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Author(s): Timothy W. Sipe and Amy R. Linnerooth

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# INTRASPECIFIC VARIATION IN SAMARA MORPHOLOGY AND FLIGHT BEHAVIOR IN ACER SACCHARINUM (ACERACEAE)<sup>1</sup>

## TIMOTHY W. $SIPE^2$ and Amy R. Linnerooth

#### Department of Biology, Gustavus Adolphus College, St. Peter, Minnesota 56082

We studied intraspecific variation in samara morphology and flight behavior within and among parent trees of *Acer* saccharinum (silver maple), with a particular focus on the effect of samara shape. Samara mass, area, wing loading, and descent rate from a 4.5-m indoor balcony were measured for 50 undamaged mature samaras from each of six parents. We found significant differences among parental types for all morphological variables and descent rate. These differences yielded a 50% range in mean dispersal potential among the six parents. There was a strong linear correlation between descent rate and square root of wing loading when mean values were plotted for each of the six parental types. But there was considerable within-parent variation for all measured variables, including substantial nonallometric variation in wing loading caused in part by poor correlations between wing area and fruit weight. Parents also differed widely in the relationship between square root of wing loading and descent rate (linear  $r^2 = 0.150-0.788$ ), with one parental type showing no significant relationship. Fruits from the same parent with similar values of the square root of wing loading showed as much as a 75–100% difference in descent rate. The usefulness of mass : area indices such as wing loading is limited by its exclusion of aerodynamically important factors such as mass distribution and wing shape, which in our case caused the six parents to behave aerodynamically almost as if they were six separate species.

Diaspore dispersal is a critical phase in the life histories of individual plants and for the persistence of populations. Many species rely on wind for dispersal, and a wide variety of diaspore morphologies have evolved to counteract the effects of gravity and prolong flight time in order to disperse more widely. Consequently, much effort has gone into categorizing morphologies and documenting their aerodynamic behaviors (Burrows, 1975; Augspurger, 1986; Matlack, 1987; Greene and Johnson, 1990; Andersen, 1993). These efforts have yielded several predictive relationships, such as the widely cited correlation between terminal descent velocity and wing loading (diaspore mass per unit area). Of the four wind-dispersed morphological categories discussed by Burrows (1975), the autorotating winged fruit (samara) is an intriguing design because it generates lift by spinning an airfoil around a central axis in a manner similar to a helicopter rotor.

The majority of published work on samaras has emphasized interspecific variation, using mean values of morphological and flight variables for each species. However, marked intraspecific variation can exist in samara morphology (Siggins, 1933; Guries and Nordheim, 1984; Matlack, 1987). Intraspecific scatterplots of descent rate vs. wing loading often show considerable variance, and wing loading (or its square root) may account for rather low fractions (40–80%) of total variation in descent rate (Green, 1980; Guries and Nordheim, 1984; Greene and Johnson, 1992; Matlack, 1992).

Such variation occurs because the aerodynamics of samara flight are complicated and depend on more than

<sup>2</sup> Author for correspondence.

just wing loading. The three-dimensional shape and mass distribution of the samara affect several components of flight behavior, including entry into autorotation, coning and pitch angles, spin rate, terminal velocity, and stability mechanisms (Norberg, 1973; Guries and Nordheim, 1984). It is not only possible but expected that samaras with the same wing area and total mass, and thus the same wing-loading values, should fly differently if shape and mass distributions differ (Augspurger and Franson, 1987). This is true even within a particular type of samara, such as the asymmetric, "nonrolling" fruits characteristic of the genus *Acer*.

There are at least two important evolutionary implications of intraspecific variation in samara morphology. First, it is conceivable that within-parent variation in dispersal potential could contribute to more uniform distributions of dispersed seed around parents, resulting in less crowding among siblings and more effective coverage of potentially suitable sites for establishment (Greene and Johnson, 1992; Augspurger and Franson, 1993). Second, selection for any particular aspect of seed dispersal within a species requires consistent differences in samara morphology among parental genotypes and selection differentials large enough to favor one parental type over another. But there are surprisingly few data on naturally occurring morphological variation within or among parents and its effects on flight behavior (Guries and Nordheim, 1984; Cwynar and MacDonald, 1987; Andersen, 1992; Augspurger and Franson, 1993).

