

Pods as sails but not as boats: dispersal ecology of a habitat-restricted desert milkvetch

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PREMISE: Adaptive seed dispersal mechanisms are fundamental to plant fitness, but dispersal advantage is scale-dependent. We tested the hypothesis that informed dispersal in response to an environmental cue enables dispersal by wind on a local scale for *Astragalus holmgreniorum*, a desert species restricted to swales and wash skirts with overland flow, but prevents longer-distance dispersal by water into unfavorable wash habitats.

METHODS: Pod biomechanics in *A. holmgreniorum* lead to major shape modifications with changes in moisture content. We performed laboratory experiments to examine the interaction of pod shape with wind and water, and conducted field experiments in *A. holmgreniorum* habitat evaluating the roles of wind, water, and seed predators on dispersal.

RESULTS: Dry pods exhibit a flattened crescent shape with partial dehiscence that facilitated wind dispersal by ground tumbling and seed scattering in laboratory experiments. Rain simulation experiments showed that even small precipitation events returned wetted pods to their cylindrical shape and opened the dorsal suture, exposing the seeds. In the field experiments, dry pods were moved locally by wind, whereas rain caused pod opening and washing out of seeds in place. Seed predators had minimal effect on pod movement.

CONCLUSIONS: *Astragalus holmgreniorum* exhibits pod structural remodeling in response to environmental change in a striking and novel demonstration of informed dispersal. Wind-driven movement of dry pods facilitates local seed dispersal, but rain causes pods to open and release seeds, ensuring that they are not transported out of suitable habitats and into active washes where they would be lost from the seed bank.

KEY WORDS antitelechory; *Astragalus holmgreniorum*; endemic; hygrochasy; informed dispersal; Mojave Desert; seed predators; wind dispersal; water dispersal.

Adaptations for seed dispersal are central to plant ecology and have been studied since the 1700s by botanists including Carolus Linnaeus (van der Pijl, 1982). Because most terrestrial plants are sessile, propagule dispersal is the only mechanism for moving from one location to another. Diaspore biomechanics play a key adaptive role in plant success through mediation of dispersal distance, as well as timing of seed release (Read and Stokes, 2006). Adaptations for seed dispersal are generally considered to be under positive selection (Howe and Smallwood, 1982), but dispersal advantage is scale-dependent and interacts with other aspects of species life history and ecology (Aukema, 2004).

For some species and environments, the vicinity of the maternal plant may be the most favorable place for progeny to establish,

resulting in selection for antitelechory (reduced dispersal capability). Dispersal in such species is limited to discharge of seeds from the fruit into the immediate surrounding area, for example, through hygrochasy, in which fruits release seeds in response to wetting (Guterman, 1994). The seeds may have further adaptations, such as mucilaginous coats, that hinder secondary dispersal (e.g., Arshad et al., 2019). This antitelechoric dispersal syndrome is quite common in desert annuals (Ellner and Shmida, 1981; van Rheede van Oudtshoorn and van Rooyen, 1999).

If a species is ecologically confined to a spatially restricted habitat surrounded by an unfavorable habitat, there should be selection for adaptations to reduce dispersal distance on a larger scale. The reduced seed wings of *Mentzelia* species that are confined to

gypsum islands are a good example (Schenk, 2013). However, a habitat-restricted species may still find it advantageous to disperse locally within a favorable habitat, to minimize density-dependent mortality due to intraspecific competition, especially kin competition, as well as to reduce potential inbreeding depression. This creates a scenario where dispersal could be under both positive and negative selection. One way that a plant species could respond under this scenario is through diaspore heteromorphy, that is, the production of two diaspore morphs with contrasting dispersal ability on the same plant. Diaspore heteromorphy has been shown to be a form of bet hedging, in which the plant produces alternative solutions to the problem of whether or not to disperse (Imbert, 2002; Baskin et al., 2014; Arshad et al., 2019). Another way to respond to two opposing dispersal selection pressures is through informed dispersal, that is, through changing diaspore phenotype in an adaptive way in response to an environmental cue (Seale and Nakayama, 2019).

Informed dispersal was originally proposed to explain how animals can respond adaptively to changes in environmental conditions by modifying their dispersal strategy (Clobert et al., 2009). The phenomenon is much less well studied in plants, but there are two documented patterns of response (Seale and Nakayama, 2019). The first pattern is a modification of seed heteromorphy. Informed dispersal takes place when the plant responds to an environmental quality cue during development by changing the proportion of dispersal morphs produced. For example, in *Heterosperma pinnatum*, the plant increases production of the more dispersible morph under conditions of water stress and intense intraspecific competition (Martorell and Martínez-López, 2014). In the second pattern of informed dispersal in plants, the diaspore undergoes “adaptive structural remodeling of dispersal-related traits in direct response to a proximal environmental cue” (Seale and Nakayama, 2019). A well-studied example is the change in pappus architecture in the common dandelion in response to increased humidity (Seale and Nakayama, 2019).

Our study addresses dispersal of a habitat-restricted desert milkvetch, *Astragalus holmgreniorum* Barneby (Fabaceae). We tested the overarching hypothesis that changes in pod shape in response to abiotic factors in the environment of this species represent an informed dispersal strategy.

Based on preliminary observations, we proposed that dry pods of *A. holmgreniorum* are adapted for short-distance wind dispersal, whereas rain triggers pod opening and seed release, acting as an antitelechoric agent to prevent longer-distance within-pod seed dispersal by water into an unfavorable habitat. To test these ideas, we examined evidence for different *A. holmgreniorum* dispersal modes in a series of laboratory and field experiments. We tested the following hypotheses: (1) that most pods would be moved only small distances by measuring post-dispersal interpod distances in the field and using these data to infer the spatial extent of maternal pod shadows (areas within which pods of an individual plant are dispersed); (2) that pods could be moved by wind, and that seeds would be dispersed as the pods tumbled across different substrates using a laboratory wind runway experiment; (3) that exposure to small rain events would cause pod opening and seed release in laboratory rain-simulation experiments. We also investigated whether (1) these dispersal modalities are operative under field conditions by following the fate of a cohort of marked pods to determine dispersal patterns, and if (2) granivorous rodents play a role in dispersal, by evaluating patterns of seed removal under different manipulated conditions in the field and rodent impacts on intact pods.

MATERIALS AND METHODS

Study species

Astragalus holmgreniorum is an endangered species endemic to the northeastern Mojave Desert near St. George, Utah, USA. The species is restricted to swales and wash skirts at the base of hillslopes of the Virgin Limestone member of the Moenkopi Formation, where it receives supplemental water in the form of overland flow during storms (Van Buren and Harper, 2003; U.S. and Wildlife Service, 2006). The species is a spring ephemeral hemicytrophite, with dormant meristems very close to the soil surface (Rominger et al., 2019). Initiation of shoot growth takes place in early February, flowering and seed production occur from March to mid-May, and by mid-June all aboveground vegetative tissue has senesced. This species is not capable of vegetative reproduction and few plants live past three growing seasons, making high seed production and the formation of a long-lived seed bank necessary for population persistence (Van Buren and Harper, 2003; Searle, 2011; Van Buren et al., unpublished data). It is only marginally adapted to the warm desert environment and relies on the supplemental water provided by overland flow to survive the dormant season.

