
Wind Dispersal of Tree Seeds & Fruits

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How-To-Do-It

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James D. Thomson
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Dynamic ecological processes often occur over short periods of time. However, laboratory exercises designed to investigate these processes often seem to take forever. In many of these exercises students merely see the results of the processes. To actually see ecologically important events taking place makes ecology exciting, more so than just tedious data collection.

At the State University of New York at Stony Brook we have tried to develop exercises that involve the students in processes as well as patterns. Here, we present two exercises on the dispersal of tree seeds by the wind. This lab was inspired by the original research of Carol Augspurger of the University of Illinois.

Dispersal of offspring can be an important aspect of the biology of an organism at many levels: colonization of new habitats (MacArthur 1972), escape from predators and pathogens (Janzen 1969) and reduction of competition with relatives, to name a few (Howe & Smallwood 1982). Dispersal seems especially advantageous in temporary habitats, but extremely general evolutionary models suggest that organisms with some capacity for dispersal can always displace non-dispersers (Hamilton & May 1977). For stationary organisms, such as plants and many marine invertebrates, dispersal may be a particularly important determinant of gene flow (Levin 1981, Levin & Kerster 1974).

Trees have a variety of dispersal mechanisms; many produce diaspores (the general term for dispersal units, which may technically be fruits, seeds, or other structures) that are adapted for dispersal by the wind. Several studies have shown the importance of these adaptations in the dispersal process (Augspurger 1986; Augspurger & Franson 1987; Augspurger & Hogan 1983; Green 1980; Guries & Nordheim 1984). Generally speaking, diaspore characteristics are likely to represent an evolutionary compromise. Seeds that contain more resources for the seedling are more likely to become successfully established but, due to their heavier weight, will not disperse as far. Green (1980), for example, proposes that the seeds of the sugar maple (which grows well in the shade), have a morphology with less dispersal potential than that of the red maple, a more opportunistic, light-requiring species that must "find" forest gaps or clearings to survive.

Diaspore Morphology

Wind-dispersed diaspores fall into several morphological groups (Burrows 1975; Harper et al. 1970; Ridley 1930). Each group has a characteristic aerodynamic behavior (rolling autogyration, undulation, tumbling, etc.) and set of equations that can be used to describe this behavior (Green 1980; Guries & Nordheim 1984; McCutchen 1977; Sheldon & Burrows 1973). Although many factors may affect the dispersal characteristics of these fruits and seeds (Burrows 1973; Sharpe & Fields 1982), most of the apparent adaptations of wind-dispersed diaspores reduce the rate of descent, thereby increasing time aloft. Since the distance a dispersal unit can be carried horizontally is dependent on the time aloft, adaptations reducing the rate of descent will serve to increase dispersal. Two aerodynamic characteristics of seeds that affect the rate of descent are the mass of the unit and its surface area. The weight of a flattened, wing-like diaspore divided by its area is called wing-loading. The square root of wing-loading has been shown to be highly correlated with the rate of descent (Augspurger 1986; Green 1980). A low wing-loading value indicates a slow rate of descent relative to a diaspore with a higher value within a morphological group.

The exercises described here are designed to investigate the properties of winged seeds and fruits. Several types of comparisons are possible. One can use variation occurring naturally among individuals within a species or among different species, or one can manipulate the weight or area of natural or artificial diaspores. Since each morphological group is aerodynamically unique, it is difficult to make interspecific comparisons using only wing-loading measures. However, diaspores with similar morphologies can be directly compared. For instance, intrageneric comparisons of natural or introduced species of ash (*Fraxinus*), maple (*Acer*), or pine (*Pinus*) would be interesting (and would be feasible in many parts of the temperate zone).

