Physical characterization of seed microsites — movement on the ground

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Summary
1. A dispersed seed must remain in a microsite long enough to imbibe water and germinate. Here the post-dispersal movement caused by wind of four asymmetric samaras of Picea engelmannii, P. abies, Pinus contorta var. latifolia and P. strobos was studied on four surface roughnesses (a smooth board, c. 250 μm, c. 750 μm and 2.0 mm). A mechanistic approach is taken to determine the chance that a seed will remain on a surface long enough to germinate.

2. The threshold or lift-off velocities for all combinations of four samaras and four surface roughnesses were determined in a wind tunnel. These measured threshold velocities were incorporated with seed mass and wing area to define the non-dimensional resistance to seed movement (B). The resistance to movement is the ratio of the force due to gravity to that developed by the wind on a given reference area.

3. The resistance to movement was used in a logistic regression to predict the percentage of seeds unmoved (remaining) on a surface with increasing wind velocity. All regressions explained a significant proportion (P < 0.05) of the variation, with $r^2 > 0.64$. Regressions had steeper slopes the greater the resistance to seed movement. The resistance equation should be species-independent, assuming a geometrically similar shape, and was so for the smoothest surface but not always so on the remaining surfaces.

4. The percentage of seeds that will be unmoved on different surfaces for different time intervals was estimated by determining the return time in a natural environment of the threshold velocities in the resistance to movement (B). Wind velocities in nature have empirically estimable return times, i.e. lower velocities occur more frequently than higher velocities. These return times were calculated for Calgary, Alberta. Heavy seeds were found to move less frequently than smaller seeds, as would be expected. On rougher surfaces, seeds remained stationary longer because the threshold velocity is larger and also the return time of that velocity is longer.

5. Finally, the timing of seed movement determined above was compared to germination times (under ideal conditions) to determine if seeds, on surfaces of different roughness, were generally stationary long enough to imbibe water and germinate. On smooth surfaces (particle sizes up to c. 750 μm), all seeds moved before adequate time had elapsed for germination. On rougher surfaces (particle sizes up to 2 mm) the distribution of the percentage of seeds remaining was positively skewed and the tail of the distribution declined more slowly. This tail defines seeds which are caught in microsites that have the highest probability of germinating.

Key-words: early seed establishment, samaras, seed germination, wind dispersal of seeds

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Introduction
A seed must remain in a particular microlocation long enough for imbibition, respiration, synthesis of nucleic acids and proteins as well as a host of other metabolic events to germinate, including the breakage of internal and/or external controls of dormancy (Bewley & Black 1985). However, after seeds have
been dispersed, they are often moved about by the wind, as well as other forces such as rain water or predators. If a seed is moved too frequently it cannot continuously imbibe water and germinate.

Empirical studies of seed movement have demonstrated that the seeds of some species move around on the ground and that seeds tend to become lodged in certain kinds of microlocations which are influenced by soil particle size and seed morphology (Sagar & Harper 1960; Harper et al. 1961; Harper, Williams & Sagar 1965; Harper & Benton 1966; Harper, Lovell & Moore 1970; Sheldon 1974; Chambers, MacMahon & Haefer 1991). The seeds of some species tend to become trapped in crevices in rough soils (Mortimer 1974). Studies have also found that secondary dispersal of seeds on the ground moves seeds farther than primary dispersal from the parent plant (Watkinson 1978; Matlack 1989).

In this study, the movement of seeds on the ground by the force of the wind will be considered, not only because it is the first step in a physical characterization of microsites, but also because we will show that, depending on the surface roughness, only a small but quantifiable number of seeds will remain in one place for a sufficient length of time to imbibe enough water to start the germination sequence. Three factors determine whether or not a seed is likely to remain in a site long enough to germinate: the size of the seed, the roughness of the ground surface and the distribution of windspeeds that occur in the area. The purpose here is to examine these three factors and show how they can be used to estimate the probability of seed movement on a particular ground surface. There can be no absolute estimate of microsite density because for any soil surface roughness, the absolute number of microsites depends both on seed size and on the windspeeds that occur in the area. However, there is a percentage of seeds that will have longer residence times than is required for imbibition and this percentage can be characterized by knowing these three factors.

This study applies the physical principles of seed movement on soil surfaces as might occur following some kinds of windthrow and after dust consumption by forest crown fires. A measure of the likelihood of no movement (i.e., resistance) relates the lift and drag forces on the seed to the force of the wind. This relationship estimates the numbers of seeds which are resistant to movement and germinate in microsites. The comparison between seed movement and germination is an attempt to begin coupling together different processes associated with early seed establishment. In this study, it is our intention to examine only those factors which cause seeds to move by the wind. Clearly the next steps should involve understanding the other factors which cause seed movement, such as rain splash and predation, as well as determining the weather budgets of different soil microsites. However, our results show not only why seeds move so frequently but also why a percentage of seeds remains stationary long enough to have a chance to germinate.

The model

SURFACE ROUGHNESS AND WIND VELOCITY

For any wind-dispersed seed, seed movement on the ground and its lodgement there is primarily a surface roughness problem. As the air moves over a surface, it creates a shear force near the ground which is the cause of seed movement. The shear force is a result of the friction that the air experiences as it moves over any surface. Wind velocity is zero at the ground surface and increases with height. The air layer just above the ground surface is slowed by friction with the ground, which reduces its velocity. Some of this momentum is then transmitted to the next layer. This continues until the wind velocity becomes independent of the ground surface (the gradient wind), which begins between 250 and 500 m above ground. The average height above the ground surface at which wind velocity is zero is called the "roughness length" and is determined by the size of the roughness elements, which in this case are soil particles.

