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WIND DISPERSAL IN CALIFORNIAN DESERT PLANTS:
EXPERIMENTAL STUDIES AND CONCEPTUAL
CONSIDERATIONS

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ABSTRACT

Because of the important role wind is alleged to have in dispersal of fruits and seeds in desert plants, diaspores were collected for experimental study of 14 species from two Sonoran Desert localities of Imperial Co., California. Field observations on natural dispersal of these species also were made. Although all 14 species were not judged to be primarily adapted to anemochory, tests on air transport capability were made using a calibrated and modified seed-blowing machine. Diaspores were tested individually and results for 20 trials averaged for each experimental condition. In one series of tests, lofting ability was determined. In other tests, a Plexiglas wind tunnel was used; the bottom of the tunnel was lined with Plexiglas, wood, and sand for three types of trials respectively. Mean surface area and mean mass were determined for the seeds and fruits of the 14 species. These figures and the ratio between surface area and mass were compared to results from the lofting and horizontal movement tests. A high presentation surface area/mass ratio was positively correlated with ease of horizontal movement (tumbling chiefly) and ease of lofting. Excellence at transport in air appears variously countered in the anemochorous species by diaspore characteristics which seem to insure lodging in crevices or depressions. More than one kind of transport in air (e.g., tumbling, floating, skidding) can be identified and particular species may exhibit these in varying proportions. Seeds with high mass have nil wind-dispersal ability and thereby may be adapted to reaching (and staying in) depressions, washes, etc. High static friction is another mechanism which maximizes lodging ability. As Asteraceae show, anemochorous ability does not always run counter to lodging ability: capability of a diaspore to attach to hairs or skin of animals runs parallel to ability to lodge in soil crevices. In the study areas and in other desert localities, ants may play some role in movement of many kinds of seeds and fruits over short distances, but destruction by ants often is excessive.

Key words: anemochory, desert ecology, dispersal, seed dispersal, wind dispersal.

INTRODUCTION

Van der Pijl (1969) regards anemochory as a derived type of dispersal, one not characteristic of primitive flowering plants. He regards this dispersal mode as highly developed in situations of biotic poverty. However, one could more easily stress not phylogenetic position or biotic poverty, but the influence of other ecological factors. Wind is abundant in most desert areas and is minimally modified by vegetation acting as windbreaks. Fleshy fruits characterize forest and

scrub areas more than desert areas. Relatively high degrees of anemochory have been reported for high latitudes (Savile 1972) and altitudes, where seed-dispersing birds are not common but wind velocities are higher than in other areas. Where seed-eating birds are not common, one expects fewer fleshy fruits adapted to bird dispersal and therefore a higher proportion of other methods of dispersal. Other potential vectors besides wind in deserts include small mammals and ants (Tevis 1958; Gordon 1980).

If anemochory ought to play an important role in deserts, studies are needed to demonstrate whether or not this is true. Both observational and experimental approaches are attempted here. As a premise for the present study, plants of two Sonoran Desert localities in Imperial Co., California, were selected. These areas had the advantage of containing trees, shrubs, herbaceous perennials, and annuals, and neither area represented a transition to any nondesert vegetation type.

When examining capability of diaspores for wind dispersal, a complex of factors must be examined. One must not rule out other means for dispersal. One must take into account various types of wind dispersal. One must consider the relationship of wind dispersal mechanisms to lodging, or "planting" of seeds and fruits. Each species has a syndrome of adaptations, and none represents any one theoretical concept in unadulterated form. Therefore the present study must be somewhat exploratory in nature.

Sheldon and Burrows (1972) studied the efficiency of pappus in Asteraceae as a mechanism for wind dispersal. They took into account effect of pappus size and shape, the effect of height at which fruits are presented for dispersal, and the influence on dispersal of environmental factors (e.g., openness of the stand). Burrows (1975) sought to group different sizes and shapes of seeds in aerodynamic terms. These two papers contain equations explaining seed dispersal in terms of such forces as drag and lift. However, these authors do not examine fully the effect of environmental factors, nor do they consider adaptations for lodging of seeds in a substrate, or subsidiary means of dispersal. Further, Burrows limits himself to primary trajectories (the trajectory from plant to ground), a factor of importance where a seed or fruit is released high above the ground surface, but of much less importance in desert areas where plants are characteristically of low stature. In desert areas not only are strong winds available for secondary transportation of seeds and fruits, vortexlike thermal currents ("dust devils") are of frequent occurrence and are capable of lofting seeds well above the desert surface. Some diaspores in deserts can roll in response to winds.

Peart (1979, 1981, 1984) discusses the adaptive significance of diaspore lodging in grasses in relation to germination and nature of substrate. He finds that awns and hairs position grass fruits with radicle pointed toward the soil. Hygroscopic movement of awns may aid in lodging of the grass fruit according to Peart's studies. The relationship between seed morphology and seedling behavior is stressed by Sheldon (1974). Lacey (1982) shows that *Daucus* diaspores travel better over snow in winter than over the surface of soil litter in autumn. Casper and Wiens (1981) consider the possibility that a rather standard rate of seed abortion in *Cryptantha* may confer lightness, and hence better dispersibility, to the quartet of calyx-enclosed nutlets in this genus, which they presume to be wind-dispersed.

Relatively little experimental work has been done, however, on wind transport of seeds and fruits. Small (1918) used a "wind tunnel" to measure dispersal

effectiveness for a few species of Asteraceae. He dropped a fruit through a hole in the top of a horizontal tube and recorded the amount of air movement needed to move a fruit the length of the tube. Small did note the effect of the environment with relation to humidity changes. The present study attempts to build on Small's methods and to expand both systematic coverage and experimental methods.

MATERIALS AND METHODS

The study localities were: (1), near Travertine Point on Highway 86 just south of the Imperial Co.–Riverside border, southwest of the Santa Rosa Mountains; and (2), near Highway S-22 in Imperial Co. west of Salton City one mile east of the Anza-Borrego Desert State Park border. Although 24 species were originally selected at these sites, the number was reduced to 14 in order to have sufficient number of fruits or seeds for each species. Seeds in the minute category were omitted because they provide great difficulties in handling during experimental procedures.

Mass and surface area were determined for the fruits and seeds of the 14 species studied, and a ratio between these two figures was also developed (Table 1). In order to determine surface area, the seed or fruit was reduced to a conic section or a series of conic sections. Trichomes were not included in these calculations, because the excessively large number (see Fig. 2, 3, 6, 10, 13) made any reasonably accurate estimate of their surface area impossible. Note is made of discrepancies between wind-transport ability and surface area based on such an undercalculation.

For measurement of wind speeds in the vertical tube of the seed-blowing machine (lofting ability) and in the wind tunnel (horizontal movement), a hot-wire anemometer was used because of its accuracy and ease of incorporation into the apparatus. The anemometer was constructed with the assistance of the Pomona College Physics Department. A "basket" wrapped with unvarnished 44-gauge wire (at 10 ohms) was attached through a Wheatstone Bridge to a microampere galvanometer and a DC power source (2 amperes; variable 6–7 volts). Measurements of wind speeds are given in cm/sec (to convert cm/sec to km/hr one multiplies by 0.036). The seed-blowing machine, property of the Rancho Santa Ana Botanic Garden, is a standard device used by those who prepare seed samples by taking advantage of the difference in lofting ability between diaspores and the chaff which accompanies them.