Manipulations

In some species [e.g., *Ailanthus altissima*, the tree-of-heaven (personal observation)], trees vary in fruit size. Where such variation is not naturally present, or when particular contrasts are desired, diaspores of a single species can be manipulated to change their aerodynamic properties (Figure 1). Some diaspores have asymmetrical wings; for example, the tree-of-heaven has a centrally placed seed in an elongated wing. The two ends of the wing are similarly shaped but one is flat while the other is twisted. This

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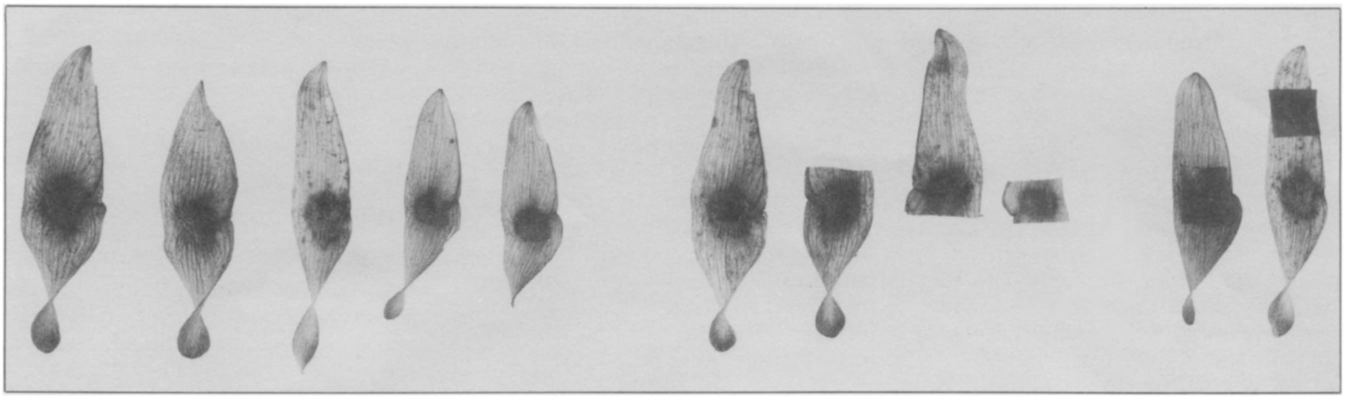

Figure 1. *Ailanthus altissima* diaspores. The group on the left displays inter-tree variation in size and shape. In the center group, treatments are shown that could be used to examine the effect of wing area and asymmetry. Tape has been added to the group on the right, changing the weight and the distribution of the weight of the diaspore.

twist gives the unit its characteristic roll. Manipulation by removing the twisted end gives a different dispersal behavior than removing the flattened end.

Wing-loading can be manipulated by changing either the weight or the surface area of the dispersal unit. Weight can be added to the diaspore by applying pieces of tape to the area that contains the seed. Additional pieces of tape would simulate even larger seeds. In some diaspores (e.g., tree-of-heaven) all or part of the seed can be removed without significantly changing the exposed surface of the dispersal unit. A change in the surface might change the air flow around the unit, confounding the effect of the weight change. The diaspore's surface area can be manipulated by removing a portion of the wing. Reducing the area will increase the wing-loading, subsequently increase the rate of descent and ultimately reduce the dispersal distance.

Diaspores with identical wing-loading properties can have different aerodynamic behaviors (Augspurger & Franson 1987). The distribution of weight on the wing and the shape of the wing will determine the type of motion during the descent. For example, changing the center of mass from the middle of the diaspore to the edge may change the motion during descent from rolling to spinning.

Artificial diaspores

Artificial diaspores can also be constructed to examine the effects of the changes in the dispersal units' mass, area, shape and symmetry. Stiff paper can be formed into wings of various sizes and shapes and will maintain its shape during the descent. The weight of the diaspore seed can be simulated by affixing weights to this wing. Augspurger and Franson (1987) used thin sheets of paraffin ("Parafilm") folded into small rectangles. The advantage to this method is that sheets of a given size will all have approximately the same weight and each artificial seed need not be weighed.

Marking Diaspore Treatments

Data collection is facilitated by color coding each species or treatment of the dispersal units to be tested. Choose colors that are easily distinguishable from each other and from the landing zone background color. We have color coded diaspores by shaking them in a bag that contained a small amount of powdered fluorescent pigment. Fluorescent pigment can be obtained from Day-Glo Color Corp., 4732 St. Clair Ave., Cleveland, OH 44103 or Hercules Inc., Coatings and Specialty Products Dept., Wilmington, DE 19899. Diaspores with these pigments are highly visible in a grass landing zone. Alternatively, quick-drying spray paint could be used to color code the diaspores. Artificial diaspores of each treatment can be constructed of different colored paper.

