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## HYDRATION HISTORY AND ATTACHMENT MORPHOLOGY REGULATE SEED RELEASE IN *CHORIZANTHE RIGIDA* (POLYGONACEAE), A SEROTINOUS DESERT ANNUAL<sup>1</sup>

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- **Premise of the study:** Most seed dispersal studies focus on the spatial aspects of propagule dissemination, i.e., the movement of seeds away from the mother plant. However, the timing of seed release can also be a critical variable influencing the probability of seedling survival. We used a biomechanical approach to analyze seed release in *Chorizanthe rigida*, a serotinous desert annual, to understand the adaptive significance of seed retention in this species.
- **Methods:** We performed pull-to-break tests on individual propagules (i.e., involucre and achene) from newly developed and older plants, under dry and wet conditions, and recorded the breaking force. We measured the involucral base area using digital images and image processing software.
- **Key results:** There is a positive correlation between the force required to detach an involucre and the size of its base area. The force required to detach involucres from soaked and older plants was lower than that for dry and new plants. This pattern provides a mechanism for the plant to regulate the number of involucres released in different rain events.
- **Conclusions:** Seed release in *C. rigida* is mediated by propagule morphology, rainfall conditions, and age of the dry plant. These factors allow this species to cope with desert environmental variability by influencing the timing and number of seeds released.

**Key words:** *Chorizanthe rigida*; delayed dispersal; desert serotiny; hygrochasy; plant biomechanics; Polygonaceae.

Seed dispersal begins with the release of the seed into the environment, continues with movement of the seed away from the mother plant, and culminates with germination of the seed (van Rheede van Oudtshoorn and van Rooyen, 1999). Either by delivering the seed to a suitable site or by enabling the use of an ephemeral resource pulse, this process is decisive; the seed is the most mobile life-stage of a plant and will greatly determine whether a plant will survive to produce more seeds. In pulse-driven ecosystems, such as deserts, where rains are infrequent and unpredictable, the timing of seed release is crucial because low soil moisture limits germination and seedling survival (Noy-Meir, 1973). In some desert plants, seed release is triggered by rainfall, a hygrochastic seed dispersal mechanism that allows them to synchronize seed release with high water availability (Friedman et al., 1978; van Rheede van Oudtshoorn and van Rooyen, 1999; Gutterman, 2002; Hegazy et al., 2006). Furthermore, in arid ecosystems with unpredictable rainfall, variability in the percentage and timing of seed germination can increase the probability of survival by allowing only a portion of the seed bank to germinate while the rest stays dormant to germinate during later water pulses as a bet-hedging strategy (Philippi, 1993;

Gutterman, 2002). Although delayed seed dispersal has received less attention, it may also contribute to variability in seed germination in serotinous desert plants, which form aboveground seed banks by retaining seeds on the mother plant and releasing fractions of them after a rainfall event for several years depending on the amount and frequency of rainfall (Friedman et al., 1978). Here we studied the mechanism of seed release in a serotinous desert plant, *Chorizanthe rigida* (rigid spineflower, Polygonaceae), using a biomechanical approach.

Biomechanics has been used to study four mechanisms of seed dispersal: (1) the kinematics of explosive dispersal of spores, pollen, and seeds with ballistic or catapult mechanisms (Witzum and Schulgasser, 1995; Murren and Ellison, 1998; Read and Stokes, 2006; Taylor et al., 2006; Endo et al., 2010; Hayashi et al., 2010; Martone et al., 2010; Evangelista et al., 2011); (2) the lift-to-drag, descent rate, and dispersal distance of wind dispersed winged propagules that exhibit “passive” dispersal (Greene and Johnson, 1993; Peroni, 1994; Vogel, 2003; Read and Stokes, 2006; Lentink et al., 2009); (3) the effect of wind on abscission, release, and dispersal distance of wind-dispersed propagules (Greene, 2005; Marchetto et al., 2010); and (4) the brittleness or ease-of-fracture of branches or stem segments for vegetative reproduction (Beismann et al., 2000; Bobich and Nobel, 2001). What all these mechanisms have in common is that they are concerned with the movement of propagules away from the mother plant, that is, how the dispersal distance is biomechanically determined. A less explored topic is the ecological and evolutionary significance of the timing of seed release. In many plants, seed release is not a random event

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(Greene, 2005; Marchetto et al., 2010) and may play a critical role in successful establishment, as the time when embryos are released to the environment has potentially important demographic consequences. In the case of species with rain-triggered dispersal mechanisms that have evolved in arid ecosystems with highly variable precipitation, the ability to release seeds after a favorable rainfall event or to regulate the number of seeds released is directly related to the plant's fitness.