The increase of velocity with height above the surface follows a logarithmic law (Sutton 1953), which can be written

\[ u(z) = \frac{u^*}{k} \ln \left( \frac{z}{z_0} \right), \]  

where \( u(z) \) is the velocity at height \( z \), \( k \) is von Karman's constant, approximately 0.4, \( z_0 \) is the roughness length in cm and \( u^* \) is the friction velocity (for symbols and units see Appendix). This equation is valid for roughness lengths not exceeding a few centimetres and for turbulent flow (Sutton 1953), which encompasses the range of roughness lengths and flow experienced in this study. When the roughness length exceeds a few centimetres, another variable, the zero-plane displacement is sometimes included in equation 1 (see Sutton (1953) for details). Equation 1 illustrates the formal relationship between the surface roughness, \( z_0 \), and the wind velocity. Although the shear stress \( (\tau) \) is not explicitly stated in equation 1, shear stress is proportional to the friction velocity \( (u^*) \) through the relationship (see Montich 1973):

\[ u^* = (\tau/p)^{1/2}, \]

Surface roughness, \( z_0 \), is an average for a particular surface and does not characterize an individual location in which a seed may be caught.

Knowing the velocity at a particular time at one height and the roughness, we can determine the velocity at any other height, at the same time. However, the velocity at any height varies over time, and this variation in velocity can be described
by a distribution function where the average return time of a particular velocity can be obtained via the inverse of its frequency.

By knowing the velocity at which seeds move, and calculating the average return time of this windspeed, the average period of time that a seed remains in one location can be estimated. From this measure, it is possible to estimate the amount of time seeds are likely to remain stationary and from that, determine whether or not a seed has adequate time (given adequate moisture) to germinate within the return time of the velocity that causes seed movement.

**SEED SIZE AND THE LIKELIHOOD OF MOVEMENT**

The likelihood of seed movement is a function of seed size, the roughness of the ground surface, and the wind velocity. The velocity of the wind that causes a seed to move will be called the threshold or lift-off velocity (Arnold & Weihs 1978). This threshold windspeed changes with different surface roughnesses and different seeds. As the surface roughness of the ground \( \left( c_0 \right) \) increases, the associated wind velocity at a specific height decreases (following equation 1), and the threshold velocity required to move the seed increases. Further, as wind velocity increases, the proportion of seeds unmoved on any surface will decrease. The seeds used in this study were single-winged asymmetrical samaras (see Augspurger (1986) for a discussion of samara morphologies).

The physical forces operating on a seed can now be combined to characterize the resistance, which relates the forces acting on the seed to the force of the wind. The model developed here is two-dimensional (i.e., vertical and parallel to the flow) and ignores the lateral or asymmetric force on the seed. Subject to this limitation, the three forces acting on a particle at rest on a flat surface include drag, lift and gravity. The force required to lift the seed is the resultant aerodynamic force in the upward vertical direction. For threshold movement along the ground the aerodynamic drag, downstream and parallel to the ground, must overcome the ground friction resulting from the difference between the weight of the seed and the lift developed, such that

\[
D = \mu(W - L),
\]

where \( W \) is the weight of the seed, \( D \) is the drag on the seed, \( L \) is the lift on the seed and \( \mu \) is the static friction coefficient.

The lift (in N) on an object is defined (Arnold & Weihs 1978) by:

\[
L = 0.5C_L\rho A_wu^2,
\]

where \( C_L \) is the coefficient of lift, \( \rho \) is the air density, \( A_w \) is the planform area of the seed (Fig. 1) and \( u \) is the wind velocity. Similarly, the drag (in N) may be calculated as:

\[
D = 0.5C_D\rho A_wu^2,
\]

where \( C_D \) is the coefficient of drag. Because the seed acts as an airfoil, the area referred to in equation 5 is the same area as in equation 4 (Ipsen 1960; Vogel 1981).

The weight of the seed is:

\[
W = mg,
\]

where \( m \) is seed mass, and \( g \) is the gravitational constant. Thus substituting equations 4–6 into equation 3 and rearranging we get

\[
C_L + \frac{C_D}{\mu} = \frac{2mg}{\rho A_wu^2},
\]

where \( \frac{2mg}{\rho A_wu^2} \) is assumed to remain constant for seeds of the same species on the same ground surface. Although it is not possible here to measure the constants \( C_L \), \( C_D \) and \( \mu \), the right side of equation 7 can be measured. This term is a dimensionless ratio of the forces on a seed and gives the resistance of a seed to motion. Henceforth this ratio will be referred to as \( B \), because Bagnold (1941) first derived an equation of motion similar to this (see also Dallavalle (1948) and Arnold & Weihs (1978)).