We studied intraspecific variation in samara mass, area, mass: area relationships, and flight behavior within and between parent trees of *Acer saccharinum* (silver maple). We selected six parents of contrasting samara morphology, with a particular focus on variation in planform wing shape. We addressed the following questions: (1) How do the parent trees differ quantitatively in samara morphology (mass, area, and mass: area relationships)? (2) Do

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Fig. 1. Representative sizes and shapes (to scale) of the six parental types of *Acer saccharinum* used in this study, with their abbreviations.

the parents differ in potential fruit dispersal as measured by total flight time (or its inverse, descent rate) from a common release point? (3) Do the parents differ in the relationship between descent rate and fruit morphology? (4) What morphological characteristics contribute to the differences in flight behavior? (5) What are the implications of these patterns for natural selection on aerodynamic behavior?

### MATERIAL AND METHODS

Mature samaras were collected in spring 1992 from six parent trees in St. Peter, Minnesota. The six parents (hereafter "parental types") produced visually distinct samaras spanning a wide range of shape and size (Fig. 1). The fruits were collected when they had dried and were being dispersed naturally. They were air-dried indoors for 3 wk and then stored in plastic bags at room temperature until the experiment was done in fall 1993. Fifty undamaged, filled fruits were selected from each type for measurements of flight time and morphology.

Flight times were measured by releasing each fruit wing downward from the end of a meter stick positioned over the edge of a 4.5-m indoor balcony. One person released all fruits and two observers independently recorded flight duration from release point to the floor using stop watches. All fruits were flown twice and the four recorded times were averaged for each fruit. These times included initial free fall and subsequent autorotation. Freefall distances generally accounted for less than onequarter ( $\approx 1$  sec) of the total 4.5-m drop distance. Our measurements represent total flight behavior, and not terminal velocity as reported by other authors (Green, 1980; Guries and Nordheim, 1984; Matlack, 1987; Greene and Johnson, 1990). We use the term "descent rate" here to avoid confusion; it is calculated as total fall distance (4.5 m) divided by measured flight duration (sec).

Descent rates were used to estimate differences in potential dispersal range within and among parental types using the equation  $D = H(V_w/V_f)$ , where D is dispersal distance, H is the height of release,  $V_w =$  mean horizontal wind velocity from point of release to ground, and  $V_f =$ mean vertical velocity during fruit fall (Cremer, 1977). For this estimation, we assumed that there was no systematic intracrown variation in samara morphology and that parental types did not differ in average release height (Guries and Nordheim, 1984). Given these assumptions, maximum differences in potential dispersal distance within or among parental types are inversely proportional to ratios between descent rates for any value of  $V_w$ . We present the results as ratios in potential areas of samara distribution (i.e., squares of distance ratios).

After flight, total fruit weight was determined to the nearest 0.1 mg with an electronic balance. Total fruit area was measured twice to the nearest 1 mm<sup>2</sup> with a LI-COR 3000 leaf area meter (LI-COR, Lincoln, NE), and the two area measurements were averaged. Wing weight, head weight, and wing area were determined after severing the seed head from the wing just posterior to the seed and perpendicular to the wing's leading edge. Wing weight (fruit weight – head weight), wing loading (total weight/ wing area), and the square root of wing loading were calculated from these data.

Summary statistics were generated for all morphology and flight variables. Kruskal-Wallis ANOVA and Student-Newman-Keuls (SNK) tests were performed on all variables to determine the significance of differences among parental types and between all possible pairs of types, respectively. We explored differences within and among parental types in the relationship between descent rate and several morphological variables by fitting linear regressions. Throughout the rest of this paper, we refer to three different components of intraspecific variation: (1) variation of individual samaras *within* each parental type (N = 50 for each type); (2) variation of individual samaras *across* all parental types (N = 300); and (3) variation *among* parental types in their mean morphology and flight values (N = 6).

