1976

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Recommended Citation

Wilson, Ruth C. (1976) "Abronia: IV. Anthocarp Dispersibility and its Ecological Implications for Nine Species of Abronia," *Aliso: A Journal of Systematic and Floristic Botany*: Vol. 8: Iss. 4, Article 11.
Available at: <https://scholarship.claremont.edu/aliso/vol8/iss4/11>

ABRONIA: IV. ANTHOCARP DISPERSIBILITY AND ITS ECOLOGICAL IMPLICATIONS FOR NINE SPECIES OF ABRONIA

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INTRODUCTION

An interpretation of the evolution of dispersal mechanisms in *Abronia* Juss. entails more than the description of anthocarps. It involves an understanding of the total reproductive ecology of each species. For *Abronia* an estimation of the possible adaptive value of dispersal mechanisms should include a consideration of: (1) anthocarp dispersibility based on morphological, anatomical, and experimental data; (2) survival after transport estimated from studies of seed coat anatomy and germination; and (3) the impact of seed loss on selection for increased or decreased dispersibility estimated from information on habitat, habit, and reproductive capacity.

The call for integrated studies dealing with dispersal ecology is eminent; e.g., Carlquist (1974). Carlquist's (1974) book, *Island Biology*, is an outstanding compendium of information and insight dealing with the interpretation of evolutionary and dispersal patterns. Although the focus of this work is primarily on the processes active in the evolution of island fauna and flora, the principles demonstrated are basic to an understanding of the potential for a species, whether from continental or insular environments, to evolve toward the most efficient dispersal strategy genetically possible for that species.

Parallels may be drawn between the ecological conditions confronting the species of *Abronia*, distributed across western North America (Standley, 1909; Wilson, 1972), and those confronting immigrants to islands (Carlquist, 1966). The populations of *Abronia* studied in this paper are confronted with large land areas, diverse topography, and geographical isolation. They grow in open, often dry, habitats.

With this in mind, I present the hypothesis that among species of *Abronia*, differences in habit, anthocarp dispersibility, and reproductive capacity may be correlated with habitat preferences as well as with conditions in surrounding habitats. Because *Abronia* species are apparently restricted to sandy "islands" and not ecologically suited to the relatively more acid, mesic sites of their continental range (Wilson, 1972), they have been subject to selective pressures reflected by differences seen in the morphology and anatomy of

their anthocarps and seeds (Wilson, 1974, 1975). Therefore, anthocarp characteristics are considered to have a positive adaptive value if they tend to increase the chances that seeds will remain in or reach ecologically suitable sites for seedling establishment.

MATERIALS AND METHODS

Field observations and collections of *Abronia* were made in California, northern Nevada, and western Arizona. Features considered relevant to an understanding of any special requirements for increased or decreased dispersibility were noted for each species.

Portions of plants were preserved as herbarium specimens, pickled using a standard FAA solution (Johansen, 1940), or dried in paper bags. Voucher specimens have been deposited at the Rancho Santa Ana Botanic Garden (Wilson, 1972).

Because dispersal with a potential for establishment is biologically significant, only mature abscised anthocarps containing a seed were considered relevant to this study.

The necessity for an understanding of the range of character variation has recently been reiterated by Dickison (1975) as stated earlier by Carlquist (1961). To evaluate the full potential for dispersibility among and within the species of *Abronia*, variation must be considered whenever possible. Therefore, when anthocarp polymorphism (Wilson, 1974) was pronounced within an inflorescence, data from each wing or lobe number category were kept separate. No fewer than 25 specimens of each category were used in experiments.

Anthocarps, harvested and allowed to dry in paper bags, were used to: (1) obtain weight and size measurements; (2) estimate anthocarp buoyancy in water; and (3) measure actual anthocarp movement under artificial wind conditions.

Anthocarp buoyancy was measured by placing anthocarps of each species into jars half filled with water and recording the number of days taken by each to sink to the bottom.