The coefficients of lift and drag, \( C_L \) and \( C_D \) (equation 7), are functions of the seed’s orientation (or angle of attack), seed shape and Reynolds number \( (Re) \) (Vogel 1981). The angle of attack measures the angle between the length of the seed or airfoil and the air flow (see Fig. 1). Firstly, the influence of the orientation of individual seeds on \( C_L \) and \( C_D \) can only be measured indirectly, and will be discussed in the context of different surfaces in the Methods section. Secondly, the change of shape between

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Fig. 1. Typical asymmetrical samaras in (a) plan view and (b) side view. (c) The angle of attack is the angle between the length of the samara or airfoil and the wind direction. (d) The typical placement of a samara between roughness elements.
species will be studied by examining the wing loading (see below), fineness ratio and aspect ratio. Wing loading measures the ratio of an object's weight to the area of the wing(s) (Vogel 1981; see below). The fineness ratio measures the relationship of seed length to height, and determines whether or not the airfoil is streamlined (Dommasch, Sherby & Connolly 1961). Aspect ratio is a ratio of the square of samara width to the planform area of the samara and identifies the slenderness of the airfoil. Equation 7 assumes that the threshold velocity of movement varies directly with seed size. From this, for winged seeds (samaras)

\[ u = \left( \frac{m}{A_w} \right)^{1/2}, \quad \text{eqn 8} \]

The quantity \( m/A_w \) is called the wing loading (Norberg 1973). Greene (1989) has shown that the wing loading of samaras increases with absolute size; that is, mass increases more rapidly than area. Because of the scaling of volume and area, and from the proportionality above and equation 7, the following should hold (Schmidt-Nielsen 1984; Greene 1989):

\[ A_w \propto m^{2.5}, \quad \text{eqn 9} \]
\[ u \propto m^{1.6}, \quad \text{eqn 10} \]

The effect of the third factor, Reynolds number, on \( C_L \) and \( C_D \) can be examined by plotting the relationship between \( B \) and \( Re \); \( Re = cu/v \), where \( c \) is some characteristic length of the object which, for the samara, was taken as the wing (Dommasch, Sherby & Connolly 1961). \( u \) is the fluid velocity, and \( v \) is the kinematic viscosity of the fluid. When velocity and kinematic viscosity are constant, the effect of the characteristic length or seed size on Reynolds number can be examined. \( C_L \) and \( C_D \) are approximately exponential for the range of Reynolds numbers considered (Dommasch, Sherby & Connolly 1961; Vogel 1981).

The resistance of seeds to movement \( (B) \), can be plotted against the percentage of seeds remaining at specific velocities. This resistance estimate can be obtained through experimentation in a wind tunnel, where a known number of seeds is exposed to increasing windspeeds on specific surfaces. If all seeds follow the same line in a plot of the number of seeds remaining against resistance, then resistance adequately describes seed movement.

**Likelihood of Seed Movement Over Time**

The threshold velocity of seed movement is used in the calculation of seed resistance to movement (equation 7) and from this the percentage of seeds moving, or those remaining stationary, at specific velocities can be estimated. Next, the percentage of seeds remaining unmoved can be related to the average return time of the threshold windspeeds to estimate the frequency of seed movement or, conversely, the likelihood of no movement. Windspeeds have a frequency distribution associated with them, from which the average return time of threshold velocities can be calculated. The distribution of return times can then be compared with the distribution of seed germination times by the method of convolution (Haugen 1968), in order to estimate the likelihood of seed germination before movement. This will identify the likelihood of seed germination on a particular surface given the windspeed distribution, the roughness of the surface, and the size of the seed (Fig. 2).

**Methods**

The four species used in this study were winged asymmetrical samaras of *Picea engelmannii* Parry (Engelmann spruce), *P. abies* (L.) Karst (Norway spruce), *Pinus contorta* Loudon var. latifolia Engelm. (lodgepole pine) and *P. sitchensis* Bong. (white pine), which represents the range of samara sizes for temperate pine and spruce (Schopmeyer 1974). *Pinus contorta* and *Picea engelmannii* seeds were obtained from Peter Lougheed Provincial Park, Alberta, Canada and *Picea abies* and *Picea sitchensis* seeds were obtained from the Petawawa National Forestry Institute, Ontario, Canada.

**Surface Roughness, Wind Velocity and Seed Movement**

Experiments were carried out to determine the rate of movement of seeds in a 30-m open-circuit, closed-throat, turbulent-flow wind tunnel. The fetch (Montith 1973) in the tunnel was greater than 100 times the height of the surface and the seed,
sufficient distance for the wind profile to acquire fully developed turbulent flow (Munro & Oke 1975; Gash 1986). The wind velocity was measured at five heights, 1.5, 5, 10, 20 and 40 cm, with a pitot tube. Profiles of velocity with height were then graphed on semi-logarithmic paper to confirm they produced a linear relationship and to estimate $z_0$.

One hundred winged seeds of *Picea engelmannii*, *P. abies*, *Pinus contorta* or *P. strobos* were uniformly placed in the working section of the wind tunnel on four different surfaces; wood (a smooth board), sand (average size: c. 250 μm), soil (c. 750 μm) and small gravel (c. 2-0 mm). The wood surface was used as a standard for comparison. Starting at a low velocity, the fan of the wind tunnel was turned on and left to run at a constant velocity for 5 min or until the seeds stopped moving. The wind tunnel was then turned off, and the number of seeds remaining counted. Seeds became aligned with the wind at much lower velocities than was required for lift-off. Seeds that lifted off the ground surface did not descend to the ground but were blown out of the wind tunnel. The velocity was then incrementally increased and the number of seeds remaining recorded at each velocity. This procedure was repeated until either no seeds remained on the surface, the wind tunnel reached its maximum velocity, or the surface itself started moving. The velocity increments were set at 2-7 m s$^{-1}$, because this is approximately the smallest velocity change possible in the wind tunnel. At least four runs (with each run made up of 100 seeds) were conducted for each species on each surface, to ensure that the distributions of movement obtained were representative of a large number of seeds. Two analyses of covariance were conducted (SAS 1985). One analysis of covariance (ANCOVA) was conducted for each set of runs, for each species on each surface, to determine if any run differed significantly from the rest. This was done by testing the percentage of remaining seeds against the runs in the wind tunnel, with resistance as a covariate. A second analysis of covariance was used then to test if seed movement differed significantly for different species on each surface, again using resistance as a covariate. Homogeneity of slopes was tested before each ANCOVA was conducted (Neter, Wasserman & Kutner 1985).