#### RESULTS

Differences among parental types in fruit traits and flight—There were significant differences among parental types for all morphological variables (Table 1). Mean fruit weight and head weight followed similar patterns since head weight accounted for the majority (85% on average) of total fruit weight. The largest type (angel wing, ANGL) was 1.6 times the mass of the smallest (dwarf, DWRF), and there were no differences between three of the intermediate types (quillpen, QLPN; longstraight, LSTR; S-curve, SCRV). All parental types differed significantly in mean wing weight, which showed a wider relative range among types than either mean fruit weight or head weight. Mean fruit area and wing area

TABLE 1. Summary of morphological and flight traits for individual parental types (N = 50) and for all six types combined (N = 300). Dispersal area ratio is an estimate of the range of potential fruit dispersal (circular area) for any constant horizontal wind velocity (see text for explanation). Parental types with the same lowercase letter are not significantly different from each other (P > 0.05) based on Student-Newman-Keuls pairwise comparisons. Parental types are ordered left to right by increasing wing loading. cv = coefficient of variation, sqrt = square root.

		Quill pen	Angel wing	Long straight	Dwarf	S-curve	Boomerang	All types
Fruit weight	mean	143.7	158.5	140.6	95.2	140.0	105.6	130.6
(mg)	max	207.0	213.4	191.9	176.5	218.9	137.7	218.9
	min	39.7	65.8	32.4	41.0	37.9	29.5	29.5
	cv	0.22	0.18	0.24	0.22	0.27	0.24	0.29
		с	d	с	а	с	b	
Head weight	mean	118.7	134.6	120.5	79.8	122.0	92.8	111.4
(mg)	max	179.2	185.4	165.4	152.6	200.4	122.7	200.4
	min	21.9	37.9	20.1	25.9	22.3	21.4	20.1
	cv	0.24	0.20	0.26	0.23	0.30	0.26	0.30
		с	d	с	а	с	b	
Wing weight	mean	25.0	23.9	20.1	15.4	18.0	12.7	19.2
(mg)	max	32.8	36.1	27.8	23.9	28.0	18.0	36.1
(6)	min	17.8	13.7	12.1	10.0	9.2	8.1	8.1
	cv	0.14	0.17	0.17	0.18	0.23	0.16	0.29
		f	e	d	b	с	а	
Fruit are a	mean	62	72	57	38	48	36	52
(mm²)	max	78	95	79	49	63	50	95
	min	45	44	38	30	29	28	28
	cv	0.12	0.13	0.15	0.12	0.19	0.14	0.29
		e	f	d	b	с	а	
Wing area	mean	52	56	44	30	37	27	41
$(mm^2)$	max	65	74	63	39	51	40	74
,	min	37	32	27	24	23	20	20
	cv	0.13	0.14	0.17	0.12	0.20	0.15	0.30
		e	f	d	b	с	а	
Wing loading	mean	2.77	2.84	3.19	3.23	3.79	3.91	3.29
$(mg/mm^2)$	max	4.13	4.01	4.67	4.52	5.60	5.46	5.60
(	min	0.89	1.13	1.02	1.17	1.13	1.38	0.89
	cv	0.20	0.18	0.23	0.17	0.22	0.23	0.25
		а	а	b	b	с	с	
Sort wing loading	mean	1.66	1.68	1.77	1.79	1.93	1.96	1.80
$(mg/mm^2)$	max	2.03	2.00	2.16	2.12	2.37	2.34	2.37
(8)	min	0.94	1.06	1.01	1.08	1.06	1.17	0.94
	cv	0.11	0.09	0.13	0.09	0.12	0.13	0.13
		а	a	b	b	с	с	
Descent rate	mean	0.89	1.00	0.93	0.97	1.06	1 09	0.99
(m/sec)	max	1 34	1.00	1 20	1 35	1.00	1.69	1 77
	min	0.63	0.77	0.55	0.66	0.75	0.60	0.55
	cv	0.17	0.19	0.15	0.15	0.18	0.20	0.19
		a	b	b	b	c	c	
Dispersal area ratio (max/min)		4.52	3.40	4.76	4.18	5.57	7.93	10.36

showed parallel patterns, spanned a twofold range from ANGL to BMRG, and also differed significantly among all parental types.

These variations in mass and area produced significant differences in mean wing loading (40% range) and mean square root of wing loading (16% range) among parents. Boomerang (BMRG) and SCRV had significantly greater square root of wing loading than dwarf (DWRF) and LSTR, which in turn were greater than ANGL and QLPN.

There were significant differences among parental types in mean descent rate, but the pattern of differences was not the same as for mean wing loading: ANGL, LSTR, and DWRF fell faster than QLPN but slower than SCRV and BMRG. The range among types in mean descent rate (0.89–1.09 m/sec, 22.5%) was comparable to the range in mean square root of wing loading (16%).