The seed pods (legumes) of *A. holmgreniorum* have an unusual and changeable shape, which is hypothesized to influence seed dispersal. They start out as fully bilocular, trigonously compressed pods with the ventral side of the fruit wall folded inward to form a double-walled partition between the valves (Barneby, 1980; Fig. 1A). The fruiting stalks are prostrate and pods become coriaceous as they mature, readily disjuncting from their receptacles (Fig. 1B). During maturation and drying, the ventral-side suture fold separates and flattens, exposing the inner partition, allowing the ends of the pod to curve dorsally, and the locules to partially dehisce at both ends. At this stage, the pods take on their characteristic crescent shape (Fig. 1C). The pods quickly return to a more linear shape upon wetting (Fig. 1E).

Study site habitat

Field studies were conducted in the natural habitat of *A. holmgreniorum* in the Mojave Desert. A location within the State Line population on the Utah–Arizona border just south of the Sun River development was chosen as a representative site. The area consists of a valley bottom at the base of small hills and plateaus. The ground surface is composed of variable amounts of rock and gravel with less than 20% living cover.

The climate at the Mojave Desert study site is characterized by relatively mild winters and hot summers, with most precipitation falling as rain in the late autumn, winter, and early spring, but summer monsoonal storms are also common in some years. May and June are consistently dry (Hereford et al., 2004), but during the warm months of July through September, 13–29% of the annual rainfall occurs, with an average of 10–20 mm total rainfall occurring over an average of three days per month (Hereford et al., 2004).

Interpod distance experiment

This study of potential pod dispersal distance was based on the premise that pods that were closer to each other in October–November (several months after initial detachment from the parent plant), would be more likely to be siblings. We located individual pods,

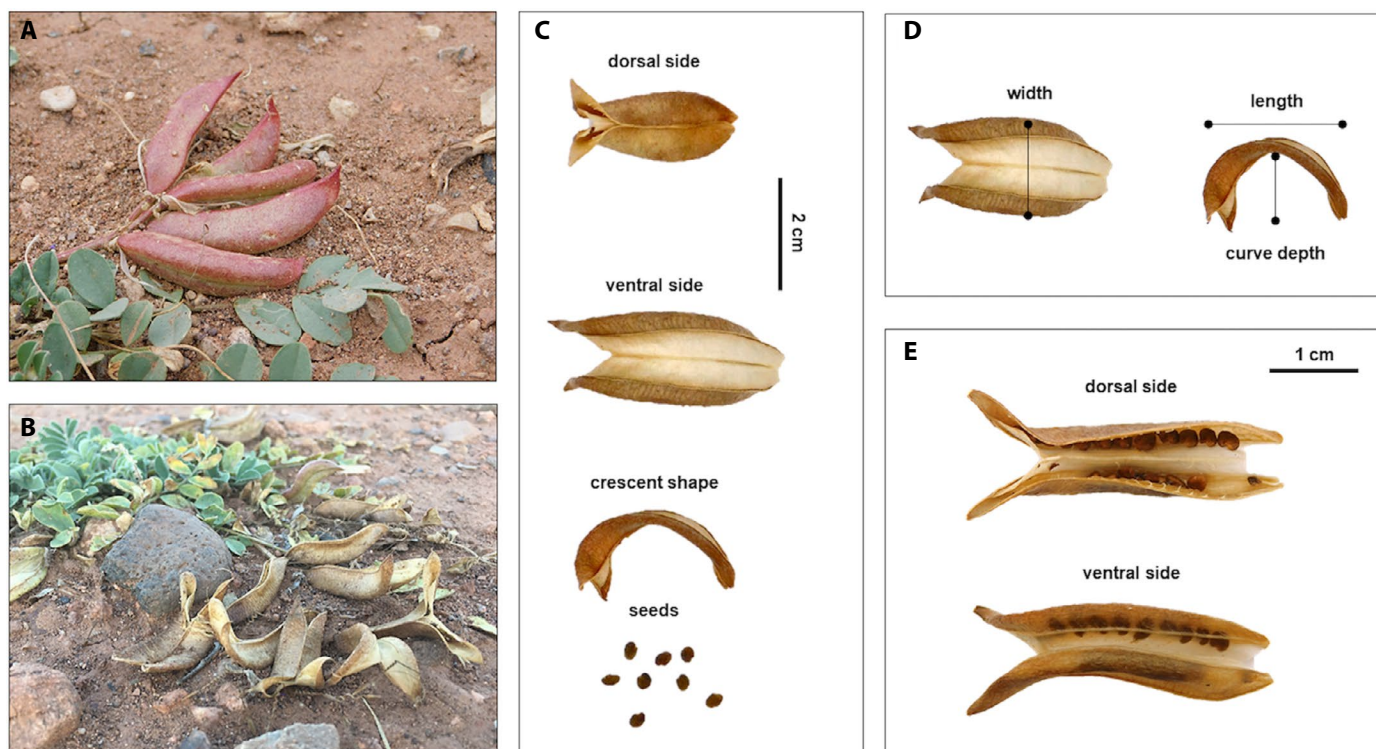


FIGURE 1. *Astragalus holmgreniorum* pods at various stages and orientations. (A) Mature pods attached to a plant growing in the field. (B) Dry pods detached and beginning to dehisce in the field. (C) Dry pods (dorsal side, ventral side, crescent shape) and seeds. (D) Pod measurements (width, length, and curve depth). (E) Wet pods (dorsal side, ventral side).

searched for all pods within a 5 m radius, then measured interpod distances between every pair of pods found. The interpod distances were binned into distance categories and fitted with a negative exponential curve to estimate maximum putative dispersal distance.

Dispersal by wind in the laboratory

To test and quantify potential for pod wind dispersal, an adjustable aluminum runway with sidewalls was constructed with a carpet fan at one end. The runway was used to expose pods to variations in surface roughness, slope, and wind velocity that occur in the natural habitat of *A. holmgreniorum*. To stabilize the sidewalls of the runway, two pieces of 5 × 10 cm lumber were cut to 40 cm lengths and secured with screws at the top ends of the runway, and flexible wire was attached to the tops of sidewalls spanning the width of the runway at three places, evenly spaced. Variation in runway surface roughness (fine, medium, and coarse) was achieved by gluing sand or aquarium gravel of two different sizes onto plywood boards. Grain size of the sand ranged from 0.5–1 mm, whereas the medium gravel ranged from 4–6 mm and the coarse gravel ranged from 6–10 mm. The plywood boards were then placed inside the floor of the aluminum runway. Clamps were used to level and secure the boards, and irrigation tubing was placed along the long edges of the boards to eliminate gaps between the board and the sides of the runway. Slope was varied by propping up the front or the back end of the runway with pieces of lumber. This resulted in downslope, level, and upslope conditions. Even with these three settings, slope varied over a narrow range (<10°). Desired wind velocities were obtained by adding screens to the carpet fan. The velocities

of low, medium, and high ranged from 3.5–5.0, 5.5–8.0, and 8.5–10.5 m·s⁻¹, respectively. These velocities correspond to a gentle, moderate, and fresh breeze, respectively, on the Beaufort Wind Scale (Beer, 2013). Velocities were measured with a handheld anemometer (Kestrel 1000 Wind Meter; Kestrel Instruments, Boothwyn, Pennsylvania, USA) at the pod launching point [40.6 cm from the fan and centered across the total width of the runway (42 cm)].