For lofting trials the vertical Plexiglas column of the seed-blowing machine was used without modification. Each seed was placed on the screen at the base of the Plexiglas column. Wind velocity was increased until the seed was supported on a cushion of air just above the screen. Microamperes were recorded with the anemometer located approximately 30 cm above the screen. Twenty diaspores per species were tested individually.

For horizontal movement trials a wind tunnel was constructed and attached to the seed-blowing machine in place of its usual vertical Plexiglas vertical tube. The wind tunnel consisted of a rectangular box ($76 \times 17.5 \times 15$ cm) made of wood but with a hinged Plexiglas top. A Plexiglas wall was attached 2 cm from one wall side to permit attachment of the anemometer. One end of the tunnel was open, the other was attached to an aluminum duct with tubing connecting to the seed-

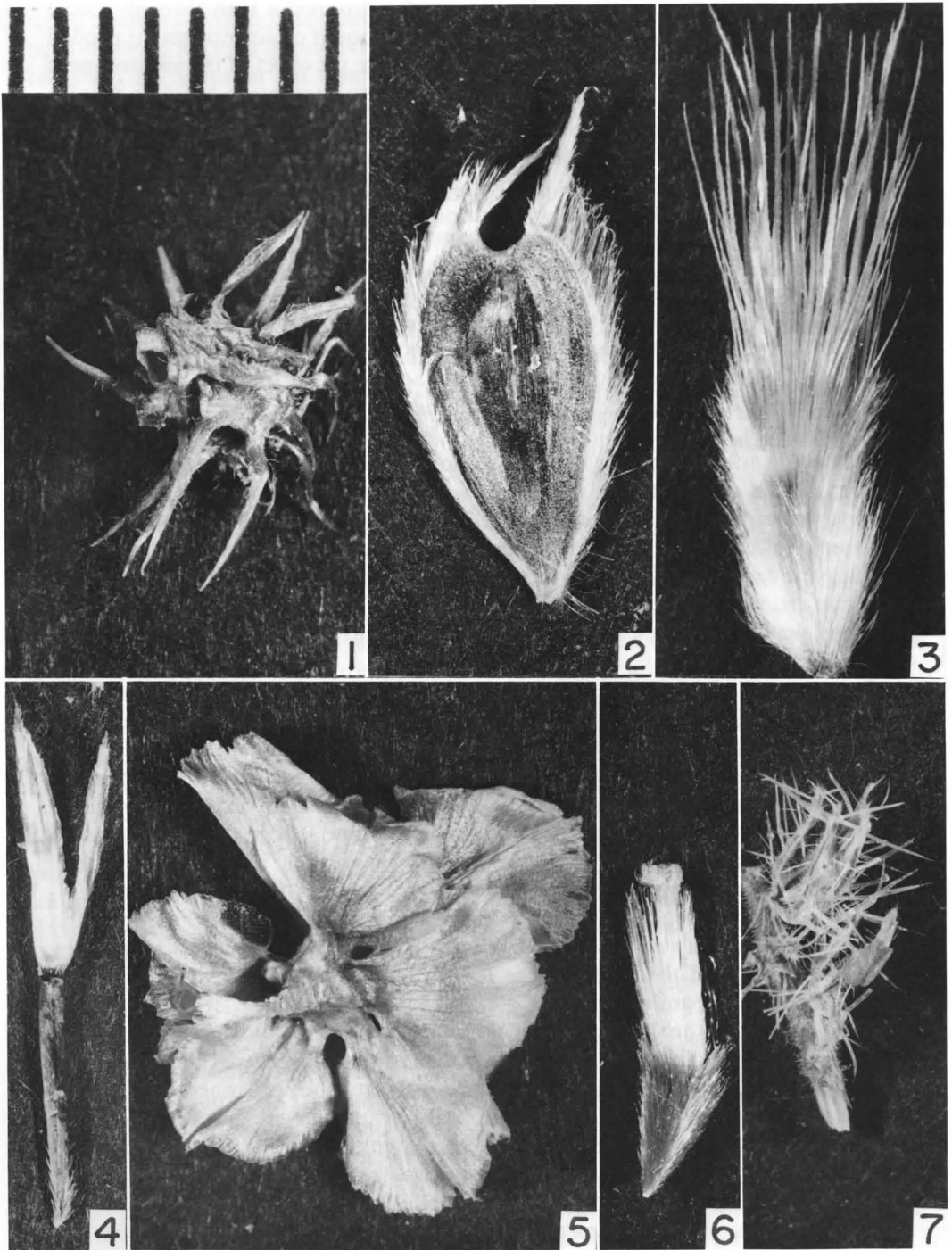


Fig. 1-7. Disseminules of Sonoran Desert plants.—1. Fruit of *Ambrosia dumosa* (some spines folded onto surface).—2. *Encelia frutescens* fruit; margin is densely hairy.—3. *Machaeranthera orcuttii* fruit (pappus bristles not reflexed in this cypsela).—4. *Chaenactis fremontii* fruit (typically fruits would bear four paleae reflexed at right angles to fruit body).—5. *Hymenoclea salsola* var. *salsola* fruiting

blowing machine. Three surfaces were prepared for use as a flooring in the wind tunnel for three series of tests: a single sheet of Plexiglas; an unfinished wooden surface; and a sand surface made by glueing sand grains onto a Plexiglas plate so that the sand would be a single grain thick. Twenty seeds of each species were tested individually on each of the three flooring surfaces. Each seed was dropped, in still air, from a height of 10 cm onto the surface of the tunnel. The top of the tunnel was left open: closing it produced turbulence and erratic readings on the anemometer. Thus the apparatus was really more in the nature of a trough than a tunnel. The wind speed was raised for each trial until a given seed was transported the length of the tunnel. A run with a given seed was judged successful only when the seed was expelled from the tunnel and did not stick or lodge. The wind speed needed to expel the seed was measured with the anemometer. Observations were made on the nature of seed orientation and movement within the tunnel.

Field studies, collection of seeds, assemblage of apparatus, and experimental work represent the work of the first author, who presented a preliminary version as a Senior Thesis at Pomona College. The second author has provided photographs of seeds and fruits (Fig. 1–14), conceptual interpretations, and text construction.

DESCRIPTION OF SEEDS AND FRUITS

The information below is organized alphabetically in terms of families, then alphabetically by genera and by species within families. The scale above Fig. 1 applies to all species.

AMBROSIA DUMOSA (Gray) Payne (Asteraceae), Fig. 1. The fruit consists of a female involucre which contains a single seed. The surface of the involucre is raised into prickles which radiate equally in all directions. The prickles are sharp-tipped and tend to penetrate and cling to skin very easily.

CHAENACTIS FREMONTII Gray (Asteraceae), Fig. 4. The fruit is a cypsela (more commonly known as an achene in Asteraceae) containing a single seed, the usual condition for the family. The base of the cypsela bears a tuft of trichomes. At the apex of the cypsela four pappus paleae are attached. Two are shown clearly in the photograph, but in most fruits four are present and these radiate from the top of the cypsela (rather than extending vertically, as shown in the photograph).

ENCELIA FRUTESCENS Gray (Asteraceae), Fig. 2. The cypsela of this species is platelike rather than cylindrical. A pair of hairy awns tip the fruit. The margin of the cypsela bears a dense fringe of trichomes.