This difference in mean descent rates among parental types translates into a 50% difference in potential area of seed dispersal for any constant horizontal windspeed.

The ranges of individual samara descent rates within parental types (0.71-1.09 m/sec) yield dispersal area ratios of  $3.4 \times$  to  $7.9 \times$ . The range of descent rates across all types (0.55-1.22 m/sec) represents an order of magnitude difference  $(10.4 \times)$  in potential dispersal area among the 300 samaras.

Correlations among morphological variables differed widely for different variable pairs and parental types (Table 2). Head weight and fruit weight were highly correlated ( $r^2 = 0.984-0.955$ ), as were wing area and fruit area ( $r^2 = 0.742-0.958$ ), for all parental types. Wing weight generally tracked wing area ( $r^2 = 0.640-0.835$ ), but neither head weight ( $r^2 = 0.210-0.412$ ) nor fruit weight (0.289-0.495) was highly correlated with fruit area.

TABLE 2. Squared correlation coefficients and probabilities of significant slopes for linear regressions among several morphological and flight variables within (N = 50) and across (N = 300) the six parental types. \*\*\* P < 0.001, \*\* P < 0.01, \* P < 0.05, ns = not significant (P > 0.05). Sqrt = square root.

Dependent variable	Independent variable	Quill pen	Angel wing	Long straight	Dwarf	S-curve	Boomerang	All types
Head weight	Fruit weight	0.992 ***	0.984 ***	0.992 ***	0.988 ***	0.991 ***	0.995 ***	0.986 ***
Wing area	Fruit area	0.923 ***	0.933 ***	0.932 ***	0.742 ***	0.958 ***	0.923 ***	0.968 ***
Head weight	Fruit area	0.290 ***	0.209 ***	0.322 ***	0.230 ***	0.412 ***	0.227 ***	0.427 ***
Fruit weight	Fruit area	0.359 ***	0.303 ***	0.384 ***	0.289 ***	0.495 ***	0.330 ***	0.526 ***
Wing weight	Wing area	0.727 ***	0.770 ***	0.669 ***	0.640 ***	0.835 ***	0.719 ***	0.863 ***
Wing area	Fruit weight	0.217 ***	0.213 ***	0.262 ***	0.256 ***	0.396 ***	0.224 ***	0.458 ***
Sqrt wing loading	Fruit area	0.006 ns	0.037 ns	0.002 ns	0.001 ns	0.003 ns	0.001 ns	0.108 ***
Sqrt wing loading	Wing area	0.008 ns	0.098 ns	0.008 ns	0.013 ns	0.003 ns	0.010 ns	0.162 ***
Sqrt wing loading	Fruit weight	0.684 ***	0.472 ***	0.629 ***	0.624 ***	0.528 ***	0.670 ***	0.138 ***
Descent rate	Fruit weight	0.328 *	0.255 ns	0.585 ***	0.616 ***	0.414 **	0.641 ***	0.067 ***
Descent rate	Sqrt wing loading	0.473 ***	0.150 ns	0.725 ***	0.580 ***	0.568 ***	0.788 ***	0.380 ***



Fig. 2. Wing area vs. fruit weight for the six parental types (N = 50 for each plot). (a) QLPN, (b) ANGL, (c) LSTR, (d) DWRF, (e) SCRV, (f) BMRG (see Fig. 1 for abbreviations). Outer lines are 95% confidence intervals.

These poor area: weight correlations extended to the relationship between wing area and fruit weight  $(r^2 = 0.213-0.396, \text{ Figs. 2, 3})$ . The low correlations between wing area and fruit weight contributed to large variation in the square root of wing loading of individual samaras both within  $(1.88 \times -2.24 \times)$  and across  $(2.52 \times)$  parental types. Of the two variables that are used to calculate wing loading, fruit weight was fairly well correlated with square root of wing loading  $(r^2 = 0.472-0.684)$ , but wing area showed no significant relationship to square root of wing loading for any parental type  $(r^2 = 0.003-0.013)$ .

**Relationships between fruit traits and flight**—Descent rate was significantly related to both square root of wing loading and fruit weight for individual samaras (N = 300) across the six parental types (Table 2; Fig. 3b, c). However, the correlation was low ( $r^2 = 0.380$ ) for square root of wing loading, and very low ( $r^2 = 0.067$ ) for fruit weight.

