SAMARA'S AERODYNAMIC PROPERTIES IN *PINUS HALEPENSIS* MILL., A COLONIZING TREE SPECIES, REMAIN CONSTANT DESPITE CONSIDERABLE VARIATION IN MORPHOLOGY

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INTRODUCTION

Seed dispersal is an important process in plant population dynamics. Typically, high concentrations of dispersed seeds are found close to the parent plant, and seed density rapidly declines with distance from the source (Willson, 1993). Increasing the variance of seed dispersal distances, regardless whether the mean is maintained or increased, leads to an increase in the area and uniformity of seed distribution (Augspurger and Franson, 1993). This is expected to be selectively advantageous due to a more efficient sampling of the environment for new favorable microhabitats, spreading of risk, and escaping the high juvenile mortality near the parent plant (Augspurger and Franson, 1993). Somatic polymorphism is one way to achieve dispersal variability, but also in monomorphic species, substantial variation might exist even within an individual plant (e.g., Sacchi, 1987). However, adaptations for dispersal may require trade-off with other fitness components. In wind-dispersed species, for example, selection for dispersal capacity may often favor small seeds, while larger seeds are frequently superior in seedling success (e.g., Rees, 1995). In addition, dispersal devices which are useful in prolonging the flight time, hence, dispersal distance, might be harmful due to increasing seed detectability to visual predators on the ground. The action of these opposing forces can lead to a wide intraspecific variation in these traits, while dispersal variability might be reduced.

Selection for a greater dispersal variability in wind-dispersed plants may act on traits that affect the height of seed release, seed abscission probability and aerodynamic properties (Burrows, 1986). Wind has a considerable contribution to dispersal variability (Greene and Johnson, 1992), but its effects, as well these of the surrounding vegetation and local topography are external to the plant control. Aerodynamic properties rely on diaspore mor-phology, and a wide variety of dispersal devices that enhance dispersal have evolved. Among these, the aerodynamics of asymmetric samaras (winged-seeds) are perhaps the best-known (Norberg, 1973; Green, 1980), as they have aerodynamic properties that can be accurately measured. Some studies have demonstrated a considerable intraspecific variation both in samara morphology and aerodynamic predictors of dispersal capacity (Guries and Nordheim, 1984; Sipe and Linnerooth, 1995).

The terminal descent velocity of wind-dispersed seeds is frequently used as an index for dispersal capacity (e.g., Green, 1980), since it reflects the time a seed can be carried away by the wind. An additional aerodynamic factor, frequently ignored, is the relaxation distance which is defined as the vertical distance traveled by a seed before it enters autorotation and reaches the terminal velocity. The relaxation distance can affect the actual dispersal distance and may be affected by other morphological factors than the terminal velocity (Guries and Nordheim, 1984). Thus, both terminal velocity and relaxation distance should be used as indices of dispersal capacity. We report here on intraspecific variation in some morphological properties and the aerodynamic predictors of dispersal capacity of the Aleppo pine (*Pinus halepensis* Mill.), the most widely distributed pine in the Mediterranean region. Since *P. halepensis* is considered a colonizing species (Acherar et al., 1984), a considerable intraspecific variation in morphological properties is expected to be found, and it should lead to a marked intraspecific

variation in dispersal capacity. However, while a considerable morphological variation does indeed exist, we found no significant variation in the aerodynamic predictors of dispersal capacity.

MATERIALS AND METHODS

A random selection of five trees, five cones from each tree and five intact samaras from each cone, totaling 125 samaras, were used in this analysis. Trees were from a natural pine stand on the western slopes of Mt. Carmel, northern Israel (32°41'N; 34°58'E). The cones were all from the same crop (third year) and all the seeds were filled. The following morpho-logical properties were measured: the samara's (seed and wing together) dimensions (maximal length, maximal width [± 1 mm] and total surface area [± 1 mm²]), and total fresh mass (± 0.1 mg). The square root of wing-loading   (= weight / area), shown in previous studies to be highly correlated with terminal velocity (e.g., Green, 1980), was calculated as (mass · gravity acceleration / area)$^{1/2}$.