Pods and seeds used in all of our experiments were obtained legally as part of a seed salvage effort on state land the previous year. Ventral side width, ventral side length, and dorsal side curve depth were measured for each pod using a digital caliper (Fig. 1D). Individual pods were weighed before and after the trials. Trials were run using 12 pods in each of the 27 treatment combinations (3 surfaces × 3 slopes × 3 wind velocities). Each pod was run in two orientations to the surface, ventral side up and ventral side down, for a total of 648 trials. Pods were exposed to the wind for a maximum of 10 s, and once movement occurred, the distance traveled was recorded. Because the runway had a finite length (150 cm) and many pods reached the end, the response variable “distance traveled” had an arbitrary maximum value and was therefore right-censored. To analyze the data, we used survival analysis (SAS Proc Lifetest). Mass loss during each pair of trials (i.e., ventral side up and ventral side down) was analyzed with analysis of variance (ANOVA, SAS Proc GLM).

Seed release in response to simulated rain

To test and quantify the effect of water on pods in the laboratory, an apparatus was designed to mimic natural summer storms in the field. Our design permitted us to apply known amounts of water

(1, 3, and 5 mm) as rain-like droplets over a 10-min period to mimic three different types of precipitation events. The apparatus consisted of a perforated aluminum plate, 18 cm × 17 cm, punched with a grid of 225 2.5-mm holes spaced 1 cm apart, mounted in a wooden frame. This was supported 45 cm above the pods, which were resting on a flat mesh strainer over a catch pan. The volume of water was applied using a thin-nozzle wash bottle, in 30-s increments, and pushed gently through the holes in the aluminum plate with a wet paintbrush in 1-min increments to achieve a repeatable treatment. For each replicate storm, 12 pods were placed in a grid on the mesh strainer below the rain simulator, six ventral side up and six ventral side down. There were three replicate storms for each precipitation amount. Following each trial, the pods were assessed, the mesh grid with pods was placed onto a paper towel to remove excess water, and the pods were left to rest for an additional 10 min followed by reassessment. Finally, the dorsal suture opening (Fig. 1E) was measured using a digital caliper. The response variables were pod opening immediately post-storm, pod opening 10 min after the storm, width of the opening of the dorsal suture 10 min after the storm, and number of seeds released. The experimental design was a randomized block design with blocks nested in precipitation amount (1, 3, or 5 mm). Pod opening was analyzed as a binary variable (open or closed) using logistic regression (SAS Proc GLIMMIX), whereas dorsal suture gap width and number of seeds released were analyzed using mixed model analysis of variance (SAS Proc MIXED).

Pod and seed movement in the field

To relate our laboratory wind runway and rain-simulation studies to the effect of abiotic factors on pod movement in the field, we installed a field dispersal study with marked pods in *A. holmgreniorum* habitat. The design consisted of 18 pod stations arranged in three rows of six stations spaced 5 m apart. At each station, 20 intact pods were placed within a 5 cm radius of a marker nail for a total of 360 pods. The pods were painted with fluorescent paint, using two-color combinations that were unique to the pods at each station. Each pod was also labeled with a unique identifier using a Sharpie-brand permanent marker. The experiment was installed on May 6, 2018, first evaluated on June 16, and finally evaluated on August 13.

Field evaluation consisted of determining the distance from the pod to the nail that corresponded to its color coding, recording the direction of pod movement from the nail to its recorded location, and noting anything unusual about pod condition (e.g., rodent chew marks) or location. We first searched for the pods during the late evening while still light and marked with flags any pods that had traveled more than 15 cm. We searched again after dark using ultraviolet flashlights for detecting the fluorescent paint on the pods, and then made one more search the next morning, when we also measured the distances and directions of pod travel. At the final evaluation, all pods found were collected into individual envelopes and examined in the laboratory to determine the number of seeds remaining.

Dispersal by seed predators

This experiment was designed to determine whether granivorous rodents might be important dispersal agents by measuring removal of *A. holmgreniorum* seeds that had been previously dispersed from their pods by other mechanisms (wind scattering, hygrochasy). To understand how seed species, spacing, position in soil, and density

affected the collecting behavior of seed predators, we installed an experiment using 6-cm plastic Petri dishes filled with sieved field soil ($n = 288$ experimental units). Each 16-dish array was replicated 18 times. Nine of the 18 arrays contained *A. holmgreniorum* seeds and the other nine contained *Oryzopsis hymenoides* (Indian ricegrass) seeds, which are typically a favored food source for desert seed predators (Auger et al., 2016). The dishes were set out flush with the soil surface at three spacings (2.25 m, 4.5 m, and 9 m), resulting in a split-plot design with three blocks, and with the factorial combination of three spacings × two seed species as the main plot. Within each species × spacing array, there were two treatments: (1) position in the soil (buried approximately 1-cm deep in soil at the bottom of the dish, or surface sown) and (2) density (low: 4 seeds per dish and high: 40 seeds per dish). The four treatments in factorial combination were included in each subplot (array). Each treatment combination had four randomly arranged replicates for a total of 16 dishes per array. We set up this experiment in early May and returned two weeks later for evaluation, after giving granivorous animals (e.g., Merriam's kangaroo rats) time to discover and utilize this new seed resource. After the two-week period, the contents of each dish (soil and seeds) were collected into a coin envelope for evaluation in the laboratory. Seeds were extracted from the soil using an appropriately sized sieve and counted.

Data were first analyzed as a split-plot design with seed species × spacing as the main plot, and position × density as the subplot in SAS Proc GLIMMIX, with seed number removed per initial seeds present in each dish as the binomial response variable. This analysis showed that species and position were highly significant whereas spacing had no significant effect (not shown). Close inspection of these results revealed that perhaps a more important measure of rodent effect was whether or not a dish had any seeds removed at all, that is, whether it had been discovered. Most dishes either had no seeds removed or all seeds removed. We reanalyzed this data set with the proportion of undisturbed dishes (replicate dishes with no seeds removed per all replicate dishes) as the response variable, using the four replicates of each treatment combination (species × position × density) in each array. We used the nine sets of four replicates (3 blocks × 3 spacings) as a sample size of nine for comparing the proportion of dishes undisturbed in each of the different treatment combinations (species × position × density).

Preliminary experiments indicated that birds and harvester ants were not important *A. holmgreniorum* seed predators; no attempt was made to further identify these potential predators.

To characterize the local rodent granivore community, we conducted three nights of trapping in May 2018. This consisted of 140 Sherman long live traps baited with rolled oats laid out over 1 ha at 5-m spacing. Traps were set at dusk and checked shortly after dawn each of the three nights. Individuals were marked to allow us to know if a recapture had occurred. As a preliminary test of whether scatter-hoarding rodents were likely to collect seeds in intact pods, we also quantified marked pods in the field dispersal study that showed signs of handling by rodents.

RESULTS

Interpod distance experiment

This experiment provided preliminary support for the hypothesis that maternal pod shadows for this habitat-restricted milkvetch

would be relatively small. We found that the number of pod pairs located at a given interpod distance decreased exponentially as a function of distance, that is, exponentially more pods were found at close interpod distances (Fig. 2). This relationship was significant ($p < 0.001$) up to 250 cm. At distances >250 cm, the relationship broke down, and there was no longer a correlation between number of pod pairs and interpod distance. This resulted in a bimodal distribution of pod-pair numbers as a function of distance. We interpreted this to mean that sibling pods were generally dispersed short distances from the maternal plant, and that pod pairs at greater distances likely represented overlapping pod shadows from different maternal plants. If this interpretation is correct, we can conclude that where the negative exponential dispersal curve drops to zero, the estimated maximum dispersal distance has been reached—approximately 400 cm.

