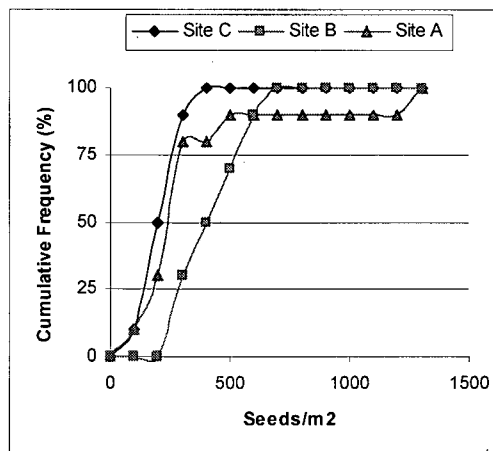
c)
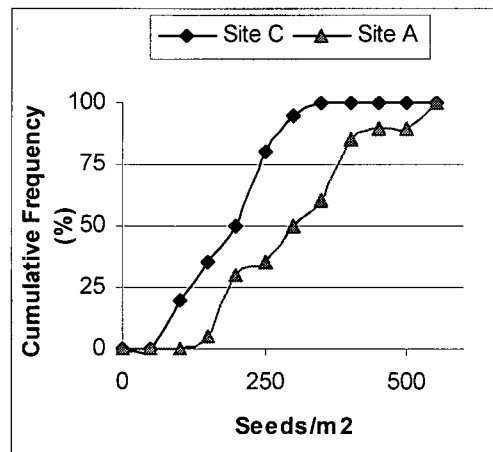
Figure 4.5. Cumulative frequency distributions of Engelmann spruce seed populations in sites A, B and C for the uncut (a), ITS (b) and at the center of the 0.1 ha (c) treatments.

a)

b)

c)
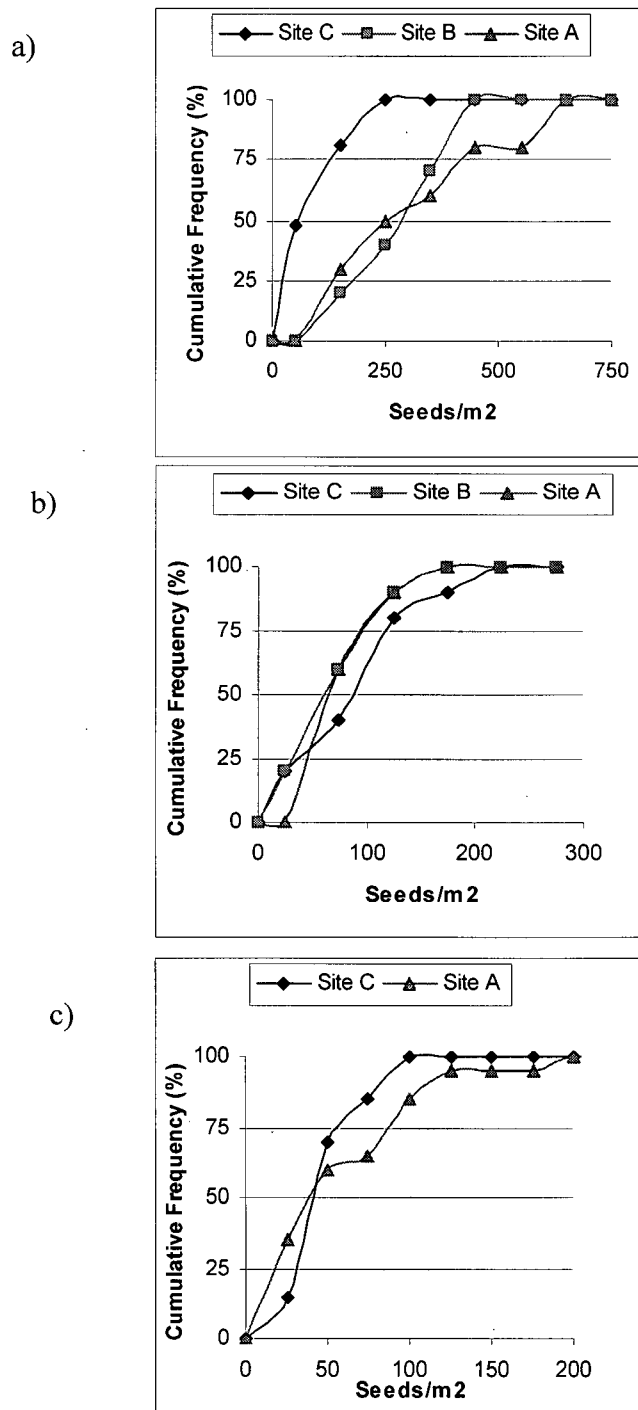
Figure 4.6. Cumulative frequency distribution of subalpine fir seed populations for sites A, B and C for the uncut (a), ITS (b) and at the center of the 0.1 ha (c) treatments.

Table 4.3. Site ranking of Engelmann spruce and subalpine fir seed supplies for Uncut, ITS and 0.1 ha treatments

	Harvest Treatment	Rank
Engelmann spruce	Uncut	A = B = C
Engelmann spruce	ITS	A = C < B
Engelmann spruce	0.1ha	A > C
Subalpine fir	Uncut	A = B > C
Subalpine fir	ITS	A = B = C
Subalpine fir	0.1ha	A = C

4.2.3 Seasonal Dispersal of Engelmann Spruce and Subalpine Fir Seed

This analysis compares seed data collected from the uncut stands in the fall and spring. Tripod traps were sampled in the fall from sites A and B. There was no location effect for Engelmann spruce in the uncut treatment. Therefore, the comparisons for spring and fall in the uncut treatment were not differentiated on the basis of location. Figure 4.7a shows that 92% of the fall Engelmann spruce population was found between 0 seeds/m^2 and 400 seeds/m^2, as compared to 49% for the spring population. The Kruskal-Wallis test indicated that the spring spruce seed population was significantly larger than the fall population (P<0.001). The median spruce seed density in spring (524 seeds/m^2) was more than three times the size of the fall's spruce density (140 seeds/m^2) (Table 4.4). It is concluded that a significant proportion of Engelmann spruce seed was dispersed after October 20th, 1997.

Table 4.4. Uncut Engelmann spruce and subalpine fir seed populations

	Median (seeds/m^2)	
	Spring	Fall
Engelmann spruce	524	140
Subalpine fir	310	176

Sites A and B had similar quantities of subalpine fir seed; however, site C had significantly fewer subalpine fir seeds relative to sites A and B (refer to 4.2.2). Subalpine fir seeds from sites A and B were combined and used for the spring and fall comparison. Figure 4.7b shows 57% of the seed densities in the fall were below 200 seeds/m^2, while

only 25% of the spring seed population was below this density. The median spring subalpine fir seed density of 310 seeds/m^2 was almost double the fall median density of 176 seeds/m^2 (Table 4.4). The Kruskal – Wallis test indicated that the spring seed population was significantly larger than the fall population (P<0.001). It is concluded that a significant proportion of subalpine fir seeds was dispersed after October 20th, 1997.

a)   b)
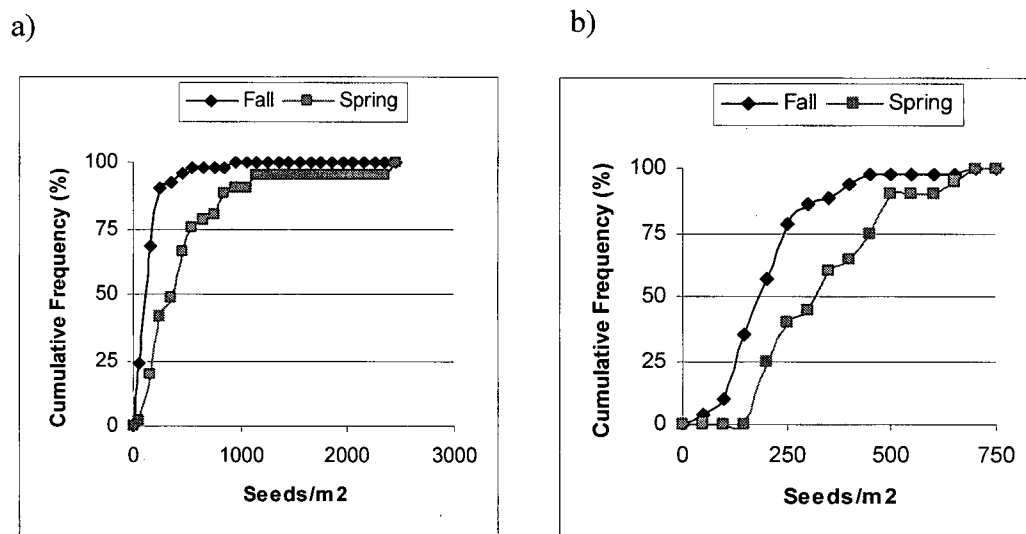
Figure 4.7. Cumulative frequency distribution of the spring and fall Engelmann spruce (a) and subalpine fir (b) seed populations

The ratio of seed collected in the spring to the number found in the fall was 3.7 for Engelmann spruce and 1.8 for subalpine fir. Snow normally covers the Sicamous Creek site by late October. In areas sheltered from the wind, the snow has minimal influence upon the spatial distribution of seed; however, in cleared openings, seeds blown along the snow considerably increases its dispersal distance (Green *et al.* 1999).

4.2.4 Engelmann Spruce and Subalpine Fir Seed Supply in the ITS and 0.1 ha Treatments Relative to the Uncut Stand

The ITS treatment removed approximately 33% of the volume from the stand. The uncut and ITS treatments were compared to determine whether this treatment

significantly reduced Engelmann spruce and subalpine fir seed supplies. Data from sites A, B and C were combined for this analysis.

The cumulative distribution of Engelmann spruce seed densities within the ITS and uncut treatments is illustrated in Figure 4.8a. The cdf plot shows that 50% of the uncut spruce seed densities were below 400 seeds/m^2, while up to 77% of the ITS seed population was below this density. The median spruce seed densities for the uncut and ITS were 395 seeds/m^2 and 249 seeds/m^2, respectively (Table 4.5). Despite the visual differences in the cdf and median values, the Kruskal – Wallis test was not able to detect a difference between the ITS and uncut spruce population at the statistical level of confidence exceeding 95% (P=0.117).

The median subalpine fir seed populations in the ITS and uncut stands were 96 seeds/m^2 and 236 seeds/m^2, respectively (Table 4.5). Figure 4.8b illustrates the cdf of the uncut and ITS subalpine fir seed populations. For the ITS stands, 87% of the traps had less than 150 seed/m^2 of fir seed, with seed densities occasionally up to 225 seeds/m^2. In the uncut treatment only 27% of the traps had a fir seed density below 150 seed/m^2 and seed densities over 600 seeds/m^2 were observed. The Kruskal – Wallis test indicated that the ITS fir seed population was significantly smaller than in the uncut stands (P<0.001). On the basis of the visual and empirical evidence, one can conclude that the fir seed population for the uncut stands was larger than the ITS seed population.

Table 4.5. Engelmann spruce and subalpine fir seed in uncut and ITS treatments

	Median (seeds/m^2)	
	Uncut	ITS
Engelmann spruce	395	249
Subalpine fir	236[*]	96[*]

[*]ITS and Uncut subalpine fir seed populations are statistically different at the 95% level of confidence (Kruskal –Wallis test)
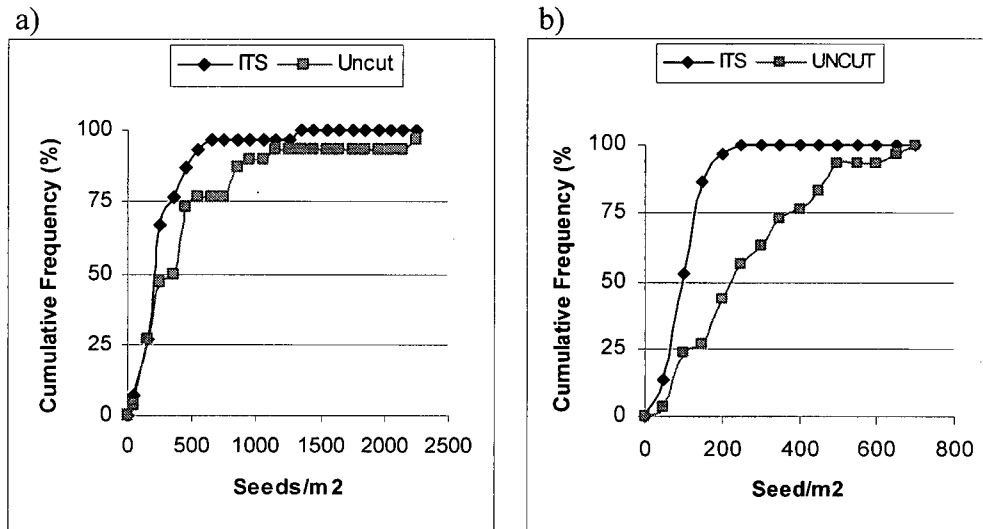
Figure 4.8. Cumulative frequency distribution of uncut and ITS Engelmann spruce (a) and subalpine fir (b) seed population.

The tripod trap data set was used to compare the density of seed in the uncut stands to that collected in the center of the 0.1 ha openings. Due to seasonal effects, both uncut and 0.1 ha data sets collected in the fall from site B were used for this comparison. In the uncut data there were two spruce seed densities that were extremely large relative to the other data; however, the cumulative frequency distributions for the uncut and 0.1 ha spruce seed populations are similar (Figure 4.9a). The Kruskal Wallis test indicated that the spruce seed population in the uncut stand was not significantly different from the center of the 0.1 ha openings (P=0.924). Based on the supporting empirical and visual evidence, it can be concluded that the spruce seed populations in the uncut and 0.1 ha treatment were similar.