Aerodynamic properties were measured in a closed-room experiment, in order to avoid any gusts. Samaras were released at a height of 2.35 m above the ground, and their descent was photographed by a 8 mm video camera with a digital time control (± 0.02 sec). The video tape was analyzed to estimate the aerodynamic properties; terminal velocity was defined as the constant descent rate in autorotation and relaxation distance as the vertical distance a samara fell until its terminal velocity was reached. Using a metric scale (± 1 cm) placed at the background, the samara's height was recorded in 0.1 seconds intervals by freezing the video picture, starting from the moment of release. The vertical distances traveled at each interval were calculated. The moment of entering terminal velocity was defined as the first time a <1 cm difference between successive intervals occurred. The descent velocity following that moment remains constant (under the above criterion) in all cases. Thus, the estimated relaxation distance is calculated as the vertical distance between the height of release and the height of entering terminal velocity, and the terminal velocity as the average rate of fall from that moment until the last record above the floor.

Nested analysis of variance was used to analyze the data. The Wilk-Shapiro test (Weisberg, 1985) was used to examine whether a variable (width, length, area, mass, wing-loading, relaxation distance and terminal velocity) conforms to a normal distribution; the last two variables match it only when log-transformed. All ANOVAs are with three levels of variation: trees, cones within trees and error.

RESULTS

Means, 95% confidence intervals and coefficients of variation of the five morphological and the two aerodynamic properties of *P. halepensis* samaras are shown in Table 1. Nested ANOVA's estimated variance components with percentages from total and significance of variation in three levels are shown in Table 2. A considerable amount of variation was found both between and within trees in all morphological properties; for mass, area and length these two sources of variation contribute together more than 70% of the total variance, with major contribution always due to differences between trees. Among morpho-logical properties, wing-loading has the lower variation both between and within trees, with the latter insignificant. The variation in the two aerodynamic properties, both between and within trees, is insignificant.

Table 1. Mean, 95% confidence intervals (CI) and coefficients of variation (CV) of five morphological properties and two aerodynamic properties of *Pinus halepensis* samaras.

Property*	Lower 95% CI	Mean	Upper 95% CI	CV
morphological:				
width	6.50	6.71	6.92	17.43
length	21.03	21.68	22.33	16.86
area	113.44	121.07	128.70	35.60
mass	21.00	22.17	23.35	29.90
(wing-loading)$^{1/2}$	41.98	42.99	44.00	13.24
aerodynamic:				
relaxation distance	0.46	0.50	0.54	44.39
terminal velocity	0.79	0.81	0.84	17.57

*Units: width and length - mm, area - mm², mass - mg, wing-loading - mg·mm·sec^{-2}, relaxation distance - m, terminal velocity - m·sec^{-1}.

The correlation between mass and area and between terminal velocity and the square root of wing-loading are of special interest in this study. However, due to the hierarchical design of our data, observations are not independent and simple correlation is inappropriate. Therefore, we calculate Pearson correlation in three levels: between seeds (n = 125), cones (n = 25) and trees (n = 5). Samara mass and surface area are significantly positively correlated in all levels (r = 0.764, df = 123, P < 0.0001; r = 0.873, df = 23, P < 0.0001 and r = 0.897, df = 3, P = 0.0389,

respectively). Terminal velocity (log-transformed) and square root of wing-loading are significantly positively correlated in the seeds and cones levels, but insignificant in the trees level ($r = 0.619$, $df = 123$, $P < 0.0001$; $r = 0.491$, $df = 23$, $P = 0.0126$ and $r = 0.387$, $df = 3$, $P = 0.5202$, respectively).

Table 2. Estimated components of variance and significance of variation of three variance sources, of five morphological and two aerodynamic properties of *Pinus halepensis* samaras.

Property	Variance components (percent of total)[a]		
	Trees	Cones within trees	Error
morphological:			
width	0.277 (19.32)*	0.406 (28.27)***	0.752 (52.41)
length	9.351 (61.28)***	2.628 (17.22)***	3.280 (21.50)
area	870.042 (42.56)***	578.879 (28.31)***	595.524 (29.13)
mass	33.481 (66.11)***	6.408 (12.65)***	10.758 (21.24)
(wing-loading)$^{1/2}$	5.007 (14.97)*	2.475 (7.40)^{NS}	25.963 (77.63)
aerodynamic:			
relaxation distance	2.424[b] (8.89)^{NS}	2.126[b] (7.80)^{NS}	22.706[b] (83.31)
terminal velocity	0.150[b] (3.41)^{NS}	0.005[b] (0.13)^{NS}	4.231[b] (96.46)

[a] Significance of variation: * - $P < 0.05$; *** - $P < 0.001$; NS - not significant. Degrees of freedom: 4 for trees, 20 for cones within trees.
[b] multiplied by 1000.

