Wind dispersal capacity of pine seeds and the evolution of different seed dispersal modes in pines

Craig W. Benkman

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Pine seed mass is isometrically related to samara shape among smaller seeded pines (< 165 mg), but not when larger seeds are included (putative bird-dispersed pines excluded). Among the largest pine seeds samara length declines with increases in seed mass. Consequently, disc-loading increases and dispersal capacity declines at an accelerating rate with increases in seed mass. The acceleration in disc-loading may arise in part from the energetic costs of constructing long-scaled cones to house the seeds and their wings. Regardless of the mechanism, the consequences for seed dispersal mode are great. For example, pine seeds weighing less than about 100 mg should be dispersed well by wind; all 38 species with seed masses less than 90 mg have adaptations for wind dispersal. Pines whose seeds weigh more than 90 mg are dispersed poorly by wind and usually have adaptations for bird dispersal (15 of 22 species).

C. W. Benkman, Dept of Biology, New Mexico State Univ., Las Cruces, NM 8803 USA.

Seed dispersal distances are a fundamental aspect of plant life histories, and have profound consequences to many aspects of plant ecology, evolution (Howe and Smallwood 1982, Willson 1992) and conservation (Tilman 1994). Thus, determining the factors influencing seed dispersal distance, and the trade-offs between them are central questions of plant biology. In a recent paper, Greene and Johnson (1993) demonstrate a trade-off between seed mass of samaras and their equilibrium descent velocities. They document that samara mass and shape are isometrically related and that equilibrium descent velocities are proportional to samara seed mass raised to the 1/6 power. Because the distance seeds disperse by wind is inversely proportional to equilibrium descent velocity (Augspurger and Franson 1987, Greene and Johnson 1990), large seeds disperse less well than small seeds (Greene and Johnson 1993). These relationships were very similar among the three plant families (Pinaceae, Aceraceae, Leguminosae) analyzed (Greene and Johnson 1993). This suggests that seed mass alone has been the main determinant of samara seed dispersal ca-

pacity and that, for example, the large cones housing Pinaceae seeds have not affected seed dispersal capacity.

Here, I present analyses of 27 species of North American *Pinus* that span a wider range of seed masses (3.5–909.0 mg; a factor of 260) than the Pinaceae studied by Greene and Johnson (1993) (2.0–255.0 mg; a factor of 128). These analyses are consistent with Greene and Johnson's (1993) finding that seed dispersal capacity declines as seed mass increases. However, seed mass is not isometrically related to samara linear dimensions, as measured by samara length; samara length decreases among the largest seeded pines. Consequently, disc-loading accelerates at larger seed masses. This acceleration in disc-loading may be due in part to the physical and energetic constraints imposed on pines for constructing a cone to house the seeds. The rapid decrease in samara seed dispersal capacity for pine seeds weighing more than about 100 mg may explain why these pines usually rely on birds to disperse their seeds.

Greene and Johnson (1993) found that descent velocity (V_f) was proportional to seed mass (m) to the 1/6th power
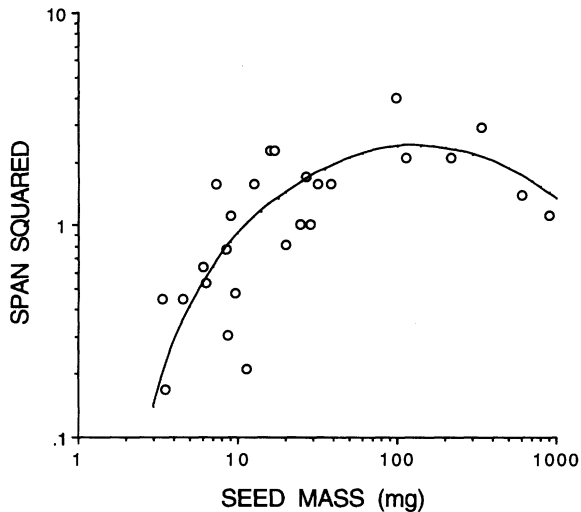
Fig. 1. The relationship between samara span squared and seed mass for 27 species of pines from North America. The curve approximates the second order polynomial equation which fits the log-transformed data well ($Y = -0.211 + 0.647X - 0.146X^2$; $R^2 = 0.55$, $df = 24$, $F = 14.7$, $P < 0.0001$).