The cumulative distribution for fir seed indicated that 80% of the traps in the center of the 0.1 ha openings had seed densities less than 150 seeds/m^2; however, only 40% of the traps in the uncut had seed densities less than this (Figure 4.9b). The Kruskal-Wallis test indicated that the uncut fir seed population was significantly greater than the 0.1 ha seed population (P=0.005). It is concluded that there were significantly fewer subalpine fir seeds in the center of the 0.1 opening compared to the uncut treatment.

a)   b)
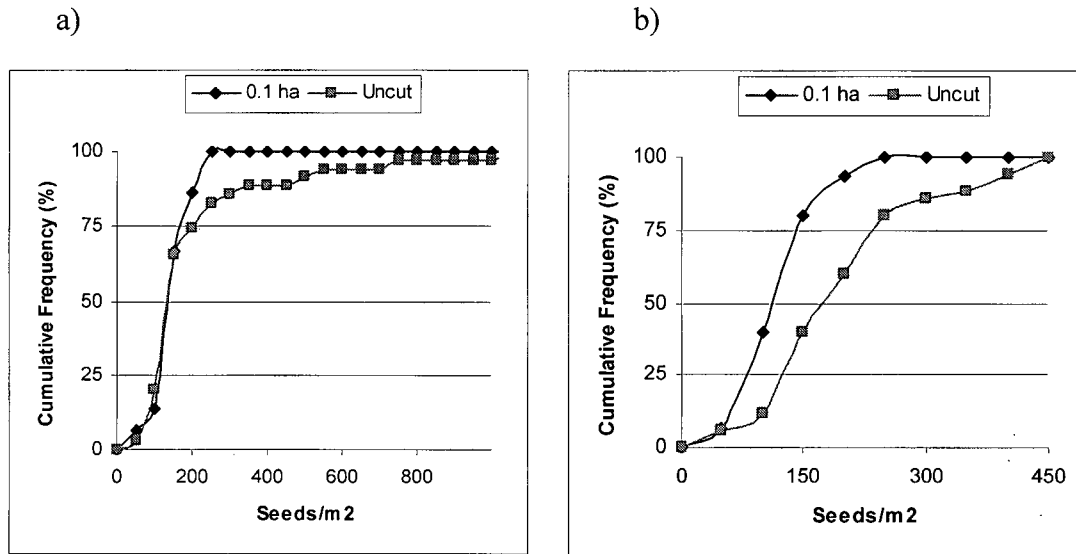
Figure 4.9. Cumulative frequency distribution of seed populations in uncut stands and the center of the 0.1 ha opening for Engelmann spruce (a) and subalpine fir (b).

The ITS and 0.1 ha treatments removed 33% of a stand's volume. Spruce is the preferred species for harvesting, and on some sites a higher proportion of spruce than fir was cut [2]. Despite the reduction of Engelmann spruce trees, it was concluded that the ITS and 0.1 ha spruce seed populations were similar to the uncut spruce population; however, the subalpine fir seed populations in the ITS and 0.1 ha treatment were significantly smaller than its uncut population. The ITS to uncut ratio for median fir seed density was 0.41, indicating there was approximately 60% fewer fir seeds in the ITS treatment. For the 0.1 ha opening, the ratio was 0.71, representing approximately 30% fewer fir seed in the center of the 0.1 ha opening relative to the uncut stand. The reduction of subalpine fir seed supply reflects the influence of fewer fir trees; however, the remaining Engelmann spruce trees appear to increase their seed production when a third of the stand's volume was removed.

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[2] Personal communication with Alan Vyse (Research Forester) on Nov. 20, 1999

4.3 Seed Dispersal into Cleared Openings

Assuming the trees surrounding a cleared area yield comparable number of seeds on all sides, the spatial distribution of seed in a cleared area is dependent primarily upon wind velocity and direction. At Sicamous Creek, Novak *et al.* (1997, unpublished) monitored wind conditions during September and October of the 1997-1998 dispersal season. For the statistical analysis of the spatial seed distribution in cleared openings, the wind data were categorized into four prevailing directions (N, E, S and W) that matched positioning of the traps to each edge. The relationship between wind azimuth and seed dispersal was assessed in terms of the number of seeds dispersed closest to an edge, relative to the overall seed deposited into the clearcut area, and to the frequency of the prevailing winds with respect to an edge.

The spatial analysis consisted of relating the open area seed density of Engelmann spruce and subalpine fir seed to the proximity of the closest source (N, E, S and W). In the 10ha and 1ha clearcut openings, the decay of seed from each edge was estimated using a negative exponential relationship between seed density and distance from the clearcut edge (Equation 3.2). The decay coefficients were compared between edges and covariance analysis was conducted on the dispersal equation from each edge to determine if site consistently influenced seed supply.

4.3.1 Wind Profile At Sicamous Creek

The average hourly wind velocity and direction were obtained from an anemometer 6m off the ground in the center of the B5 10 ha clearing. At this location, friction from the clearcut edge reduced wind velocity. Assuming Engelmann spruce and subalpine fir trees are 29m in height (Greene and Johnson 1996), Equation 2.11 was used to adjust the velocity of the recorded wind data to u_r. The adjusted median wind speeds in Table 4.6 reflect the velocity above the canopy. The overall arithmetic mean and median wind velocities were 2.9m/s and 2.7 m/s, respectively. The frequency distribution of the 1255 hours of wind about the arithmetic mean had a positive skewness coefficient ($\gamma_1 = 0.57$,

P=0.01); however, when transformed by natural logs the distribution had a negative skew ($\gamma_1 = -1.1, P<0.001$) (Snedecor and Cochran 1989). The northerly winds had the highest mean velocity at 3.4 m/s; however, given that the overall standard error of the hourly wind velocity was 1.4 m/s, the average directional velocities were not statistically different.

Table 4.6. September and October prevailing winds at SCSSRP study site (Source: Novak *et al.* 1997, unpublished) [a]

	North	East	South	West	All Winds
Azimuth (in °)	316-45	46-135	136-225	226-315	0-359
Number of hrs.	82	210	495	468	1255
Mean (m/s)	3.4	3.0	3.0	2.8	2.9
Std. Dev. (m/s)	1.7	1.2	1.4	1.4	1.4
Median (m/s)	3.4	3.0	2.7	2.6	2.7
Min (m/s)	0.1	0.2	0.2	0.4	0.1
Max (m/s)	7.8	6.3	7.4	8.3	8.3
Freq of hrs. (%)	6.5	16.7	39.4	37.3	100
Rank	4	3	1	2	-

[a] Hourly mean wind velocities recorded by the anemometer in B5 clearcut were adjusted by Equation 2.11 to account for the friction from the surrounding edges

The frequency of hours recorded for each prevailing wind was the best indicator of the relative difference between wind directions, given their mean velocities are comparable. During the 1997 fall dispersal season there were fewer northerly winds (6.5%) than the other wind categories (Table 4.6). Southerly winds (39.4%) were most frequent, followed by westerly winds (37.3%) and easterly winds (16.7%). The relationship between the frequency of prevailing winds and the quantity of seed dispersed closest to its respective edge is assessed in the following section.

4.3.2 Prevailing Winds and Seed Dispersal

Typically, seed dispersal studies have access to data from only one or two edges. The orientation of the seed traps in the 10 ha and 1 ha clearcuts were used to assess wind azimuth and seed dispersal from all four edges. The seed share equations quantitatively

assessed the relationship between the seed supply from the closest edge, and the frequency of an edge's prevailing wind. The assumptions of the wind/seed dispersal analysis were that each edge had a homogeneous supply of seed and the average wind velocity and variability were the same for each wind direction. It should be noted that the 1255 hours of wind data were collected in September and October and do not represent the entire dispersal season. For this analysis, it is assumed that this wind data recorded during these two months are representative of the entire dispersal season. The relationship between prevailing winds and seed dispersal was estimated with the Engelmann spruce and subalpine fir data sets in the 10 ha and 1 ha clearcuts. If the relationships identified were statistically significant, then comparisons were undertaken between the parameters of the 10 ha and 1 ha share equations.

Equations 4.1 a and b are the 10 ha seed share equations for Engelmann spruce and subalpine fir, respectively. The share equation for spruce had an intercept of 0.096 and slope of 0.614. The intercept and slope were both significantly different than 0 and 1, respectively. However, the slope (0.614) was also significantly different than zero (P=0.001). This suggested that the frequency of prevailing winds blowing over each edge could explain a significant proportion in the variation in Engelmann spruce seed supply between edges. Using the wind data in Table 4.6, Equation 4.1a estimates that 32.5% of spruce seeds will be dispersed closest to the west edge (0.096+0.614*.373). Substituting the wind frequencies from the north, east and south into equation 4.1 predicts that 13.6%, 19.9% and 33.8% of Engelmann spruce seed will fall in closest proximity to the N, E and S edges, respectively. The intercept represents constant factor for each edge that is not accounted for by wind frequency. For example, of the 32.5% of all spruce seed deposited closest to the west edge, 9.6% is not reflected in the frequency of the wind from the west. The seed share equation for subalpine fir had an intercept of 0.065 and slope of 0.74 and were not significantly different than 0 or 1, respectively. Therefore, the proportion of fir seed closest to an edge in a 10 ha clearing has a 1 to 1 relationship with wind frequency.

$$\%ES_{kj} = \quad 0.096 \quad + \quad 0.614 \quad *W_j$$
$$(P = 0.048)^1 \quad (P = 0.022)^2$$

$n = 56$ **4.1a**

$$\%SF_{kj} = \quad 0.065 \quad + \quad 0.738 \quad *W_j$$
$$(P = 0.278)^1 \quad (P = 0.216)^2$$

$n = 56$ **4.1 b**

where:

^{1} = Probability of the intercept not being equal to zero
^{2} = Probability of the slope not being equal to one

Equation 4.2 a and b show the 1 ha seed share equations for Engelmann spruce and subalpine fir, respectively. The Engelmann spruce share equation had an intercept of 0.194 and a slope of 0.224; these were significantly different than 0 and 1, respectively. The slope of 0.224 was significantly different than zero ($P<0.001$) indicating that some of the difference in the supply of seed closest to an edge is attributed to the frequency of the respective prevailing wind. For subalpine fir, the seed share equation had an intercept of 0.159 and a slope of 0.366, which were significantly different than 0 and 1, respectively. The slope was significantly different than zero ($P<0.001$), indicating prevailing wind did account for some of the variation in seed supply between edges. The greater slope coefficient in the subalpine fir seed share equation suggested that the spatial orientation of its seeds was more influenced by wind direction than the Engelmann spruce seed. Fir seed has a greater terminal velocity than spruce, and airborne fir seeds are less likely to be carried beyond the quadrant situated closest to the nearby edge.

$$\%ES_{kj} = \quad 0.194 \quad + \quad 0.224 \quad *W_j$$
$$(P < 0.001)^1 \quad (P < 0.001)^2$$

$n = 152$ **4.2a**

$$\%SF_{kj} = \quad 0.159 \quad + \quad 0.366 \quad *W_j$$
$$(P < 0.001)^1 \quad (P < 0.001)^2$$

$n = 152$ **4.2 b**

where:

^{1} = Probability of the intercept not being equal to zero
^{2} = Probability of the slope not being equal to one

Overall, the 1 ha share equations had a smaller slope and larger intercept than the 10 ha share equations. For Engelmann spruce, the 1 ha slope coefficient was one-third the size of the 10 ha slope coefficient. For subalpine fir, the slope coefficient was half the

size. A smaller slope parameter indicates a weaker relationship between prevailing winds and the seed supply found closest to the respective edge. For spruce and fir the 1 ha seed share equations, the value of the intercept increased by approximately 0.1 over their 10 ha counterparts. In the 1 ha clearcut, the traps positioned perpendicular to the closest edge were closer to the three remaining edges than in the 10 ha clearcut. For example, in the 1 ha clearcut, traps perpendicular to the north edge were 50m from the east and west edges, while in the 10 ha clearing the east and west edges were 165m away. More seed from the three remaining edges (secondary seed sources) in the 1 ha clearcuts is the probable cause for the reduced seed share relationship for the 1 ha openings.

4.3.3 Seed Dispersal in the 10 ha Clearcut

As cleared openings increase in size, windward winds are a primary factor influencing seed dispersal. The negative exponential function (Equation 3.2) estimated seed dispersal spatially from each edge. This analysis assesses the exponential decay of seed from each edge. The second component draws upon the estimated dispersal equations to identify source effects associated with site (A, B and C) and whether an edge consistently supplies more or less seed relative to another.

4.3.3.1 Seed Dispersal and Rate of Decay with Distance

The negative exponential decay equation was estimated from Engelmann spruce and subalpine fir seed data collected between 0m and 90m from the closest edge. Table 4.7 shows the resultant dispersal parameters; namely the source effect (b_0) and the decay effect (b_1) for Engelmann spruce. The decay coefficient estimated the exponential reduction in seed density for every meter away from the closest edge. An assumption of covariance analysis is that the decay coefficient must be constant between sites A, B and C in order to test for different source effects. If the b_1 were not the same between sites, the data from the site with the unique decay coefficient would be analyzed independently. For example, in Table 4.7 the decay coefficient for the west edge at site C ($b_1 = -0.031$) was significantly larger than sites A and B ($b_1 = -0.015$). Therefore, the site C data were

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analyzed independently. The separate equation for the west edge (site C) was based upon five seed traps and the unique decay rate was more likely the result of a small sample (n=5) than of dispersal conditions at the site.

The decay coefficient was constant across sites A, B and C for the north (b_1=-0.018), east (b_1=-0.015), and south (b_1=-0.032) edges. The statistically significant decay coefficients ranged from $-$ 0.032 for the south edge (sites A, B and C) to $-$0.015 for the west edge (sites A and B) and east edge (sites A, B and C). The decay coefficient for the north edge (-0.018) was not significantly different than zero (P=0.1257) indicating that distance was not a critical factor in determining the quantity of seed found between 0 to 90 meters from the north edge. This was not the case for the east, south and west edges, where the probability that the decay coefficients are equal to zero ranged from 0.001% to 0.033%, indicating that spruce seed density declined with distance from these edges.

Table 4.7. Regression equations for the dispersal of Engelmann spruce seed in 10 ha clearcut areas [1]

Edge (sites)	b_0	b_{0A}	b_{0B}	b_1	r^2	Obs.
North (ABC)	3.301 (P<0.001)	-	-	-0.018 (P=0.126)	0.18	14
East (ABC)	4.072 (P<0.001)	1.22 (P<0.001)	-	-0.015 (P=0.002)	0.77	15
South (ABC)	4.431 (P<0.001)	1.538 (P=0.029)	1.538 (P=0.029)	-0.032 (P=0.004)	0.67	15
West (AB)	4.152 (P<0.001)	0.44 (P=0.081)	-	-0.015 (P=0.003)	0.77	10
West (C)	4.929 (P<0.001)	-	-	-0.031 (P=0.033)	0.96	5

where:

[1] $N_{xi} = \exp(b_0 + b_{0A} + b_{0B} + b_1 x)$, where N_{xi} is the quantity of seed estimated at distance x in site "i"; and x is the perpendicular distance from the closest edge

[2] P-values of the regression coefficient are enclosed in brackets

The dispersal equations estimated for subalpine fir seed were determined from the combined tripod/box data set. Referring to Table 4.8, the decay coefficient for the north edge is not significantly different than 0 (P=0.969). The decay coefficients for the north (b_1=0) and south (b_1=-0.028) edges were statistically similar between all sites, while the

east and west edges were separated to reflect differential decay parameters on a given site. The decay coefficients for the east edge in site C and the west edge in site A were not significantly different than zero, while the decay parameters for the east (sites A and B) and west (site B and C) were statistically different than zero. Since the latter estimates for the east and west edges were based upon twice the number of observations, the parameters which indicate no decay in the seed density were likely due to the sample not being representative of the spatial distribution of seeds.

The statistically significant decay parameters for Engelmann spruce had a larger range than subalpine fir. For Engelmann spruce, the decay parameter ranged between –0.015 and –0.032, compared to –0.022 and –0.028 for subalpine fir. From the north edge, the decay parameters for both species were not significantly different than zero. The lack of a consistent spatial seed pattern from the north edge likely reflects the effect of infrequent northerly winds. Most of the seed production along the north edge was dispersed into the treed area by leeward winds. A larger sample of traps from the north edge would have increased the likelihood of detecting a spatial pattern from the few seeds blown into the 10 ha opening from the north edge.