Laboratory Exercises

The mass and area of seeds or fruits are easily measured and manipulated by students. Additionally, students can construct artificial dispersal units that vary in these properties. From simple calculations of wing-loading, predictions of the rates of descent for each category of dispersal unit can be formulated. After the dispersal units have been collected and prepared, students can release the seeds or fruits in either a natural or laboratory setting, thereby observing the dispersal process. The differences in dispersal distance or time aloft are readily related to the aerodynamic characteristics of the diaspore.

Two types of exercise are: determining rates of fall in still air and measuring displacement distances from a release point. The still air exercise is designed to be conducted indoors, while the horizontal wind exercise is conducted outdoors. Each may be used independently to investigate the influence of morphological differences of various dispersal units, or they may be combined for a more complete understanding of the dispersal process.

1. Still Air Exercise: Rate of Descent of Dispersal Units

Rationale

The purpose of this exercise is to determine the rates of descent for diaspores without the influence of horizontal winds and to relate this information to measured differences in their aerodynamic properties. Since diaspores with slower rates of descent will spend more time aloft, they will have the potential to achieve greater dispersal distances (Augspurger 1986). Questions or hypotheses can be formulated and tested by students who investigate the role of diaspore morphology in the dispersal process. It is important to keep these questions rather simple. Although both mass and diaspore area are taken into account by wing-loading, it is best to examine one variable at a time, i.e., examine the effect of diaspore weight or area separately, but not both together. If the question is too complicated, it is difficult to intuitively understand the cause of the differences in rates of descent.

Equipment & mechanics

The most difficult aspect of this exercise is finding a suitable place to release the diaspores. Ideally, the drop site should allow the diaspores to fall a distance approximately equal to the height of the tree from which they were obtained. Since some diaspores will drift laterally even in draft-free areas, the release point should be above the center of a large landing zone. A large building such as a school gymnasium, theatrical stage, or auditorium is ideal. The easiest system is to manually release the diaspores from a balcony or catwalk. An alternative release mechanism can be fashioned and attached to a pulley system that can be raised above the landing zone. The area required for the landing zone will depend on the lateral movement of the particular dispersal units being tested.

The area of the diaspores can be determined by tracing the outline of the dispersal unit onto millimeter graph paper and counting the number of intersecting lines within this area. The area of the diaspore will be given in square millimeters. Alternatively, a transparent millimeter grid can be lain over a seed or fruit and the number of intersections can be tallied. Thirdly, the area of an irregularly-shaped diaspore can be determined indirectly by tracing the outline of the diaspore on a piece of paper and weighing on a sensitive balance the paper contained inside this outline. The weight can be converted to an estimate of the area; multiply this weight by a conversion factor composed of the measured area of a regularly-shaped piece of paper divided by its weight.

A balance for weighing the dispersal units, a meter tape to measure the release height and stopwatches for recording descent time are the only other equipment required.

Analysis & discussion

The rate of descent can be calculated as height divided by time. Although the terminal velocity of the diaspore is technically the best descriptor of descent (Green 1980), this calculated rate provides a reasonable means of comparing various diaspores. The time to reach terminal velocity is a minor portion of the total descent time, if the dispersal units are released from a sufficient height (Augspurger 1986; Guries & Nordheim 1984). Since we are considering dispersal characteristics of trees, the time should be an insignificant portion of the seed or fruit's descent period.

Rate of descent can be plotted against the square root of wing-loading for each morphological type of diaspore. For more sophisticated students, morphological types can be compared using a regression analysis. Discussion of the results might center around tradeoffs between the seed size and number, and the costs and benefits of achieving greater dispersal distances.

Figure 2. *Ailanthus altissima* diaspores in the mowed grass of the landing zone.

2. Horizontal Wind Exercise: Dispersal Distance

Rationale

Like the exercise described above, this examines the influence of the aerodynamic properties of the diaspore on dispersal potential. Here we are interested in the distance the dispersal unit is laterally displaced from the release point. Of course, the actual distance each seed or fruit travels is subject to the additional variables of the wind's direction, strength and variability during the period the diaspore is aloft after release from the parent tree. No absolute conclusions can be drawn about the distances a given diaspore will travel. However, comparisons of distances obtained by diaspores of different aerodynamic properties that were released at the same moment will yield relevant information about the dispersal process. The questions and hypotheses are similar to those of the Still Air Exercise.