Dispersal by wind in the laboratory

Results of the laboratory wind dispersal trials supported our hypothesis that dry *A. holmgreniorum* pods would be readily moved

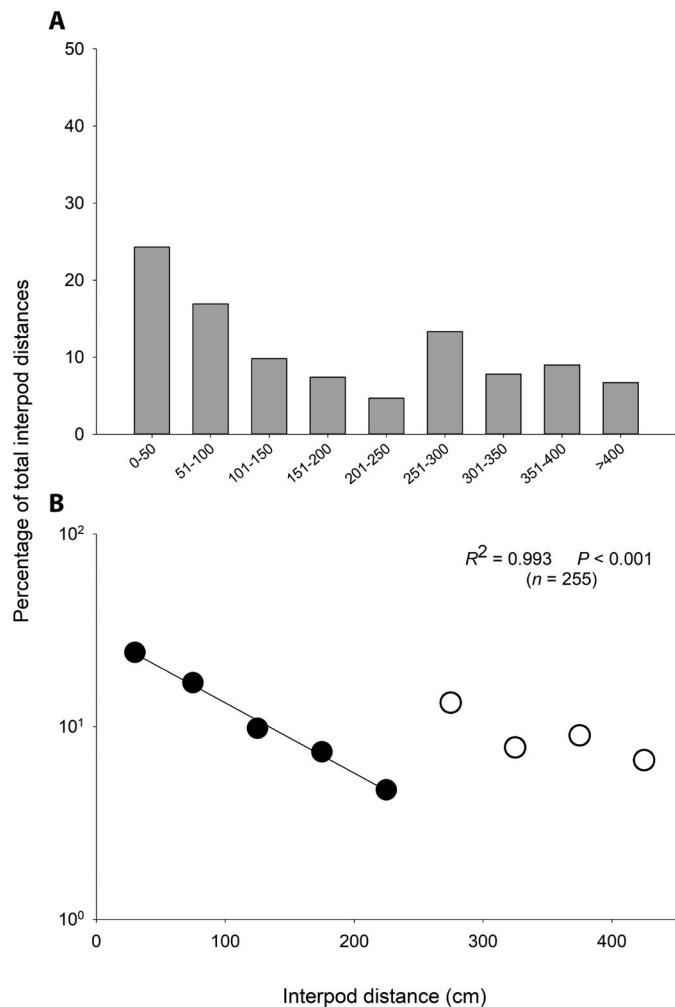


FIGURE 2. Interpod distances measured between *Astragalus holmgreniorum* pods in the field in October–November 2017. (A) The percentage of interpod distances in each of nine distance categories. (B) A negative exponential curve fitted to the data for pod pairs with interpod distances of 250 cm or less (black symbols) with a y-axis on a logarithmic scale.

by simulated wind and would release seeds as they moved (see Appendix S1 video recording). As expected, all three treatments (surface, slope, and wind velocity) had significant effects on distance traveled ($p < 0.001$; Fig. 3). On average, pods traveled farther across a smoother surface, on a downslope, and at higher wind velocities. There was no significant effect of pod orientation (ventral side up or down), or pod mass on distance traveled.

More interesting were the significant interactions we observed between surface and velocity, between slope and velocity, and between surface, slope, and velocity. The effect of surface roughness was much more pronounced at low vs. high wind velocities. For example, pods on the coarse surface traveled only 6% as far as those on the fine surface under low wind velocity, but traveled 72% as far under high wind velocity (Fig. 3). This pattern was present, but not nearly as extreme, for the slope-by-velocity interaction. In this case, pods on an upslope traveled 66% as far as those on a downslope under low wind velocities, but 82% as far under a high wind (Fig. 3). With respect to the three-way interaction, on the fine surface the effect of slope was evident only at low wind velocity. On the medium surface there was little effect of slope at any wind speed, whereas on the coarse surface, there was very little movement on any slope at low wind velocity. At high, and especially at medium, wind velocity, there was a strong effect of slope (Fig. 3). When pod measurements of width, length, and curve depth (Fig. 1D) were included individually as covariates in the survival analysis, increased width ($df = 1$, $\chi^2 = 16.0$, $p < 0.001$) and increased curve depth ($df = 1$, $\chi^2 = 16.6$, $p < 0.001$) significantly increased the distance travelled, showing that pod shape influences aerodynamic properties; however, their inclusion in the model did not change the patterns described above.

The difference in pod mass before and after the paired trial for each pod was used to evaluate seed loss during the trials. The average mass of a single seed was 6 mg. All three main effects significantly influenced mass loss (Fig. 4). Fine and medium surfaces caused more mass loss than did the coarse surface. Downslopes and upslopes caused more mass loss than did the level slope. High wind velocity caused 225% more mass loss than did low velocity, and medium-velocity mass loss was intermediate. There were two-way interactions between surface and slope and between slope and velocity (Fig. 4). Mass loss was especially high on the medium surface with an upslope. Across all surfaces, mass loss was greatest on the upslope with high wind velocity and lowest on the level slope with low wind. The three-way interaction was also significant ($p = 0.009$; Fig. 4). This was because one treatment combination, medium surface on an upslope with high wind velocity, resulted in approximately twice the mass loss of any other treatment. This indicates that on average, every pod in this treatment combination lost a seed on its two brief trips down the runway, whereas in most of the other treatment combinations less than half of the pods lost a seed. The combination of sufficient roughness on an upslope with a high wind velocity apparently provided enough jarring of the pods as they bounced along the runway to optimize seed dispersal.

Seed release in response to simulated rain

Our simulated storms were small and of short duration, yet were extremely effective in inducing pod opening, supporting our hypothesis that exposure to wetting causes pod shape change and release of seeds. Pods opened during a simulated 10-min rainfall event and continued to open during 10 min post-storm. Precipitation amount (i.e., total rainfall in a 10-min period) had a significant positive

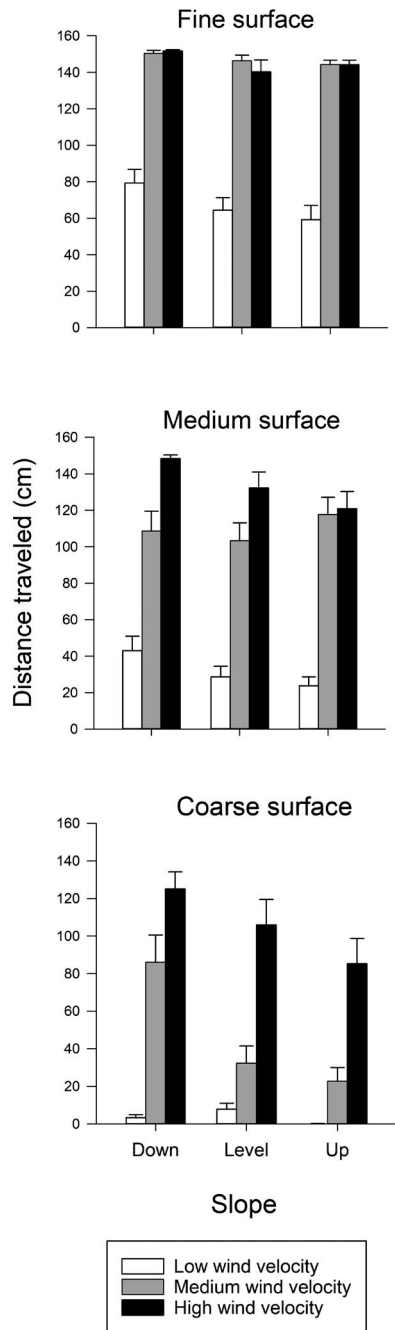


FIGURE 3. The effects of Surface (Sur), Slope (Slo), and Velocity (Vel), and their interactions on the distance traveled by *Astragalus holmgreniorum* pods on a 150-cm-long runway exposed to artificial wind in the laboratory. Error bars = standard error of each mean.