Individual parent types diverged markedly in these relationships (Table 2; Figs. 4, 5). ANGL showed no significant relationship of descent rate to either fruit weight or square root of wing loading. Four of the remaining types showed a higher correlation of descent rate to square root of wing loading than to fruit weight, while DWRF showed the reverse. Parental types with significant slopes showed widely different correlations:  $r^2 =$ 0.328–0.641 for fruit weight,  $r^2 = 0.473$ –0.788 for square root of wing loading.

In contrast to relationships based on individual samaras (within or across types), there was a strong linear correlation between descent rate and square root of wing loading when mean values were plotted for the six parental types (Fig. 6). Five of the types fell on a line ( $r^2 = 0.965$ for these five), while ANGL deviated noticeably from this line.



Fig. 3. Wing area vs. fruit weight (a), descent rate vs. fruit weight (b), and descent rate vs. square root of wing loading (c) for individual samaras of all six parental types combined (N = 300 for all plots). Outer lines are 95% confidence intervals.

#### DISCUSSION

The existing literature on fruit weight vs. morphology has focused mostly on interspecific comparisons. The underlying assumptions for these studies are that dispersal behavior plays a significant role in population persistence, and that natural selection can work within a species to shape fruit morphologies that enhance dispersal potential. Four conditions must be met if natural selection is to operate on aerodynamically important morphological traits such as wing loading: (1) sufficient phenotypic variation for the trait, (2) sufficient selective differentials among parents, (3) sufficient heritability for the trait, and (4) sufficient correlation between the morphological trait (e.g., wing loading) and the function in question (e.g., descent rate).

Our data are relevant to the first and last of these four conditions. The significant differences in mass, area, and



Fig. 4. Descent rate vs. fruit weight for the six parental types (N = 50 for each plot). (a) QLPN, (b) ANGL, (c) LSTR, (d) DWRF, (e) SCRV, (f) BMRG (see Fig. 1 for abbreviations). Outer lines are 95% confidence intervals.

mass: area ratios we found in *Acer saccharinum* demonstrate that there is considerable phenotypic variation in samara morphology among and within parents. Furthermore, our narrowly selected samples suggest we have not included the full range of morphological variation for this species. In general, mass and area variables showed wider variation among the six parental types we studied (66– 106%) than wing loading (40%) and the square root of wing loading (16%), which is expected (Greene and Johnson, 1992). These morphological differences yielded a 50% range in mean dispersal potentials among the parent trees.

The fourth condition for effective selection is that variations in fruit morphology need to be highly correlated with variations in descent rate both among and within parents. If flight behavior does not vary predictably with morphological variation, there can be no effective selection among parents for this relationship, regardless of whether mean values for the morphological and flight variables differ among parents. We found a very high correlation between mean descent rate and mean square root of wing loading for the six parental types (Fig. 6). This result is in agreement with interspecific studies, where single data points represent entire species (e.g.,



Fig. 5. Descent rate vs. square root of wing loading for the six parental types (N = 50 for each plot). (a) QLPN, (b) ANGL, (c) LSTR, (d) DWRF, (e) SCRV, (f) BMRG (see Fig. 1 for abbreviations). Outer lines are 95% confidence intervals.

Guries and Nordheim, 1984; Augspurger, 1986; Greene and Johnson, 1993; but see Matlack, 1987 for nonrolling samaras). However, even though we found highly significant *slopes* between flight time and the square root of wing loading within five of the six parental types (Fig. 5), the *correlations* were surprisingly low and differed considerably among the types ( $r^2 = 0.150-0.788$ ). Within a single parent, fruits with similar values of the square root of wing loading could show a 75–100% difference in descent rate (Fig. 5). Remarkably, one type (ANGL) showed no significant relationship at all between wing loading and descent rate.