*Chorizanthe rigida* is a winter desert annual, growing only 2–10 cm high, and found across the Sonoran and Mojave deserts of North America. It forms an aboveground seed bank by

retaining seeds in its lignified, spiny, stout stems for several years (Fig. 1A). Its seed dispersal is triggered by rainfall events. The seeds, contained in involucre formed by three bracts holding one central achene (Fig. 1B), are held on to the branch by a hygrochastic-tissue base that swells and softens when wet, allowing the detachment of the whole dispersal structure or propagules (achenes + involucres) when triggered by the pounding of raindrops (Fig. 1C, D). Undispersed involucres remain attached to the plant as the lignified tissues redry (Ellner and Shmida, 1981; van Rheede van Oudtshoorn and van Rooyen, 1999; Felger, 2000; Baldwin et al., 2002). The involucres of

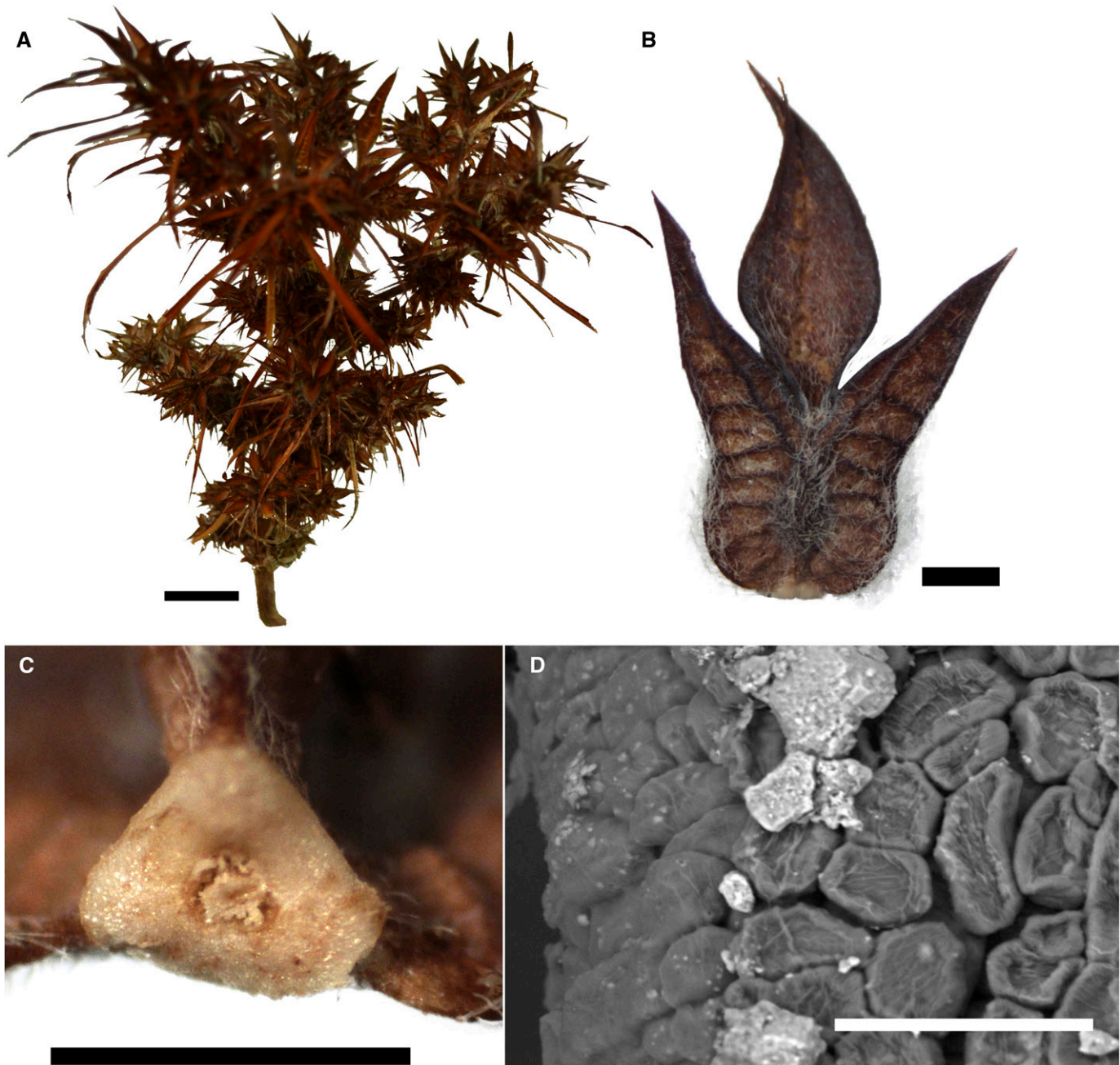


Fig. 1. (A) *Chorizanthe rigida* whole dry plant, (B) involucre, (C) involucre base, and (D) electron-microscope image (1500 $\times$ ) of dehydrated cells of the dehiscence tissue at the base of the involucre.