effect on the fraction of pods that opened (defined as sufficiently open to see inside at mid-pod, ~0.2 mm) both immediately post-storm and 10 min post-storm (Fig. 5). Precipitation amount also significantly affected how widely the pods opened (the width of the gap at mid-pod 10 min post-storm; Fig. 5), but did not significantly affect the number of seeds that were shaken loose from the pods by raindrops or that fell out 10 min post-storm (Fig. 5). Number of seeds released was extremely variable with zero as the most frequent value. These results demonstrate that even small amounts of precipitation can cause pods to open via hygrochasy so that seeds can be washed out. This could prevent seeds within pods from being transported out of suitable habitats by overland flow.

Pod orientation (ventral suture side down or ventral suture side up) significantly affected the percentage of pods that opened immediately post-storm (Fig. 6), with 52% more ventral-side-down pods opening than ventral-side-up pods. However, the effect was no longer significant 10 min post-storm (Fig. 6). Pods that were ventral-side down had a significantly wider pod gap (139% wider) than ventral-side-up pods 10 min post-storm (Fig. 6). There were no significant interactions between pod orientation and rain amount.

Pod and seed movement in the field

Results of the field pod dispersal study supported the hypothesis that pod movement by wind and water in the field is primarily over short distances, but that long-distance travel in overland flow does occur. At the first evaluation (June 16), we relocated 88% of the marked pods (315 of 360). Eighty-three percent of the relocated pods (262 of 315) were still within 15 cm of their original location (Table 1). Of the 53 pods that moved more than 15 cm, 33 (61%) were recorded to the north or northeast of their original location. The remaining 39% were distributed in the direction of movement nearly evenly among the remaining cardinal and intercardinal directions. There was no recorded precipitation in the area during the period from experimental installation to the first evaluation.

At the final evaluation (August 13), we relocated 73% of the marked pods (262 of 360). Pod travel distances increased overall, with only 45% (119 of 262 pods) still within 15 cm of their original positions (Table 1). An additional 70 pods were within 15–50 cm, and 31 more were within 100 cm. Twenty-three pods were between 100 and 200 cm from the origin, whereas 19 of those located had traveled greater distances. Of these 19 pods, 15 were within 600 cm of the origin. Four of the pods had travelled distances >1500 cm, apparently carried by water down the wash adjacent to the study plots. The maximum distance recorded was 2827 cm. It was evident upon arrival at the study site that there had been recent heavy rain that had generated overland flow through the plot area, especially on the lower margins, closer to the wash. In fact, there were two significant rainstorms between the two evaluations, with rainfall totaling 6 mm on July 20, and 8 mm on August 12 (PRISM Climate Group, 2019). It is likely that more pods

Effect	df	Wald χ^2	P-value
Surface	2	183.7	<0.001
Slope	2	38.1	<0.001
Velocity	2	699.1	<0.001
Sur x Slo	4	5.0	0.290
Sur x Vel	4	15.8	0.003
Slo x Vel	4	10.8	0.029
Sur x Slo x Vel	8	35.3	<0.001

FIGURE 4. The effects of Surface (Sur), Slope (Slo), and Velocity (Vel), and their interactions on mass loss by *Astragalus holmgreniorum* pods as they dispersed seeds moving along on a 150-cm-long runway exposed to artificial wind in the laboratory. Error bars = standard error of each mean.

were carried down the wash but could not be located, because the few that were found were nearly buried in mud.

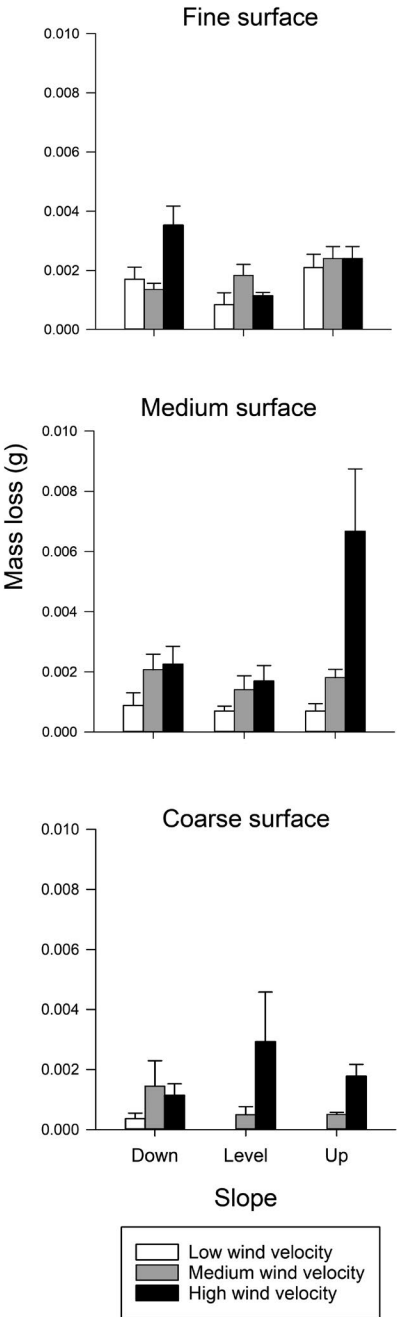
On the final evaluation date, we systematically collected the pods as we carried out the distance measurements and brought them back to the laboratory to evaluate the number of seeds remaining in each pod. In the laboratory, we discovered that the great majority (85%) of pods (222 of 262) no longer contained any viable seeds. This was true regardless of whether the pods had moved appreciably; there was no relationship between seed number per pod and distance travelled. Less than 5% of the pods contained more than one remaining seed, and only three pods contained more than five seeds. The maximum number of seeds remaining in any pod was nine. Roughly a third of the pods recovered contained dried mud inside, including both those that had traveled a long-distance and those that had not. This long-distance pod movement apparently did not result in significant long-distance seed movement, however, because seeds were apparently quickly washed out of open pods during the first stages of a rainstorm.

Dispersal by seed predators

This experiment demonstrated that granivorous rodents collect *A. holmgreniorum* seeds and could potentially act as mid-distance dispersers. Overall, *A. holmgreniorum* seed dishes were discovered at a significantly lower rate than were *O. hymenoides* dishes (37% vs. 77% of dishes discovered; $p < 0.001$; Fig. 7), indicating that *A. holmgreniorum* seeds are a less-preferred food source. Position in the soil (buried or surface-sown) was also significant for both species ($p < 0.001$), with buried seeds much more likely to escape discovery and collection. Perhaps surprisingly, there was no significant effect of seed density on the proportion of dishes disturbed for the two species ($p = 0.648$; Fig. 7). There were no significant interactions among species, position, and/or density (Fig. 7). Taken together, our findings support the hypothesis that granivores will harvest and potentially disperse *A. holmgreniorum* seeds, especially seeds on the soil surface, over a range of densities and spacings.