Table 4.8. Regression equations for the dispersal of subalpine fir seed in 10 ha clearcut areas [1]

Edge (sites)	b_0	b_{0A}	b_{0B}	b_1	r^2	Obs.
North (ABC)	0.857 (P=0.099)	-	-	0 (P=0.969)	0	14
East (AB)	3.356 (P<0.001)	-	-	-0.022 (P=0.001)	0.44	26
East (C)	1.518 (P=0.010)	-	-	0 (P=0.894)	0	13
South (ABC)	2.275 (P<0.001)	1.400 (P=0.029)	1.400 (P=0.029)	-0.028 (P=0.005)	0.66	14
West (BC)	2.750 (P<0.001)	-	1.608 (P<0.001)	-0.026 (P<0.001)	0.74	30
West (A)	3.334 (P<0.001)	-	-	-0.006 (P=0.247)	0.10	15

where:

[1] $N_{xi} = \exp(b_0 + b_{0A} + b_{0B} + b_1 x)$, where N_{xi} is the quantity of seed estimated at distance x in site "i"; and x is the perpendicular distance from the closest edge
[2] P-values of the regression coefficient are enclosed in brackets

4.3.3.2 Site Effect on Engelmann Spruce and Subalpine Fir Seed Supply

The source parameter b_0 represents the background seed at sites A, B and C unless a differential b_{0A} and/or b_{0B} was statistically significant. If this was the case then the source parameter for site A was $b_0 + b_{0A}$, while site B was $b_0 + b_{0B}$. The dispersal equations in Tables 4.7 and 4.8 were integrated from 0m to 100m to estimate the total number of seeds in a 1m wide corridor running perpendicular from the respective edge. The quantities of seed at each site, for a given edge, were compared to determine if particular sites consistently supplied more or less seed.

Table 4.9 shows the supply of Engelmann spruce seed from 0m to 100m for each site and edge. Summing the contribution from each edge, site A (28373 seeds) was estimated to supply the most spruce seed, followed by site B (19313 seeds) and site C (11074 seeds). In terms of each edge, Site A supplied either more or an equivalent amount of spruce seed as sites B and C. All the edges at Site C supplied fewer spruce seeds than at site A, with the exception of the north edge where spruce seed supply was equivalent between sites. Despite the 'total' amount of spruce seed at site B being larger than at site C, differences between sites B and C were not consistent. Site B supplied more spruce seed from the south edge than site C; however, for the west edge, site C supplied more spruce seed than site B.

Table 4.10 shows the supply of subalpine fir seed from 0m to 100m for each site and edge. There were fewer subalpine fir seeds at site C than sites A and B, with the exception of the north edge. Differences in fir seed supply between sites A and B are not consistent. The relatively small difference of 671 'total' subalpine fir seeds between sites A and B is attributed solely to the west edge.

Table 4.9. Estimated total number of Engelmann spruce seeds in a corridor 1m by 100m running perpendicular into the 10 ha clearcut from the center of the respective edge [1]

Edge	Site A	Site B	Site C	Mean
		-Total Seed-		
North	1259	1259	1259	1259
East	10293	3039	3039	5457
South	11724	11724	2518	8656
West	5111	3292	4259	4221
Total	28387	19313	11074	19592

[1] $\int_0^{100} \exp(b_0 + b_{0A} + b_{0B} + b_1 x)dx$

Table 4.10. Estimated total number of subalpine fir seeds in a corridor 1m by 100m running perpendicular into the 10 ha clearcut from the center of the respective edge [1]

Edge	Site A	Site B	Site C	Mean
		-Total Seed-		
North	224	224	224	224
East	1159	1159	462	927
South	1323	1323	326	991
West	2109	2781	557	1816
Total	4816	5487	1549	3958

[1] $\int_0^{100} \exp(b_0 + b_{0A} + b_{0B} + b_1 x)dx$

In the 10 ha clearcut, the relative composition of Engelmann spruce and subalpine fir seed changed dramatically from the composition in the uncut stand. In the uncut stands, the median seed population of Engelmann spruce was 1.7 times that of subalpine fir seed. Only one of the twelve 1m corridors had an estimated ratio below that of the uncut stand. For all the edges, the ratio of Engelmann spruce to subalpine fir seed ranged from 1.2 to 8.9, with an overall mean of 5.5 (Table 4.11). The increased ratio shows that relatively more Engelmann spruce seed were dispersed into the cleared opening.

Table 4.11. Estimated ratio of Engelmann spruce seed to subalpine fir seed in a
10 ha clearcut

Edge	Site A	Site B	Site C	Mean
		-Seed Ratio-		
North	5.6	5.6	5.6	5.6
East	8.9	2.6	6.6	6.0
South	8.9	8.9	7.7	8.5
West	2.4	1.2	7.6	3.8
Mean	5.9	3.5	7.1	5.5

4.3.3.3 The Influence of Edge Orientation on the Spatial Dispersal of Seed

When an open area closest to a given edge consistently had a different amount of seed
relative to the other edges, the common factor is likely the pattern of winds during seed
dispersal (Franklin and Smith 1974). The resultant 10 ha dispersal functions for
Engelmann spruce and subalpine fir are illustrated in Figures 4.10-4.11, respectively.
These figures along with Tables 4.9 and 4.10 were used to compare the dispersal of
Engelmann spruce and subalpine fir seed for each edge and assess the relationship with
prevailing winds.

A larger number of Engelmann spruce and subalpine fir seeds were dispersed from
the south and west edges, with the north edge contributing the least (Figures 4.10 and
4.11). Tables 4.9 and 4.10 indicate more seed was found closer to the south and west
edges, with the exception of the east edge at site A for Engelmann spruce and the east
edge at site C for subalpine fir. For example, at site B, 2781 and 1323 subalpine fir seeds
were supplied from the west and south edges, respectively, and exceeded the seed
supplied from the east (1159) and north edges (224). Fewer Engelmann spruce (1259)
and subalpine fir (224) seeds were estimated to be dispersed into the 100m^2 transect
perpendicular from the north edge. Southerly (39.4%) and westerly (37.3%) winds were
more frequent at Sicamous Creek than the easterly (16.7%) and northerly (6.5%) winds;
therefore, seeds produced along the southerly and westerly edges had more opportunity to
be carried into the 10 ha cleared opening.
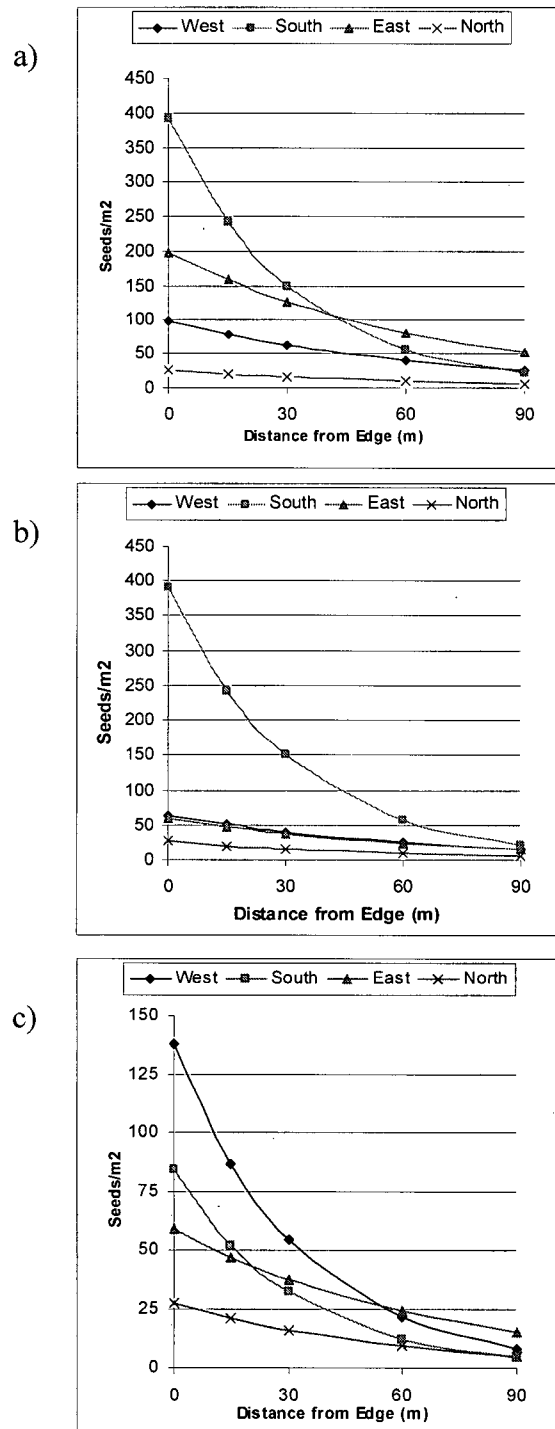
Figure 4.10. Regression equations estimating Engelmann spruce seed dispersal at sites A (a), B (b) and C (c) in the 10 ha clearcuts

a)

b)

c)
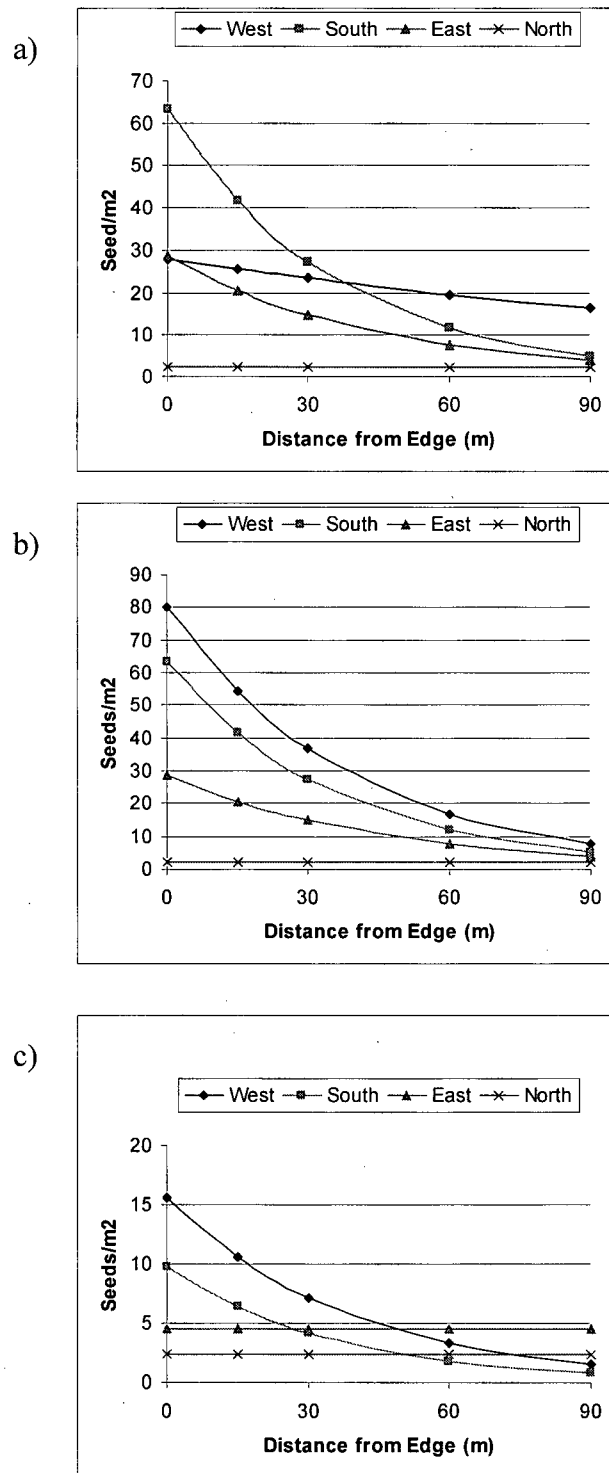
Figure 4.11. Regression equations estimating subalpine fir seed dispersal at sites A (a), B (b) and C (c) in the 10 ha clearcuts

4.3.4 Seed Dispersal into 1.0 ha Clearcut

This section utilizes the 10 ha seed dispersal equations for Engelmann spruce and subalpine fir to predict the seed densities in the 1 ha opening. These predictions will be compared to the mean seed densities recorded at various distances from the edge. This will assess whether the dispersal characteristics in the 10 ha clearing are similar to the 1 ha clearing. The negative exponential decay function was estimated by regression from seed data at 16.5m, 33m and 50m from each edge. The estimated parameters were used to examine the spatial distribution of seed, as well as the influence of location and edge on the seed dispersal.

4.3.4.1 Predicting 1 ha Seed Dispersal with 10 ha Dispersal Equations

The 10 ha dispersal equations for site B (Table 4.7 and 4.8) were used to predict the quantity of Engelmann spruce and subalpine fir seed supplied in the 1 ha opening at site B. Figures 4.12 and 4.13, respectively, display the predicted and observed spatial seed density of spruce and fir along the north-south and west-east corridors for the 1 ha openings.

For their respective edges, the 10 ha dispersal equations under-predicted the observed seed supply at 16.5m and 33m, with the exception of the south edge for spruce and the west edge for fir. For example, in Figure 4.12b the west 10 ha dispersal equation predicted the Engelmann spruce seed densities at 16.5m and 33m away from the west edge to be 77 seeds/m^2 and 60 seeds/m^2, respectively; however, the mean values at these locations were 140 seeds/m^2 and 98 seeds/m^2. The consistent under-prediction of seed supply by the 10 ha dispersal equation for their respective edge, is an indication that the three remaining edges were secondary seed suppliers for the 1 ha openings. In Figure 4.13a, the west and east edges were 50m on either side of the N-S corridor and were estimated to supply 10 seeds/m^2 and 2 seeds/m^2, respectively, to all locations along the N-S corridor. Throughout the N-S corridor, the estimated supply of seed from the south edge far exceeded the estimates from the north.