($V_f \propto m^{1/6}$) (Greene and Johnson 1993). This, they argued, was a result of an isometric relationship between seed mass and shape, where planform area of the entire samara (A_w) is proportional to samara mass to the 2/3rd power ($A_w \propto m^{2/3}$). Since $A_w^{0.5}$ is strongly correlated with samara length (Greene and Johnson 1993), the relationship between samara length (total length of seed and seed wing) squared and samara mass should be allometric. However, a plot of seed mass and samara length measurements compiled by McCune (1988; I exclude putative bird-dispersed pines) for 27 species of *Pinus* (Fig. 1) shows that the relationship is not allometric (seed wing masses are not available, so I use seed mass rather than samara mass; this should not alter the relationships qualitatively) because the quadratic term of a quadratic equation fit to log-transformed data (Fig. 1) is significant ($P < 0.007$). Samara length initially increases with increases in seed mass, reaches an asymptote at a seed mass of about 165 mg (Fig. 1), and then declines. Only one of the 12 species of Pinaceae studied by Greene and Johnson (1993) had a seed mass ≥ 165 mg, which could explain why they found an isometric relationship. Indeed, if the analyses are limited to pine seeds weighing less than 165 mg, then the exponent (*b*) to the relationship samara length squared = *a*(seed mass)^b is 0.613 (SE = 0.14; $P < 0.0005$), which is similar to 0.667 as predicted by Greene and Johnson (1993).

Given the above relationship (Fig. 1), descent velocity should not be allometrically related to pine seed mass. Since disc-loading, which is samara mass (I use seed mass) divided by length of the samara squared, is highly correlated with descent velocity (Norberg 1973, Guries and Nordheim 1984, Augspurger and Franson 1987),

disc-loading (*Y*) should not be allometrically related to pine seed mass (*X*). The relationship is not allometric since the quadratic term of a quadratic regression fit to log-transformed data ($Y = 1.26 - 0.54X + 0.37X^2$, $r^2 = 0.82$, $df = 24$, $F = 54.15$, $P < 0.0001$; *Y* has *X* as its numerator, so they are not strictly independent) is significant ($P < 0.002$). Again, the differences between these results and those of Greene and Johnson (1993) are related to the inclusion of larger seeded pines. For example, if the analyses are restricted to pine seeds weighing less than 220 mg, as in Greene and Johnson (1993), then the quadratic term is insignificant ($P > 0.1$).

The acceleration in disc-loading may be related to the energetic costs of constructing long-scaled cones to house the seeds and their wings, resources that otherwise might be used to produce more seeds (e.g., Cohen and Motro 1989). For example, *P. sabiniana* Dougl. (606 mg seeds) and *P. torreyana* Parry (909 mg seeds) would require cone scales over 22.8 cm and 27.9 cm long, respectively, to maintain a disc-loading of the largest pine seeds (324 mg) dispersed presumably well by wind (*P. coulteri* D. Don); these lengths are nearly as long as some *P. lambertiana* Dougl. cones (Munz and Keck 1959), which are the longest pine cones in the world. Such a constraint might explain the strong relationship between disc-loading and seed mass for the largest pine seeds (Fig. 2). Second, physical constraints may limit the size of cone that can be held near a branch tip. For instance, *P. coulteri* cones (the heaviest of all pine cones) are produced only along the trunk and main branches (Borchert 1985), whereas most other pines produce cones on branch tips throughout the canopy (Benkman, pers. obs.). These costs are not incurred by the cone-less plants in the other two families (Aceraceae and Leguminosae) analyzed by
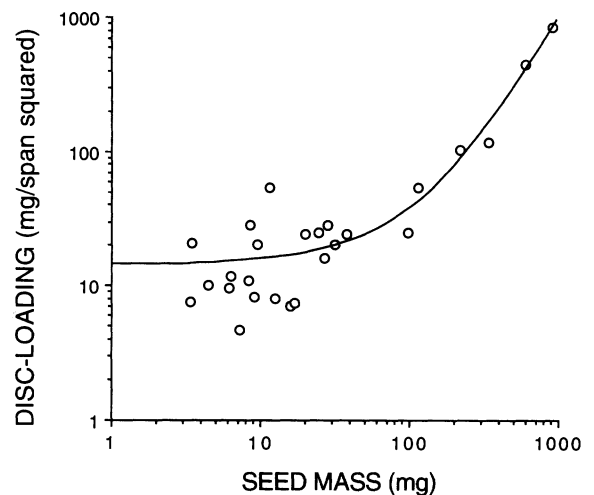

Fig. 2. The relationship between disc-loading and seed mass for 27 species of pines from North America. The curve represents a best fit second order polynomial equation fit to untransformed data ($Y = 14.137 + 0.151X + 0.001X^2$; $R^2 = 0.99$, $df = 24$, $F = 1625$, $P < 0.0001$).

Greene and Johnson (1993). The absence of such costs could explain why samara size and shape vary isometrically and dispersal capacity does not decline as rapidly with increases in seed mass in these two families.