From three nights of trapping, the greatest number of individuals captured each night were Merriam’s kangaroo rats (*Dipodomys merriamii*). Thirteen was estimated as the minimum number of Merriam’s kangaroo rats known to be in the area based on capture-recapture data—a population considered to be of moderate size based on the 1-ha trapping grid (Auger et al., 2016). We also captured antelope ground squirrels (*Ammospermophilus leucurus*) five times; these are mainly diurnal rodents that consume seeds but are omnivores rather than granivores. Two cactus mice (*Peromyscus eremicus*) were trapped at locations at the edge of suitable *A. holmgreniorum* habitats. This species is also an omnivore rather than a specialist on seeds. We conclude from this observational study that Merriam’s kangaroo rats are likely to be the principal *A. holmgreniorum* rodent seed predators and dispersers at this study site.

Evaluation of chew marks in the pod dispersal study revealed that only 3% of the pods showed any sign of handling by rodents,



Effect	df	F	P-value
Surface	2	7.6	<0.001
Slope	2	4.6	0.010
Velocity	2	19.2	<0.001
Sur x Slo	4	2.4	0.047
Sur x Vel	4	0.9	0.474
Slo x Vel	4	2.4	0.047
Sur x Slo x Vel	8	2.6	0.009

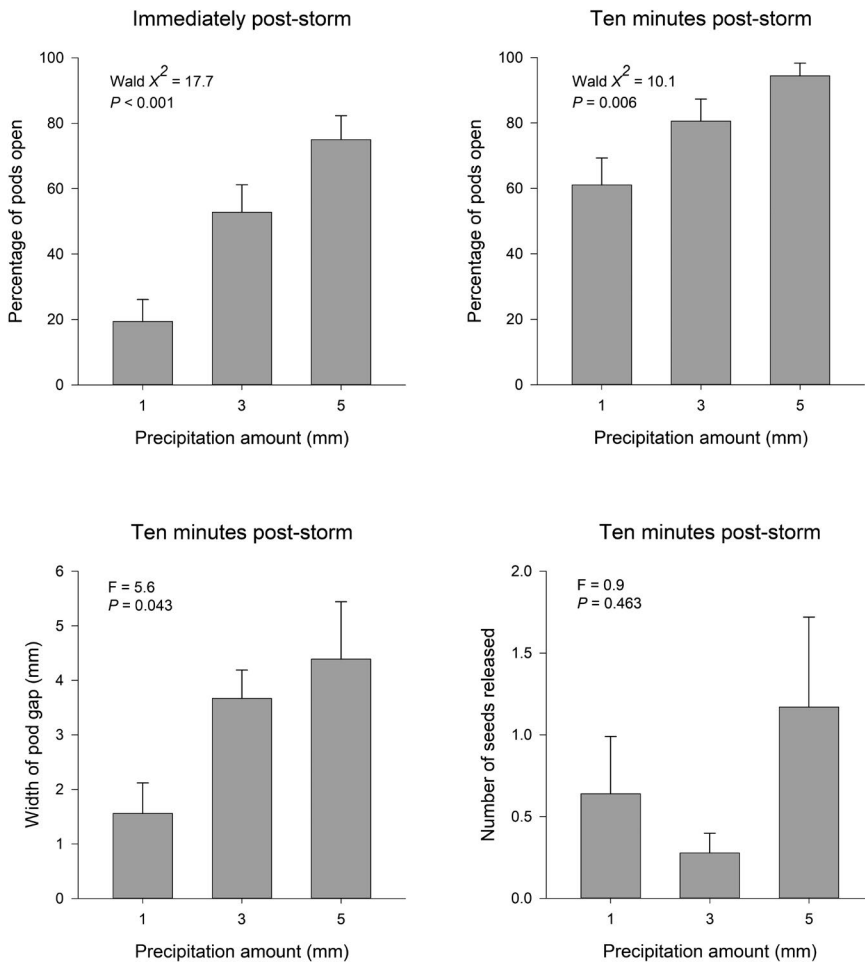


FIGURE 5. The effect of precipitation amount in a 10-minute simulated rain period on the percentage of *Astragalus holmgreniorum* pods open immediately post-storm and 10 minutes post-storm, and the width of pod gap in the dorsal suture and number of seeds released 10 minutes post-storm. Error bars = standard error of each mean.

and none of these pods were opened. Missing pods were likely also not removed intact by Merriam's kangaroo rats, because these rodents carry individual seeds in fur-lined cheek pouches and would not be able to carry away intact pods.

DISCUSSION

Pod biomechanics enable informed dispersal

The physics of plant movement has received considerable research attention both historically (Darwin and Darwin, 1881) and more recently (Read and Stokes, 2006; Forterre, 2013). Movement of dead tissues, such as mature pericarp tissue, is usually driven by hydration/dehydration motors that contribute to movement via the reversible shrinking and swelling of cells and tissues. Studies of fruit dehiscence have usually focused on movement-inducing hygroscopic changes that happen during drying (Elbaum and Abraham, 2014). Specialized tissues within the fruit wall respond to dehydration by contracting, twisting, or coiling. Speed of motion is inherently limited by the rate of water movement through

the tissue, but some plants have evolved mechanical instability mechanisms that can release stored energy, resulting in irreversible rapid motion during drying (Forterre, 2013; Poppinga et al., 2019). Species with ballistic seed ejection in response to water (Witztum and Schulgasser, 1995) or even before dehydration (Galstyan and Hay, 2018) also use such mechanisms, in addition to changes in water content or turgor pressure gradients.

The movement exhibited by pods of *A. holmgreniorum* is more subtle. Tissues in the ventral partition of *A. holmgreniorum* pods play a key role in pod shape change. The flattening of the ventral partition in response to slow dehydration of freshly matured fruits results in gradual pod curving but only partial dehiscence, whereas the hygrochastic return to near-cylindrical shape and the complete opening of the dorsal suture happens much more quickly. For pods submerged in water, pod opening and seed release can take place in less than 1 min. This relatively fast response to wetting results in pod dehiscence during the first few minutes of even a low-intensity rainstorm. The pods can undergo repeated cycles of shape change in response to environmental cues, but once the seeds have been released by rain, these changes no longer function in dispersal. Only the shape change and release of seeds following the first wetting event represent an element of informed dispersal.

Dispersal by wind

Wind is one of the most common seed dispersal agents, and various morphological adaptations to wind dispersal are seen in

the plant kingdom, particularly in the Fabaceae (Fahn and Zohary, 1955; Fahn and Werker, 1972). Studies of wind-dispersed species have identified categories of diaspores and their associated dispersal strategies (Fahn and Werker, 1972; van der Pijl, 1982; Augspurger, 1989; van Rheede van Oudtshoorn and van Rooyen, 1999), yet for many species the dispersal strategies remain unknown.