The "total" prediction summed the contribution of seed predicted along the north –
south (west - east) line from all four edges. The "total" prediction consistently
overestimated the number of spruce and fir seeds collected at 16.5m, 33m 50m, 67m and
83.5m from the north or east edges. As distance from the edge increased, the relative
difference between the forecasted and the observed mean seed density also increased. At
16.5m, 33m and 50m, the forecasted seed densities exceeded the observed densities by
multiples of 1.5, 2.0 and 2.6, respectively. As distance from the edge increased, the
growing relative difference between the forecasted and actual mean seed density suggests
that the decay of seeds from the edge is greater for the 1 ha clearcut than for the 10 ha
clearcut. The lower forecasted seed density could possibly be attributed to reduced
horizontal wind speeds in the 1 ha clearings.

a)   b)
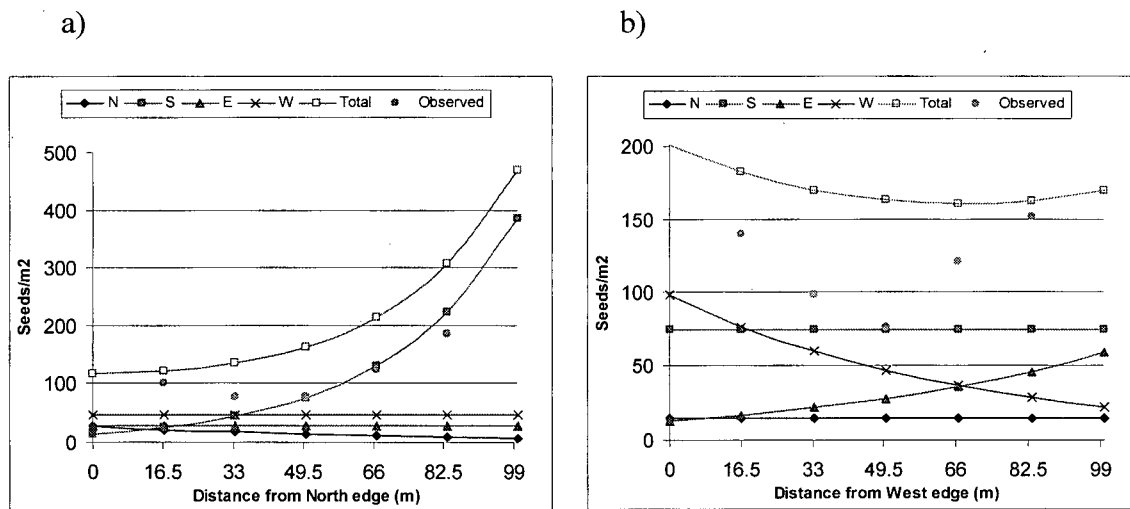
Figure 4.12. The spatial distribution of Engelmann spruce seed in the 1 ha
clearcut. The 10 ha dispersal equations (site B) predicted supply of seed from
each edge into a 1m corridor running perpendicular from (a) the center of north
edge to the center of the south edge, or (b) the center of the west edge to the
center of the east edge.

a)   b)
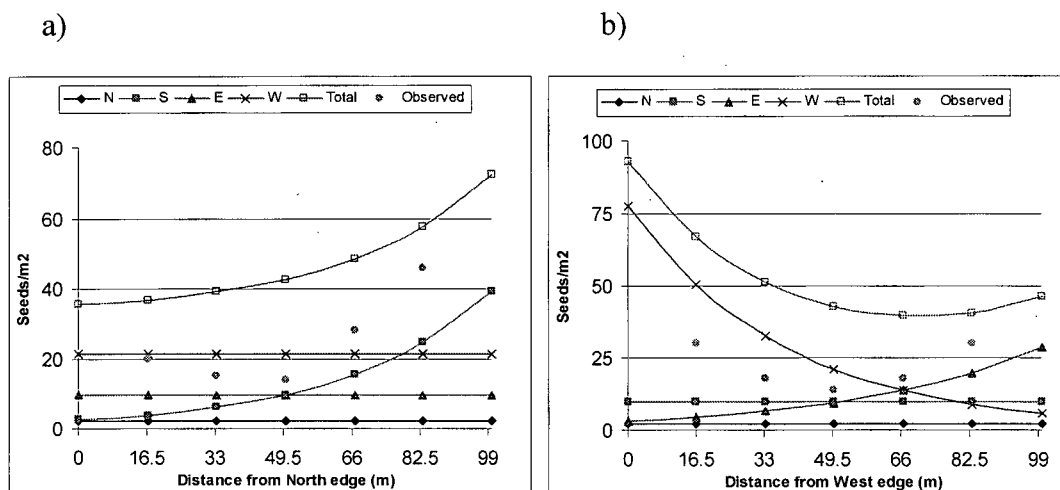
Figure 4.13. The spatial distribution of subalpine fir seed in the 1 ha clearcut.
The 10 ha dispersal equations (site B) predicted supply of seed from each edge
into a 1m corridor running perpendicular from (a) the center of north edge to the
center of the south edge, or (b) the center of the west edge to the center of the
east edge.

4.3.4.2 Seed Dispersal and Rate of Decay with Distance

For the dispersal of Engelmann spruce and subalpine fir seeds in the 1 ha treatment,
Tables 4.12 and 4.13 show that the decay coefficients (b_1) were comparable between sites
and were significantly ($\alpha=0.05$) different than zero, with the exception for the north edge.
The significant decay coefficients for Engelmann spruce ranged from –0.014 for the west
edge to -0.025 for the south edge (Table 4.12). The 1 ha decay parameters were not
consistently different than the 10 ha coefficients, which ranged from –0.015 to –0.032
(Table 4.7). For subalpine fir, the 1 ha decay coefficients ranged from -0.029 for the east
edge to -0.047 for the south edge (Table 4.13). They were consistently greater than their
respective decay parameters for the 10 ha clearcut, which ranged from 0 to –0.028 (Table
4.9).

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Table 4.12. Regression equations for the dispersal of Engelmann spruce seed in 1 ha clearcut [1]

Edge (sites)	b_0	b_{0A}	b_{0B}	b_1	r^2	Obs.
North (ABC)	4.450 (P<0.001)	0.334 (P<0.026)	0.334 (P<0.026)	-0.008 (P<0.104)	0.25	61
East (ABC)	5.350 (P<0.001)	-	-	-0.022 (P=0.001)	0.29	59
South (ABC)	5.593 (P<0.001)	-	-	-0.025 (P<0.001)	0.46	60
West (ABC)	5.007 (P<0.001)	-	-	-0.014 (P<0.001)	0.16	59

where:

[1] $N_x = \exp(b_0 + b_{0A} + b_{0B} + b_1 x)$; where N_x is the number of seeds estimated at distance x, and and x is the perpendicular distance from the closest edge

[2] P-values of the regression coefficient are enclosed in brackets

Table 4.13. Regression equations for the dispersal of subalpine fir seed in 1 ha clearcut [1]

Edge (sites)	b_0	b_{0A}	b_{0B}	b_1	r^2	Obs.
North (ABC)	3.01 (P<0.001)	-1.335 (P<0.001)	-	-0.01 (P<0.33)	0.27	61
East (ABC)	3.84 (P<0.001)	-1.07 (P<0.001)	-	-0.029 (P<0.001)	0.36	83
South (ABC)	4.438 (P<0.001)	-	-	-0.047 (P<0.001)	0.30	60
West (ABC)	3.547 (P<0.001)	-0.735 (P=0.011)	0.827 (P=0.005)	-0.033 (P<0.001)	0.40	84

where:

[1] $N_x = \exp(b_0 + b_{0A} + b_{0B} + b_1 X_\perp)$; where N_x is the number of seeds estimated at distance x, and x is the perpendicular distance from the closest edge

[2] P-values of the regression coefficient are enclosed in brackets

4.3.4.3 Comparison of the Source Parameter in the 1 ha and 10 ha Dispersal Equations

The source parameters (b_0, b_{0A}, b_{0B}) reflects the constant background amount of seed available from the closest, opposite and adjacent edges. Comparisons between the 10 ha and 1 ha source parameters revealed that the 1 ha estimates were equal or exceeded the 10 ha source parameters. For the 10 ha opening, 20 spruce seeds and 3 fir seeds were estimated at 16.5m from the north edge. For the 1 ha clearing there were 104 spruce

seeds and 17 fir seeds at 16.5m from the north edge. The increased amount of seed is likely due to the contribution of seed from secondary sources. Furthermore, given the low frequency of northerly winds, the north edge may not have contributed many seeds to the east, west and south corridors. Therefore, the size of the source parameters for the east, west and south edges should be inflated less, due to fewer seeds originating from the north edge. This was confirmed by the estimates of b_0 for the east, west and south edges being marginally larger for the 1 ha clearcuts than the 10 ha clearcuts.

4.3.4.4 Location Effect on Engelmann Spruce and Subalpine Fir Seed Supply

The dispersal equations in Tables 4.12 and 4.13 were integrated between 0m and 50m to assess the influence of site on Engelmann spruce and subalpine fir seed supply. In a 1m corridor running perpendicular to each edge, a total of 23511 spruce seeds were estimated to be dispersed at sites A and B, while 22111 spruce seeds were estimated for site C (Table 4.14). The quantity of spruce seeds estimated at each site was the same, with the exception of the north edge where site C supplied fewer spruce seeds than sites A and B. Overall, the number of Engelmann spruce seeds dispersed in the 1 ha openings was not influenced by site.

For subalpine fir, site B supplied more seed than site A for the north, east and west edges (Table 4.15). Site C supplied more seed from the north and the east edges than site A. Differences between sites B and C were small, having an equivalent supply of fir seed from each edge except for the west edge where Site B had more fir seed. When the estimates from each edge were combined, site A had the fewest fir seeds (2667 seeds) followed by site C (4505 seeds) and site B (5598 seeds).

Table 4.14. Estimated Engelmann spruce seeds in a corridor 1m wide and 50m long running perpendicular into the 1 ha clearcut from the center of the respective edge [1]

Edge	Site A	Site B	Site C	Mean
		-Total Seed-		
North	4928	4928	1215	4462
East	6386	6386	6386	6386
South	7664	7664	7664	7664
West	4532	4532	4532	4532
Total	23511	23511	22111	23044

[1] $\int_0^{50} \exp(b_0 + b_{0A} + b_{0B} + b_1 x)\,dx$

Table 4.15. Estimated subalpine fir seeds in a corridor 1m wide and 50m long running perpendicular into the 1 ha clearcut from the center of the respective edge[1]

Edge	Site A	Site B	Site C	Mean
		-Total Seed-		
North	210	798	798	602
East	421	1228	1228	959
South	1628	1628	1628	1628
West	407	1943	850	1067
Total	2667	5598	4504	4256

[1] $\int_0^{50} \exp(b_0 + b_{0A} + b_{0B} + b_1 x)\,dx$

Table 4.16. Estimated ratio of Engelmann spruce seed to subalpine fir seed in a 1 ha clearcut

Edge	Site A	Site B	Site C	Mean
		-Seed ratio-		
North	23.5	6.2	4.5	11.4
East	15.2	5.2	5.2	8.5
South	4.7	4.7	4.7	4.7
West	11.1	2.3	5.3	6.3
Mean	8.8	4.2	4.9	6.0

For the 1 ha clearing, the ratios between Engelmann spruce seed and subalpine fir seed exceeded the uncut ratio of 1.7. The overall mean seed ratio was 6.0 (Table 4.16). The increased seed ratio in the 1 ha clearings was consistent with the findings in the 10 ha clearings, indicating a higher proportion of Engelmann spruce seed are dispersed by wind.

4.3.3.5 The Influence of Edge Orientation on the Spatial Dispersal of Seed

The 1 ha dispersal equations for subalpine fir and Engelmann spruce are plotted in Figures 4.14 and 4.15, respectively. With the exception of site C for subalpine fir, fewer seeds were dispersed from the north edge. The largest supply of Engelmann spruce and subalpine fir seed was dispersed from the south edge. Table 4.14 and Figure 4.15 show that more subalpine fir seeds were located in areas closest to the south edge (1628 seeds) than the north, east or west edges. Despite westerly winds (37.3%) being relatively more frequent than easterly winds (16.7%), more spruce and fir seeds were found closer to the east edge than the west edge. However, for both species, the south edge consistently supplied the most seed and the north edge supplied the least amount of seed, indicating a positive correlation between seed dispersal from an edge and the frequency of the respective prevailing winds.
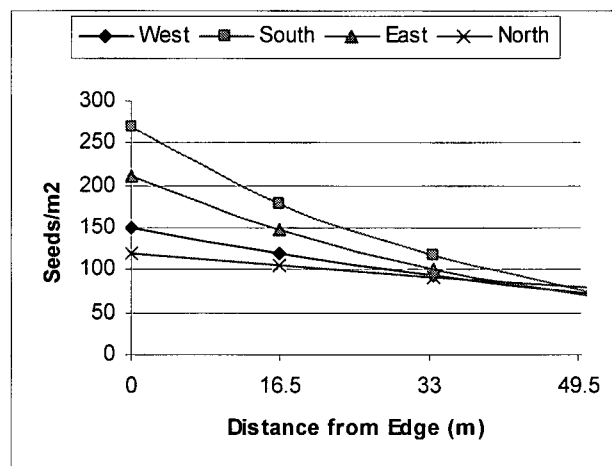
Figure 4.14. Regression equations estimating Engelmann spruce seed dispersal from sites A, B and C in the 1 ha clearcuts (north intercept site C is not included)

73

a)

b)

c)
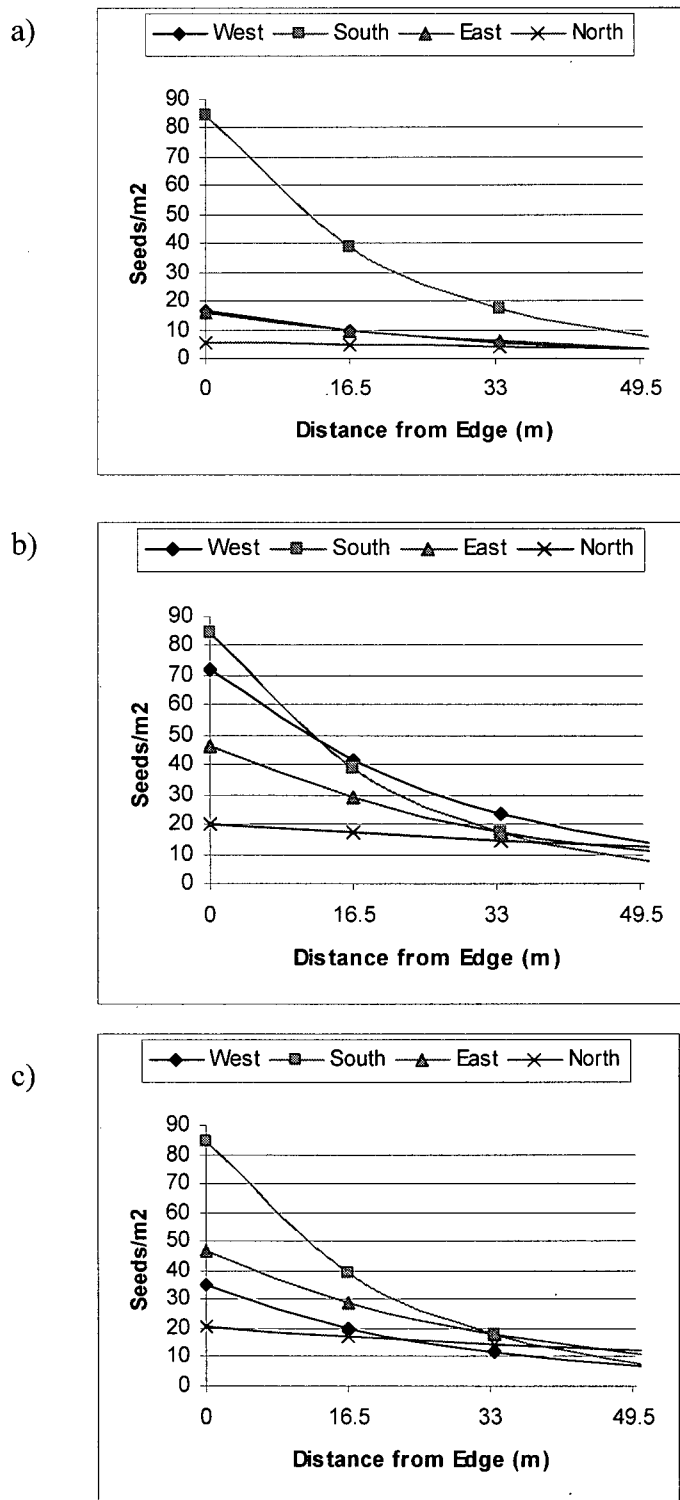
Figure 4.15. Regression equations estimating subalpine fir dispersal at sites A (a), B (b) and C (c) in the 1 ha clearcuts

4.3.5. Comparison of Seed Supply in 10 ha and 1 ha Clearcut Openings Relative to Uncut Stands

The dispersal equations for the 10 ha clearing were integrated between 0m and 100m to estimate the supply of Engelmann spruce and subalpine fir seed for a 1m wide corridor within the clearing running perpendicular to the center of each edge. The 10 ha mean corridor supply of spruce and fir seeds from all edges and sites was 4898 seeds and 989 seeds, respectively. In the uncut stands, the median seed densities were 395 seeds/m^2 for spruce and 236 seeds/m^2 for fir. Figure 4.16 illustrates the relative area of uncut forest that supplied the equivalent quantity of seed found in the 100m^2 corridor from each edge. The supply of seed in a 12.4m^2 uncut patch for Engelmann spruce and 4.2m^2 uncut patch for subalpine fir would be equivalent to the amount of seed in the 100m^2 corridor in the 10 ha clearcuts.