The actual movement of anthocarps under artificial wind conditions was measured. The mean distance moved was calculated for each species from distances moved by individual anthocarps placed, one at a time, at the same position in front of the wind source. Each anthocarp was allowed to move until it would no longer move. Because the wind velocity diminishes at distances away from the starting point, the anthocarps that moved the farthest may be said to require the lowest wind velocity to initiate their movement.

Germination was considered to determine: (1) effect of anthocarps on germination; and (2) seed and seedling salt tolerances. Seedlings were checked to note any damage to their development resulting from the pre-treatment of their seeds with either sea water or freshwater. Unfortunately, only preliminary germination studies were possible.

Because a seed does not always develop in every anthocarp, the number of seeds set per number of anthocarps developed in a single inflorescence was recorded for inflorescences from plants of each species. Dried materials

often fragment; therefore, fixed materials were used to obtain complete inflorescences.

Seed and anthocarp weights (Wilson, 1974) were used to calculate percent seed weight per total dispersal unit weight.

Surface area in mm^2 was measured for the broadest side from a graphic representation of the average anthocarp type considered to have the greatest dispersal potential in terms of wing and lobe categories. Surface area in mm^2 per 0.001 gram of dispersal unit weight was calculated from weight and surface area data. This ratio was used to estimate the potential for each anthocarp type to be moved by wind.

ANTHOCARP DISPERSIBILITY

Five criteria may be used to describe anthocarp dispersibility in the *Abronia* species studied: (1) anthocarp morphology; (2) weight distribution between seeds and anthocarps; (3) anthocarp weight to surface area ratios; (4) actual movement of the anthocarps under experimental conditions; and (5) anthocarp buoyancy in water (TABLE 1; Figs. 1-9).

When taken together, these criteria may be used to suggest potentials for anthocarp dispersal (TABLE 2; Fig. 10). Keep in mind that the actual dispersal of each species in its particular habitat depends upon local conditions and wind velocities. In the final interpretation of the actual dispersal of the anthocarps, at least three factors should be considered: (1) the availability of wind or water; (2) the distances between suitable sites for seedling establishment; and (3) the types of hazards or unsuitable habitats between suitable sites.

The absence of fleshy, edible portions on mature anthocarps suggests that they are not carried internally by animals. Likewise, no obvious anatomical structures are found in the anthocarps to suggest external animal transport.

Viscid trichomes on the exteriors of *Abronia maritima* Nutt. ex Wats. anthocarps remain sticky even when air dried, but are not believed sufficiently viscid to attach the anthocarps to either animal feathers or fur for significant distances. Perhaps the mucilage from these trichomes covers the anthocarp surfaces and makes them more buoyant.

Developing anthocarps do not all show the same degree of variability within their inflorescences. Anthocarp polymorphism (Wilson, 1974) may give the species a wider range of dispersal potentials. Morphological variability of anthocarps may be correlated with differential dispersibility both among the species and within a single species.

Anthocarps were cut open to reveal body cavity size and seed position for each of the nine species of *Abronia* studied (Figs. 1-9). Because seed and anthocarp sizes are so variable among the species, percent seed weight to total dispersal unit weight was calculated to facilitate a comparison of weight distribution between seeds and anthocarps of nine *Abronia* species (TABLE 1).

Percent seed weight percentages may be divided into three categories: (1) high, 80% + seed weight for *A. alpina* Bdg.; (2) intermediate, 40-60% seed weight for *A. nana* Wats. ssp. *covillei* (Heimerl.) Munz, *A. crux-maltae*

TABLE 1. Percentages of seed weight to total weight, mean mm² surface area per 0.001 gram, and results from movement by air and flotation experiments for the anthocarps and seeds of nine *Abronia* species.