*C. rigida* and their hydrochastic dehiscent tissue vary in size within individuals and among populations (Felger, 2000). Because the base of the involucre controls seed release, such size variation can have important consequences for both the timing of seed release and the number of propagules released in response to environmental conditions.

Here we explored the relationship between the basal cross-sectional area of involucre pedicels of *C. rigida* and their ease of release. We tested the hypothesis that for pedicel base area to be a selective trait contributing to the plant's fitness there should be a correlation between these two variables. We employed a biomechanical approach to measure the force needed to detach propagules. We predicted that the force needed to detach involucres with larger base areas will be higher than that used for involucres with smaller base areas. We also predicted that wet involucres would detach more easily than dry involucres and that the force needed to detach involucres from older plants (i.e., plants from past years) would be lower than that needed for newly grown plants.

## MATERIALS AND METHODS

**Sampling**—Individuals of *Chorizanthe rigida* were collected from populations in the Mojave and Sonoran deserts in California (USA), in the central part of the biogeographic range of the species. Plants belonging to the 2009–2010 cohort were collected at the end of the growth season (summer 2010) to avoid tissue weathering and decomposition. To perform additional tests on the effect of weathering on seed release, we also collected individuals that showed visible signs of weathering, indicating they had established at least 1 yr before the 2009–2010 cohort.

**Tensometer experiment**—The force causing involucre detachment ( $F_b$ , breaking force) was measured by conducting pull-to-break tests using a tensometer. The tensometer consisted of a precision scale attached to a Test Stand for Force Gauge (Phase II AFG-1000, Calright Instruments, San Diego, California, USA). Either a Pesola Micro-Line Spring Scale (PESOLA AG, Baar, Switzerland; capacity: 1 N, precision: 0.01 N) or a Pesola Medio-Line Spring Scale (capacity: 3 N, precision: 0.02 N) was used depending on the size of the involucre. To improve readability, we used a drag-pointer recorder in the medium-line (3 N) scale to mark the breaking force, whereas for microscale readings (<1 N) breaking force was recorded visually because friction in the drag-pointer could add significant bias in very low readings. The crocodile clamp at the other end of the scale was directly attached to large involucres (Fig. 2). Smaller involucres were secured with a mini surgical clamp (Mini Bulldog Serrefines, Fine Science Tools, Foster City, California, USA) with a serrated jaw of 6 × 22 mm dimensions) that was attached to the crocodile clamp.

During measurements, each individual was tightly secured on a vise from its taproot at the base of the plant, and the crocodile or hemostatic clamp was placed at the seed holding portion of the involucre while still dry. Care was taken to place the plant so that the involucre–clamp–pesola system was at a 90° angle from the workbench. If the involucre was not released after applying the force, it was manually removed to avoid reusing the same involucre twice. Information on release or no-release was also recorded. After setting up the involucre to the clamp, we initially measured the force needed to release dry involucres. Afterward, we measured wet involucres by applying water with a dropper to soak the entire involucre. The smallest involucres soften quicker and were tested ca. 5 min after soaking, the medium-size involucres were tested after ca. 15 min, and the largest involucres were given 30 min to soak before testing. The period of wetting was decided according to the range of the measuring instruments. Tensile force was applied by releasing the lever of the stand at a slow and constant rate until the involucre was released from the plant, and breaking force ( $F_b$ ) was recorded. Not all involucres could be tested because after initial wetting many of the smaller propagules became so loose that they were released as they were attached to the mini-clamp, before any tensile strength could be applied. Conversely, some of the larger involucres failed to detach within the force range of our largest tensometer (3 N). The basal cross-sectional area of these recalcitrant involucres was significantly larger than that