For legumes, Augspurger (1989) found that the majority of wind-dispersed diaspores are indehiscent. The few dehiscent fruit categories that she reported tended to have few seeds, reflecting the evolutionary trend toward decreased seed numbers in wind-dispersed legumes (Dudik, 1981). The added weight of more seeds should negatively affect aerodynamics. The pods of *A. holmgreniorum* seem to run counter to this expectation. They are dehiscent and contain 18 seeds on average (Searle, 2011) but still show aerodynamic capabilities, as demonstrated in the current study. A small group of species within the Fabaceae has evolved a nonaerial wind dispersal strategy of tumbling across the ground in open habitats (Augspurger, 1989). From our studies we conclude that *A. holmgreniorum* falls into this category of chamae-anemochores (ground tumbler dispersed by wind). However, our finding that the legume itself is the primary dispersal unit and that seeds are dispersed from

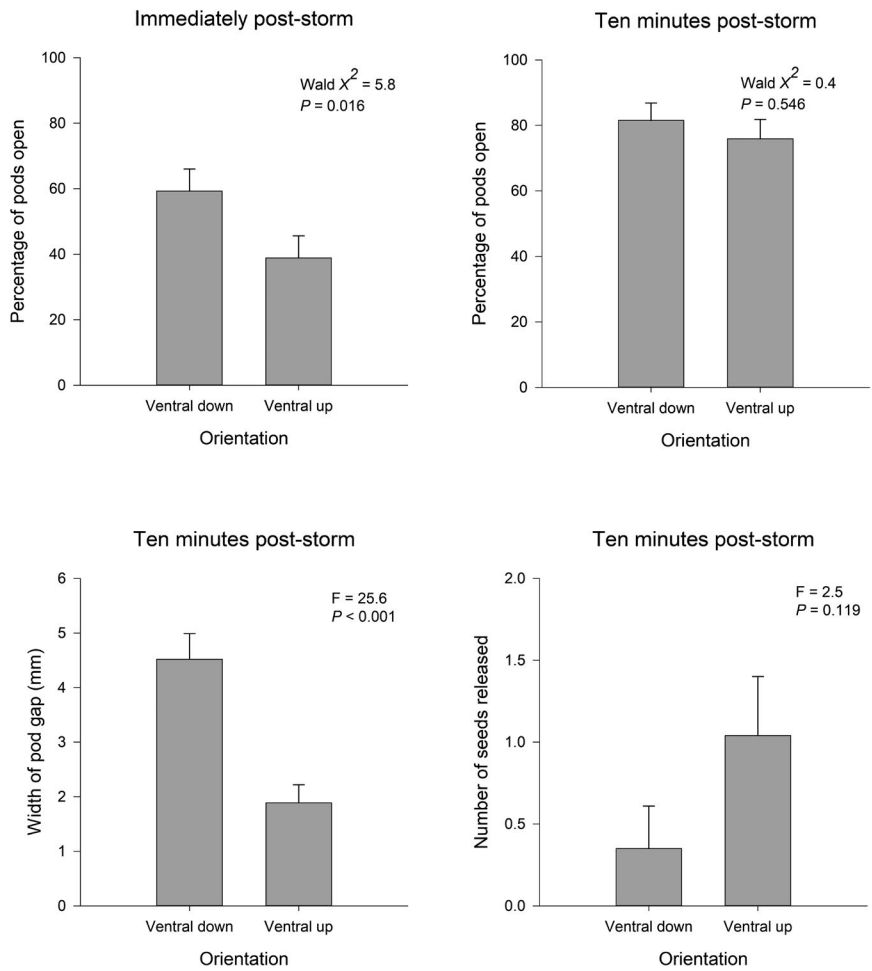


FIGURE 6. The effect of pod orientation during a 10-minute simulated rain period on the percentage of *Astragalus holmgreniorum* pods open immediately post-storm and 10 minutes post-storm, and width of pod gap in the dorsal suture and number of seeds released 10 minutes post-storm. Error bars = standard error of each mean.

the partially dehiscent legume as it tumbles along the ground appears to be unique. The more common form of chamae-anemochory is the annual tumbleweed life form, in which the entire plant breaks off at the soil surface and disperses seeds or fruits as it tumbles in the wind (van der Pijl, 1982).

Pods of herbaceous plants that experience dry desert conditions may be more likely to be dispersed by wind than those of more mesic environments. Because *A. holmgreniorum* occurs in open areas with little vegetative cover (Stubben, 1997), its pods on the ground can be moved by wind. Field anemometer data recorded near the ground over the summer at the study site showed that wind velocities used in the laboratory experiment ($3.5\text{--}10.5\text{ m}\cdot\text{s}^{-1}$) were in a realistic range.

Dispersal of seeds from the partially dehiscent pods as they bounced along the ground was highly dependent on the combination of surface roughness, slope, and wind velocity, all of which vary widely under field conditions in the Mojave Desert. This indicates that the dispersal of *A. holmgreniorum* seeds from pods during wind movement can be complex and possibly microsite-specific. For example, high densities of seeds can accumulate in response to surface microtopography and in the wind shadows

of shrubs (Brown et al., 1979). Higher rates of seed deposition in favorable habitats can improve rates of recruitment and influence population dynamics (Nathan and Muller-Landau, 2000; Levin et al., 2003) and has been termed “directed dispersal” (Wenny, 2001). It is not known whether seed scatter during wind dispersal in *A. holmgreniorum* has this effect. Because seeds of a given cohort germinate over many years, seed aggregations are not easily detected by identifying high-density seedling patches of this species.

The negative exponential dispersal curve we found in our interpod distance study (Fig. 2) is similar in pattern to the idealized curves presented by Willson and Traveset (2000) and also agrees well with pod movement distances in our field study with marked pods (Table 1). The directional patterns of pod dispersal we observed in the marked pod experiment reflected prevailing south and southwest winds, but also occasional erratic wind directions, further supporting the conclusion that these pods were moved by wind.

Hygrochasy as a mechanism to time seed release, prevent dispersal, and reduce predation

We have shown that the pods of *A. holmgreniorum* exhibit hygrochasy. Hygrochasy functions in many species as a mechanism for timing seed release during germination-triggering rain events (Gutterman, 1990, 1994; Martínez-Berdeja et al., 2014). This is not likely to be the case for *A. holmgreniorum* because its seeds are physically dormant and not germinable at dispersal (Searle, 2011; Rominger et al., 2019). Instead, when the fruit

itself functions as a diaspore, as in *A. holmgreniorum*, hygrochasy and subsequent washing out of the seeds can act to curtail maladaptive within-pod dispersal.

Gutterman (1990, 1994) concluded that mature fruits that remain closed when dry function to protect seeds from predation during the desert dry season, particularly from ants, and that

TABLE 1. Travel distances for marked pods ($n = 360$) in the field pod dispersal experiment installed in *Astragalus holmgreniorum* habitat on May 6, 2018.