HYMENOCLEA SALSOLA T. & G. var. *SALSOLA* (Asteraceae), Fig. 5. As in *Ambrosia*, the fruit of this species is a female involucre which contains a single seed. Radiating from the involucre in all directions are platelike appendages.

MACHAERANTHERA ORCUTTII (Vasey & Rose) Cronquist & Keck (Asteraceae), Fig. 3. The cypsela of this species is cylindrical, densely covered by trichomes. The apex of the cypsela bears numerous bristles. The bristles may reflex outward

←

head; some wings are folded onto surface of this fruit (normally they radiate in all directions).—6. *Psathyrotus ramosissima* fruit; corolla enclosed by pappus bristles.—7. *Cryptantha angustifolia*, fruiting calyx showing sharp stiff hairs; portion of inflorescence axis is attached. (Magnification scale for all figures is above Fig. 1 [divisions = 1 mm].)

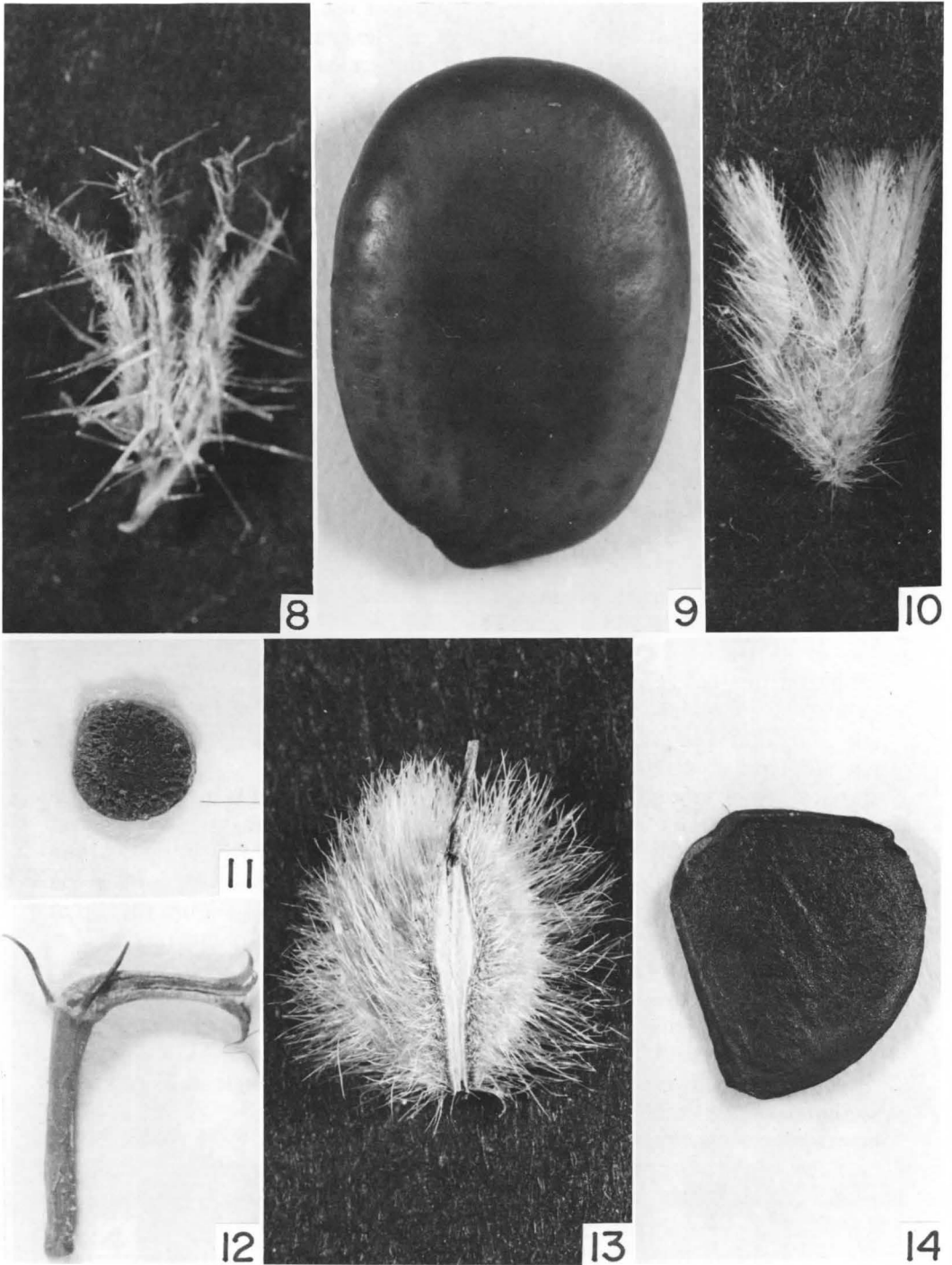


Fig. 8-14. Disseminules of Sonoran Desert plants.—8. *Cryptantha nevadensis*, var. *nevadensis*, fruiting calyx, showing sharp stiff hairs.—9. *Cercidium floridum* seed, broader surface shown.—10. *Dalea mollissima*, fruiting calyx (legume enclosed within the calyx).—11. *Eremalche rotundifolia*, achene, showing disklike shape.—12. *Chorizanthe brevicornu* subsp. *brevicornu*, involucre with hooked

when humidity is low; when humidity is higher, the bristles tend to be more nearly upright as shown in the photograph. Fruits tested all had bristles well reflexed outwardly.

PSATHYROTES RAMOSISSIMA (Torr.) Gray (Asteraceae), Fig. 6. The body of the cypsela is conical, densely covered by trichomes. The apex of the cypsela bears a tube of bristles which do not tend to reflex very much. The dried corolla is often retained on the fruit, as shown in Fig. 6.

CRYPTANTHA ANGUSTIFOLIA (Torr.) Greene (Boraginaceae), Fig. 7. As is true of many Boraginaceae, *C. angustifolia* has four nutlets which tend to be retained within the fruiting calyx although they may fall out during the maturation or dispersal process. The nutlets are about 1 mm long. The portion shown in the photograph is one fruiting calyx plus portions of another sepal and of the inflorescence axis. The sepals and dried inflorescence axis are very brittle and tend to break irregularly. The sharp, tangled trichomes tend to group fruiting calyces together somewhat, so that the disseminule can sometimes be more than a single fruiting calyx. The sharp stiff trichomes tend to penetrate skin and remain embedded.

CRYPTANTHA NEVADENSIS Nels. & Kenn. var. NEVADENSIS (Boraginaceae), Fig. 8. The fruiting calyx in this species tends to separate from the inflorescence axis singly more frequently than that of *C. angustifolia*. The fruiting calyx of *C. nevadensis* is larger than that of *C. angustifolia*, as are the nutlets, each of which is about 2.5 mm long. The nutlets tend to fall out of the calyx during maturation and dispersal, although they may be retained indefinitely. The trichomes on the sepals are like those of *C. angustifolia* in being stiff, intricately displayed, and capable of penetrating and lodging in skin.

CERCIDIUM FLORIDUM Benth. (Fabaceae), Fig. 9. The diaspore of this species is a somewhat flattened oval seed, although the legume may tend to remain unopened and thus disperse as a several-seeded unit occasionally. The seed does not float in water, and its surface is smooth and hard.

DALEA MOLLISSIMA (Rydb.) Munz (Fabaceae), Fig. 10. The disseminule of this species is the fruiting calyx in which the small unopened legume is enclosed. The one- (sometimes two-) seeded legume remains within the fruiting calyx indefinitely. The fruiting calyx is tipped by five calyx teeth which are densely clothed with trichomes, as is the calyx tube.