Seed mass was determined on an electronic balance. The planform area was digitized with a video camera connected to a microcomputer with an Oculus 300 Real Time Image Digitizing and Processing Board (Coreco Inc., Ville St.-Laurent, Que.). Digitized images were processed using the Video Image Processing System (AWB Software Consultants Ltd., Calgary, Alta.).

**TEST OF MODEL ASSUMPTIONS**

Resistance to movement depends on orientation, shape and Reynolds number. These must be examined separately. The influence of seed orientation on seed resistance to movement, $B$ (equation 7), can only be measured indirectly. All seeds on smooth surfaces were similarly orientated, parallel to the ground surface and the air flow, with an angle of attack of 0° (Fig. 1c). Thus the relationships between $C_L$, $C_D$, size and $Re$ will be examined on a smooth surface, where the angle of attack is minimal. Lift increases from zero to some maximum at an angle of approximately 18°, and then decreases again (Dommasch, Sherby & Connolly 1961). Thus, increasing the angle of attack from 0° to 18° increases lift force, but an angle less than 0° retards the lift. Drag is never zero, and increases up to very high angles of attack (Vogel 1981). As ground surface roughness increases, the angle of attack becomes more varied. It is assumed that as the surface becomes rougher, the heavy end of the samara (weighed down by the seed) will more likely end up in a crevice with the wing pointing up (see Fig. 1d). This will constitute a negative angle of attack, and require a larger threshold velocity to compensate. The limitation of this approach is inherent in the two-dimensional model of resistance used by Baghold (1941) and Arnold and Weilhs (1978). A two-dimensional model is a first approximation and a three-dimensional model would give a more complete understanding of sidleslipping or the lateral moments. Asymmetrical moments on an isolated wing (the ratio of rolling moment produced by sidleslipping to the sidleslipping which produces it) would clearly introduce a major increase in complication in a model which ecologists will already find difficult. At this point, the advantage gained is not obvious.

The influence of shape on the resistance to movement was examined using the wing loading, fineness ratio and aspect ratio measures. Single-factor analyses of variance were conducted to determine if these measures differed significantly between species. The effect of $Re$ can be studied at different velocities and a plot of the inverse of $Re$ vs. $B$ (resistance to movement) identifies their relationship.

**RETURN TIME OF WIND VELOCITY**

Estimates of the return time of windspeed were obtained by using gradient windspeed measures and then deducing the winds at lower levels. Gradient windspeeds were used because they are unaffected by surface conditions and do not have the inherent difficulties of surface anemometer records (Davenport & Baynes 1972; Davenport 1982). This method was also used because ecologists rarely have access to windspeed data collected over a long enough period in an area similar to their study area (at the necessary height(s)). First, gradient windspeed measures were obtained from radiosonde data at 1524 m above sea level (approximately 400 m above the ground...
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(T. Rhodes, personal communication) from the University of Calgary Meteorological Station. If the measurements were not taken exactly at 1524 m a.s.l., linear interpolation (cf. Davenport & Baynes 1972) was used to obtain the windspeed at the appropriate height. Radiosonde data were taken every 12h, from June until August, 1978, 1980 and 1982, and June until September 1979 and 1981. The gradient windspeed values and their frequencies were then plotted on Weibull probability paper (Takle & Brown 1978).

Secondly, using a method developed by Davenport (1961a,b, 1964, 1982) and Davenport & Baynes (1972), the gradient wind measurements were used to estimate windspeeds at lower heights, such as 10 m. With this method, direct estimates of wind-speed by surface anemometers are unnecessary, because the gradient windspeed can be traced down to the height of interest.

The velocity at any specific height, \( u(z) \), lower than the gradient height, can be calculated using the power-law equation:

\[
 u(z) = u_0(z/zh)^n, \tag{eqn 11}
\]

where \( u_0 \) is the gradient wind, \( zh \) is the height of the gradient wind, and \( n \) the power-law exponent (Davenport 1982). The power-law exponent was determined empirically to range from 0.07 to 0.11 (with larger exponents representing rougher surfaces) from profiles taken in recent crown fire burns where all canopy and understory foliage and small branches have been removed by burning (E.A. Johnson & G.I. Fryer, unpublished data). The power-law (equation 11) can be matched to the logarithmic profile (equation 1) at any reference height, \( z_R \), using the following relationships found by comparing the magnitudes and slopes of the two profiles:

\[
 n = \frac{1}{\ln(z_R/zh)} \quad \text{and} \quad zh = z_R (C_v/k_a)^{-1/n}, \tag{eqn 12}
\]

where \( C_v \) is the geostrophic drag coefficient, \( k_a \) is von Karman's constant and \( a \) is empirically determined (Davenport 1982). Both laws are used because the lower part of the boundary layer is better represented by a logarithmic law, in the range 0 to 30 or 50 m (Counihan 1975). Power-law estimates at heights close to the ground are less reliable than estimates obtained from the logarithmic law at the same height, but the power-law fits the data better than the logarithmic law over a greater height range, such as at the gradient height (Counihan 1975). Therefore, the power-law was used to obtain the estimated return times of certain velocities which coincided with velocity estimates from the wind tunnel, obtained from the logarithmic law. The return time of the power-law estimates were then used as the return times of the threshold velocities which were determined in the wind tunnel.