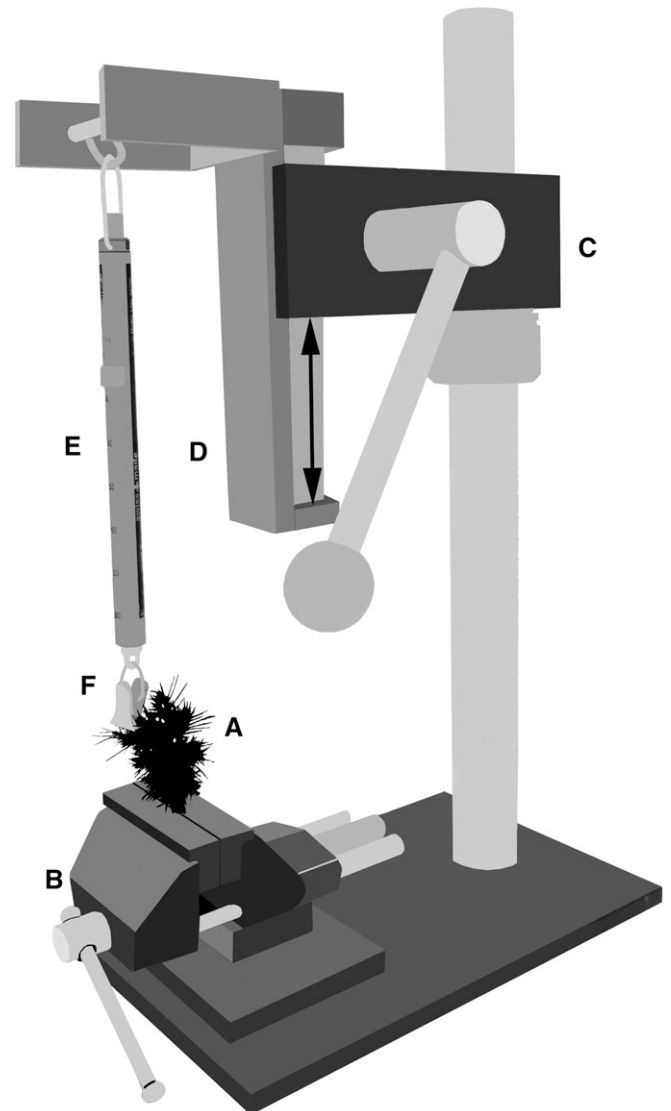


Fig. 2. Tensometer set-up consisting of (A) individual of *Chorizanthe rigida* (B) clamp, (C) stand, (D) mobile gauge-holding device, (E) force gauge, and (F) a crocodile clamp. The gauge-holding device is activated mechanically; it is placed at the lowest end of its mobility range by turning the lever counter-clockwise. Releasing the lever causes the device to move upward applying tensile force to the clamped propagule.

of the experimentally detached ones ( $1.32 \pm 0.09 \text{ mm}^2$  vs.  $0.86 \pm 0.03 \text{ mm}^2$ ;  $t = 4.67$ ;  $df = 53$ ;  $P < 0.0001$ ).

**Morphological measurements**—Involucre images (frontal and base views) were obtained using a dissecting scope (Nikon SMZ 745T) and a digital camera (Infinity 1). Two morphometric variables were measured from the involucre images: (1) involucre base cross-sectional area and (2) the area of the seed receptacle in the involucre (referred hereafter as involucre size), measured as the projected area of the involucre's central "belly", without the bracts. Areas were defined with points marked using a custom program made in Matlab 7.5 with the Image Processing Toolbox 6.0 (MathWorks, Natick, Massachusetts, USA).

**Statistical model and analyses**—We performed two separate analyses. First, we analyzed data from new plants that had been subject to involucre soaking. We obtained breaking force estimates for a total of 221 involucres (we did not include data from involucres that did not detach during the tensile test). We tested for a linear relationship between the breaking force measured experimentally

and the pedicel base cross-sectional area with an intercept of zero. We also tested the effect of involucre size as a covariate in a linear model to analyze the possible additive effect of involucre size on the breaking force.

Second, we analyzed the effect of the base area, wetting (with two levels: wet and dry), and weathering (with two levels: old and new) on the force needed to release the involucre, and the interactions between base area and wetting, base area and weathering, and hydration and weathering. We also tested whether wetting, weathering, and their interaction affected the breaking strength (force divided by the base area). A total of 253 involucre were examined in this second analysis, including new and older plants, tested under dry and wet conditions, and excluding those involucre that did not detached under the maximum tensile force of our equipment.

## RESULTS

In the analysis of new plants, we found a significant positive correlation between the force necessary to detach the involucre and the base area ( $r^2 = 0.42$ ;  $F_{1,219} = 156.8$ ;  $P < 0.0001$ ), and the intercept did not differ significantly from zero ( $-0.96 \pm 0.60$ ;  $P = 0.11$ ; Fig. 3). The mean squares regression slope, an indication of the average tensile strength of the tissue, was  $6.1 \pm 0.9$  (SE)  $\text{kN/m}^2$  (the standard unit of  $1 \text{ kN/m}^2$  is equivalent to a breaking force of  $1 \text{ mN/mm}^2$  of involucre base cross-sectional area). We did not find a correlation between breaking strength (in  $\text{kN/m}^2$ ) and the base area of the involucre ( $r^2 = 0.006$ ;  $F_{1,221} = 1.257$ ;  $P = 0.263$ ), suggesting that breaking stress is constant for all base areas. Additionally, once the main effect of base area had been included into the model, we analyzed the effect of involucre size on the force needed to detach the involucre, and we did not find a significant effect ( $r^2 = 0.01$ ;  $F_{1,219} = 2.7$ ;  $P = 0.1$ ), in accordance with the hypothesis that base area resistance is independent of propagule size.