EREMALCHE ROTUNDIFOLIA (Gray) Greene (Malvaceae), Fig. 11. The fruit of *E. rotundifolia* is an indehiscent one-seeded carpel (therefore an achene) which is disklike in shape, about 0.2 mm thick. The surface contains small pits or concavities.

CHORIZANTHE BREVICORNU Torr. subsp. BREVICORNU (Polygonaceae), Fig. 12. The five- or six-hooked bracts (Fig. 12, upper right) of this plant enclose an achene 1–2 mm long; the achene remains within the calyx and is not readily loosened. In addition to the involucre, portions of the inflorescence axis and bractlets may be shed together, as shown in Fig. 12. The recurved and sharply pointed nature

← bracts, a pair of bracts, and attached pedicle (below).— 13. *Larrea tridentata*, one carpel (adaxial face shown) of the five carpels which usually remain attached.— 14. *Hesperocallis undulata* seed, illustrating disklike shape. (Magnification scale for all figures is above Fig. 1.)

of the bracts permits them to hook firmly into skin. The bractlets are sharply tipped enough to have a similar action even if they are not recurved at their tips.

LARREA TRIDENTATA (Sessé & Moc. ex DC.) Cov. (Zygophyllaceae), Fig. 13. The fruit of *Larrea* consists of five united one-seeded carpels. After maturation these may break apart, so that units ranging from one to all five carpels may disperse together. Each carpel is densely covered by long trichomes which are not stiff enough to penetrate into skin. When the five carpels are shed as a unit, the fruit has a spherical shape, uniformly covered by trichomes. Such intact fruits were studied in the present paper; the photograph (Fig. 13) represents one of the carpels, showing an adaxial face of the carpel where it was united with others.

HESPEROCALLIS UNDULATA Gray (Liliaceae), Fig. 14. The only monocotyledon in the present study, and therefore last in this listing, *Hesperocallis* has notably large disk-shaped seeds about 5 mm in diameter and approximately 0.5 mm thick. The seed is not winged in any way, and is only moderately rough.

RESULTS AND DISCUSSION

An obvious feature which emerges from Table 1 is that surface area and mass are independent variables, although they do tend to parallel each other (with some notable deviations, as in *Hesperocallis*). The reader should take note of the fact that trichomes have been omitted from the surface-area calculations, and thus hairier fruits are notably undercalculated with respect to surface area.

Table 2 gives the results of lofting and horizontal movement tests. One feature which is obvious from this table is that the rank order of the species in lofting ability is quite different from the rank order of the species in terms of horizontal movement. The reason for this is that two types of motion in air are involved. The lofting test reveals ability of a fruit or seed to float in air. The wind-tunnel tests demonstrate the ability of a fruit or seed to undergo a tumbling motion or a skidding motion. The three surfaces utilized in the wind-tunnel tests reveal different degrees of static friction. The least friction is exhibited by the Plexiglas floor of the wind tunnel. For some species, the wood provides the maximum friction; for others, the sand surface does.

Seeds and fruits in the wind-tunnel tests showed a characteristic shift in their positioning at speeds below those needed to blow them out of the tunnel. Seeds and fruits assume positions of minimal wind resistance by becoming oriented with bristles, spines, or pappus (if asymmetrically present on the seed or fruit) downwind. Although diaspores were dropped from a height of 10 cm and allowed to position themselves randomly, all seeds or fruits of a particular species attained the same orientation once the wind current was turned on.

On the Plexiglas surface, *Cryptantha angustifolia* required the least air velocity to achieve diaspore movement. Table 2 shows standard deviation in wind-tunnel tests; values range from a high of 21.2% for *Encelia frutescens* to a low of 7.2% for *Cercidium floridum*. The explanation for these figures seems to be that behavior of any flattish object in a wind current is inconsistent. A flat seed is more subject to various minute aerodynamic forces. The point at which "lift" is a significant enough force to overcome the seed-surface interface "vacuum" is highly variable.

The unpainted wood surface of the wind tunnel showed that particular morphological characteristics of the diaspore were important in offering various degrees of contact with the microscopic irregularities of the surface. The fruits of

Table 1. Surface area to mass ratios, mass values, and surface areas for fruits or seeds of 14 desert species, ranked by surface to mass ratio (rankings according to mass and to surface area specified numerically; trichomes omitted from surface-area figures).

Species	Surface area to mass ratio	Mass, g	Rank	Surface area, mm ²	Rank
<i>Cryptantha nevadensis</i>	83,000	3.1×10^{-3}	9	253.3	4
<i>Machaeranthera orcuttii</i>	59,600	7.0×10^{-3}	5	417.5	1
<i>Cryptantha angustifolia</i>	41,200	1.5×10^{-3}	12	61.9	8
<i>Psathyrotes ramosissima</i>	31,500	6.0×10^{-4}	13	18.9	13
<i>Chaenactis fremontii</i>	30,300	5.5×10^{-4}	14	16.7	14
<i>Ambrosia dumosa</i>	20,400	6.4×10^{-3}	7	129.7	5
<i>Dalea mollissima</i>	20,400	2.4×10^{-3}	10	48.3	9
<i>Hymenoclea salsola</i>	15,700	7.3×10^{-3}	3	113.9	6
<i>Eremalche rotundifolia</i>	12,700	1.6×10^{-3}	11	30.1	12
<i>Larrea tridentata</i>	11,200	2.4×10^{-2}	2	262.2	3
<i>Chorizanthe brevicornu</i>	9570	3.1×10^{-3}	8	29.2	11
<i>Hesperocallis undulata</i>	6600	7.0×10^{-3}	4	46.5	10
<i>Encelia frutescens</i>	1310	6.7×10^{-3}	6	86.9	7
<i>Cercidium floridum</i>	961	2.8×10^{-1}	1	268.9	2

Machaeranthera orcuttii required the least wind velocity for movement, perhaps because the high surface to mass ratio (see Table 1) overcame any friction provided by the wood grain. This species also had the lowest standard deviation (8.1%) in this test. The greatest wind velocity needed for movement in this test was exhibited by seeds of *Cercidium floridum*. The highest deviation (23.9%) was shown by *Chaenactis fremontii*, perhaps because position of the four pappus paleae and the way they intersect the wood surface may vary considerably.

On the sand surface, the species requiring the least velocity for movement was *Cryptantha nevadensis*. In all species except for *Encelia frutescens* and *Eremalche rotundifolia* lower wind velocities were required for movement on the Plexiglas surface than on the sand surface. Percent deviations for the sand surface were generally higher than for the two other surfaces, indicating that minute irregularities underneath a seed or fruit tend to make some diaspores of a species cling more, others less, than with a more uniform surface. *Cercidium floridum* showed the least deviation on the sand surface, as it did on the Plexiglas surface. *Chaenactis fremontii* showed the highest deviation on the sand surface, as it did on the wood surface.