Species and distance moved groups	Number of wings or lobes	Mean			Number of days taken for anthocarps to sink
		Percent ^a seed weight	mm ² /0.001 ^b gram	Distance moved by air (cm)	
EXTREMELY SHORT					
<i>A. alpina</i>	0	81	1.5	201	1.5
SHORT					
<i>A. latifolia</i>	5	19	1.6	274	9.5
<i>A. maritima</i>	5	13	1.7	300	15.0
<i>A. turbinata</i>	0	71			4.0
	3-5	53	3.9	300	5.5
LONG					
<i>A. umbellata</i>	0	40			3.5
	3-5	27	5.1	371	3.5
<i>A. pogonantha</i>	0	74			3.5
	2	50	8.6	373	4.0
	3	55			4.0
<i>A. nana covillei</i>	5	43	8.1	419	4.0
<i>A. villosa</i>	0	21			3.5
	1-2	25			3.5
	3-5	20	4.9	422	3.5
EXTREMELY LONG					
<i>A. crux-maltae</i>	2-4	46	9.4	455	2.0

^a Mean anthocarp plus seed weights from Wilson (1974) and mean seed weights from Wilson (1975).

^b Surface areas measured for one side of an anthocarp from a graphic representation of a typical anthocarp for each species.

Kell., *A. pogonantha* Heimerl., and *A. turbinata* Torr.; and (3) low, about 10-30% seed weight for *A. maritima* Nutt. ex Wats., *A. latifolia* Eschs., *A. umbellata* Lam., and *A. villosa* S. Wats., respectively.

Surface area per dispersal unit weight, mm² per 0.001 gram, was used to estimate the potential of anthocarps for wind dispersal. Anthocarps with a high surface area to weight ratio are considered to have a high potential for movement by wind in contrast to anthocarps with lower surface area to weight ratios. Based on surface area to weight ratios alone (TABLE 1) the potential for dispersal by wind may be represented by four categories: (1) low for *A. alpina*, *A. maritima*, and *A. latifolia*; (2) intermediate for

←

Figs. 1-9. Anthocarps of nine *Abronia* spp. cut open to show relative seed size and position, and body-cavity size.—1. *Abronia maritima*.—2. *A. latifolia*.—3. *A. umbellata*.—4. *A. villosa*.—5. *A. turbinata*.—6. *A. nana covillei*.—7. *A. pogonantha*.—8. *A. alpina*.—9. *A. crux-maltae*.

A. turbinata, *A. umbellata*, and *A. villosa*; (3) high for *A. nana covillei* and *A. pogonantha*; and (4) extremely high for *A. crux-maltae*.

Abronia species are presented in TABLE 1 according to four actual distance-moved categories as follows: (1) extremely short, below 210 cm; (2) short, between 211 cm and 310 cm; (3) long, between 311 cm and 425 cm and (4) extremely long, 426 cm and above. Anthocarps that move only short distances are considered to require the highest wind velocities to initiate their movement.

Low dispersal potentials and short distances moved in anthocarps of *A. alpina*, *A. maritima*, and *A. latifolia* result from two different anthocarp conditions. Anthocarps of *A. maritima* and *A. latifolia* are extremely large and bulky as indicated by their low percent seed weight percentages and low surface areas per 0.001 gram; whereas the anthocarps of *A. alpina* are small and wingless with a high percent seed weight and a low surface area per 0.001 gram.

During movement experiments the small tapered ends of *A. turbinata* anthocarps were observed to turn toward the direction of the moving air allowing the air to move across their surfaces and hold them down. When turned sideways to the moving air, the anthocarps were not moved forward but were repositioned by the moving air.

Abronia villosa appears to move farther than would be expected according to its dispersal potential (TABLE 1). Perhaps the alternating convex and concave surfaces of its wings aid in providing this anthocarp with a greater potential for movement than can be estimated from surface area to weight ratios alone. In the field *A. villosa* anthocarps were observed to spin along the ground in the wind turning like propellers.