In the second set of analyses, we found a significant effect of base area, hydration, weathering, and the interaction between base area and hydration, base area and weathering, and hydration and weathering. However, quantitatively, most of the variation was explained by base area and hydration (Fig. 4; Table 1). In agreement with these results, we also found a significant effect of hydration, weathering, and the interaction between

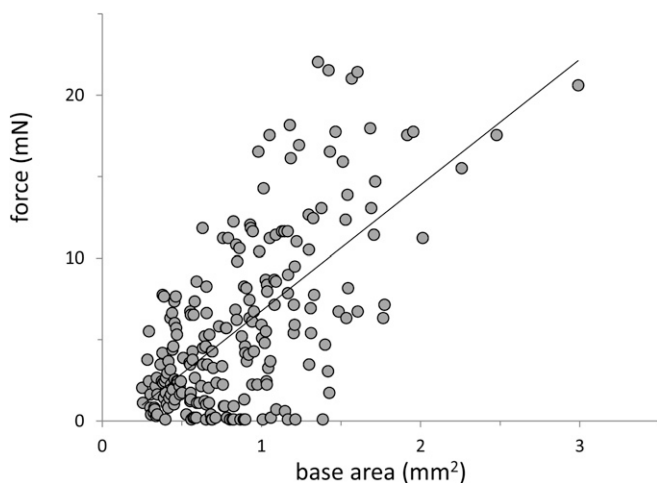


Fig. 3. Correlation between involucre base area and the force ( $F$ ) necessary for involucre detachment ( $r = 0.65$ ;  $df = 219$ ;  $P < 0.0001$ ). The slope of the fitted least-squares line defines the mean breaking strength, or area-specific tensile breaking force ( $F_b = 6.1 \pm 0.9 \text{ kN/m}^2$ ).

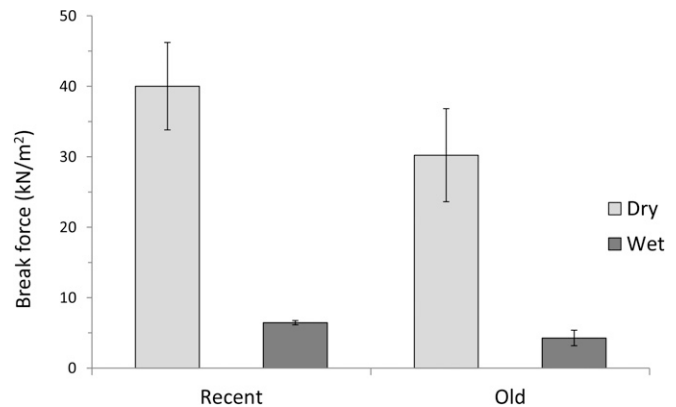


Fig. 4. Effects of plant age and pedicel wetting on the involucre breaking force (mean  $\pm$  SE;  $n = 3$  for recent plants with dry pedicels,  $n = 221$  for recent wet,  $n = 6$  for old plants with dry pedicels,  $n = 26$  for old wet). Different letters indicate significantly different ( $P < 0.05$ ) means for a  $t$  test with unequal sample sizes.

hydration and weathering on breaking stress, with a quantitatively larger effect of hydration (Table 2).

## DISCUSSION

The force needed to detach involucre and the base area of involucre was positively correlated in new plants subjected to soaking (Fig. 3), indicating that thicker pedicels tend to retain seeds more strongly than thinner ones. We also found a significant effect of wetting and weathering on the force needed to detach the involucre (Fig. 4). Thus, given similar bases, wet and older involucre release seeds more easily than involucre that are dry or have not been subject to weathering. Collectively, these results indicate that seed release in *C. rigida* is regulated by the biomechanical properties of the involucre pedicel. On the other hand, we did not find a positive correlation between the area-specific tensile strength and the cross-sectional area of the involucre, implying that the mechanical properties of involucre pedicels were similar for all sizes. The force needed to detach a propagule from a plant is best predicted as the product of the tensile strength of the base of the pedicel and its cross-section area, as predicted by standard material resistance theory (Vogel, 2003).

In *C. rigida*, as in other hygrochastic species, the determinants of pedicel softening and seed release are related to the properties of cells and tissues. The biomechanical properties of plant tissues are greatly determined by the cell wall and the nature of the middle lamellae, including the structure and orientation of the cellulose fibrils (Burgert and Fratzl, 2009; Geitmann, 2010; Weinkamer and Fratzl, 2011) and the proportion of hemicellulose (Chanliaud et al., 2002; Ryden et al., 2003; Cosgrove and Jarvis, 2012), pectin (a hydrophilic molecule; Cosgrove, 1997; Whitney et al., 1999), and lignin (a hydrophobic molecule) in the wall (Boudet, 2000; Donaldson, 2001; Jones et al., 2001; Sperry, 2003; Peter and Neale, 2004). These compounds can strongly affect how changes in humidity impact the biomechanics of plant tissues. Most hygrochastic plants show active opening of plant organs, such as capsules, inflorescences, or entire plant branches, caused by the moisture-driven antagonistic response of two different dead-cell tissue layers where a swelling tissue with thick cell walls expands

TABLE 1. ANOVA table showing the effect of base area, hydration, weathering, and the interactions on the force needed to detach the involucre.