In the lofting tests, difficulties were experienced in obtaining data for *Encelia frutescens* and *Chaenactis fremontii* because few fruits of these species conformed to the criterion of this test, that of riding on a cushion of air just above the bottom screen of the seed-blower tube without falling. For these two species, therefore, data presented are based on fewer than 20 trials. The order in which species are listed in Table 2 is the order of lofting capability. The broad surfaces of the flat achene of *Encelia frutescens*, the pappus paleae of *Chaenactis fremontii*, and the trichomes of *Dalea mollissima*, coupled with the low mass of fruits of these species may explain high lofting ability in these species. Low lofting ability seems correlated with condensed form coupled with greater mass. The low deviation of *Ambrosia dumosa* may relate to uniformity in these spherical but moderately heavy fruits. The high deviation in lofting of *Hesperocallis undulata* may be

Table 2. Velocities required for movement of seeds and fruits of 14 desert species, together with standard deviation (expressed as a percentage of the velocity) and rank of species (rank for lofting is the order of species at left); in the wind-tunnel tests, three kinds of flooring have been used.

Species	Lofting		Wind tunnel: Plexiglas floor			Wind tunnel: Wood floor			Wind tunnel: Sand floor		
	cm/sec	SD %	cm/sec	SD %	Rank	cm/sec	SD %	Rank	cm/sec	SD %	Rank
<i>Encelia frutescens</i>	47.2	—	171.9	21.2	11	157.0	13.1	9	145.7	21.1	10
<i>Chaenactis fremontii</i>	49.0	—	97.7	9.8	8	110.3	23.9	8	107.2	23.5	7
<i>Cryptantha nevadensis</i>	50.7	6.6	56.6	12.0	1	84.4	21.7	2	67.6	11.4	1
<i>Dalea mollissima</i>	50.7	6.9	74.1	11.1	3	95.4	18.5	5	87.1	15.8	4
<i>Machaeranthera orcuttii</i>	52.6	8.1	62.8	8.3	2	52.6	8.1	1	84.8	12.8	2
<i>Psathyrotes ramosissima</i>	54.6	9.4	96.8	12.9	7	175.4	11.5	11	122.9	12.5	9
<i>Cryptantha angustifolia</i>	60.3	9.0	79.0	9.4	5	93.0	15.1	4	102.9	12.4	6
<i>Hymenoclea salsola</i>	61.2	12.5	81.5	9.0	6	107.4	10.9	7	92.9	11.3	5
<i>Eremalche rotundifolia</i>	62.3	8.3	225.3	18.1	13	196.5	13.0	13	185.7	15.2	11
<i>Hesperocallis undulata</i>	64.9	20.4	184.7	14.8	12	175.4	11.5	12	218.8	19.2	13
<i>Chorizanthe brevicornu</i>	73.4	7.8	135.5	17.9	10	167.8	12.8	10	189.0	19.9	12
<i>Ambrosia dumosa</i>	87.9	4.9	102.6	10.2	9	102.3	10.9	6	117.6	11.7	8
<i>Larrea tridentata</i>	89.9	5.8	76.3	9.5	4	88.4	8.3	3	86.8	8.1	3
<i>Cercidium floridum</i>	101.6	7.5	278.1	7.2	14	544.8	—	14	467.7	6.9	14

explained by the fact that these seeds, although disklike in shape, may vary considerably in outline, ranging from circular to oval or polygonal. These kinds of variations may result in large standard deviations because the effect of shape is great where the seed acts as an airfoil. As noted earlier, diaspores with airfoillike characteristic tended to show much higher standard deviation than those in which movement by wind did not tend to involve sailing or kitelike motions.

The velocities required to loft seeds and fruits (Table 2) range from 47.2 cm/sec, which equals 1.7 km/hr (1.06 mi/hr) to 544.8 cm/sec, which equals 19.6 km/hr (12.3 mi/hr). These velocities may seem unexpectedly slow for seed movement when one compares them to known windspeeds in deserts, not to mention hurricane velocities. However, one must remember that the lofting experiment utilizes a condition quite unlikely to occur in nature: a vertical stream of air. Most air currents in desert areas tend toward the predominantly horizontal planes of the landscape, and thus lofting of seeds would require far greater velocities (together with kinds of gusting that would lift seeds from the substrate) than the experimental condition. The experimental velocities which induced horizontal transport in the wind tunnel are somewhat greater than those which induced lofting in the vertical tube. However, the horizontal movement velocities are also much less than one might expect on the basis of winds in nature. Horizontal transport in nature requires traversing of much more irregular terrain than the relatively smooth flooring of the wind tunnel (even sand or wood) offers. With these considerations, one can understand discrepancies between experimental velocities and the nature of winds in desert areas available for transport of anemochorous diaspores.

The reader is reminded that surface area of trichomes was not included in surface-area figures, so that hairier seeds and fruits ought to have greater lofting and horizontal transport capability than the figures of Table 1 might suggest; in fact, hairy seeds and fruits do have enhanced dispersibility (Table 2).

ANALYSIS OF SPECIES

Based upon field observations, morphology, and experimental data, an attempt is made here to present an image of where each species falls with respect to adaptations to anemochory and to other dispersal adaptations. The species are listed in the same order as in the morphology descriptions earlier.

AMBROSIA DUMOSA. The fruit of this species ranks in an intermediate position with respect to surface area and mass, but its lofting ability is low and its tumbling ability medium. There is little doubt that because prickles easily enter and remain in skin, fruits of this species disperse by catching on skin and fur of small mammals. However, the tumbling characteristics are good enough to widen dispersal range from the parent plant prior to attachment to mammals. This can be observed in the wild. Shreve (1951, p. 159) noted the prickles "improve the chance that the fruit will lodge in a spot favorable for germination." *Ambrosia dumosa* is a good example of how adaptations for travel on animals may simultaneously be adaptations for lodging. The morphology of the fruit does not, however, secure lodging of the fruit of *Ambrosia dumosa* with radicle pointed downward as is true in grasses (Peart 1979, 1981, 1984), and the value of lodging mechanisms may be more in the nature of adherence to substrate so that germination can occur, as opposed to continuous travel of the fruit. Small quantities of *Ambrosia dumosa* fruits are collected by harvester ants (Gordon 1980); the ants seek these fruits,

she claims, because of the high protein content of embryos. Ants may have the net effect of destroying some of the fruits rather than providing any appreciable degree of transportation of them to favorable germination sites.

CHAENACTIS FREMONTII. Fruits are excellent at lofting, very likely because of the broad but light surfaces of the four pappus paleae. The fruits are much less good at tumbling; tips of the pappus paleae become lodged in crevices, but more importantly rest on the achene base and the tips of two of the four pappus paleae in the fashion of a tripod, and the stability of this configuration requires moderate wind velocity to initiate tumbling. Thus, an ideal dispersal event for *Chaenactis fremontii* would involve lofting of the fruits directly from the mature head (where they tend to spread apart and where their pappus paleae are displayed and face potential wind currents). Once the fruit has fallen to the ground, further travel via tumbling or becoming airborne again is likely to be much less. The pointed tips of the pappus paleae and of the achene base may tend to lodge the fruit in sand and gravel crevices. During the field observations, the first author noted ants carrying fruits of *Chaenactis fremontii*; fruits were grasped by the hairy achene base, and carried upright with the pappus paleae above the ant. Collection of *Chaenactis fremontii* fruits by ants has been recorded by Tevis (1958). Although ants very likely destroy many of the fruits, some fruits may be carried to suitable germination sites by ants and eventually may germinate. Note should be taken that the pappus paleae move hygroscopically, and thus are likely to act in lodging of the fruit in the same fashion that hygroscopic awns in grasses act (Peart 1979, 1981, 1984). The configuration of the *Chaenactis* fruit results in lodging of the fruits with radicle downward, conferring a germination advantage like that reported by Peart (1979, 1981, 1984) for grass fruits.