Travel distance	June 16 evaluation		August 13 evaluation	
	Pods recovered	% of recovered pods	Pods recovered	% of recovered pods
0–15 cm	262	83.2	119	45.4
15–50 cm	21	6.7	70	26.7
50–100 cm	21	6.7	31	11.8
100–200 cm	6	1.9	23	8.8
200–600 cm	5	1.6	15	5.7
>1500 cm	0	0	4	1.5
Total recovered	315	88% of total pods	262	73% of total pods

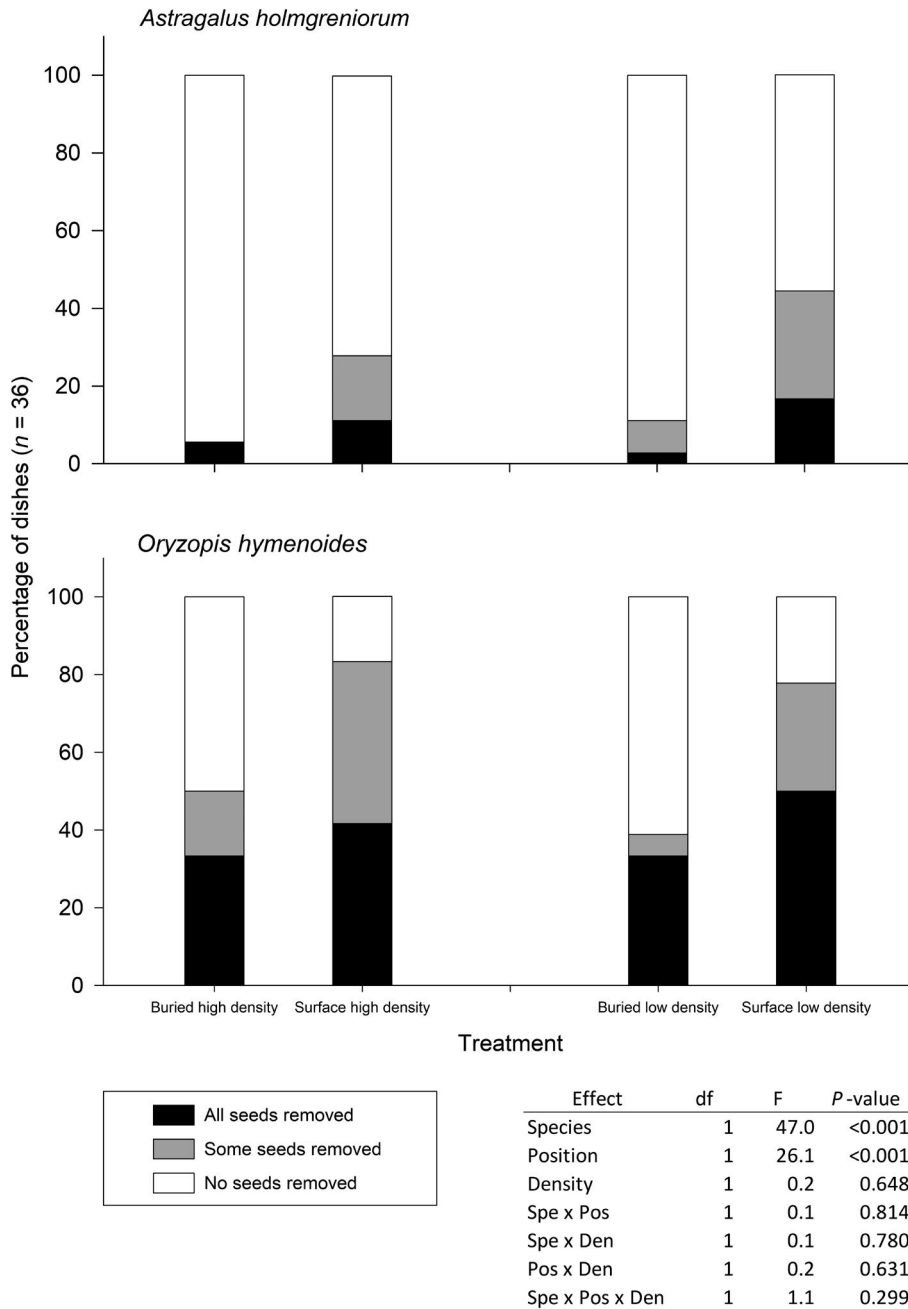


FIGURE 7. The effects of Species (Spe), Position (Pos), and Density (Den), and their interactions on the percentage of field-soil-filled, 6-cm Petri dishes with all seeds, some seeds, or no seeds removed in each of four treatment combinations shown separately for *Astragalus holmgreniorum* and *Oryzopsis hymenoides*. Position refers to position in the soil of the petri dish (buried approximately 1-cm deep or surface-sown). Density is either low: 4 seeds per dish or high: 40 seeds per dish. The response variable in the analysis was a proportion of dishes with no seeds removed.

hygrochasy is a mechanism to ensure their release when seed predators are less active. In our marked pod experiment, seed predators largely ignored the coriaceous dry fruits, supporting this hypothesis for *A. holmgreniorum*. Very few dry pods had any rodent chew marks, perhaps because the excessive time required to remove seeds in situ could expose the animal to increased predation risk (Auger et al., 2016). Once the pods became wet and

seeds were washed out, we observed that the seeds were often quickly buried in mud, effectively preventing further movement following release and also providing protection from predation. Birds and harvester ants cannot detect buried seeds, whereas rodent seed predators use olfaction for detection. Because seeds of *A. holmgreniorum* do not take up water, they are not readily detectable by olfaction even when the ground is wet (Paulsen et al., 2013).

Merriam's kangaroo rats in our field experiment removed some seeds of *A. holmgreniorum*, indicating that these seeds would likely be consumed or cached if readily available on the surface. These scatterhoarding rodents could act as mid-distance dispersal agents for *A. holmgreniorum*, because their home ranges can be at least 100 m in diameter (Auger et al., 2016). The fact that the seeds are not highly preferred increases the likelihood that they would be cached rather than consumed, and the chances of cache discovery would be reduced because detection of physically dormant seeds would be difficult. However, the evidence suggests that rodents play only a minor role in *A. holmgreniorum* seed dispersal.

CONCLUSIONS

We conclude from these experiments that wind is the most likely primary dispersal agent for *A. holmgreniorum*, given that pods can readily be moved under conditions likely to be encountered in the field, and in fact were moved along the ground by wind under field conditions. The distances moved may not ordinarily be very great, but the potential for longer-distance dispersal by wind, e.g., in dust devils, clearly exists. We also showed that seeds are shaken from the pods during wind dispersal, which provides a mechanism for seed scattering away from the maternal plant. Pod hygrochasy may reduce seed predation but functions primarily to limit dispersal by water, acting as an antitelechoric agent to prevent seed dispersal within pods in overland flow to sites that are outside suitable habitat for the species.

The dispersal syndrome of *A. holmgreniorum* we have described presents aspects that are in direct opposition to each other, i.e.,

one aspect promotes seed dispersal in dry pods and the other prevents seed dispersal when pods are wet. This syndrome represents a novel and striking example of informed dispersal (Martorell and Martínez-López, 2014; Seale and Nakayama, 2019) where dispersal-related traits are modified in an adaptive way in response to an environmental cue, namely the rainfall that causes pod hydration, shape change, and seed release into a suitable habitat.

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AUTHOR CONTRIBUTIONS

S.E.M. and S.H. conceived the ideas and designed the methodology. All authors (S.E.M., S.H., and M.T.S.) took part in data collection, analysis, and writing of the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. A short video example of Dispersal by Wind in the Laboratory.

APPENDIX S2. A summary of the data files.

APPENDIX S3. The Dispersal by Wind in the Laboratory data.

APPENDIX S4. The Simulated Rain in the Laboratory data.

APPENDIX S5. The Dispersal by Seed Predators in the Field data.

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