Source	df	F	r <sup>2</sup>	P
Base area	1	113.4	0.18	<0.001
Hydration	1	175.6	0.28	<0.001
Weathering	1	27.9	0.04	<0.001
Base area × hydration	1	32.1	0.05	<0.001
Base area × weathering	1	18.6	0.03	<0.001
Hydration × weathering	1	21.3	0.03	<0.001
Residuals	246			
Total	252			

perpendicularly to the orientation of cellulose microfibrils (Fahn and Werker, 1972; Ellner and Shmida, 1981; Gutterman and Ginott, 1994; van Rheede van Oudtshoorn and van Rooyen, 1999; Hegazy et al., 2006; Burgert and Fratzl, 2009; Pufal et al., 2010). *Chorizanthe rigida*, however, does not show active movement of organs. Instead, tissue at the base of its involucre swells and softens when wet, allowing the detachment of the involucre by the pounding of raindrops, tightly holding the involucre again when the base dries up again. Despite the absence of active movement, the final effect on seed release is similar to the opening and closing of hygrochastic capsules because it allows the plant to release or retain propagules through changes in the hydration of the swelling tissue at the base of the involucre (Fig. 1). Furthermore, decreased tensile strength in the sun- and weather-exposed involucre in older plants is likely caused by changes in the composition and structure of the cell wall. Weathering of cellulosic materials causes lignin degradation and cellulose depolymerization (Buschle-Diller and Zeronian, 1993). Tissue weathering in deserts is caused by a suite of abiotic processes including photodegradation, physical fragmentation, and leaching caused by wind or water erosion, and biotic decomposition processes caused by soil microbiota (Montaña et al., 1988; Austin and Vivanco, 2006).

The biomechanical features of *C. rigida* seed dispersal may have important ecological implications. A hygrochastic seed dispersal mechanism allows this species to synchronize seed release to rainfall events, as reported for other desert annual species (Friedman et al., 1978; van Rheede van Oudtshoorn and van Rooyen, 1999). Furthermore, *C. rigida* is distributed in desert areas with winter and biseasonal (winter and summer) rainfall patterns. Involucre with larger base areas could be more strongly held to the plant, preventing seed release in response to false rain cues, such as a small winter rainfall event or a summer storm when high temperatures would not allow survival of a desert winter annual.

Plants are formed by a collection of modules, and changes in meristem growth can result in important variation in form and size of these individual plant parts (Martone et al., 2010).

TABLE 2. ANOVA table showing the effect of hydration and weathering on the breakage force.

Source	Df	F	r <sup>2</sup>	P
Hydration	1	130.1	0.32	<0.001
Weathering	1	10.0	0.02	0.002
Hydration × weathering	1	16.5	0.04	<0.001
Residuals	249			
Total	252			

Intraindividual variation in modular structures can play a major role in the way a given plant copes with environmental variation by giving different survival probabilities to different parts of the plant. Our results showed that there is variability in the breaking force needed to detach the involucre. Plants may release more or fewer involucre from their aboveground seed bank according to a rainfall threshold, as an adaptive bet-hedging dispersal strategy to cope with rain unpredictability. Although our experiments did not simulate the exact conditions for seed release from this plant in the field, the approach allows us to assess biomechanically which involucre are more likely to be dislodged. Our data may underestimate the true magnitude of biomechanical variation in propagule ease of release because we could not adequately measure the tensile strength of the smaller and the larger involucre, which would have added additional variation to the extremes of the data range. Finally, as shown by our results, weathering, in the form of long-term exposure to solar radiation and rainfall events, also increases the ease of seed release. Thus variation in involucre dispersal increases with the age of the plants' cohorts.

Commonly, seed release in plants occurs when fruits reach maturity, with the opening of the abscission tissue in the dried-out pedicels or capsular sutures. Hygrochastic (i.e., water-triggered) opening is present in the capsules of some desert families, such as Liliaceae, Agavaceae, and Onagraceae. Plants with hygrochastic abscission of the fruit pedicel, are unusual in nature and, in North American deserts they belong mostly in the Polygonaceae. *Chorizanthe rigida* provides a good system to study the importance of moisture cues in seed release of desert plants and the demographic consequences of timing of seed release. Comparing the force needed to release seeds across other desert taxa, many of which provide seeds that sustain the complex guild of desert granivores, should provide broad ecological information on wind and animal dispersal. For example, it would be informative to test whether larger-seeded species require larger animals as vectors and whether their propagules require more force to detach.