An implication of the relationship between disc-loading and seed mass in pines (Fig. 2) is that wind dispersal should be a highly effective mode of dispersal for pine seeds weighing less than about 100 mg. However, the effectiveness of wind dispersal should decline with further increases in seed mass. All pines with seeds weighing less than 90 mg ($n = 38$ species) are apparently adapted for wind dispersal (Lanner 1980, Tomback and Linhart 1990, Vander Wall 1990), whereas only seven of 22 species with larger seeds rely on wind dispersal (based on Table 3 in Tomback and Linhart 1990). The bird-dispersed pines with the smallest seeds, *P. pumila* Regal and *P. flexilis* James, have seed masses averaging 92 (Tomback and Linhart 1990) and 92.6 mg, respectively. Because bird-dispersed pines have proportionately thinner seed coats than wind-dispersed pines (Vander Wall and Balda 1977, Balda 1980), *P. pumila* and *P. flexilis* would probably weigh over 100 mg, if they had seed coats of comparable thickness as wind-dispersed seeds.

Alternatively, the lower size threshold for pines to evolve adaptations for bird dispersal could arise because potential seed dispersers, such as nutcrackers (*Nucifraga* spp.), do not harvest and cache sufficient numbers of smaller less profitable seeds. This is unlikely. Clark's nutcrackers (*N. columbiana* Wilson) cache sufficient quantities of 60 mg *P. ponderosa* var. *ponderosa* Laws. seeds (seed mass data from Benkman, unpubl.) in autumn to survive on them for most of the year (Giuntoli and Mewaldt 1978). Clark's nutcrackers even harvest and cache the 11.6 mg seeds of *Pseudotsuga menziesii* (Mirb.) Franco (Giuntoli and Mewaldt 1978, Lanner 1980, Vander Wall and Balda 1981, Vander Wall et al. 1981), and nutcrackers may even be important dispersers of 25 mg seeds of *P. longaeva* D. K. Bailey (Lanner et al. 1984, Lanner 1988; seed mass based on the closely related *P. aristata* Engelm). Presumably these pines have not evolved adaptations to facilitate bird dispersal because wind dispersal is so effective.

In contrast, pines having seeds larger than 100 mg are more likely to benefit from evolving adaptations to promote animal dispersal because they are poorly dispersed by wind. Indeed, the four largest pine seeds (disc-loading > 90 mg/cm²; see Fig. 2) are unlikely to even autorotate, so that the small wings will not act to increase dispersal distance by wind (D. F. Greene, pers. comm.). Elsewhere, I have argued (Benkman et al. 1984, Benkman 1995) that adaptations facilitating seed dispersal by nutcrackers also facilitate seed predation by tree squirrels (*Sciurus* and *Tamiasciurus*), which rapidly harvest whole cones. Consequently, pines do not evolve adaptations for bird dispersal in regions where tree squirrels are abundant. Six of the seven species with seeds larger than 100 mg that have not developed adaptations facilitating seed dispersal by birds occur in forests where tree squirrels are common

(see Benkman et al. 1984). The seventh species, *P. canariensis* C. Smith, is restricted to the Canary Islands where suitable dispersers (i.e., jays and nutcrackers) are absent (Bannerman 1963).

Unable to effectively evolve means of wind dispersal or seed dispersal by birds, these large-seeded pines may be prime candidates to benefit from secondary dispersal. Although seeds of several different species of conifers are secondarily dispersed by rodents (West 1968, Abbott and Quink 1970), only one study provides compelling evidence of a net benefit from secondary seed dispersal by rodents (Vander Wall 1992a,b). It was done on the large-seeded *P. jeffreyi* Grev. & Balf. in A. Murr. (113.6 mg seeds). On the other hand, small-seeded conifers, whose seeds are dispersed well by wind, do not appear to benefit from ground-foraging rodents (e.g., 11.6 mg *Pseudotsuga menziesii* seeds; Sullivan 1978). Large-seeded pines are more likely to benefit from secondary seed dispersal because the larger the seed the more kernel mass that can be cached per unit time (see Vander Wall and Balda 1977, Lanner 1980, Vander Wall 1988) and, if equal amounts of kernel are later retrieved and eaten regardless of seed size, a higher proportion of large-kerneled seeds than small-kerneled seeds will be left uneaten potentially to germinate. Other pines with large-sized seeds (e.g., *P. lambertiana, P. coulteri, P. sabiniana*) may accrue a net benefit from mammals that harvest and cache seeds. In addition, the high disc-loading of large seeds may promote secondary seed dispersal by concentrating the seed shadow so that individual ground-foraging rodents encounter and cache more seeds. This might also account for the decline in samara span length for the largest seeded pines (Fig. 1).

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