The dispersal equations for the 1 ha clearing were integrated from 0m and 50m to estimate the seed supply from each edge to the center of the clearing. Figure 4.17 illustrates the relative area of uncut forest that supplied the equivalent amount of seed found in the 50m^2 corridor from each edge. For spruce and fir the 1 ha mean corridor seed supply was 5761 seeds and 1064 seeds, respectively. It would take 14.6 m^2 of uncut forest to supply the 5761 Engelmann spruce seeds and 4.5m^2 of uncut forest to supply 1064 subalpine fir seeds. The 1 ha corridor was half the size relative of the 10 ha corridor; however, each had a similar quantity of Engelmann spruce and subalpine fir seed. This suggests secondary sources were contributing a significant amount of seed in the 1 ha clearing.

Greene and Johnson (1996) conclude that 90% of the seeds originate from an area no further back from the edge than twice the height of the stand. The evidence from the 1997-1998 dispersal season at Sicamous Creek suggests that seed is supplied from trees exceeding 15m within the forest and likely confirms Greene and Johnson's conclusion.
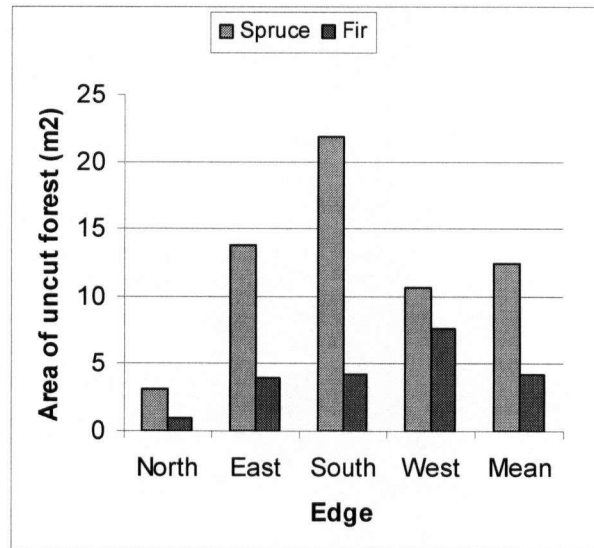
Figure 4.16. Illustration of the area of uncut forest that supplies the equivalent quantity of seed found in the 100m^2 in the 10 ha clearcut.
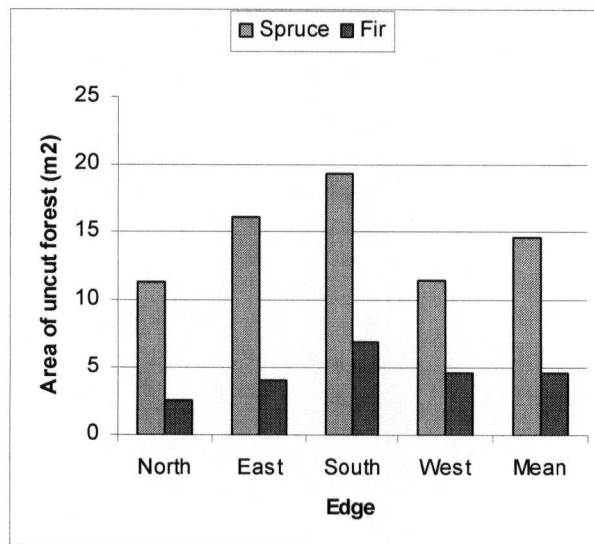
Figure 4.17. Illustration of the area of uncut forest that supplies the equivalent quantity of seed found in the 50m^2 corridor in the 1 ha clearcut.

4.3.6 Summary of Seed Dispersal into Cleared Openings

Wind velocities and frequencies at Sicamous Creek were grouped by azimuth into four categories (N, E, S and W). The mean wind velocity did not differ significantly between directional categories with an overall mean of 2.9 m/s. Winds from the north made up only 6.5% of all of the wind hours recorded. Southerly winds (39.4%) were most frequent, followed by westerly (37.3%) and easterly (16.7%) winds.

The dispersal equations specified for each edge, as well as the seed share equations, showed the number of seeds dispersed closest to an edge was correlated positively with the frequency of its respective prevailing wind. The north edge consistently supplied fewer seeds, while the majority of seed was supplied by the south edge. The 10 ha seed share equations had nearly a one to one relationship with prevailing wind frequencies, while the 1 ha seed share equations had a smaller correlation parameter. Each edge in the 1 ha clearcut was a possible seed source. The larger source parameter (b_0) in the 1 ha dispersal equations relative to the respective 10 ha equations suggests more seed was contributed by adjacent and opposite edges in the 1 ha clearing.

For the 10 ha and 1 ha dispersal equation, the decay parameter from the north edge was not significantly different than zero, indicating that the seed supply was constant irrespective of the distance from the north edge. For the 10 ha clearcuts, the decay parameters for the E, S and W edges were significantly different than zero and ranged from -0.015 to -0.032 for Engelmann spruce and –0.022 to -0.028 for subalpine fir. For the 1 ha clearcut the decay parameters for Engelmann spruce were comparable (-0.014 to –0.025) to the respective 10 ha decay parameters; however, they were larger for subalpine fir (-0.029 to –0.047). Greene and Johnson (1996) suggested that the wind velocity drops more rapidly in smaller openings. Assuming slower wind speeds in the smaller openings, the rate of decay in the 1 ha openings was expected to be greater than the 10 ha openings. The subalpine fir 1 ha decay parameters were consistently greater than the 10 ha parameters; however for Engelmann spruce this was not the case.

Covariance analysis was used to identify if a site significantly influenced the Engelmann spruce and subalpine fir seed supply in the 10 ha and 1ha openings. For the 10 ha clearcut, site C supplied fewer spruce seeds; however, for the 1 ha opening there was no consistent difference between sites. There was consistently less subalpine fir seed at site C in the 10 ha opening and site A for the 1 ha opening.

Seed in the 1 ha clearing did not appear to be dispersed as far as in the 10 ha clearing. When the 10 ha dispersal equations were applied to forecast seed dispersal in the 1 ha clearings, they consistently overestimated the recorded seed density. The difference between the predicted seed density and the observed density increased with distance from each edge. Fewer seeds reaching the middle of the 1 ha clearings may be attributed to slower wind speeds carrying seed a shorter distance downwind.

The ratio between Engelmann spruce seed and subalpine fir seed for the 10 ha (5.5:1) and 1 ha (6.0:1) clearcut openings was significantly larger than in the uncut stands (1.7:1). The increased ratio suggests that spruce seed were more amenable to wind dispersal than fir seed. Engelmann spruce seeds have a lower terminal velocity and a smaller surface area than subalpine fir seeds. The lower terminal velocity enables seed to be airborne longer and a smaller surface area reduces the likelihood of seed being caught up in the canopy. These are two factors enabling spruce trees that are located deeper into the uncut forest, to contribute more seed into an opening relative to subalpine fir.

5.0 Development and Validation of Seed Dispersal Model (DISPERSE)

DISPERSE is a spatial seed dispersal model developed to account for the primary variables influencing seed dispersal in cleared openings. This chapter will summarize model development and assess its ability to estimate Engelmann spruce and subalpine fir seed dispersal in the 10 ha and 1 ha clearings at Sicamous Creek. The chapter concludes by assessing the effects of clearcut width and orientation on the spatial distribution of seed.

5.1 Development of DISPERSE

DISPERSE was developed to account for the primary variables influencing seed dispersal in cleared openings. It is coded in Visual Basic 4.0 For Applications and is accessed through Excel 7.0. The model requires approximately 1 MB of hard drive space. Descriptions of the input data, an overview of the dispersal algorithm and the resulting output of the spatial distribution of seed in a clearing are summarized in the following discussion.

5.1.1 Input Data

To operate the area source model the user must provide three components: 1) wind information, 2) species characteristics and 3) a description of the dimensions and geographic orientation of the clearcut. Up to 20 different wind directions can be supplied to DISPERSE. For each wind direction, the user must identify its azimuth, mean velocity, the reference height it was recorded at and the frequency it occurred during the dispersal season. Table 5.1 illustrates data for three wind directions used in one simulation. These data will enable the model to determine the windward and leeward winds with respect to each edge and simulate seed dispersal into the clearing. The mean wind velocity and reference height are required for the non-dimensional dispersal parameter T (Equation 2.16).

Greene and Johnson (1996) assumed 50% of the winds are windward to an edge and only these winds carry seeds into an opening. The remaining 50% of winds are leeward, and blow seed back into the forested edge. In their dispersal function (Equation 2.19), the density of seed in the uncut stands (BQ) is multiplied by 0.5, to represent that 50% of the seed are dispersed into the clearing. In DISPERSE, the actual proportion of windward winds replaces 0.5 assumed by Greene and Johnson (1996).

Table 5.1. Wind and species information used for DISPERSE simulation

	Direction 1	Direction 2	Direction 3
Wind azimuth (degrees)	225	45	120
Frequency (%)	30.0	20.0	50.0
Reference median wind velocity (m/s)	4.0	3.5	4.3
Reference wind height (m)	10	10	10

	Species 1	Species 2
Height of source (m)	29	29
Terminal velocity of seed (m/s)	0.61	0.8
Median density of seed in an uncut stand (#/m^2)	395	236

DISPERSE simulates seed dispersal for as many tree species as data are provided. Height of source, terminal velocity of the seed and seed density in the uncut stands are required input data as they are needed for the area source dispersal equation (Equation 2.19). Table 5.1 provides species information for Engelmann spruce and subalpine fir.

Dimensions of the open area must be provided before DISPERSE can run. A grid of raster cells represents the opening. The resolution of the raster cell is defined by the user. The user is queried on the length of the north and west edges. The dispersal model assumes that the edges of the clearing form a square or rectangle. The geographic orientation of the clearcut must be specified to determine the angle that a prevailing wind would blow across the treed area. Finally, the user is asked to identify if any of the edges are not a source of seed and these edges are excluded from the dispersal algorithm.

5.1.2 Structure of the Area Source Model

Macros within DISPERSE simulate how each wind direction disperses seed into the clearing from each edge (see Appendix I). A description of how a wind direction is modeled by the dispersal algorithm will be illustrated with a southwest prevailing wind (225^0). Figure 5.1 illustrates the orientation of the wind with respect to the clearing. DISPERSE uses the spreadsheet configuration to represent the clearcut. The user defines the resolution of the cells representing the cleared area. For this example, 25 raster cells (10m by 10m) in 5 rows and 5 columns represent the 50m by 50m cleared area in the simulation.

The DISPERSE algorithm simulates seed dispersal one species at a time. For species 1, DISPERSE predicts seed dispersal resulting from wind direction 1 (225^0). Once Species 1 and Wind Direction 1 are selected, the next step is to adjust the wind direction for the spatial orientation of the clearcut. If the clearcut is not oriented exactly N-S, the direction (azimuth) is adjusted to determine the resultant angle that the wind blows across each of the edges. In this example, the clearcut runs along the N-S axis and no adjustments are required.

The second step is to determine which of the edges are windward to the southwest prevailing wind. DISPERSE only uses windward edges to disperse seed into the clearing. In Figure 5.1, the SW prevailing wind is windward to the west and south edges. DISPERSE then checks if the windward edges are a source of seed. DISPERSE will only simulate seed dispersal from edges that have seed. Each edge in Figure 5.1 has a seed supply.

0,0	0,1	0,2	0,3	0,4	0,5	0,6
1,0	1,1	1,2	1,3	1,4	1,5	1,6
2,0	2,1	2,2	2,3	2,4	2,5	2,6
3,0	3,1	3,2	3,3	3,4	3,5	3,6
4,0	4,1	4,2	4,3	4,4	4,5	4,6
5,0	5,1	5,2	5,3	5,4	5,5	5,6
6,0	6,1	6,2	6,3	6,4	6,5	6,6
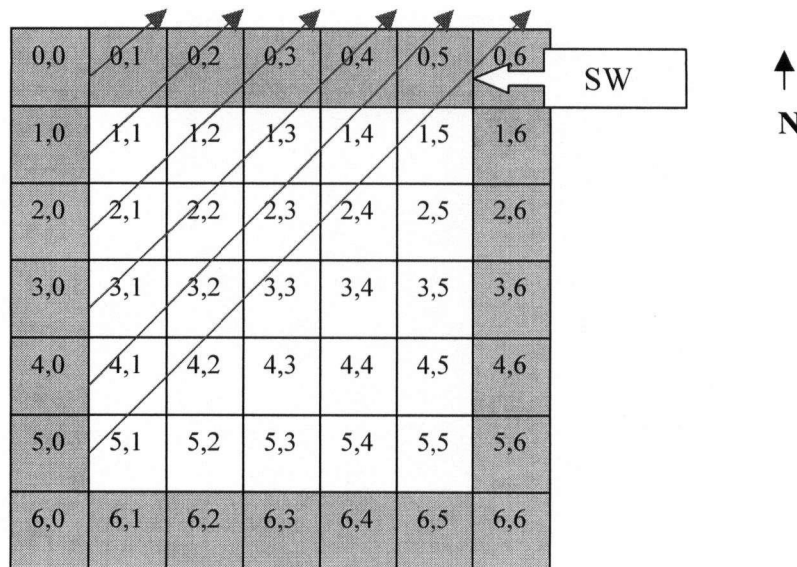
Figure 5.1. A 50m by 50m clearing is represented by 25 raster cells (5 rows, 5 columns) with DISPERSE. In this illustration a SW prevailing wind (225^0) disperses seeds from the west edge.