**Conclusion**—Seed dispersal in *C. rigida* is controlled by involucre base area and wetting and weathering of the propagules. The biomechanical properties of involucre release and dispersal in *C. rigida* are ecologically and evolutionarily relevant because survival and establishment depend on the correct timing of seed release to a favorable winter rainfall.

#### LITERATURE CITED

- AUSTIN, A. T., AND L. VIVANCO. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature Letters* 442: 555–558.
- BALDWIN, B. G., S. BOYD, B. J. ERTTER, R. W. PATTERSON, T. J. ROSATTI, AND D. H. WILKEN. [eds.] 2002. The Jepson desert manual: Vascular plants of southeastern California. University of California Press, Berkeley, California, USA.
- BEISMANN, H., H. WILHELMI, H. BAILLERES, H. C. SPATZ, A. BOGENRIEDER, AND T. SPECK. 2000. Brittleness of twig bases in the genus *Salix*: Fracture mechanics and ecological relevance. *Journal of Experimental Botany* 51: 617–633.
- BOBICH, E. G., AND P. S. NOBEL. 2001. Vegetative reproduction as related to biomechanics, morphology and anatomy of four cholla cactus species in the Sonoran desert. *Annals of Botany* 87: 485–493.
- BOUDET, A. M. 2000. Lignins and lignification: Selected issues. *Plant Physiology and Biochemistry* 38: 81–96.
- BURGERT, I., AND P. FRATZL. 2009. Plants control the properties and actuation of their organs through the orientation of cellulose fibrils in their cell walls. *Integrative and Comparative Biology* 49: 69–79.