Germination rates

The time required for *Pinus contorta* seeds to germinate was determined by submerging the seeds in aerated water. Both stratified and unstratified seeds were used. Seeds were stratified by keeping the seeds moist at 4°C for 60 days (Schopmeyer 1974). Seeds were considered to have germinated when the radicle emerged (Bewley & Black 1985). The seeds were surrounded by water and then aerated, so no contact problems arose between the soil surface and the seed coat, with respect to water uptake. This germination time represents the minimum under ideal conditions. The *Picea abies* and *Pinus strobus* seeds had low viability and consequently could not be used as accurate tests of these species' germination rates.

Timing of seed movement with germination

The resistance of seeds to movement can be compared with the percentage of seeds unmoved in the wind tunnel, so that seed resistance can be used to estimate the percentage of seeds unmoved on a particular surface. The next step is to couple the percentage of seeds unmoved with the average return time of windspeeds in nature. This is done by calculating the return time of the threshold velocities of seed movement from the power and logarithmic laws of wind in nature. Finally, the germination rates of seeds can then be included, so we may estimate the chances of germination of the seeds that remain over time, or the chances of seed germination before movement. This is accomplished by the method of convolution (Haugen 1968). The return times for seed movement and the germination times were examined and when the two overlapped, the probabilities of each were multiplied, as in the convolution method.

Results

Seed movement and assumptions

The movement of all four species on each wind tunnel surface could be represented by a logistic function:

\[
 E(P_t) = \frac{\exp(\beta_0 + \beta_1B)}{1 + \exp(\beta_0 + \beta_1B)}, \tag{eqn 13}
\]

where \( E(P_t) \) is the predicted estimate of the percentage of seeds remaining, \( B \) is the seed resistance to movement, and \( \beta_0 \) and \( \beta_1 \) are the intercept and slope from linear regression analysis, respectively (Neter, Wasserman & Kutner 1985). \( P_t \) was logistically transformed \((\ln[P_t/(1-P_t)]\) and each observation was weighted by the inverse of the variance of a logit \((nP_t\{1-P_t\}) \), where \( n \) is the total number
of seeds) to account for the known dependence between the mean and variance so that linear regression analysis could be performed. All regression equations explained a significant proportion \((P < 0.05)\) of the observed variation and the coefficients of determination \((r^2)\) were never below 0.64 (Table 1). The slope and intercept of the linear regression analyses are independent of each other \((r^2 = 0.007, n = 16; P > 0.05)\).

In Fig. 3, the shape of the curve changes with different surfaces. In general, for any surface, the steeper the slope, the greater the resistance of seeds to movement. This means that on rougher surfaces, seed movement is more variable and some seeds are unmovable by the wind for long periods, so there is an increase in the proportion of unmovable seeds on these surfaces. Thus, sites in which seeds remain stationary for longer periods can be described in terms of wind velocity; seeds that do not move with each increasing velocity can be thought of as being in ‘safe’ microsites for windspeeds up to that particular velocity.

The slopes depended upon the species and the surface type (test of heterogeneity of slopes: \(F_{5,758} = 6.10, P < 0.001\)). Based on a-posteriori contrasts, the slopes of the percentage of remaining seeds vs. resistance were not significantly different on wood for all four species \((P < 0.001)\). Here the angle of attack was at a minimum, and seed movement was expected to be the same. This result empirically validates the use of the resistance equation to explain the movement of asymmetric samaras on smooth surfaces by wind. On sand the slope of the percentage of Pinus contorta seeds remaining against resistance differed significantly from the other three species, and Picea engelmannii differed significantly from Pinus strobus \((P < 0.001)\). On sand, more differences in movement occurred than was expected, because the roughness of sand was lower than that of the soil and gravel and the orientation of the seeds was assumed to be more uniform. On soil and gravel, only the slopes for Pinus contorta and P. strobus seeds differed significantly \((P < 0.001)\).

Next, the effects of Reynolds number and seed shape (and indirectly orientation) on the resistance \((B)\) were examined. No significant relationship was found between \(Re\) and \(B\) \((r^2 = 0.170, n = 12, P > 0.05)\). Thus, for the range of samara sizes examined here, their performance was unaffected by size. The results of the analyses of variance revealed differences between species for wing loading, fineness ratio and aspect ratio. The average wing loading differed significantly between species \((\text{ANOVA}; F_{3,116} = 23.25, P < 0.001)\). The wing loadings of Picea engelmannii and Pinus contorta were not significantly different but the wing loadings of Picea abies and Pinus strobus were both significantly different from each other and the other two species (Tukey’s multiple comparisons; \(P < 0.05\)). The species also had different average fineness ratios \((\text{ANOVA}; F_{3,116} = 144.90, P < 0.001)\). The fineness ratios of Picea engelmannii and P. abies were not significantly different but the fineness ratios of Pinus strobus and P. contorta differed significantly from each other and the other two species (Tukey’s multiple comparisons; \(P < 0.05\)). Lastly, the average aspect ratio measures differed significantly between species \((\text{ANOVA}; F_{3,116} = 49.73, P < 0.001)\). The aspect ratios of Picea engelmannii and P. abies were not significantly different from each other and