DISPERSE predicts the influence of a 225^0 wind on the windward edges (West and South). The arrows in Figure 5.1 represents the direction of the SW prevailing wind and the direction seed is dispersed from the west edge. Given the dispersal angle, a straight vector is drawn between each originating cell (R_iC_0) and the first cell that falls outside the dimensions of the clearcut. Any raster cell falling within the dimensions of the clearcut, and intersected by the straight vector, is a destination cell for seed from the originating cell. However, when a vector passes through two rows in one column (R_iC_j and $R_{i+1}C_j$) seed is deposited into the top raster cell ($R_{i+1}C_j$). For example in Figure 5.1, the vector running from R_5C_0 passes through cells R_5C_1 and R_4C_1. DISPERSE deposits seed into cell R_5C_1, leaving cell R_4C_1 to receive seed from cell R_4C_0. This prevents a destination raster cell receiving seed from two originating cells from the same wind direction. The Pythagorean theorem is used to solve for the distance between the originating cell (R_iC_0) and the center of any destination cell. Distance, wind information, and seed species characteristics are substituted into the area source equation (Equation 2.19) to simulate the amount of seed that each destination cell receives from the uncut edge.

Beginning with the first windward edge (west), seed is dispersed from the middle of right side of cell R_0C_0. In Figure 5.1, the SW prevailing wind does not carry seed from R_0C_0 into the clearing and therefore for the west edge, this raster cell is not a source of seed for the clearing. Once a seed is dispersed to all the qualifying destination cells, DISPERSE shifts the originating position down one row (R_1C_0) and the same procedure is repeated. This procedure is repeated for each originating cell until it reaches one row past the end of the clearcut ($R_{i+1}C_0$). At this point, the simulation of seed dispersal ends. Once cell R_6C_0 was reached, the dispersal algorithm stops.

The clearcut is then rotated so that cells $R_0C_0 - R_5C_0$ represents the next windward edge for wind direction 1 (south edge). The north and east edges are skipped by dispersal algorithm because wind direction 1 (225^0) is not windward to these edges. DISPERSE adjusts the resultant wind angle to account for the rotation of the clearcut. The new resultant angle is used to disperse seeds from the south edge using the same procedure. Following the completion of wind direction 1 on the south and west edges, DISPERSE proceeds to wind directions 2 and 3. Once simulation of all wind directions is complete DISPERSE prints out the spatial distribution of seed.

5.1.3. Output from the Model

A worksheet is created by DISPERSE to represent the predicted spatial distribution of seed in the opening (Figure 5.2). Each grid cell is represented by a shade of grey, to indicate its relative seed density as compared to the other grid cells in the clearing. A darker shade represents a relatively higher seed density. The output worksheet is organized into columns. Columns 1-4 illustrate seed dispersed from the West, North, East and South edges, respectively. The first grid of cells in row 1, columns 1-4, shows the total distribution of seed dispersed from each edge. Rows 2-4 exhibits the distribution of seed predicted for wind directions 1 through 3 on each edge (W, N, E and S). For example, row 2, column 4, predicts the influence of wind direction 1 (225^0) on the south edge. The overall total (Grand Total) seed distribution for the entire clearcut is found in row 1, column 5. The 'Grand Total' is the sum of the 'Total' grids of each edge.

The output of DISPERSE illustrates the influence of each wind direction on each edge, as well as the overall spatial distribution of seed in the entire clearcut.
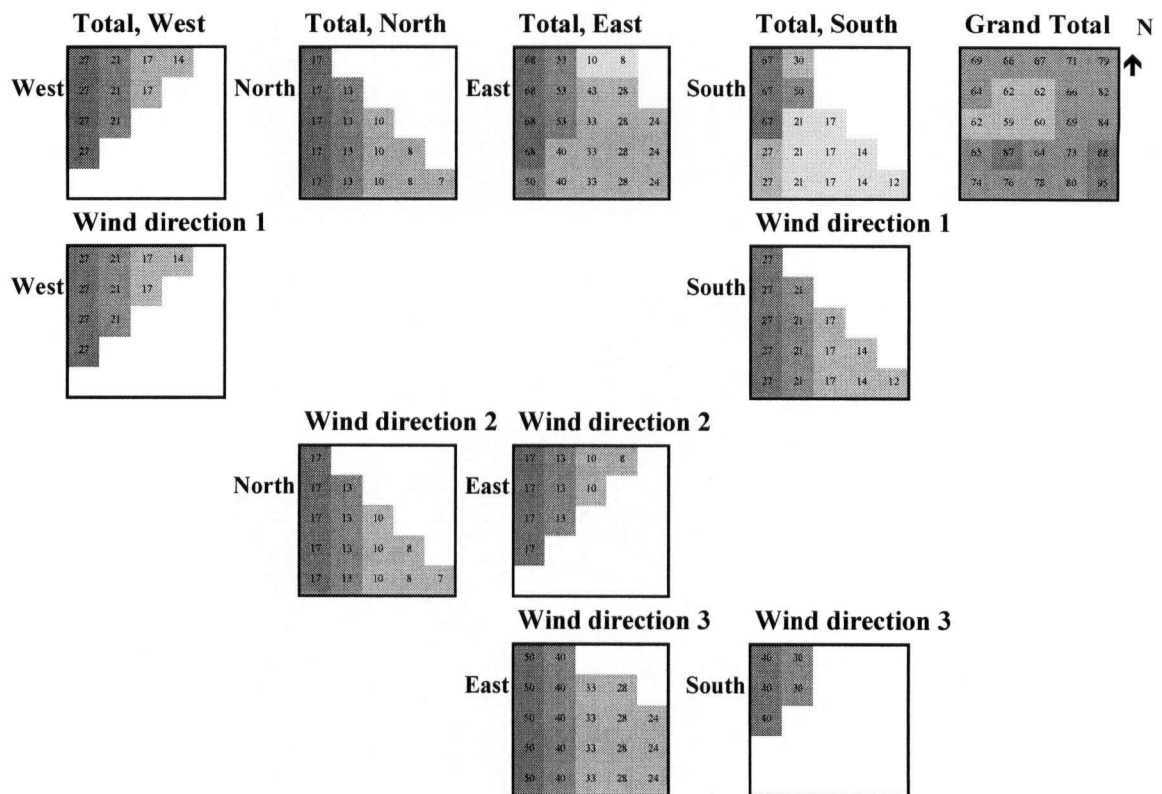
Figure 5.2. Output from DISPERSE, illustrating the spatial distribution of seed using input data from Table 3.1. Columns 1-4 represent the west, north, east and south edges of the clearing, respectively. Rows 2-4 represent seed dispersal by prevailing wind direction 1, 2 and 3, respectively. Row 1 is the vertical addition of seed resulting from each of the prevailing wind directions on either the west, north, east and south edges. Row 1, column 5 (Grand Total) illustrates the predicted spatial distribution of seed in the clearing.

5.2 Simulation of Area Source Model

The objective of this section is to assess the accuracy of Greene and Johnson's (1996) area source model and incorporate it into DISPERSE. The section consists of three components. Firstly, the seed and wind data collected in the 10 ha clearcut were used to validate and recalibrate the area source dispersal equation ($\exp(-2.64T^{0.72})$). The recalibrated equation was then incorporated into DISPERSE. Secondly, the spatial distribution of seeds in the 10 ha and 1 ha openings were simulated by DISPERSE and its accuracy was assessed relative to the observed seed values. Thirdly, using the seed and wind data collected at Sicamous Creek, DISPERSE was used to determine the influence of the orientation and width of a clearcut opening on the spatial distribution of seed within a clearing.

5.2.1 Validation of DISPERSE

The spatial distribution of the Engelmann spruce and subalpine fir seed data from the 10 ha clearcuts were used to validate and recalibrate Greene and Johnson's (1996) area source model. These adjustments were in turn incorporated into DISPERSE. This section overviews the seed and wind data used for validation and then assesses Greene and Johnson's (1996) model in terms of accounting for the quantity of seed at an edge, as well as the spatial distribution of seed in the 10 ha cleared opening.

5.2.1.1 Seed data

Seed traps for the 10 ha clearcuts were oriented in transects passing through the center of an edge and running perpendicular to the center of the opposite edge (refer to Figure 3.6). Due to the orientation of seed traps, predictions in the corner of the clearcut could not be tested. The validation of the spatial simulation of Engelmann spruce seed dispersal used the tripod trap data set, while the tripod/ box trap observations were used for subalpine fir. The density of seed found in the uncut stands relied upon the traps placed in the uncut stands during the 1997-1998 dispersal season. Due to the skewness of

the seed densities in the uncut stands, the median seed density values were selected to represent the base seed density to be dispersed in the simulation.

5.2.1.2 Wind data

For September and October of the 1997-1998 dispersal season Novak *et al*. (1997, unpublished) recorded the direction and hourly wind speed in the B5 10 ha clearcut at Sicamous Creek. For model validation it is assumed that the recorded wind data represent the wind conditions for the entire dispersal season. Referring to Figure 5.3, the wind data were grouped into eight directional categories. For each 45^0 category, the midpoint within the 45^0 radius was used to represent the direction of the wind. For example, the SSW prevailing winds are represented by an angle of 202.5^0. Table 5.2 summarizes each 45^0 category in terms of its median wind velocity and relative frequency during the dispersal season.

The categorization of wind in DISPERSE depended upon the geographic orientation of the clearing. The winds had to be organized in a way that no prevailing wind categories would run parallel along an edge. For example, if the west edge of a clearing were tilted 22.5^0 to the east, the SSW prevailing would run parallel to the west edge. Wind categories had to be organized so that each prevailing wind category was windward of two edges in the clearing. This ensured that DISPERSE accounted for the frequency of windward winds blown across each edge in the clearing. Therefore, if a cleared opening were oriented NNE to SSW, the eight wind categories would have to be centered around each of the following directions; N, NE, E, SE, S, SW, W and NW. Since the majority of the clearcuts at Sicamous Creek are oriented N-S, the eight wind groupings in Table 5.2 are used in the simulations.
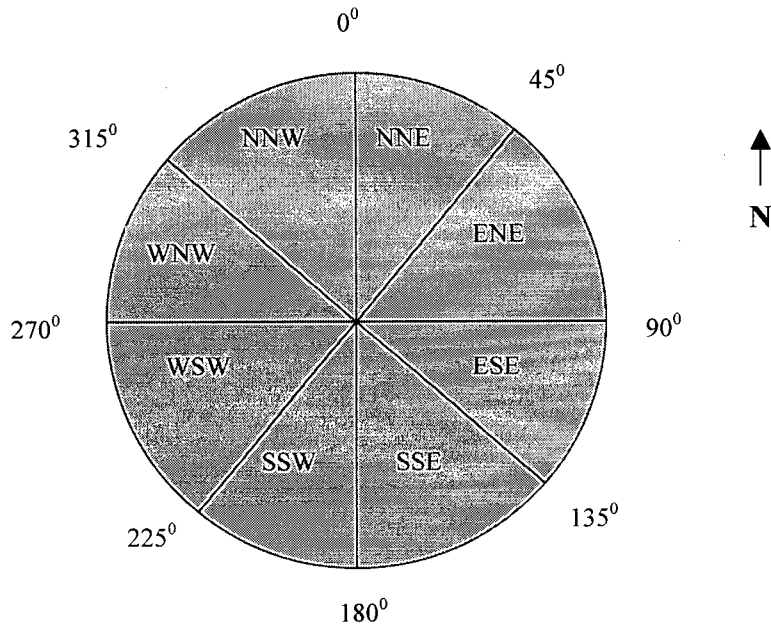
Figure 5.3. Illustration of the prevailing wind categories used in DISPERSE

Table 5.2. Statistical description of eight wind categories used in DISPERSE

	NNE	ENE	ESE	SSE	SSW	WSW	WNW	NNW
Direction (degrees)	22.5	67.5	112.5	157.5	202.5	247.5	292.5	337.5
Freq. of hrs. (%)	1.8	2.6	14.1	20.1	19.4	22.4	14.9	4.7
Adj. Median Vel. (m/s)	2.6	2.5	31	3.0	2.3	2.2	3.4	3.6

Source: Novak *et al.* (1997, unpublished)
[1] Hourly wind velocities recorded in September and October (1997) by anemometer in B5 clearcut. Wind velocities were adjusted by Equation 2.11 to account for the friction from the surrounding edges

5.2.1.3 Quantity of Seed at the Edge

The Greene and Johnson (1996) area source model assumes that the edge has half the density of seed relative to the uncut stands. Therefore, the median uncut seed density should be equivalent to the median seed density along the edge doubled. The uncut spruce (P=0.017) and subalpine fir (P=0.002) seed populations were larger than the seed population along the edge doubled. In the 10 ha clearings, the median seed densities from the four edges of the forest were 102 seeds/m^2 and 78 seeds/m^2 for Engelmann

spruce and subalpine fir, respectively. These densities were 26% and 33% of their uncut seed densities. Overall, there was significantly less than half the amount of seed at the edge relative to the uncut seed supply

5.2.1.4 Rate of decay from the edge

The decay function $(\exp(\tau T^{\phi}))$ determines the frequency of seeds in the cleared area relative the number available at the edge as the distance from the edge changes. Greene and Johnson (1989) validated τ and ϕ with 12 data sets that accounted for a variation in terminal velocity and tree height, but that did not include the corresponding wind data during dispersal. They assumed abscission was non-random with respect to wind velocity and a value of 7.87m/s was substituted for $\overline{u}_g$ in each of the data sets to determine the T variable.

The area source model (Equation 2.19) assumed the hourly wind speeds were distributed lognormally around the geometric mean ($\overline{u}_g$). Analysis of the wind data collected at Sicamous Creek shows that the distribution of wind speeds had a slight positive skew; however, they were not distributed lognormally. The median prevailing wind speed for the respective edge was substituted for $\overline{u}_g$, under the assumption that seed abscission was a random process. For Engelmann spruce and subalpine fir, the observed seed densities at 15m, 30m, 60m and 90m were divided by the density of seeds at the edge (0m). The observed decay of seed was compared to the frequency of seed predicted by two decay functions; one with non-random abscission and the other with random abscission.

Figures 5.4 and 5.5 illustrate the predictions of the decay function when either 7.87 m/s or the median windward wind speed was substituted for u_r in the T variable (Equation 2.17). In these figures, the predicted decay of seed is compared to the actual decay of seed observed in the 10 ha clearcut openings. When the median prevailing wind speed was substituted for $\overline{u}_g$ the decay function for both species consistently under-

predicted the density of seed in the opening. The substitution of 7.87 m/s for $\bar{u}_g$ resulted in accurate predictions of seed density as distance from an edge increased. The results appear to confirm the Greene and Johnson (1996) assumption of nonrandom abscission; however, this conclusion is inconsistent with the winds observed during the fall of 1997.