Although the dispersal units of *A. pogonantha* have a high potential for movement, they fall short of this calculated potential during experiments. Wings, in *A. pogonantha*, are small and develop at a 180° angle of each other on the most common two-winged type. Because this anthocarp type is very flat, when on a flat surface, there is little exposed structure to catch the moving air.

Slightly inflated crests at the tops of the lobes of *A. nana covillei* anthocarps provide extra surface area which increases their potential for movement, regardless of wind direction.

Although the anthocarps of *A. crux-maltae* generally develop only two main wings, they usually develop a third or fourth smaller wing or ridge perpendicular to the larger wings. These anthocarps are set at an angle by the smaller wings. During experiments turbulence appeared to build up under the tilted edges of these anthocarps, even at low wind velocities, and would cause them to move along a few centimeters at a time in a stop-and-go fashion.

Upon closer examination of the data in TABLE 1, the relationship of the effects of surface area to weight ratio and percent seed weight to total dispersal unit ratio on the actual movement of the anthocarps under artificial wind conditions can be identified.

Although the surface area to weight ratios are similar for *A. nana covillei* (8.1 mm²/0.001 g) and *A. pogonantha* (8.6 mm²/0.001 g), *A. nana covillei*

traveled 11% farther with 6% less surface area per 0.001 g but 14% less percent seed weight.

The surface area to weight ratios are similar for *A. villosa* ($4.9 \text{ mm}^2/0.001 \text{ g}$) and *A. umbellata*, yet, *A. villosa* traveled 12% farther with 4% less surface area per 0.001 g but 26% less percent seed weight.

The surface area to weight ratios are similar for *A. alpina* ($1.5 \text{ mm}^2/0.001 \text{ g}$) and *A. latifolia* ($1.6 \text{ mm}^2/0.001 \text{ g}$), yet, *A. latifolia* traveled 27% farther with 6% more surface area per 0.001 g and 77% less percent seed weight.

The surface area to weight ratios are similar for *A. alpina* and *A. maritima* ($1.7 \text{ mm}^2/0.001 \text{ g}$), yet, *A. maritima* traveled 33% farther with 12% more surface area per 0.001 g and 84% less percent seed weight.

These comparisons demonstrate that when surface areas are similar percent seed weight becomes a major factor in the actual movement of the anthocarps.

Interestingly, *A. turbinata* ($3.9 \text{ mm}^2/0.001 \text{ g}$) and *A. maritima* ($1.7 \text{ mm}^2/0.001 \text{ g}$) moved the same distance, 300 cm. *Abronia turbinata* anthocarps were found to have 56% more surface area per 0.001 g, but 75% more percent seed weight than *A. maritima*.

A similar comparison may be made between *A. villosa* and *A. nana covillei*. *Abronia nana covillei* anthocarps fell short of the distance traveled by *A. villosa* anthocarps by only 0.7% with 40% more surface area per 0.001 g, but had 53% more percent seed weight than *A. villosa*.

When *A. villosa* and *A. crux-maltae* ($9.4 \text{ mm}^2/0.001 \text{ g}$) anthocarps are compared, *A. crux-maltae* anthocarps moved 7% farther with 48% more surface area per 0.001 g and 56% more percent seed weight.

Weight distribution, general morphology, and the size of the body cavity of the anthocarps are all related to the potential buoyancy of the dispersal unit in water. Data from flotation experiments are recorded in TABLE 1. An anthocarp with a large body cavity and thick parenchymatous anthocarp walls may be expected to float, e.g., *A. maritima* (Fig. 1). In fact, *A. maritima* anthocarps remained afloat much longer than anthocarps of other species. Some took up to 18 days to sink. Anthocarps of *A. latifolia* were also found to be relatively more buoyant when compared to anthocarps of other species. Both *A. maritima* and *A. latifolia* are coastal species.

The two species found to contain the least buoyant anthocarps, *A. alpina* and *A. crux-maltae*, are found growing in habitats away from major waterways. The small anthocarps of *A. alpina* (Fig. 8) were held on the surface of the water by surface tension. When the water was swirled slightly, some of these anthocarps sank immediately.