ENCELIA FRUTESCENS. Fruits of this species are excellent at lofting, but relatively poor at horizontal movement on a surface (Table 2), providing an interesting irony. *Encelia frutescens* characteristically occurs on stony slopes, hills, and mesas (Munz 1974; Shreve 1951). Perhaps in such localities updrafts catch fruits when the heads of this plant mature and shatter, and thereby fruits are carried mostly to nearby rocky slopes and occasionally to more distant slopes. Once the fruit has fallen to the ground, it is not likely to skid or become lofted again, although the high standard deviation (Table 2) suggests events of lofting will vary considerably. The shape of this fruit and its tendency not to be moved horizontally would tend to result in its lodging in crevices readily, although not necessarily with radicle oriented toward the ground.

HYMENOCLEA SALSOLA. The fruit of *Hymenoclea salsola* is similar to that of *Ambrosia dumosa* except that it bears wings rather than prickles. Wings provide better lofting and better horizontal transport capability as compared to the fruit of *Ambrosia dumosa* (Table 2). *Hymenoclea* fruits seem well adapted to wind transport, especially by tumbling. Dispersal of these fruits by animals is undoubtedly negligible. Some *Hymenoclea* fruits were found in formicaries of *Vermessor pergandei* (Mayr) (Wheeler and Wheeler 1973).

MACHAERANTHERA ORCUTTII. Fruits are excellent at horizontal movement (Table 2); the lofting ability is only slightly less striking (note that despite the rank order, the air speed necessary to loft fruits of this species is only 5.4 cm/sec faster than for the best-lofting species). The large number of bristles and trichomes raise the fruit of *Machaeranthera orcuttii* above a surface, and with this large presen-

tation of surface area, it tends to be carried horizontally better than those species in which a diaspore rests close to a surface. Other species of *Machaeranthera*, such as the desert species *M. canescens* (Pursh) Gray, have much lighter fruits equally well equipped with trichomes and bristles, and one suspects that *M. orcuttii* would be inferior to *M. canescens* in dispersal ability, perhaps an example of loss of dispersibility (e.g., Carlquist 1966). The range of *M. orcuttii* is very small (Imperial Co., California, and adjacent Baja California) compared to that of *M. canescens*, and one would expect a moderate degree of loss of dispersibility with respect to this restricted range. In a series of other genera, comparison of lofting ability of seeds revealed that species adapted to restricted areas had lower lofting ability than did congeners with wider ranges (Carlquist, unpublished). The lofting ability of *M. orcuttii* is doubtless enough for it to reach cliffs and slopes within its range; it does tend to occur on rocky canyons (Shreve 1951). The trichomes on the achene would aid the fruit of *M. orcuttii* to lodge in crevices, and it may be an example of a fruit morphology in which wind dispersal is high while lodging ability is still present to a marked degree. The comments above for *Chaenactis fremontii* apply here.

PSATHYROTES RAMOSISSIMA. Virtually the same at lofting ability (perhaps because of dense covering of fruits with trichomes) as *Machaeranthera orcuttii*, *P. ramosissima* is appreciably less good at horizontal movement. The pappus of *P. ramosissima* is somewhat less well developed and often less well reflexed than that of *M. orcuttii*, and only this minor difference makes it slightly less dispersible. Fruits of *P. ramosissima* have been reported to have been collected by ants, but this doubtless accounts for little dispersal.

CRYPTANTHA ANGUSTIFOLIA. The fruiting calyces of this species release nutlets at various times during the dispersal process, so it must be considered to have a two-phase dispersal system. The lofting and horizontal movement values (Table 2) are high enough so that one must consider that this species has a definite anemochorous capability even though that may not be its primary adaptation. The tendency of the sharp, stiff hairs to stick in skin assures epizoochorous transport. Although the fruiting calyces of *C. angustifolia* are smaller than those of *C. nevadensis*, they are less good at wind transport. This could be attributed to some tendency of calyces to cling to each other or to a tendency of calyces to break from the plant together with pieces of the inflorescence axis. High protein content of seeds makes the nutlets attractive to ants, which forage for *S. angustifolia* nutlets in large quantities (Gordon 1980; Tevis 1958).

CRYPTANTHA NEVADENSIS. The fruiting calyces are like those of *C. angustifolia* but are more easily detached from each other and from the axis. The handling of fruiting calyces illustrates quite convincingly their ability to become attached to fur and fabric, but if not attached, they have excellent wind-dispersal characteristics (Table 2). The fruiting calyces of *C. nevadensis* show that epizoochorous dispersal capability does not always run counter to anemochorous dispersal capability. The low mass of fruiting calyces of *C. nevadensis* and the tendency for hairs to hold the calyces above a surface (thereby giving greater effective presentation area) help to account for excellent air-movement abilities of this species. One should note such features as the high standard deviation on the wood surface, which illustrates the tendency for hairs to catch on the wood grain. When nutlets leave the fruiting calyces, they would tend to lodge in sand because they are so

similar to sand grains in size and shape. Lodging ability is maximized by separation of nutlets from the calyx, just as epizoochorous and anemochorous dispersal modes are maximized during retention of nutlets within the calyx.

CERCIDIUM FLORIDUM. The large, smooth seeds of this species rank at the bottom of the listings for either lofting or for horizontal movement by air (Table 2). One should not infer from this that the morphology of the seed of *Cercidium* is not related to air dispersal: it may be related to anemochory, but in a negative way. *Cercidium floridum* tends to grow in or near streambeds and washes (Shreve 1951; Munz 1974). The seeds, when tested, do not float and even if seeds remained in unopened pods, the pods would not likely float very far. However, the high mass and (for that mass) low surface area render the seed of *Cercidium floridum* unlikely to be picked up by wind, but to the extent it is moved at all, it is likely to tumble downward, either by gusts of wind or flash floods, into washes and streambeds much as gravel is preferentially carried into such depressions. Thereby, negative ability at wind dispersal has the effect of planting *Cercidium floridum* seeds in their preferred habitat, with minimal chance that they will be carried out of that habitat. During the process of downwashing into streambeds and washes, abrasion probably gradually reduces the dormancy typical of legumes with very thick seed coats, so that the closer a seed is to the bottom of a wash, the more likely it will germinate. *Cercidium floridum* is a good example of a probable adaptation for lodging and for gradual downward movement within a terrain by its shape, weight, and bulk, and for staying planted in a favorable site. All too often such probable adaptations are dismissed in the literature as examples of “no known” or “no obvious” dispersal mechanism. Ellner and Shmida (1981) depart from that pattern in their use of the term antitelechory for seeds such as those of *Cercidium*. Seeds of *C. floridum* have been reported in ant formicaries (Wheeler and Wheeler 1973), but this is not likely to result in much transport of seeds, perhaps at best only occasional burying of seeds beneath the soil surface. One may well ask how seeds adapted to downwashing ever get upstream. Very likely occasional events of seed carriage and ingestion by granivorous birds account for upslope establishments.