During September and October the highest adjusted hourly wind speed was 8.3 m/s, and only two of the 1255 recorded hourly wind speeds were above the non-random abscission velocity of 7.87 m/s assumed by Greene and Johnson (1996). However, the recorded speeds are hourly averages and gusts during some hours would exceed the threshold non-random abscission velocity determined by Green and Johnson (1996). Despite this fact, the low incidence of mean hourly winds exceeding 7.87 m/s suggests that 7.87 m/s may not represent the median nonrandom abscission speed. For each of the 12 seed dispersal data sets used for validation, Greene and Johnson (1996) assumed that $\bar{u}_g$ was 7.87 m/s in the determination of τ and ϕ. The wind data at Sicamous Creek suggests that this assumption is incorrect and biases the estimates of τ and ϕ. Until a better understanding of non-random abscission is documented to adjust $\bar{u}_g$, random abscission will be assumed for DISPERSE and τ and ϕ will be adjusted to reflect the median wind speed recorded at Sicamous Creek.
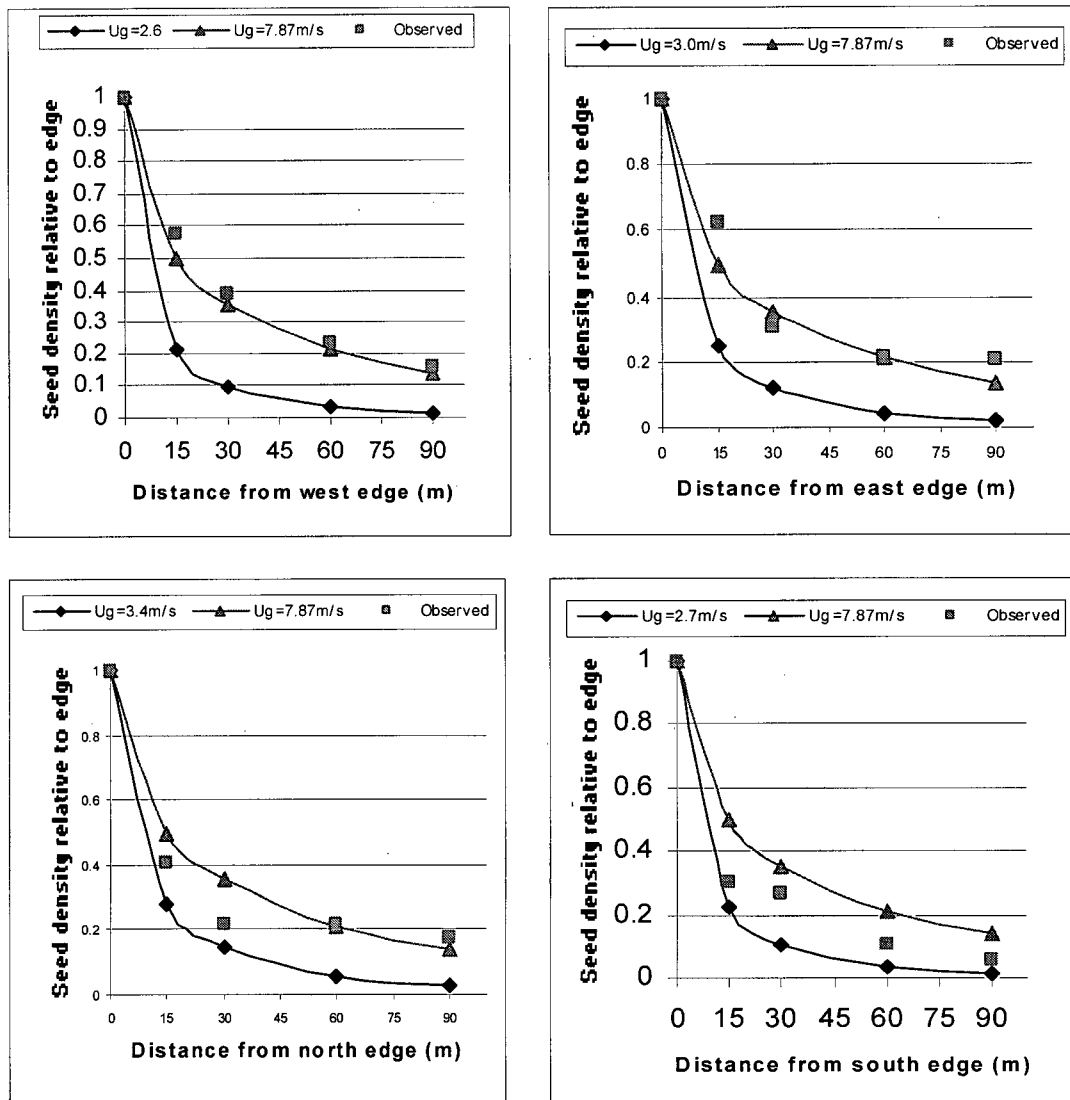
Figure 5.4. Seed dispersal function $(\exp(-2.64T^{0.72}))$ (Green and Johnson 1996), where the geometric mean wind speed $(\bar{u}_g)$ is either 7.87m/s or median wind speed from the prevailing direction. The nonrandom abscission seed dispersal with 7.87m/s and the random abscission seed dispersal with 3.4 are compared to the observed mean density of Engelmann spruce seeds in 10 ha clearcuts relative to the seed density at each edge.
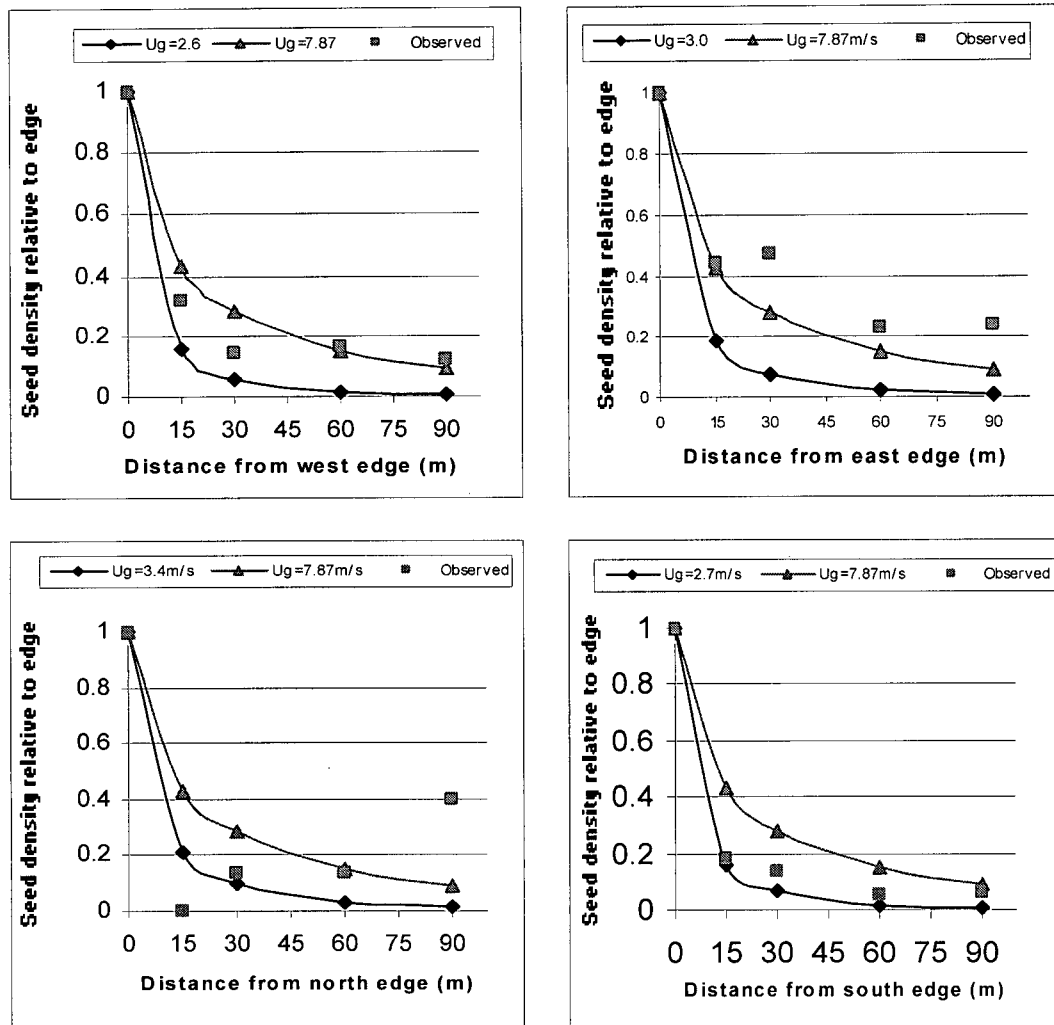
Figure 5.5. Seed dispersal function $(\exp(-2.64T^{0.72}))$ (Green and Johnson 1996), where the geometric mean wind speed ($\bar{u}_g$) is either 7.87m/s or the median wind speed from the prevailing direction. The nonrandom abscission seed dispersal with 7.87m/s and the random abscission seed dispersal with 3.4 are compared to the observed mean density of subalpine fir seeds in 10 ha clearcuts relative to the seed density at each edge.

5.2.1.5 Recalibration of Greene Johnson Area Source Model for DISPERSE

The 10 ha seed share equation (section 4.3.2) indicates that the proportion of seeds falling along each edge is correlated with the frequency of its respective prevailing winds. The respective median seed density along the edge for Engelmann spruce and subalpine fir was 26.3% and 33% of their median seed density in the uncut stands. The midpoint between these two relative densities is 30%. Instead of taking the edge density to be 50% of the uncut stands, which was assumed by Greene and Johnson (1996), DISPERSE assumes the seed density at the edge to be 30% of the uncut seed density. Equation 5.1 scales 30% upwards or downward in proportion to the windward winds.

$$WE = \frac{WW}{50\%} * P * \overline{SU} \qquad\qquad 5.1$$

where:

WE = seed density on windward edge (seeds/m^2)
WW = the percent of windward winds
P = proportion of seed at the edge relative to the uncut stand
$\overline{SU}$ = median seed density in the uncut stand (seeds/m^2)

If the proportion of seed at the edge were half of the uncut density and 50% of winds are windward, Equation 5.1 predicts the same quantity of seed at the edge as Greene and Johnson's area source model. According to the 10 ha observations, P is 0.30. Equation 5.1 reduces the seed density on the edge by 70% relative to the uncut seed density, but retains the relative influence of the windward winds in determining the amount at each edge.

For $\exp(\tau T^{\phi})$, the parameter estimates for τ and ϕ are based on the assumption of non-random abscission. The distribution of hourly winds at Sicamous Creek suggests 7.87 m/s is not the correct estimate for $\overline{u}_g$. DISPERSE assumes random abscission and the median non-random abscission speed of 7.87 m/s was replaced by the median wind speed (2.74 m/s) recorded at Sicamous Creek. Referring to Figures 5.4 and 5.5, the area source model developed by Greene and Johnson (1996) accurately predicts the spatial

distribution in the 10 ha clearing. Using the solver function within Excel (Orvis 1996), τ and ϕ were adjusted to fit the Greene and Johnson (1996) dispersal curve, when 2.74 m/s was substituted for $\overline{u}_g$. Since $\overline{u}_g$ was smaller, the T parameter was greater, which resulted in τ increasing from -2.64 to -1.24; however, ϕ remained the same at 0.72. The revised decay function ($\exp(-1.24T^{0.72})$) with a median wind speed of 2.74 m/s forecasted seed to be dispersed identically to ($\exp(-2.64T^{0.72})$) when 7.87 m/s was assumed. Therefore, the seed densities that corresponded to $\overline{u}_g = 7.87$ m/s in Figures 5.4 and 5.5 were identical to the estimates from the revised equation.

The adjustment of the Greene and Johnson (1996) decay function from non-random to random abscission about a median wind speed of 2.74 m/s assumed that the parameters -1.24 and 0.72 were statistically consistent with the spatial seed dispersed at Sicamous Creek. This assumption was tested with the ratio of the observed mean seed density at x meters from the closest edge (N_x) to the mean seed density at the respective edge (N_0) for Engelmann spruce and subalpine fir. The nonlinear function ($\exp(\tau T^{\phi})$) was solved so that the values of τ and ϕ minimized the residual sum of squares between the predicted and observed ratios of seed density. Equation 5.2 was estimated:

$$\frac{N_x}{N_0} = \exp(-1.33T^{0.61}) \qquad\qquad \textbf{5.2}$$

$$n = 39 \qquad r^2 = 0.93 \qquad \sigma = 0.092$$

The estimates for τ (-1.33) and ϕ (0.61) were not significantly different from -1.24 and 0.72, solved for the non-random adjusted decay function. Therefore, -1.24 and 0.72 were accepted as appropriate estimates for τ and ϕ, respectively.

Greene and Johnson's (1996) area model was calibrated assuming that wind dispersed seed perpendicular from the windward edge. Perpendicular dispersal of seed from each edge causes the seed from adjacent edges to be double counted in the corners of an opening. DISPERSE is a multi-wind seed dispersal model that accounts for the direction that seed is dispersed from an edge.

There is an 180^0 array of windward winds blowing across an edge and on average seed in DISPERSE is carried downwind from an edge at an angle of 45^0 (135^0). This causes the simulated seed to be airborne further than the same point perpendicular to an edge. The distance variable x in equation 2.18 was multiplied by 1.4 to account for the 40% increase in average distance that seed was simulated to be airborne in DISPERSE. With the distance component in the T variable inflated by 40%, the solver function in Excel recalibrated τ to be -1.02 while ϕ remained the same (0.72).

The winds at Sicamous Creek were grouped into either eight categories (Table 5.1) or four categories, namely NE, SW, SE and NE. DISPERSE was simulated to determine if the number of wind categories influenced the accuracy of the predicted spatial distribution of Engelmann spruce and subalpine fir seed in the 10 ha openings. For each simulation, the spatial distribution of seeds along the N-S and W-E corridors were compared to the predictions made by Greene and Johnson's (1996) area source model. Simulations using either eight or four wind categories predicted similar spatial distribution of seed in the 10 ha clearings. However, the residual errors measuring the difference between the simulated seed densities and the observed seed densities were greater when four wind directions represented all wind azimuths. This indicated that the accuracy of simulated predictions of seed dispersal increased when more directional categories represent wind velocity and wind frequency. The accuracy of the prediction by DISPERSE also confirms that τ is adjusted appropriately.