<table>
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<th>Species</th>
<th>Surface</th>
<th>Intercept ((\beta_L))</th>
<th>Slope ((\beta_0))</th>
<th>Coefficient of determination ((r^2))</th>
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<td>Wood</td>
<td>-2.80</td>
<td>44.25 (2.26)</td>
<td>0.88</td>
<td>54</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sand</td>
<td>-2.89</td>
<td>72.90 (6.81)</td>
<td>0.72</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soil</td>
<td>-2.12</td>
<td>54.83 (4.49)</td>
<td>0.71</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gravel</td>
<td>-0.37</td>
<td>88.83 (6.71)</td>
<td>0.81</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>Pinus strobus</td>
<td>Wood</td>
<td>-3.82</td>
<td>42.77 (3.10)</td>
<td>0.80</td>
<td>51</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sand</td>
<td>-1.77</td>
<td>28.72 (2.78)</td>
<td>0.70</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soil</td>
<td>-0.72</td>
<td>32.99 (3.32)</td>
<td>0.64</td>
<td>57</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gravel</td>
<td>0.50</td>
<td>34.59 (3.34)</td>
<td>0.72</td>
<td>44</td>
<td></td>
</tr>
</tbody>
</table>
the aspect ratios of *Pinus strobus* and *P. contorta* were also not significantly different from each other (Tukey's multiple comparisons; \( P < 0.05 \)). It appears that the shape does differ between species, although not consistently (Table 2). The two *Picea* species were similar except for wing loading, and the two *Pinus* species were only similar in aspect ratio. The two smallest samaras, *Picea engelmannii* and *Pinus contorta*, had similar wing loadings. The slope of the relationship between the velocity at which 50% of the seeds moved on wood and the wing loading of the seed (see Table 2) was not significantly different from the expected value of 0.5 (\( r^2 = 0.429, n = 17, P > 0.05 \)). The data also conformed to the expected slope of 0.67, as seen in equation 9 for the relationship between the mass and planform area of the samaras (\( r^2 = 0.744, n = 120, P > 0.05 \)). The slope of average mass vs. the velocity at which 50% of the seeds moved on wood was not significantly different from 0.167 (\( r^2 = 0.677, n = 17, P > 0.05 \)). Over the range of mass and area, the seeds were geometrically similar in size and, consequently, larger seeds required higher wind velocities to move them.

In general, *Pinus contorta* seed movement differs from that of the other three species. Despite not having significantly different wing loadings
of the seeds becomes increasingly varied. This may account for the differences in slope between species.

**Wind Velocity and Return Time**

The wind profiles in the wind tunnel showed a significant linear relationship ($P < 0.05$) between the logarithm of height and velocity ($r^2$ in all cases $>0.9$). The logarithmic law was then used to estimate the wind speed at 10 m. The frequency of occurrence or the average return time of wind speed at 409 m for Calgary is plotted on Weibull probability paper in Fig. 4. By using the 10-m wind speed estimates as well as the gradient wind speed return times with equation 11, estimates of the return times of the threshold wind speeds were obtained. Figure 5 illustrates how long seeds are likely to remain stationary on a given surface. Notice how the curve shifts to the right with larger exponents; i.e., the return time of the threshold velocity increases on rougher surfaces, decreasing seed movement. The length of time seeds remain stationary then increases, with greater seed movement return times on gravel.

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**Fig. 4.** Cumulative probability distribution of windspeed ($\text{m s}^{-1}$) at 409 m plotted on Weibull probability paper (University of Calgary Meteorological Station) ($n = 705$). The right-hand side of the figure shows the estimated average return times of the velocities.

(See Table 2), *Picea engelmannii* and *Pinus contorta* seed movement was significantly different on sand. Thus equation 7 does not appear to incorporate all of the differences in seed shape and movement, as is consistent with a model that does not include side-slip and lateral moments. However, the seed movement of all species on wood was not significantly different but on rougher surfaces the orientation

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**Fig. 5.** Percentage of seeds unmoved against the return time of the threshold velocity for seed movement of four conifers. The lines represent the return-time estimates with the appropriate power-law exponents, between 0-07 and 0.11 (see text for explanation). (a) *Picea abies* on wood, exponent of 0.07 (●) and 0.08 (○); (b) *Pinus strobus* on gravel, exponent of 0.08 (●) and 0.09 (○); (c) *Picea engelmannii* on soil, exponent of 0.09 (●) and 0.10 (○); (d) *Pinus contorta* on gravel, exponent of 0.10 (●) and 0.11 (○).
Seed movement on the ground

Stratified seeds of *Pinus contorta* and *Picea engelmannii* germinated much more quickly than unstratified seeds of both species (Fig. 6). In general, more *Picea engelmannii* seeds germinated than *Pinus contorta* and more quickly, with *Picea engelmannii* taking 135 h for 50% of the seeds to germinate and *Pinus contorta* taking 358 h for 50% of the seeds to germinate.