The thin wings of *A. crux-maltae* anthocarps showed no special resistance to water uptake and absorbed water quickly. Buoyancy is reduced further in *A. crux-maltae* anthocarps by the limited air space between the body cavity and its large seed (Fig. 9).

Anthocarps of *A. umbellata* appear not to have any special capacity for long-term flotation, yet this species occurs on offshore islands.

Four important parameters can be taken from TABLE 1 and standardized for the sake of comparison. Relative percentages for these four parameters are recorded in TABLE 2.

TABLE 2. Relative percentages of percent seed weight per total weight, mm² surface area per 0.001 gram, distance moved by air and flotation times for the anthocarps and seeds of nine *Abronia* species.

Species and habitat groups	Number of wings or lobes	Relative Percent			
		Percent ^a seed weight	Surface ^b area	Distance ^c moved	Flotation ^d time
COASTAL					
<i>A. maritima</i>	5	16	18	66	100
<i>A. latifolia</i>	5	23	17	65	63
<i>A. umbellata</i>	3–5	33	54	81	23
DESERT					
<i>A. villosa</i>	3–5	25	52	93	23
<i>A. pogonantha</i>	2	62	91	82	27
<i>A. crux-maltae</i>	2–4	57	100	100	13
MONTANE					
<i>A. nana covillei</i>	5	53	86	92	30
<i>A. turbinata</i>	3–5	65	41	66	37
<i>A. alpina</i>	0	100	16	44	10

^a 81 percent seed weight per total weight equals 100%.

^b 9.4 mm²/0.001 gram equals 100%.

^c 455 cm moved by air motion equals 100%.

^d 15 days taken to sink equals 100%.

Extremes among the *Abronia* species for dispersibility potentials as seen in *A. maritima*, *A. crux-maltae*, and *A. alpina* anthocarps are dramatized by the graphic representation of their relative percentages for: (1) relative percent seed weight; (2) relative surface area; (3) relative distance moved; and (4) relative flotation time (Fig. 10).

In *A. maritima*, anthocarps show a low potential for movement by wind but float far longer than those of any other species tested. The anthocarps of *A. maritima* scored the lowest relative percent seed weight, a low relative percent surface area, a low relative percent distance moved, and the highest relative percent flotation time.

In *A. crux-maltae*, anthocarps have an extremely high potential for wind dispersal and an extremely low potential for flotation. The anthocarps of *A. crux-maltae* scored an intermediate relative percent seed weight, the highest relative percent surface area, the highest relative percent distance moved and the next to the lowest relative percent flotation time.

In *A. alpina*, anthocarps lack any special potential to be conveyed by either wind or water other than in some fortuitous way. *Abronia alpina* is considered an example of reduced dispersibility within the genus (Wilson, 1970). The anthocarps of *A. alpina* scored the highest relative percent seed weight, the lowest relative percent surface area, the lowest relative percent distance moved, and the lowest relative percent flotation time.

Fig. 10. Representation of four dispersal-potential parameters as relative percentages for three *Abronia* spp. from diverse habitats: flotation time; distance moved by artificial wind; percent seed weight to total dispersal unit weight; and surface area in mm^2 per 0.001 gram. Habitats included are coastal foredunes for *A. maritima*, widely scattered Carson Desert dunes for *A. crux-maltae*, and high, sandy, meadow edges in the southern Sierra Nevada for *A. alpina*. Relative percentages are taken from TABLE 2.

SURVIVAL AFTER DISPERSAL

Abronia species often occur near saline environments; therefore, some degree of salt tolerance or protection from salt is predicted for the seeds, since many dispersing anthocarps may fall into or cross areas of high salinity.