Figures 5.6 and 5.7 illustrate the spatial distribution of Engelmann spruce and subalpine fir seed predicted by DISPERSE, relative to the mean seed density observed in the 10 ha clearings. The eight wind categories specified in Table 5.2 are used for the simulations. Overall, DISPERSE accurately estimated the density of seed. The largest forecasted errors were along the edge. For example, the spruce seed density closest to the south edge was under-estimated in spite of having the largest share of windward winds. The under- or over-estimation of seed densities from an edge tended to follow the same pattern. For example, DISPERSE consistently over-estimated the density of fir seed from the north edge, and under-estimated the quantity of spruce seed from the south and east

edges. In general, the accuracy of DISPERSE predictions improved as distance from the edge increased. Accuracy in areas with lower seed densities is relatively more important than precision close to the forest edge where seeds are more plentiful.

a)   b)
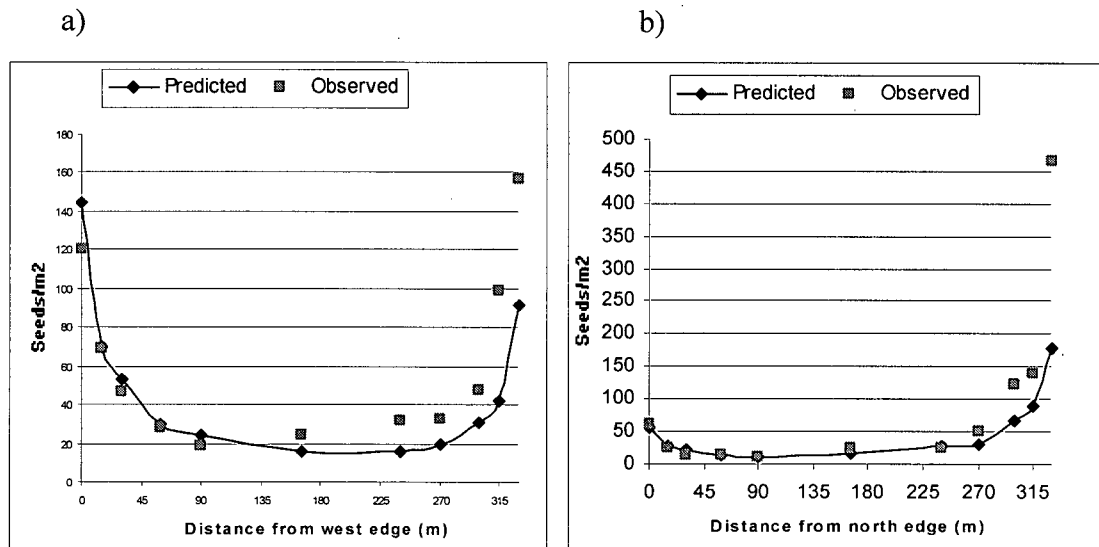
Figure 5.6. Simulation of Engelmann spruce seed dispersal in a 10 ha clearcut using the adjusted dispersal function ($-1.02T^{0.72}$) and eight wind directional groupings.

a)   b)
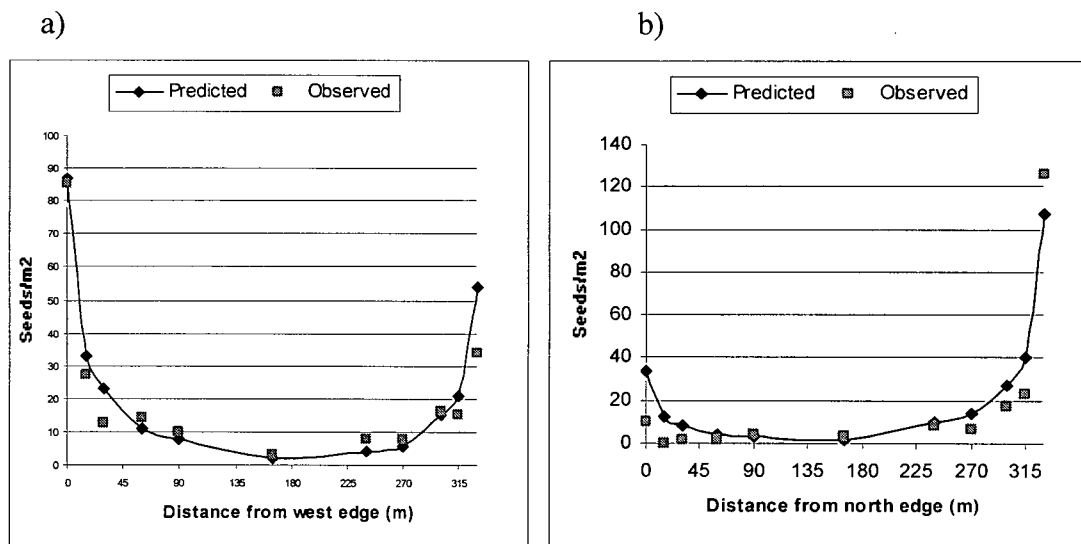
Figure 5.7. Simulation of subalpine fir seed dispersal in a 10 ha clearcut using the adjusted dispersal function ($-1.02T^{0.72}$) and eight wind directional groupings.

5.2.2 Simulation of DISPERSE in 10 ha and 1 ha Clearing

Figures 5.8 and 5.9 illustrate the simulated spatial distribution of seed in the 10 ha clearings for Engelmann spruce and subalpine fir, respectively. Each figure depicts a 10 ha clearing with a width and length of 330m, and each cell representing a 10m by 10m area. In both figures, there is more seed near the south and west edges than the north and east edges, illustrating the positive correlation between the quantity of seed found closest to an edge and the frequency of its respective prevailing winds.

The most distinct difference between the predicted spatial distribution of Engelmann spruce and subalpine fir was the area delineated by the lowest seed density. Fewer subalpine fir seeds were in the center of the 10 ha opening relative to Engelmann spruce. The dispersal characteristics of the two species were identical, except subalpine fir seed had a greater terminal velocity (0.8m/s) than Engelmann spruce seed (0.61m/s). Therefore, the simulated ratio of spruce seed to fir seed increased as distance from the edge increased.

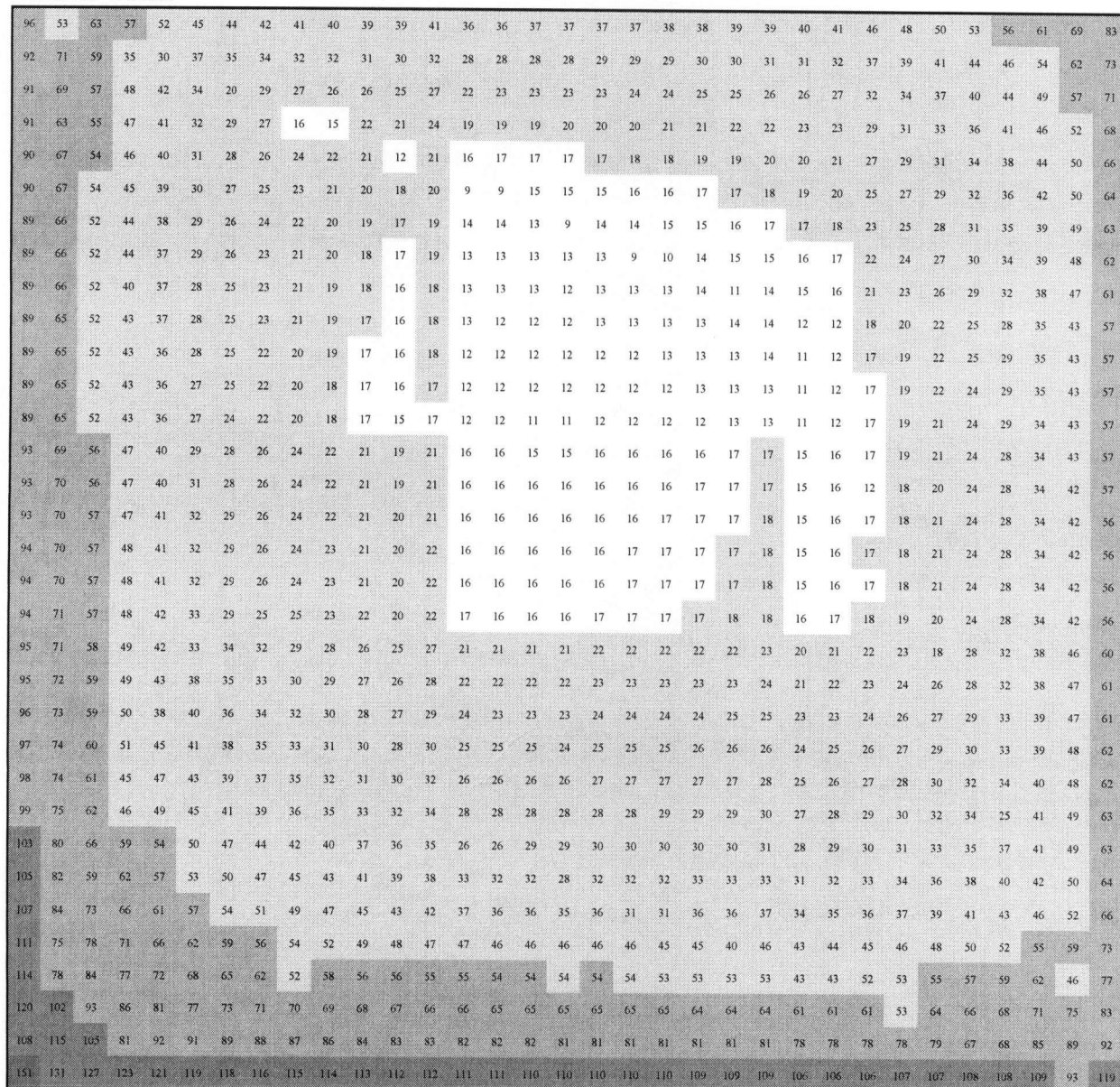| 96	53	63	57	52	45	44	42	41	40	39	39	41	36	36	37	37	37	37	38	38	39	39	40	41	46	48	50	53	56	61	69	83
92	71	59	35	30	37	35	34	32	32	31	30	32	28	28	28	28	29	29	29	30	30	31	31	32	37	39	41	44	46	54	62	73
91	69	57	48	42	34	20	29	27	26	26	25	27	22	23	23	23	23	24	24	25	25	26	26	27	32	34	37	40	44	49	57	71
91	63	55	47	41	32	29	27	16	15	22	21	24	19	19	19	20	20	20	21	21	22	22	23	23	29	31	33	36	41	46	52	68
90	67	54	46	40	31	28	26	24	22	21	12	21	16	17	17	17	17	18	18	19	19	20	20	21	27	29	31	34	38	44	50	66
90	67	54	45	39	30	27	25	23	21	20	18	20	9	9	15	15	15	16	16	17	17	18	19	20	25	27	29	32	36	42	50	64
89	66	52	44	38	29	26	24	22	20	19	17	19	14	14	13	9	14	14	15	15	16	17	17	18	23	25	28	31	35	39	49	63
89	66	52	44	37	29	26	23	21	20	18	17	19	13	13	13	13	13	9	10	14	15	15	16	17	22	24	27	30	34	39	48	62
89	66	52	40	37	28	25	23	21	19	18	16	18	13	13	13	12	13	13	13	14	11	14	15	16	21	23	26	29	32	38	47	61
89	65	52	43	37	28	25	23	21	19	17	16	18	13	12	12	12	13	13	13	13	14	14	12	12	18	20	22	25	28	35	43	57
89	65	52	43	36	28	25	22	20	19	17	16	18	12	12	12	12	12	12	13	13	13	14	11	12	17	19	22	25	29	35	43	57
89	65	52	43	36	27	25	22	20	18	17	16	17	12	12	12	12	12	12	12	13	13	13	11	12	17	19	22	24	29	35	43	57
89	65	52	43	36	27	24	22	20	18	17	15	17	12	12	11	11	12	12	12	12	13	13	11	12	17	19	21	24	29	34	43	57
93	69	56	47	40	29	28	26	24	22	21	19	21	16	16	15	15	16	16	16	16	17	17	15	16	17	19	21	24	28	34	43	57
93	70	56	47	40	31	28	26	24	22	21	19	21	16	16	16	16	16	16	16	17	17	17	15	16	12	18	20	24	28	34	42	57
93	70	57	47	41	32	29	26	24	22	21	20	21	16	16	16	16	16	16	17	17	17	18	15	16	17	18	21	24	28	34	42	56
94	70	57	48	41	32	29	26	24	23	21	20	22	16	16	16	16	16	17	17	17	17	18	15	16	17	18	21	24	28	34	42	56
94	70	57	48	41	32	29	26	24	23	21	20	22	16	16	16	16	16	17	17	17	17	18	15	16	17	18	21	24	28	34	42	56
94	71	57	48	42	33	29	25	25	23	22	20	22	17	16	16	16	17	17	17	17	18	18	16	17	18	19	20	24	28	34	42	56
95	71	58	49	42	33	34	32	29	28	26	25	27	21	21	21	21	22	22	22	22	22	23	20	21	22	23	18	28	32	38	46	60
95	72	59	49	43	38	35	33	30	29	27	26	28	22	22	22	22	23	23	23	23	23	24	21	22	23	24	26	28	32	38	47	61
96	73	59	50	38	40	36	34	32	30	28	27	29	24	23	23	23	24	24	24	24	25	25	23	23	24	26	27	29	33	39	47	61
97	74	60	51	45	41	38	35	33	31	30	28	30	25	25	25	24	25	25	25	26	26	26	24	25	26	27	29	30	33	39	48	62
98	74	61	45	47	43	39	37	35	32	31	30	32	26	26	26	26	27	27	27	27	27	28	25	26	27	28	30	32	34	40	48	62
99	75	62	46	49	45	41	39	36	35	33	32	34	28	28	28	28	28	28	29	29	29	30	27	28	29	30	32	34	25	41	49	63
103	80	66	59	54	50	47	44	42	40	37	36	35	26	26	29	29	30	30	30	30	31	28	29	30	31	33	35	37	41	49	63	
105	82	59	62	57	53	50	47	45	43	41	39	38	33	32	32	28	32	32	32	33	33	33	31	32	33	34	36	38	40	42	50	64
107	84	73	66	61	57	54	51	49	47	45	43	42	37	36	36	35	36	31	31	36	36	37	34	35	36	37	39	41	43	46	52	66
111	75	78	71	66	62	59	56	54	52	49	48	47	47	46	46	46	46	46	45	45	40	46	43	44	45	46	48	50	52	55	59	73
114	78	84	77	72	68	65	62	52	58	56	56	55	55	54	54	54	54	53	53	53	53	43	43	52	53	55	57	59	62	46	77	
120	102	93	86	81	77	73	71	70	69	68	67	66	66	65	65	65	65	65	64	64	64	61	61	61	53	64	66	68	71	75	83	
108	115	105	81	92	91	89	88	87	86	84	83	83	82	82	82	81	81	81	81	81	81	78	78	78	78	79	67	68	85	89	92	
151	131	127	123	121	119	118	116	115	114	113	112	112	111	111	110	110	110	110	110	109	109	109	106	106	106	107	107	108	108	109	93	119

Figure 5.8. The spatial distribution of Engelmann spruce seed in the 10 ha clearcut openings simulated by DISPERSE. The simulated seed density (seeds/m^2) appears in each cell. Cells are shaded from light to dark grey to indicate the relative increase in seed density.