This unexpected result raises two questions about wing loading and its relationship to flight behavior. First, is the source of variation in wing loading within a parent predictable—in particular, does it represent ontogenetic allometry? Second, why are the correlations between wing loading and descent rate so low? These questions are important because variation in wing loading within a parent has significant implications for seed dispersal shadows, including the hypothesis that controlled variation in samara wing loading (Augspurger and Franson, 1993) or terminal velocity (Greene and Johnson, 1992) may produce a more uniform seed distribution. Selection would



Fig. 6. Mean descent rate vs. mean square root of wing loading for the six parental types. The linear regression is fitted through all types except ANGL, since ANGL showed no significant relationship between descent rate and wing loading. Outer lines are 95% confidence intervals. A = ANGL, B = BMRG, D = DWRF, L = LSTR, Q = QLPN, S =SCRV (see Fig. 1 for abbreviations).

be most effective in favoring within-parent wing loading variation if it was under some form of parental regulation, such as developmental allometry, and if there was a high correlation between wing loading and descent rate.

Greene and Johnson (1993) documented an interspecific allometric relationship between samara mass and planform area in which area increased as only the onesixth power of mass as overall samara size increased. Thus larger fruits necessarily have higher wing loadings. If this principle were to operate ontogenetically within a parent, we would expect within-parent variation in wing loading. However, the correlation between wing area and fruit weight should be fairly tight, regulated by a predictable sequence of mass: area ratios during development. For Acer saccharinum, planform areas (entire fruit or just the wing) were not highly correlated with samara mass (entire fruit or just the head) (Table 2). In particular, wing area was not correlated with wing loading for any parental type. The problem is not the use of linear regressions on arithmetic axes, since the scatterplots (e.g., Fig. 2) show no consistent nonlinear relationships between these variables that would be captured by fitting allometric (exponential) curves. We conclude that wing loading variation within our parent trees does not exhibit strong allometric linkage between samara area and mass.

With respect to the second question, the surprising aspect of our data is not variation in wing loading per se, but the poor correlation between wing loading and descent rate. Regardless of whether the variation arises allometrically or through environmental factors beyond parental control, previous research would suggest that wing loading should be able to explain more of the variation in descent rates.

This assumes, however, that samara shape remains constant as wing loading varies within or across parents. Our results clearly demonstrate that samara shape differs substantially among parents and may be as important as wing loading in controlling flight behavior. Shape is not conserved among parental types of different size in *Acer saccharinum*. Our two largest types (QLPN and ANGL) are very different in shape from the two smallest types (BMRG and DWRF). Shape is not conserved within types of similar size, either: QLPN is clearly different from ANGL, while BMRG does not resemble DWRF at all (Fig. 1). The result is that wing loading does not decline with overall samara size among parents, and mean descent rates can differ even when mean wing loading values are similar (e.g., QLPN vs. ANGL, or BMRG vs. DWRF).

A careful consideration of the aerodynamic impacts of wing shape helps to explain these results. ANGL was different from all other parental types in this study. It showed no predictive relationship between descent rate and either fruit weight or square root of wing loading (Figs. 4, 5), and it fell out of line with the other five types in the otherwise tight linear relationship between mean descent rate and mean square root of wing loading (Fig. 6). ANGL had the largest head and total fruit weight, but also the largest wing area, which produced a very low wing loading. We would have predicted a slow descent rate for ANGL relative to the other types, and ANGL was indeed significantly slower than SCRV, DWRF, and BMRG. But it was also faster than LSTR, which had a higher wing loading than ANGL. The ANGL wing is strongly curved in planform (Fig. 1). This reduces the effectiveness of the wing in generating lift per unit area, since the amount of lift produced by an airfoil with constant cross-sectional shape is a function not only of total wing area, but also of planform shape and spin rate. Angular velocity increases distally, and a chord section of constant area generates more lift the farther it is from the seed. Since this relationship is nonlinear (i.e., lift increases with the square of air velocity over the airfoil section), wings with the same total area but different planform shape (e.g., short, wide vs. long, narrow) will not generate equal amounts of lift (Norberg, 1973). This is the reason helicopter rotors are long, narrow, and not curved in planform. ANGL's large wing area produces a lower wing loading, but this masks a loss of lift efficiency due to its nonideal bent wing shape. QLPN, which like ANGL also has a heavy fruit and a large wing area, has a straighter wing than ANGL, generates more lift per unit wing loading, and descends slower than ANĜL.

Shape considerations may also explain the contrast between LSTR and DWRF in descent rate. These two types had statistically indistinguishable wing loadings. LSTR (140 mg on average) was substantially heavier than DWRF (95 mg) and yet LSTR flew over 0.5 sec (17%) longer than DWRF (P < 0.001). Like ANGL, although without an obvious bend in planform, DWRF has a more compact wing (large width : length ratio), which reduces lift per unit total wing area as compared to LSTR.