Preliminary germination studies suggest that the anthocarps of some *Abronia* species may inhibit germination until ample leaching has been accomplished. Thus, the seeds presumably would germinate in the presence of low-salt soils and ample water. In *Atriplex halimus* L. seedlings do not tolerate the same high sodium chloride concentrations as the adult forms. Successful germination occurs after heavy rains when the salt content of the habitat reaches its lowest salt level (Mayer and Poljakoff-Mayber, 1963). Beadle (1952) and Kadman-Zagavi (1955) both reported that the dispersal unit of *Atriplex* species (morphologically bracts fused around the fruit and seed) inhibits germination. Soaking for at least 24 hr is required to leach out the inhibitors in the bracts and fruit.

Some parallels can be drawn between *Atriplex* and *Abronia* species, often associated in similar xeric habitats. Seeds of all but one species of *Abronia* tested did not germinate when left in their anthocarps without at least 48 hr leaching time. Only the seeds of *A. nana covillei* were found to germinate and grow inside their anthocarps without leaching. Seeds and seedlings of *A. villosa* and *A. alpina* showed the capacity to grow after a sea water soaking. The seedlings of *A. pogonantha* and *A. turbinata* (known to reach montane as well as desert habitats), and *A. nana covillei* showed little salt tolerance. Seeds of these species pretreated with sea water, germinated but their radicles did not grow normally and soon became deformed.

Because seeds of *A. pogonantha* and *A. turbinata* did not germinate until their seed coats were removed, it appears that their seed coats may inhibit embryo growth until adequate pretreatment, possibly leaching, has occurred.

SELECTIVE IMPACT OF SEED LOSS THROUGH DISPERSAL

The total number of seeds produced over a period of time by a population depends in part on: (1) the size of the individual plants; (2) the length of the growth season (regulated in part by annual or perennial habits); (3) the breeding system; and (4) the presence or absence of effective pollinators throughout the blooming season. After the seeds are produced they may be eaten or destroyed in a number of ways. Unfortunately, only a guess at the full impact of anthocarp dispersal on seed loss or establishment can be made.

Seed longevity was not tested, but certainly must be important for the carry-over of viable seeds from one year to the next. Seeds of *A. villosa* collected in 1968 germinated in low percentages (30%) in the fall of 1975. One may only imply that large numbers of seeds are carried over through the drier years in a dormant condition.

Differences in seed production which occur among the nine species of *Abronia* studied are presented in TABLE 3.

Low seed-set percentages and total numbers of seeds per inflorescence in the coastal species, *A. latifolia*, *A. maritima*, and *A. umbellata*, indicate a reduced reproductive capacity for the populations sampled. In these three species individual plant size is large and the blooming period may extend throughout the year under favorable weather conditions. All other species listed in TABLE 3, except *A. alpina*, showed relatively high seed-set percentages and total numbers of seeds per inflorescence. Although *A. alpina* develops only 4-5 flowers and only 2-3 seeds per inflorescence on the aver-

TABLE 3. Mean numbers of seeds and anthocarps, and seed-set percentages per inflorescence for nine species of *Abronia*.

Species and habitat groups	Mean no. seeds	Mean no. anthocarps	Percent seeds per inflorescence
COASTAL			
<i>A. maritima</i>	3.9	11.2	34
<i>A. latifolia</i>	2.0	16.8	12
<i>A. umbellata</i>	5.3	12.7	42
DESERT			
<i>A. villosa</i>	15.1 ^a	19.3	78
	19.0 ^b	19.8	95
<i>A. pogonantha</i>	15.2	19.4	78
<i>A. crux-maltae</i>	15.4	15.6	99
MONTANE			
<i>A. turbinata</i>	24.6	32.4	76
<i>A. nana covillei</i>	14.1	18.0	79
<i>A. alpina</i>	2.3	4.0	56

^a Plants from Thousand Palms, California.^b Plants from Basin Road on Highway 15, California.

age, it has a 56% seed-set percentage. This percentage is still higher than percentages recorded for the coastal species.