Figure 7 is the convolution of seeds remaining over time (Fig. 5) and the germination times of seeds (Fig. 6), and shows the likelihood of seed germination before movement for *Picea engelmannii* (stratified and unstratified) and *Pinus contorta* (stratified) seeds on gravel. *Pinus contorta* and *Picea engelmannii* seeds would move before germination on wood, sand and soil, and consequently the curves in Figs 5 and 6 for these surfaces did not overlap in time. The effects of windspeed, surface roughness and seed size on seed movement have all been incorporated in Fig. 7. Moving from left to right on the bottom axis of Fig. 7, initially few of the seeds have been moved by wind, but also few of the seeds have had time to germinate. After a longer period, more seeds will have had time to germinate but they will also have had a greater chance of being moved by the wind. The highest point on the graph will occur when the maximum number of the seeds has not yet moved but has had sufficient time to germinate. On the right side of the axis, the majority of seeds will have moved and will also have had time to germinate. This tail, given a generally similar germination pattern within a species, is a function of the seed movement. The tail is consequently a function of wind speed and surface roughness. The length of the tail is significant because it defines the microsites in which seeds can be trapped even at high windspeeds. The extent of the tail will of course be due in part to the instability of the ground surface itself.

In general, more seeds will have a chance to germinate if the return time of the windspeed is long and the germination rate is as fast as possible (assuming appropriate moisture conditions). *Picea engelmannii* seeds have a greater chance of germinating before moving than do seeds of *Pinus contorta*. Although we could not estimate germi-

**Fig. 6.** Cumulative germination percentages of seeds of *Pinus contorta* (stratified (•) and unstratified (●)) and *Picea engelmannii* seeds (stratified (○) and unstratified (●)).

**Fig. 7.** Expected number of seeds of two conifer species that remain unmoved by the wind long enough to germinate on gravel (power-law exponents of 0.10 (○) and 0.11 (●)): (a) stratified *Pinus contorta*; (b) stratified *Picea engelmannii*; (c) unstratified *P. engelmannii*. 
nation for *Picea abies* and *Pinus strobus*, published estimates are available. For *Picea abies*, germination rates vary from 10–22 days (USDA Forest Service 1948; Schopmeyer 1974) to 7–21 days (Edwards 1987). If *Picea abies* seeds do not start germinating for 10 days and the distribution of wind velocities used in this paper are assumed, then seed movement on all four surfaces is estimated to occur before germination. If the *Picea abies* seeds begin germinating within 7 days, then, although more than 50% of the seeds on gravel are estimated to have moved, there are seeds still present to germinate (*Picea abies* seeds will still have moved by 7 days on wood, sand and soil). For *Pinus strobus*, germination rates vary from 12–39 days (USDA Forest Service 1948) to 7–28 days (Edwards 1987). If *Pinus strobus* seeds do not begin germinating for 12 days and the distribution of wind velocities presented in this paper are assumed, then the movement of the total population of *Pinus strobus* seeds on all four surfaces is estimated to occur before germination. If the *Pinus strobus* seeds begin germinating within 7 days, then, although less than 40% of the seeds on gravel are estimated to remain, there are still seeds present to germinate (*Pinus strobus* seeds are estimated to have moved by 7 days on wood, sand and soil).

**Discussion**

The results of this study appear to support Harper's (1977) suggestion that seed movement on the ground will influence the potential number of seeds available for germination and establishment. Fundamental to the identification of these microsites, in which seeds germinate and establish, for wind-dispersed seeds is the relationship between seed movement on the ground and the physical properties of the ground surface. Seed movement is influenced by the surface roughness of the ground, the distribution of windspeeds that occur in the area, and seed size. These three factors influence the length of time that a seed remains stationary and therefore the time available to imbibe water and germinate. Resistance (B), which is proportional to the ratio of gravity to the force of the wind, encompasses these three variables. The physical properties of the surface and the wind distribution are incorporated into the resistance equation (7) through the windspeed at a particular height. This is because the windspeed changes with height, and is influenced by the roughness of the ground surface. The dimensions of the seed enter the resistance equation through wing loading (see Table 2). For a given windspeed distribution, resistance translates into time because the windspeeds causing seed movement are associated with specific return times. The curve that results shows the decline in the number of seeds remaining unmoved over time (Fig. 5). Conversely, the number of seeds germinating on any surface increases over time (Fig. 6). By coupling the increasing chance of germination over time with the decreasing chance of remaining stationary over time, the chance of germination before movement can be determined (Fig. 7). These curves differ for all species and surfaces. However, in general, the seed movement of all four species, *Picea engelmannii*, *P. abies*, *Pinus contorta* var. *latifolia* and *P. strobus*, will occur before germination on wood, sand and soil. On gravel, the times to germination vs. movement begin to overlap and a curve similar to Fig. 7 will result.

What does this rather intricate discussion do for our understanding of the idea of microsites? It would appear that on rough surfaces there is a certain number of seeds (Fig. 5) which is rather securely trapped and will not be moved by winds which do not cause the surface material also to move. These trapped seeds are more likely to germinate if water is available and predation does not occur. Consequently, the distribution of seeds remaining at different windspeeds, shown in Fig. 7, gives an idea of the chance of a seed finding a microsite. The tail of the curves in Fig. 7, or the extent of these microsites for any particular surface, is due largely to the roughness of the ground surface. The ground surface roughness is a function of both wind speed and roughness length equation 1. If, for a particular area, the windspeed, at a reference height, is assumed to be the same, then the roughness length is the important variable. Roughness lengths are generally an order of magnitude less than the height of the roughness elements (Montieth 1973). Consequently the number of seeds that remain (Fig. 7) is a function of the roughness elements. The physical reason for this is that as the roughness elements get larger, the roughness stress component of the surface total stress (proportional to $u^*$; see equation 2) increases but the intervening surface stress component decreases (Lyles 1977). In other words, the proportionality of surface stress between the seeds and roughness elements changes, with the stress on the seeds decreasing as the roughness element gets larger.