Equipment & mechanics

The optimal site is one where the diaspores are exposed to a wind that blows steadily and where there are no nearby obstructions to cause eddies that might obscure differences in aerodynamic performance. It is also important that the seeds or fruits are free to fall to the ground without striking any objects such as shrubs or fences that might obscure differences in dispersal potential. A landing zone of mowed grass, as opposed to pavement, causes the diaspores to stay where they land, rather than blowing along the ground (Figure 2). A flagpole located on an athletic field has worked well for us. The existing flag-raising mechanism is easily adapted for raising a container of diaspores to any desired height. A line could also be suspended between buildings, trees, or stadium bleachers and a rope thrown over the line (Figure 3).

Our container is a plastic bucket with a friction fitting lid. Eyebolts are placed in the lid and the bottom of the bucket. The line of the flagpole is attached to the eyebolt on the bottom of the bucket for hoisting. A second line allows the lid to be pulled off and out of the way (don't let anyone get hit by the falling lid!), allowing the diaspores in the bucket to simultaneously begin their descent. Trial drops of a few dispersal units will help establish the best release height for the actual test. Diaspores should be neither extremely aggregated nor diffused in distribution.

Mapping the exact coordinates of every dispersed diaspore in relation to the release point would provide the most accurate description of the results of the dispersal process. However, since there may be a large variance in the distance traveled by diaspores of a particular morphology and wing-loading, large numbers of each diaspore type may be needed. The mapping process would be extremely tedious, and data analysis would require a computer. A somewhat less demanding variant would be to measure only the radial distance traveled by each diaspore, swinging a measuring tape anchored at the release point.

A more practical method of characterizing dispersal distances is to divide the landing area into zones or quadrats and count the number of each type of diaspore. The sophistication of the students and the type of questions to be answered will influence the type of quadrat design used. For simply comparing dispersal distances of different diaspores, the landing area can be divided into consecutive circles using meter tapes. Boundaries can be marked with powdered chalk, or one can simply swing the tape to decide on borderline diaspores. By choosing the radii after the release, you can ensure that each zone contains a manageable number of diaspores. Four to six distance categories, chosen to contain roughly equal numbers, should allow good discrimination of different diaspore types. For more sophisticated analyses of the data, it is better to establish a grid system of smaller square quadrats of equal area. We strongly recommend collecting each diaspore type into separate bags labeled with the quadrat identification and diaspore type since having a lot of students carrying partial collections around invites confusion. Diaspores can then be counted immediately, or later in the lab.

This exercise can be completed in one long laboratory period or broken into shorter periods. Preparation and manipulation of four treatments of 700 to 1000 *Ailanthus* diaspores required about a half hour for a class of 25. We recovered 70 to 80 percent of the diaspores from mowed grass. This yielded more than adequate sample sizes. A trial drop, grid construction and collection of diaspores from two release exercises required less than two hours.

Analysis & discussion

The type of statistical analysis depends on sophistication of the students, the information desired and the type of quadrat design used. A comparison of the relative dispersal distances for various types or treatments of dispersal units can be analyzed using a chi-square test of independence for data organized into a contingency table. The chi-square test of independence is explained in most elementary statistics texts, such as Walpole (1983), and can be taught in conjunction with the exercise. The null hypothesis is that there will be no difference between the different types of dispersal units in their frequency of distribution in each quadrat. Significant deviation from this expectation will yield a chi-square value greater than the critical value and will indicate that the diaspores do not have similar dispersal patterns. Inspection of quadrat tallies for paired comparisons should indicate which unit has the greater dispersal potential. One advantage of this method of analysis is that it allows the use of the sector quadrat sampling technique which requires much less effort to set up and fewer quadrats.

Though more time-consuming, a grid of equal-area quadrats will allow a better characterization of some additional biologically important parameters. Once diaspores of each type or treatment have been counted for each quadrat you can calculate means and standard errors for three biologically important measures of dispersal: the distance from the drop point, the distance from the centroid of the distribution and the crowding (a measure of dispersion). These analyses require knowledge of more advanced statistical procedures not explained here (see Augspurger & Franson 1987).