DALEA MOLLISSIMA. This species demonstrates how a legume species can be quite positively adapted for anemochory. The numerous trichomes on the fruiting calyces (Fig. 10) are not stiff enough or otherwise adapted to penetrating and staying in skin or fur, although one cannot rule out occasional attachment. The excellence of *D. mollissima* at lofting is equalled by its excellence at horizontal movement (Table 2). Had trichomes been included in the surface-area calculations, *D. mollissima* would very likely have ranked higher on the list of species in Table 1, perhaps even first. The fruiting calyces ought to be very good at tumbling until lofted by a gust of wind, a two-phase air-dispersal event doubtless visible in other species, although in some desert plants tumbling will predominate (e.g., *Larrea*), whereas in others, lofting will. The tendency for fruiting calyces of *D. mollissima* to be conical in shape with trichomes pointing toward the calyx-lobe tips makes it resemble the hairy fruits of many Asteraceae. As in those Asteraceae, this configuration tends to maximize lodging ability (when injected into a crevice by the pointed end of the cone, the orientation of the hairs will tend to prevent it from escaping the crevice) with wind-dispersal ability.

EREMALCHE ROTUNDIFOLIA. One can cite packing considerations as reasons for production of disk-shaped seeds. However, one can entertain possible adaptive

value for such a seed shape in *Eremalche*. Tevis (1958) has claimed that harvester ants "were unable to break into the circular fruit, which stayed tightly compressed until dry—at which time it burst open, like a flower, exposing a ring of ripe seeds which many ants could assault together." However, the ultimate taking of the achenes by ants may thereby be delayed until the achene wall is hard enough to resist predation; occasional fruits may be carried by ants to favorable sites without consumption, although ants cannot be considered a good source of dispersal for this species. Like all other diaspores in the present study, the achenes of *Eremalche rotundifolia* lack elaiosomes. A diaspore with an elaiosome has an effective mechanism for yielding nutrition to an ant while minimizing the chance of embryo destruction. *Eremalche rotundifolia* may often be found in washes (Munz 1974) and local colonies. The shape of fruits of *Eremalche*, although unlike the shape of seeds in *Cercidium*, may have a similar effect: minimizing the chance of pickup by wind, maximizing downwash by wind and water and maximizing lodging. This may tend to promote precinctiveness, a concept cited in loss of dispersibility of seeds (Carlquist 1966). However, Ellner and Shmida (1981) claim that antitelechory does not serve to recapture a habitat for the species, but has other explanations. Further studies are needed in this interesting field.

CHORIZANTHE BREVICORNU. The curved, sharp teeth of the involucre bracts attach very easily and persistently to skin, fur, or other surfaces. The nut contained within the bracts is thereby effectively carried by animal vectors. One can hardly doubt that *Chorizanthe brevicornu* is designed for epizoochory. Part of this adaptation is presentation of minimal surfaces to the wind, so that lofting and horizontal movement are less likely to happen (note the relatively low surface area to mass ratio, Table 1), and when they do happen, movement is likely to be arrested by hooking of the involucre tips or bractlet tips onto irregularities of the substrate. *Chorizanthe brevicornu* grows very close to the ground, so that small mammals are likely to come into contact with disseminules as they pass the plant, and thus wind dispersal from a plant to the ground surface, as in *Ambrosia dumosa*, is not an integral part of the dispersal adaptation for *C. brevicornu*. The marked adaptation for hooking onto an animal surface runs parallel to the adaptation for lodging of the disseminule, not counter to it (although one should note that epizoochorous mechanisms, if very efficient, account for adherence to an animal but not for ultimate fall from that animal surface to the ground).

LARREA TRIDENTATA. Shreve (1951) in discussing the fruits of this species says that, "owing to the lightness of the fruits and their hairy coverings, they are blown about to a slight extent and washed away by rain to a much greater extent." He does not give his reasons for claiming predominance of hydrochory. Certainly in the wind-tunnel tests, the fruits of *Larrea tridentata* (entire fruits, not separate carpels) ranked third or fourth. Such high ranking in tumbling ability cannot be dismissed as a byproduct of some other kind of dispersal, it can only represent a primary adaptation to tumbling. The ability at lofting is much less good, and *Larrea* represents a species in which one type of adaptation to travel in air is not correlated with another. This is doubtless due to the relatively great mass of the *Larrea* fruits (Table 1), which rank 13, the same rank as in the list of lofting abilities. However, given the excellent tumbling abilities of *Larrea* fruits and the longevity of shrubs in this species, over a few generations fruits could be blown across the entirety of desert areas (at least the intercontiguous ones) of North

America. The good tumbling ability of *Larrea* fruits may be attributed to the fact that stiff trichomes radiate equally in all directions from the surface of this spherical fruit. Thus the body of the fruit is propped above the surface of the ground and not only does wind reach all surfaces on the windward side of a fruit, little force is required because the tumbling motion is more like the rolling of a ball as compared to the end-over-end motion necessary to move fruits of, say, *Chaenactis*, or the skidding motion one can see in *Eremalche*. The trichomes on *Larrea* fruits are not stiff and do not penetrate skin or fabrics well. One cannot rule out occasional events of epizoochorous travel, and this may explain the occurrence of the genus in both North and South America, but such events are doubtless quite infrequent.

HESPEROCALLIS UNDULATA. The seeds of this species are in shape much like the achenes of *Eremalche rotundifolia*, and many of the same comments might apply to both species. In fact, despite some difference in mass, the lofting abilities of the two species are very close, and so are the results from wind-tunnel tests. *Hesperocallis undulata* tends to form local colonies (Munz 1974), so low capability for wind dispersal tends to maintain a heavy concentration of seeds in the areas ecologically best suited for their survival. This is an excellent strategy for survival of a species with relatively specialized ecological requirements provided that occasional events of longer-distance transport can occur. When one notes that the wind velocity needed to move seeds of *Hesperocallis* horizontally is only about 6.8 km/hr (4.2 mi/hr), occasional transport of seeds across distances of relatively great length can easily be postulated. Transport of seeds of *Hesperocallis* by water or by animals can be hypothesized to be minimal and can be ruled out for all practical purposes.

CONCLUSIONS ABOUT DISPERSAL CONCEPTS

The 14 desert species represent several different modalities of anemochory, and some species are primarily epizoochorous rather than anemochorous. The experimental data permit some new conclusions, since distinctions of a quantifiable nature are revealed: for example, the differences between lofting and tumbling modes.

Chorizanthe brevicornu represents maximal adaptation among the species studied for epizoochory. The efficient hooklike structures are few and provide minimal surface for reaction to wind currents. Epizoochorous design does not need to exclude anemochory, as shown by *Cryptantha nevadensis* (and, to a lesser extent, *C. angustifolia*), which excels at both lofting and tumbling. One may hypothesize that a fruiting calyx of *C. nevadensis* may sometimes be caught on a small animal surface; if not, it may disperse by lofting or tumbling. The tendency of stiff trichomes or hooks in *Cryptantha* and *Chorizanthe*, respectively, to catch on skin or fur can have a positive value in lodging of the diaspores in sites suitable for germination. In *Cryptantha*, the series of dispersal options is enhanced by the tendency of nutlets to fall from the fruiting calyx at various times after maturation. The nutlets are the size of sand grains and may travel much like sand granules when winds blow. The presence of nutlets within sand leads to their remaining in place to a much greater degree than their traveling, and the fall of nutlets from a calyx can therefore be considered essentially a lodging or planting mechanism,

ending efficient travel by wind or on an animal surface. *Ambrosia dumosa* seems to show features balanced between epizoochory and anemochory.