DISCUSSION

The main, apparently unexpected, result of this study is that *P. halepensis* samaras exhibit substantial intraspecific variations in morpho-logy and mass, but insignificant ones in aerodynamic predictors of dispersal capacity. Intraspecific variation in diaspore morphology can produce substantial variation in dispersal capacity (Morse and Schmitt, 1985). The considerable amount of variation due to differences between trees in mass, area and length may be an expression of a high genetic control over these traits. If these variations are at least partially genetically based, natural selection might favor certain genotypes. If *P. halepensis* is indeed a pioneering species, selection should have favored an increase in variance of dispersal capacity of its seeds. However, no variation in dispersal capacity was found.

One explanation for this is that variation in dispersal distances may still exist, but is controlled by factors other than aerodynamic ones (e.g., wind, height of release, etc.), as has been demonstrated in previous studies (Greene and Johnson, 1992; Augspurger and Franson, 1993). If this is correct, why invest resources in a special dispersal device? Furthermore, wings might be responsible for an increased cost in increasing the risk of predation, since the seed is more easily detectable to visual predators on the ground, as the wing protrudes above the surface like a flag. Observations on post-dispersal predation of *P. halepensis* seeds have shown that it is very intensive (Schiller, 1979). On Mt. Carmel, 100% seed losses within several days, mostly by ants but also by visual predators as rodents and birds, were frequently recorded (R. Nathan, unpublished data).

Another explanation is that trade-offs with other fitness components play a central role. This holds if traits which influence dispersal capacity are affected by other selection pressures, thus reducing variability in dispersal capacity while increasing the variation of these traits, as we found. Strong selection for competitive ability of the seedling may cause a shift toward larger seeds. Thus, the high intraspecific variation found in samara's mass can be attributed to the effect of dispersal-competition trade-off. Greene and Johnson (1993) raised the question whether this trade-off necessarily exists; why relatively heavy seeds may not have relatively large wings and thus, by maintaining wing-loading, suffer no reduction in dispersal capacity? They conclude that there is a biomechanical limitation on the effectiveness of the wing as a function of size, hence larger samaras are necessarily more poorly dispersed. Benkman (1995) proposed that wing length in *Pinus spp.* is limited by physical and energetic constraints imposed on constructing larger cones with scales long enough to house samaras with long wings. Once again, the large wing has an additional cost, as it might increase mortality inflicted by seed-predators. Thus, the high intraspecific variation found in samara's area and especially length, can be attributed to the effect of dispersal-predation avoidance trade-off. Predation may act also on seed mass variation, but here no single direction is expected; while ants might favor small seeds, rodents tend to select larger seeds. The expected overall outcome of the dispersal-competition and dispersal-predation avoidance trade-offs is a larger variability in samara's mass, area and length, but smaller variation in dispersal capacity. This implies that

even for a colonizing species dispersal capacity may not be the major fitness component. Rather, a compromise between dispersal capacity and other fitness components such as competitive ability of seedlings and predator avoidance of seeds, determine the morphological properties of this species.

Our finding that samaras of *P. halepensis* exhibit considerable variation in morphological properties but not in aerodynamic ones contradicts results of previous studies on wind-dispersed plants (e.g., Morse and Schmitt, 1985). Wing-loading, the ratio between weight and surface area, has proved to be a useful index of terminal velocity (e.g., Green, 1980). Similarly, terminal velocity and (square root of) wing-loading were found to be positively correlated in our sample (it is significant between seeds and cones; the insignificant correlation between trees is probably due to the small sample). It stands to reason that heavy seeds with small wings (high wing-loading) would fall faster than light seeds with large wings (low wing-loading). If the variations in mass and area are positively correlated, i.e., heavy seeds tend to have large wing and vice versa, wing-loading should remain unchanged. We found such a correlation in our sample in all levels, and, accordingly, wing-loading exhibited the lower variation among morphological properties. The same correlation was found in five other *Pinus spp.*, among other species with asymmetric samaras, and has been attributed to a flight stability constraint (Greene and Johnson, 1993). The question how *P. halepensis* is able to colonize successfully new, randomly located sites, despite low dispersal variability of its seeds resulting from trade-offs and physical constraints, remains unresolved. Perhaps rare events of long-distance dispersal are relatively more common in this species, due to other factors such as high abscission threshold and more sufficient turbulence effect.

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