The highest average number of seeds (24) per inflorescence is recorded for *A. turbinata* (TABLE 3).

ECOLOGICAL IMPLICATIONS

Müller's (1955) paper contains a summary of data collected by earlier workers on the dispersal of fruits and seeds, but information is not included for *Abronia* although *Atriplex* and *Rumex* L. species were sampled in detail.

Wind can be incidentally related to the movement of most seeds or fruits. The importance of wind as a primary dispersal agent for anthocarps of *Abronia* species only becomes evident when the anthocarps of one species are moved by wind to significantly greater distances than the anthocarps of other species. Likewise, if the anthocarps of a species are significantly more buoyant than those of another species, then water may be important for their dispersal.

Of the species studied, perennials tended to grow in coastal and montane habitats, while annuals were typically found in desert habitats (Wilson, 1972).

Plant habit, size, and habitat are considered for *A. maritima*, *A. villosa*, *A. crux-maltae*, *A. alpina*, *A. nana covillei*, and *A. turbinata* to illustrate their possible relationship to anthocarp evolution in *Abronia*.

Species in coastal habitats are known to hybridize when sympatric (Tillett, 1967). In the populations of *A. maritima* studied, seed-set percentages and total numbers of seeds per inflorescence were low. The perennial habit of this species which may produce seeds over long periods may be compensating for its otherwise lowered seed production. Individuals of *A.*

maritima, situated on foredunes where anthocarps may be washed or blown into the sea, may benefit from buoyant anthocarps that can float even for short distances and then be cast back onto the beach. Because *A. maritima* does not compete well inland (Purer, 1936), dispersal by wind to any distance from the foredune habitat must result in seed loss.

High seed-set percentages and total numbers of seeds per inflorescence were recorded for the desert species. These high figures are possibly correlated with an annual habit and a general isolation of these species from one another.

Abronia villosa grows in the hottest and driest parts of the Sonoran, Colorado, and Mojave deserts often near saline lakes or alkaline flats. The hard bodies of *A. villosa* anthocarps may protect the seeds from desiccation or salt damage. In the southern deserts where strong winds are common, winged anthocarps may be blown long distances. Anthocarp polymorphism, a striking characteristic in *A. villosa*, results in a wide array of dispersal unit shapes and weights, each with a different potential for movement. Some anthocarps may be dispersed over long distances while others may remain near their site of origin. Further, anthocarps of *A. villosa* are sufficiently buoyant to be transported during flash floods. Seeds of this relatively weedy species germinate after late summer rains and may come into bloom by fall. Plants may grow through the winter and continue to bloom well into the summer provided adequate moisture.

The small, delicate annual plants of *A. crux-maltae* were recorded to have the highest seed-set percentages for any of the nine species studied. Narrow soil tolerances, widely scattered dune habitats, an annual habit, and high fertility appear to be correlated with the evolution of anthocarps which are easily dispersed by wind. That the anthocarps of this species show both the highest potential for wind dispersal and the longest actual distance moved during wind experiments is no surprise.

Montane species, except *A. alpina*, generally produce intermediate to high numbers of seeds per inflorescence, and have good seed-set percentages. In *A. alpina* the total number of seeds produced per year is low because individual plants are small, numbers of flowers per inflorescence are low, and its growing season is generally short. This small perennial shows low actual anthocarp movement by wind and a low calculated potential for wind dispersal. These anthocarps do not float for very long. The wingless anthocarps in *A. alpina* are not difficult to postulate when so many *Abronia* species are known to develop both wingless and winged anthocarps in the same inflorescence. Under natural conditions seeds of *A. alpina* may be lost when they reach the adjacent meadows where they cannot grow. High dispersibility may have a negative selective value for this species. High dispersibility would carry seeds away from ecologically suitable habitats, especially where suitable sites are separated by wide unsuitable areas and ridges. Therefore, reduced dispersibility may be favored as anthocarps with the best dispersibility continue to be lost (Wilson, 1970).