- BUSCHLE-DILLER, G., AND S. H. ZERONIAN. 1993. Weathering and photodegradation of cellulose. In C. Heitner and J. G. Scaiano [eds.], Photochemistry of lignocellulosic materials. ACS Symposium Series, 177–189. American Chemical Society, Washington, D.C., USA.
- CHANLIAUD, E., K. M. BURROWS, G. JERONIMIDIS, AND M. J. GIDLEY. 2002. Mechanical properties of primary plant cell wall analogues. *Planta* 215: 989–996.
- COSGROVE, D. J. 1997. Relaxation in a high stress environment: The molecular bases of extensible cell walls and cell enlargement. *Plant Cell* 9: 1031–1041.
- COSGROVE, D. J., AND M. C. JARVIS. 2012. Comparative structure and biomechanics of plant primary and secondary walls. *Frontiers in Plant Science. Mini Review Article* 3: 1–6.
- DONALDSON, L. A. 2001. Lignification and lignin topochemistry: An ultrastructural view. *Phytochemistry* 57: 859–873.
- ELLNER, S., AND A. SHMIDA. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* 51: 133–144.
- ENDO, Y., J. SAKAMOTO, Y. KASHIWANO, H. YOKOTA, S. NAKAMURA, AND E. KINOSHITA. 2010. A biomechanical study on burst mechanisms of plant fruit: Stress analysis of pericarps before bursting. *Journal of the Mechanical Behavior of Biomedical Materials* 3: 512–519.
- EVANGELISTA, D., S. HOTTON, AND J. DUMAIS. 2011. The mechanics of explosive dispersal and self-burial in the seeds of the filaree, *Erodium cicutarium* (Geraniaceae). *Journal of Experimental Biology* 214: 521–529.
- FAHN, A., AND E. WERKER. 1972. Anatomical mechanisms of seed dispersal. In T. T. Kozłowski [ed.], Seed biology, 152–221. Academic Press, New York, New York, USA.
- FELGER, R. S. 2000. Flora of the Gran Desierto and Río Colorado of northwestern Mexico, 398–400, 403–403. University of Arizona Press, Tucson, Arizona, USA.
- FRIEDMAN, J., N. GUNDERMANN, AND N. ELLIS. 1978. Water response of the hydrochastic skeletons of the true rose of Jericho. *Oecologia* 32: 289–301.
- GEITMANN, A. 2010. Mechanical modeling and structural analysis of the primary plant cell wall. *Current Opinion in Plant Biology* 13: 693–699.
- GREENE, D. F. 2005. The role of abscission in long-distance seed dispersal by the wind. *Ecology* 86: 3105–3110.
- GREENE, D. F., AND E. A. JOHNSON. 1993. Seed mass and dispersal capacity in wind-dispersed diaspores. *Oikos* 67: 69–74.
- GUTTERMAN, Y. 2002. Survival adaptations and strategies of annuals occurring in the Judean and Negev Deserts of Israel. *Israel Journal of Plant Sciences* 50: 165–175.
- GUTTERMAN, Y., AND S. GINOTT. 1994. Long-term protected 'seed bank' in dry inflorescences of *Asteriscus pygmaeus*; Achene dispersal mechanism and germination. *Journal of Arid Environments* 26: 149–163.
- HAYASHI, M., S. P. GERRY, AND D. J. ELLERBY. 2010. The seed dispersal catapult of *Cardamine parviflora* (Brassicaceae) is efficient but unreliable. *American Journal of Botany* 97: 1595–1601.
- HEGAZY, A. K., H. N. BARAKAT, AND H. F. KABIEL. 2006. Anatomical significance of the hydrochastic movement in *Anastatica hierochuntica*. *Annals of Botany* 97: 47–55.
- JONES, L., A. R. ENNOS, AND S. R. TURNER. 2001. Cloning and characterization of *irregularxylem4* (*irx4*): A severely lignin-deficient mutant of *Arabidopsis*. *Plant Journal* 26: 205–216.
- LENTINK, D., B. DICKSON, J. L. VAN LEEUEN, AND M. H. DICKINSON. 2009. Leading-edge vortices elevate lift of autorotating plant seeds. *Science* 324: 1438–1440.
- MARCHETTO, K. M., M. B. WILLIAMS, E. JONGEJANS, R. AUHL, AND K. SHEA. 2010. Applications of particle image velocimetry for seed release studies. *Ecology* 91: 2485–2492.
- MARTONE, P. T., M. BOLLER, I. BURGERT, J. DUMAIS, J. EDWARDS, K. MACH, N. ROWE, M. RUEGGEBERG, R. SEIDEL, AND T. SPECK. 2010. Mechanics without muscle: Biomechanical inspiration from the plant world. *Integrative and Comparative Biology* 50: 888–907.
- MONTAÑA, C., E. EZCURRA, A. CARRILLO, AND J. P. DELHOUME. 1988. The decomposition of litter in grasslands of northern Mexico: A comparison between arid and non-arid environments. *Journal of Arid Environments* 14: 55–60.
- MURREN, C. J., AND A. M. ELLISON. 1998. Seed dispersal characteristics of *Brassavola nodosa* (Orchidaceae). *American Journal of Botany* 85: 675–680.
- NOY-MEIR, I. 1973. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4: 25–41.
- PERONI, P. A. 1994. Seed size and dispersal potential of *Acer rubrum* (Aceraceae) samaras produced by populations in early and late successional environments. *American Journal of Botany* 81: 1428–1434.
- PETER, G., AND D. NEALE. 2004. Molecular basis for the evolution of xylem lignification. *Current Opinion in Plant Biology* 7: 737–742.
- PHILIPPI, T. 1993. Bet-hedging germination of desert annuals: beyond the first year. *American Naturalist* 142: 474–487.
- PUFAL, G., K. G. RYAN, AND P. GARNOCK-JONES. 2010. Hygrochastic capsule dehiscence in New Zealand alpine *Veronica* (Plantaginaceae). *American Journal of Botany* 97: 1413–1423.
- READ, J., AND A. STOKES. 2006. Plant biomechanics in an ecological context. *American Journal of Botany* 93: 1546–1565.
- RYDEN, P., K. SUGIMOTO-SHIRASU, A. C. SMITH, K. FINDLAY, W. REITER, AND M. C. McCANN. 2003. Tensile properties of Arabidopsis cell walls depend on both a xyloglucan cross-linked microfibrillar network and rhamnogalacturonan II-borate complexes. *Plant Physiology* 132: 1033–1040.
- SPERRY, J. 2003. Evolution of water transport and xylem structure. *International Journal of Plant Sciences* 164: S115–S127.
- TAYLOR, P. E., G. CARD, J. HOUSE, M. H. DICKINSON, AND R. C. FLAGAN. 2006. High-speed pollen release in the white mulberry tree, *Morus alba* L. *Sexual Plant Reproduction* 19: 19–24.
- VAN RHEEDE VAN OUDTSHOORN, K., AND M. W. VAN ROOYEN. 1999. Dispersal biology of desert plants: Adaptations of desert organisms. Springer, Berlin, Germany.
- VOGEL, S. 2003. Comparative biomechanics: Life's physical world, 301–341. Princeton University Press, Princeton, New Jersey, USA.
- WEINKAMER, R., AND R. FRATZL. 2011. Mechanical adaptation of biological materials—The examples of bone and wood. *Materials Science and Engineering C* 31: 1164–1173.
- WHITNEY, S. E. C., M. G. E. GOTHARD, J. T. MITCHELL, AND M. J. GIDLEY. 1999. Roles of cellulose and xyloglucan in determining the mechanical properties of primary plant cell walls. *Plant Physiology* 121: 657–663.
- WITZTUM, A., AND K. SCHULGASSER. 1995. The mechanics of seed expulsion in Acanthaceae. *Journal of Theoretical Biology* 176: 531–542.