The model we present is not without its limitations. Seeds move frequently on smoother surfaces but are trapped and move less frequently on rougher surfaces, as one intuitively thinks. On the smoothest surface, wood, all seeds moved similarly, and the dimensionless variable, resistance (B), appeared to describe the mechanism of movement. On the rougher surfaces, however, the resistance equation did not completely explain seed movement: all four species did not move similarly, and *Pinus contorta* in particular moved differently. *Pinus contorta* has the smallest wing loading as well as the largest fineness ratio, which indicates it is the most slender samara, perhaps suggesting why a greater velocity is required to initiate movement. The wing loading, fineness and aspect ratios of the four species were
different, although the differences were not reflected consistently in seed movement. The movement of all four species was the same on the smoothest surface, where it was assumed that the orientation of the seeds was the same, indicating that the resistance equation adequately described seed movement. On the rougher surfaces, however, not all of the seeds moved in a similar manner, and on these surfaces the orientation of the seeds was variable. This suggests that the orientation of the seeds is a factor influencing seed movement and that the resistance equation, in describing seed movement on rougher surfaces, is incomplete. The source of the problem may be that a three-dimensional model of seed movement, which also incorporates the lateral force on a seed, is required to replace the two-dimensional model of resistance used here.

In this study, the surfaces used were relatively smooth when compared to the variety of surfaces encountered in a natural setting. However, these surfaces may be considered comparable to some specific conditions in the field, where movement could play a significant role in successful germination. A high-intensity crown fire, the most common form of disturbance in Picea engelmannii and Pinus contorta forests, consumes large amounts of the debris and litter, often leaving only standing tree boles. In a recent burn the wind profile followed the logarithmic law and the roughness was determined to be similar to the roughness of the soil or gravel used in the wind tunnel (E.A. Johnson and G.I. Fryer, unpublished data). However, the conditions existing in a recent burn have been simplified. No other obstructions or vegetation were present in the flow of the wind expressed here, which could change the distribution or return time of the wind velocities in a real situation.

In the identification of microsites, the effect of non-equilibrium airflow resulting from heterogeneous surface conditions must be considered. In the preceding estimates of seed movement, equilibrium air flow and a homogeneous surface were assumed. In the field with heterogeneous surface conditions, the magnitude of roughness change will influence the distance required for the air flow to equilibrate. Several investigators have studied the behaviour of wind over changes in surface roughness (Bradley 1968; Angle 1975; Jackson 1976; Jarvis, James & Landsberg 1976; Arya 1982). The complex behaviour of air flow after large changes in ground surface roughness elements currently limits the characteristic time and length at which seed movement can be studied. Studies of these air-flow phenomena as well as studies of seed movement in the field over changes in roughness are the next logical steps to take in studying seed movement. Once the behaviour of air flow under non-equilibrium conditions is better understood, the characteristic time and length at which seed movement can be studied will decrease.

This will approach the level of explanation desired in most studies of seed-microsite movement (for example, Green 1983; Geritz, de Jong & Klinkhammer 1984).

Seed movement is not the only factor influencing germination and establishment and provides only part of the answer in the process of identifying successful germination. In this study, only the movement of single-winged asymmetric samaras on surfaces of moderate roughness has been considered, although other types of winged and plumed seeds may follow similar movement patterns. Further, the effect of rainfall on the seeds has not been examined, nor have the moisture conditions that exist in microsites on different surfaces. However, the comparison made here between seed movement and germination was an attempt to begin coupling together the different processes associated with germination: water uptake and seed movement. The next step would be to determine empirically the water budgets of the sites in which seeds become trapped in the field. In this way, the variables responsible for successful seed germination and establishment can be combined in a stepwise manner to produce a physical model for predicting the probability of seed establishment in different habitat locations.

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Appendix. Symbols used in the text.

Seed movement on the ground

\[ A_w \] total planform area of samara (cm\(^2\))

\[ B \] seed resistance to movement

\[ C_v \] geostrophic drag coefficient

\[ C_D \] coefficient of drag

\[ C_L \] coefficient of lift

\[ D \] drag force (N)

\[ g \] gravitational acceleration (981 cm s\(^{-2}\))

\[ h \] height of samara (cm)

\[ k \] von Karman constant (0-4)

\[ l \] length (chord) of samara (cm)

\[ l/h \] fineness ratio

\[ L \] lift force (N)

\[ m \] total samara mass (g)

\[ mL \] total samara mass (g)

\[ mL/A_w \] wing loading (g cm s\(^{-2}\))

\[ n \] power-law exponent

\[ Re \] Reynolds number

\[ u \] velocity (cm s\(^{-1}\))

\[ u_G \] velocity independent of the ground surface roughness (cm s\(^{-1}\))

\[ u^* \] friction velocity (cm s\(^{-1}\))

\[ v \] kinematic viscosity (cm\(^2\) s\(^{-1}\))

\[ w \] width (span) of wing (cm)

\[ w^2/A_w \] aspect ratio

\[ z \] height (cm)

\[ z_G \] height at which the wind profile is independent of the ground surface (cm)

\[ z_R \] reference height (cm)

\[ z_0 \] roughness length (cm)

\[ z_0 \] change in roughness (mm)

\[ \rho \] density of air (g cm\(^{-3}\))

\[ \tau \] shear stress (g cm\(^{-1}\) s\(^{-2}\))

\[ \mu \] static friction coefficient