Abronia nana covillei appears to have evolved toward more efficient dispersibility at low wind velocities, typical of montane habitats. Because *A. nana covillei* has a perennial habit and a good reproductive capacity, at

least from the standpoint of numbers of seeds produced, the continual dispersal of its anthocarps may not have the same negative effect for this species as is implied for *A. alpina*. The populations of this species are isolated in much of its range. In the Big Bear area it has become rare. The anthocarps of this species are relatively thin walled and are perhaps harvested by animals for their seed. Many questions remain to be answered concerning the ecology of *A. nana covillei*. The caespitose habit and extensively branched, well-developed root system of *A. nana covillei*, unlike those found in either the desert or coastal species, suggest a long evolutionary history as a perennial for this species. By contrast, coastal perennials look much like enlarged, overgrown annuals.

In *A. turbinata*, annuals with a good potential for anthocarp dispersal are prevalent in populations which grow at the lower, drier, elevations of its range where unsuitable habitats are easily crossed by wind-blown dispersal units. In contrast, perennials with lower potential for anthocarp dispersal are common in populations of the more mesic, higher elevations where suitable habitats are widely separated and isolated by mountain ridges. Reduced dispersibility among the high-elevation populations may lead to ever greater isolation of the populations. Evolution toward reduced seed loss and increased productivity may explain the increased frequency of smaller anthocarp lobes and perennial plants in isolated high-elevation populations of *A. turbinata*.

The following are believed to be of adaptive value because they are interpreted as increasing the chances for some seedling establishment in ecologically suitable sites for the species listed: (1) extremely buoyant anthocarps and perennial habit in *A. maritima*; (2) anthocarp polymorphism and weedy annual habit in *A. villosa*; (3) anthocarps with a high potential for wind dispersal and large seeds in *A. crux-maltae*; (4) anthocarps with a capacity for dispersal at low wind velocities and perennial habit with a high reproductive capacity in *A. nana covillei*; (5) reduced anthocarp lobes, perennial habit, and high numbers of seeds per inflorescence for populations of *A. turbinata* in the more mesic, isolated parts of its range; and (6) wingless anthocarps with low dispersibility and perennial habit in *A. alpina*.

SUMMARY

Field observations, morphological data, and experimental findings are combined with information about the distribution and habitats of each species.

Adaptive changes toward increased or decreased anthocarp dispersal by wind or water are postulated for nine *Abronia* species.

Anthocarp and seed weights, and anthocarp dimensions were used to calculate dispersal potentials which are contrasted with the actual movement of the anthocarps tested under artificial wind conditions.

Anthocarp dispersibility, survival after dispersal, and selective impact of seed loss through dispersal are discussed. Seed germination, seedling salt tolerance, and reproductive capacity are discussed as being relevant to an interpretation of the evolution of dispersal mechanisms in *Abronia* species.

Because *Abronia* species seem adapted to intermittent, unstable, nonsaline, pioneer habitats, often adjacent to saline or otherwise ecologically closed environments, it is hypothesized that the anthocarps and seeds of most of the species of *Abronia* examined have evolved in such a way that wind-blown or sea-drifted dispersal units are moved across ecologically unsuitable habitats into pockets of suitable habitats where the seedlings may grow.

Extremes in anthocarp modifications are represented by *A. maritima*, *A. crux-maltae*, and *A. alpina*.

The combination of percent seed weight per total dispersal unit weight, surface area in mm² per 0.001 gram, actual distance moved under artificial wind conditions, and flotation time anthocarp characteristics suggests that: (1) in *A. maritima*, from coastal foredune habitats, anthocarps have evolved toward flotation; (2) in *A. crux-maltae*, from Carson Desert dunes, anthocarps have evolved toward wind dispersal; and (3) in *A. alpina*, from sandy borders of alpine meadows of the southern Sierra Nevada, anthocarps have evolved toward reduced dispersibility.

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