In the remaining species, adaptations appear to represent some version of anemochory, coupled with some mechanisms for lodging of disseminules in a favorable site. The tests show that there is more than one category of wind dispersal, and any given species may represent a balance between two (or more) types. The vertical column of air provided by the unmodified seed-blowing machine measured lofting ability clearly. The wind tunnel measured tumbling, a quite different type of action, as well as skidding.

Tumbling may represent a rolling motion in the case of diaspores which are roughly spherical (*Ambrosia dumosa*, *Hymenoclea salsola*, *Larrea tridentata*). In other cases, an end-over-end motion is achieved if there is a tripodlike configuration, as in *Chaenactis fremontii*. The tendency of a diaspore to be supported on trichomes and thereby better exposed to the air current improves its ability to tumble, as shown by *Larrea tridentata*. *Larrea tridentata* fruits are just a little too heavy to be good also at lofting. Similarly constructed but lighter disseminules are also excellent at lofting (*Cryptantha angustifolia*, *C. nevadensis*, *Dalea mollissima*, and the hairier fruits of Asteraceae: *Machaeranthera orcuttii* and *Psatthyrotes ramosissima*). Casper and Wiens (1981) hypothesize wind transport in *Cryptantha flava* Payson because a constant rate of ovule abortion lightens the disseminule and aids wind transport.

Diaspores which lie quite flat on a surface show far less wind-transport capability unless they are very light. The flat surfaces of the *Encelia frutescens* fruit and the pappus paleae of *Chaenactis fremontii* fruits as well as the low mass of these fruits account for excellence of these species at lofting. The tripodlike configuration of the *Chaenactis fremontii* fruit and the marginal hairs of *Encelia frutescens* fruits tend to catch wind currents, accounting for the ability of fruits in these species to become lofted rather than cling to a surface. Broad surfaces in these species, which may be likened to the surfaces of a kite, can be said to constitute a distinctive lofting mechanism. *Hymenoclea salsola* fruits have winglike appendages which catch the wind; fruits in this species are less good at tumbling or lofting than those of *Chaenactis fremontii* or *Encelia frutescens* merely because of their greater mass.

In lofting, high surface area to mass ratio plus a low mass are essential features. Trichomes (not included in the calculations) doubtless increase surface area considerably and account, for example, for why fruiting calyces of *Dalea mollissima* rank higher in lofting or horizontal transport (Table 2) than they do in the listing of species by surface to mass ratio (Table 1). The area which is presented to the wind surface (termed presentation area elsewhere in this paper) is more important than the total area in this regard; a diaspore raised above a substrate by being supported on trichomes is more effective at horizontal motion than a flat diaspore which lies on a substrate. Increase in mass, even if surface area is great, results in lowered success in lofting, but tumbling ability may be retained if other features are still optimal, as shown by *Larrea tridentata* and, to a lesser extent, *Hymenoclea salsola*. Species in which lofting ability outweighs tumbling ability may characterize rocky slopes and cliffs, sites reached by lofting well but very poorly by tumbling motions. In the present study, *Encelia frutescens* and *Machaeranthera orcuttii*, both excellent at lofting, occupy such sites.

A concept which may be called "negative anemochory" ("antitelechory" of Ellner

and Shmida 1981) is hypothesized to explain mass and surface characteristics of seeds or fruits that are somewhat flattened (*Cercidium floridum*) or disklike (*Eremalche rotundifolia*, *Hesperocallis undulata*). These species have smooth and relatively heavy seeds or fruits which can be said to avoid both lofting and horizontal movement by wind currents. The advantage of this configuration is potentially twofold: to permit downwash of fruits or seeds into washes (habitats to which *Cercidium floridum* and *Eremalche rotundifolia* are, in fact, adapted); and to permit most disseminules to stay near the parent plant. Ellner and Shmida (1981), working with diaspores of Old World desert areas, discount the latter idea, which they term recapturing of the habitat. Instead, they suggest that what they term antitelechory is a byproduct of selection for other factors, such as widening of the season during which germination occurs, strategies with respect to flooding, or prevention of excessive foraging. Ellner and Shmida (1981) show that antitelechory is virtually absent in scrub of the Mediterranean area, but occurs in about 22% of the Old World desert species they studied. Further study is needed, but negative anemochory appeals to us as a genuine phenomenon related to reaching suitable habitats. Fruits and seeds which show negative anemochory may tend to travel much as gravel might, gradually settling to lower elevations and lodging there. Negative anemochory may have a significance not merely in downwash where suitable habitats are topographically lower, but in prevention of continued transport, insuring that a diaspore stays in a suitable habitat long enough to become covered and to germinate. High winds could provide for occasional events of longer-than-normal transport for species in this category, accounting for why species with poor transport reach some distant localities. The idea that species with poor dispersal tend to recapture a habitat of small extent or with specialized conditions should be tested on a case-to-case basis, for it may operate in some species but not in others. In lofting trials of diaspores of genera in which two or more species, differ with respect to geographical range and narrowness of ecological requirements, species poorer at dispersal were found to have more restricted range or requirements (Carlquist, unpublished).

The requisites of optimal anemochory might seem at first glance to run entirely counter to those optimal for lodging but in fact they do not. Lofting ability compatible with lodging ability is shown well in fruits of certain Asteraceae in the present study (*Chaenactis fremontii*, *Machaeranthera orcuttii*, and *Psathyrotes ramosissima*) and in *Dalea mollissima*; Peart (1979, 1981, 1984) has shown distinctive lodging mechanisms in certain grass fruits. These species show a distinctive morphology: a conical configuration with trichomes and bristles pointing away from the tip of the cone. The pointed end of the cone tends to enter a crevice (it turns out to be the heavier end, since more light bristles predominate at the broad end of the cone). Once such a fruit has entered a crevice, the orientation of the hairs would tend to lock the fruit in the crevice. In the Asteraceae, the radicle end of the embryo is at the pointed end of the cone, also favoring germination of fruits lodged with the pointed end into the substrate; Peart stressed this for grasses. During the lofting phase of transport, fruits of Asteraceae like those mentioned above act in a parachutelike fashion, a behavior somewhat different from the kitelike configuration of *Encelia frutescens* fruits.

One of the features of this study which deserves special mention is the fact that air speeds required to loft or horizontally move a diaspore were rather low: 1.7 km/hr to a maximum of 19.6 km/hr, with most species falling in the lower half

of this range. One can object that vertical air currents and transport across flat and relatively smooth surfaces, the conditions provided by the seed-blowing machine and the wind tunnel, respectively, are infrequent in the wild. However, even if transportation in nature is not so unimpeded as in the experimental conditions, the low velocities needed to move seeds and fruits in this study are striking when one notes that winds in the desert regions studied exceed 100 km/hr several times per year. Diaspores are available for transport on such occasions because seed-banking is considerable and high winds tend to occur in late summer and autumn. Such exceptional winds can account for longer-than-normal transport events, and also show why lodging mechanisms—a much-neglected adaptation in seeds and fruits—are a very real necessity in the dispersal economy of a plant. Lodging mechanisms may themselves be a complex of factors: ways to induce cessation of movement, ways to insure entrance into the substrate, and, as stressed by Peart, ways of orienting a diaspore so as to point the radicle downward into a crevice.

Although the concepts discussed above are based on studies of desert species, they offer interesting possibilities for interpretation of anemochory in other areas. We need to explore modes of anemochory, the degree to which they are alike or mutually exclusive, and the degree to which they coexist in any given species with other dispersal modes, such as epizoochory, and with adaptations for lodging.

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