Finally, BMRG seems to be the least well adapted for long flight. It has a fairly low fruit weight, the lowest wing area, the highest wing loading, and fastest descent rate. It is also possible that the terminal hook on the BMRG wing (Fig. 1) is contributing to lower lift efficiency. The negative impact of wing-tip vortices becomes more serious as tip breadth increases. The ideal wing tapers near the tip to minimize these vortices, which means that the maximum chord distance should be located somewhat back of the wing tip (Norberg, 1973). The terminal hook on BMRG is thus a less ideal shape as compared to a shape like LSTR.

This discussion assumes that spin rates and three-dimensional samara orientation during autorotation are the same among parental types, since actual lift is determined not only by the potential lift per unit wing area but also by the rate of air flow over the airfoil. For autorotative samaras, this depends on the total planar area (disk area) swept by the spinning wing per unit time, which is proportional to spin rate. Although we were not equipped to measure spin rate or three-dimensional orientation, it is likely that they are affected by samara mass distribution and wing shape in ways that do not necessarily parallel wing loading. Our observations during experimental flights suggest a qualitative ranking of spin rates of  $DWRF \ge ANGL \ge QLPN > SCRV \ge LSTR \ge BMRG.$ This pattern is consistent with the results we have discussed. For example, (1) the faster spin rates of DWRF and ANGL did not overcome their nonideal wing shapes. and (2) the slower spin rate of BMRG compounds the effect of high wing loading and hooked wing shape to produce the fastest descent rate.

We measured flight in still air and did not separate initial freefall from autorotative terminal velocity. In general, it is more difficult to predict precise samara behavior during freefall and entry into autorotation than during stable autorotation. Wing loading is thought to be more influential during stable autorotation than during freefall (Guries and Nordheim, 1984), and it is likely that wing loading would have been more highly correlated with terminal velocity than with total descent rate in still air. Wing shape is particularly important for entry into autorotation (Norberg, 1973; Guries and Nordheim, 1984), and Greene (1990) has demonstrated that modest turbulence can hasten entry into autorotation. But the effects of wing shape differences on the time required to reach stable autorotation in still vs. turbulent air have not been studied (Greene, personal communication, University of Calgary). Thus it is difficult to judge whether our still air measurements exaggerated or diminished shape-related contrasts in total descent rates among parental types as compared to what would happen under modest turbulence. At the very least we can say that natural selection will see total flight behavior, not just autorotation, and that selection for any one component of aerodynamic behavior (such as terminal velocity) may be modified by other effects of samara morphology (such as freefall and entry into autorotation). This is why we measured total flight time and not just terminal velocity.

We conclude that wing loading is a useful index of potential aerodynamic behavior, but it does not capture all the effects that morphological traits may have on flight since it does not explicitly take into account samara mass distribution or shape. Comparable problems may result from the use of indices such as aspect ratios, which measure departure of a given shape from a circle of the same area, to quantify wing shape (Greene and Johnson, 1993). Wings of different planform shape could generate similar aspect ratios but quite different aerodynamics. Samara shape clearly interacts in important ways with total mass, area, and mass: area traits in affecting flight behavior. Furthermore, this occurs intraspecifically with strong contrasts in samara morphology among parents. Our six parental types behaved almost as if they were six separate species, and this suggests caution in interpreting the aerodynamic or ecological comprehensiveness of empirical relationships based on single data points for entire species, especially when species means are based on small sample sizes (frequently <30 and as low as 1–5 in the published literature). The significance of this point can be appreciated by pondering which of the six parental types studied here should be used to represent the entire species *Acer saccharinum*.

Finally, we conclude that there is a large amount of within-parent variation in wing loading and descent rates caused at least in part by poor correlations between wing area and fruit weight. The origin of this within-parent variation is unclear at present, but the generally low correlations between wing loading and descent rate may slow selection for any particular mean wing loading value, or for a range of wing loading values, within a species.

We are currently exploring ways of quantifying wing shape that measure the degree to which samaras of given mass and planform area depart from design efficiencies based on aerodynamic principles. We also hope to measure dispersal under natural conditions from parent trees with contrasting samara morphology. These studies will help clarify the impact that variations in samara morphology within and among parents have on dispersal enhancement.

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