Organizing a Competition: Selection Under Constraints

Students can compete to design the optimal diaspore, given some biologically realistic constraints, especially if more than one week can be spared for the exercise. For example, each student could be allowed say 50 g (total) of Parafilm (for seeds) and thin paper (for wings). Within that constraint of "reproductive effort," any morphology that could be assembled with glue would be accepted, as long as the Parafilm was compressed into a discrete seed-like mass. All the seed lots from the class would then be pooled and dropped simultaneously. The winner would be the morphology that produces the largest number of "successful" colonists from the fixed investment in materials, with "success" ideally including both seed weight and dispersal distance. The most elegant way of including these aspects would be to measure the radial distance of each diaspore, then calculate:

$$\text{probability of success} = f\,(\text{seed weight}) * g\,(\text{distance})$$

where f and g are simple functions announced to the students in advance. The overall success or fitness of a morphology would simply be the sum, over all the seeds of that type, of the probabilities of success. Rather than measuring all dispersal distance, you could simply select some distance as the success/failure cutoff. The only difficulty here is that it would be hard to specify this distance as part of the contest rules, because it is best chosen after the drop for the reasons explained above.

The competitive nature of such an exercise should help spice up students' participation (especially if their grades reflect the success of their dia-

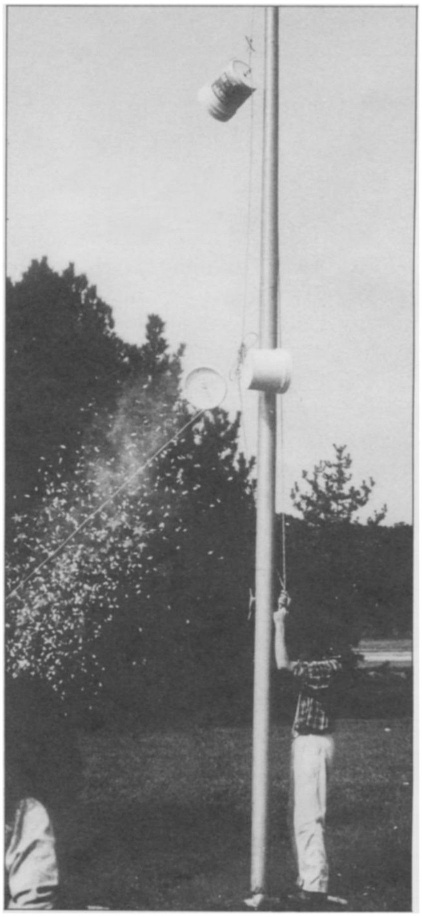

Figure 3. Plume of *Ailanthus altissima* diaspores being carried by the wind.

spores!); it should also form an ideal basis for a discussion of the evolution of optimal structures under conflicting constraints. A critical point to develop in discussion is that improvements in the design of real organisms depend on what morphology is already present; organisms can become stuck on local adaptive peaks. For example, one can imagine that the best possible winged morphology is still not as effective as any number of plumed morphologies, but a tree with winged diaspores will not be capable of evolutionarily trading wings for plumes because the gradual intermediate conditions would be worst of all. Thus, students should not be surprised if they can design novel structures that are "better" than natural ones.

Additional Questions for Discussion

1. Many plant species have seeds that germinate best in certain microhabitats. Can you imagine any ways in which the morphology of wind-dispersed diaspores might promote selective dispersal to particular microhabitats?
2. Contrast wind dispersal with dispersal by birds or bats. Fleshy fruits that attract vertebrates would seem to be more expensive to make than winged seeds —are there compensating advantages?
3. We have discussed only primary dispersal, or dispersal from the parent to the landing point. Consider situations in which secondary dispersal may be important as well: think of the city tree *Ailanthus,* for example, which often germinates in pavement cracks or storm sewers.
4. Consider seasonal timing of dispersal. Are some seasons more favorable than others? Consider winter release in terms of question 3. At what seasons do wind-dispersed species in your area release their seeds?
5. How much force is required to separate a diaspore from its point of attachment? What are the consequences for dispersal?

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