

Comparing recruitment success of *Dudleya* species

Danielle Amoroso

Master's Candidate

California State University, Northridge

Danielle.amoroso@csun.edu

Golden Gate National Recreation Area

Background

The genus *Dudleya* Britton & Rose (Crassulaceae) includes about 45 species that are succulent perennials. The genus has many species that display a variety of morphologies, from large rosettes about a half a meter in diameter to petite geophytes less than 10 cm across (Yost 2013). *Dudleya* are often found on rocky outcrops in the California mountains, which are suitable locations for studying colonization and recruitment (Lopez et al. 2009; Ryti 1984). The different species of the genus have come under much scrutiny, as they are difficult to discern, and have a tendency to hybridize (Moran 1951b; Uhl and Moran 1953; Yost et al. 2013). The species, in general lack apomorphic characteristic and show highly variable morphologies (Moran 1951a, 1960; Yost 2013). The species distinctions are based on stem morphology and petal orientation (Moran 1960; McCabe 2012; Yost 2013). The intraspecific variation of the genus has resulted in recognized species complexes (McCabe 2012; Yost 2013), which tend to be divided across their range.

I am studying the earliest life stages of the plant, which fall into the classification of the regeneration niche. While the term 'niche' is used frequently in ecology, it has many sub-definitions. The niche, in a general definition is the plant's total relationship with its environment, including biotic and abiotic factors. Grinnell

(1917) described the niche of the California Thrasher (*Toxostoma redivivum*) as the habitat it occupied and the behavioral adaptations it had developed to deal with those factors. Hutchinson (1957) described a species' niche as a "n-dimensional hyper volume", meaning that many factors were attributed to the niche as a whole. In 1977, Grubb elaborated on niche theory by focusing on the *regeneration niche* (or recruitment niche). He was interested in what it took for a species to persist and replace deaths within its population, and what determined that a seed would mature into a sexually reproductive adult. It "is an expression of the requirements for a high chance of success in the replacement of one mature individual by a new mature individual of the next generation, concerning all the processes and characters" (Grubb 1977, pp. 119). These characters include dispersal in space and time, germination, seedling establishment, and further development to the immature plant.

Seed germination and seedling establishment are crucial phases in the life of a plant, mainly due to the vulnerability of seedlings (Dodd and Donovan 1999; Clarke and Davison 2004; Baily et al. 2012; Warren and Bradford 2011; Martinez-Villegas et al. 2012). Seedling vulnerability is especially critical for plants that inhabit rock outcrops, and areas that have high seedling mortality. Regeneration of plant communities begins with the emergence of seedlings to replace deaths within the population, which was first generally discussed by A. S. Watt in 1947. The numbers of recruits of new generations isn't only important within the population itself, but is also important in the theory of evolutionary divergence (Grubb 1977). Differences in the community begin at the time of regeneration when new seedlings

are recruiting into their realized niche, and becoming sexually mature individuals. In 1955, A.S. Watt emphasized that there are four main phases of a plant's life, which is reflected by physiological age. The four stages are pioneer, builder, mature, and degenerate. The pioneer stage will be the focus of this study, and the way the different species pairs recruit into their regeneration niche, as seedling recruitment is often the central limitation to any population restoration (James et al. 2011) and persistence.

The germination of a seed, emergence through the substrate and the transition to being a successful recruit within the population has been found to be the most limiting factor for a number of native plant species, and their subsequent recruitment (Dodd and Donovan 1999; James et al. 2011). Cervera et al. (2006) found that seedlings are more vulnerable than adults due to extreme environmental fluctuations that can occur at the substrate surface, especially in semi arid and arid environments like those throughout California.

Over half of all *Dudleya* are considered "endemic," "uncommon," "rare," or "threatened" (Bartel in Hickman 1993). Conservation of an imperiled plant, or rare species conservation often requires a thorough understanding of its reproductive ecology (Weekley et al. 2010). Factors that may contribute to a rare species' decline tend to be due to small population sizes, breeding constraints, habitat fragmentation, and alteration of disturbance regimes (Weekley et al. 2010), as well as the high numbers of invasive species present in California. Since many of the *Dudleya* species are native to restricted habitats as well, they have become habitat specialists. These habitats have narrow ranges, which in turn, creates a narrow

niche for *Dudleya* to persist in. These specialist species experience many ecological challenges than their congeners that have broader habitats (Miller-Struttmann 2013). These ecological challenges require the species to develop differences in reproductive traits that may contribute to their range restriction (Miller-Struttmann 2013). These differences in reproductive traits may concern seedling success and the ability for the maternal plant to create ample seeds for the propagation of the next generation.

Differences in recruitment success are likely to reflect a trade-off between seed size and seed number (Jakobsson and Eriksson 2000). Although seed number is difficult to quantify in *Dudleya*, seed size has been interesting to investigate. Seed size is a key trait in plant life history. Large seeds are generally seen to promote recruitment in places with greater competition for resources, in shade, or under drought or mineral depravity (Westoby et al. 1996; Jakobsson & Eriksson 2000). Jakobsson & Eriksson found a positive relationship between seed size and recruitment success, and that larger seeds produce larger seedlings. Donath and Eckstein (2010) believe that large seeds also have larger (longer) radicles, which may have a better chance of contacting soil. Small seeds and small radicles may be at a disadvantage in microsites thick with litter or bryophytes. Small seeds may be advantageous in terms of dispersal and colonization at microsites (Moles & Westoby 2004). It has been found that the body size of the maternal individual can influence any correlation between seed size and seed numbers (Venable 1992), these measurements can be standardized to account for maternal size. Location dependent variations have also been found contributing to seed size variation

(Kuniyal et al 2013; Ellison 2001; Dlamini 2011). Considering the effects of the phylogenetic relationships among the species using phylogenetic independent contrasts will allow for accounting of phylogeny (Felsenstein 1985). It will be interesting to see if the tendency to maintain their ancestral states (phylogenetic conservatism) is found in these species. This tendency of failure to adapt to new environmental conditions has been called a key factor in speciation due to isolation of populations (Wiens 2004). Although it seems that *Dudleya* are happy to speciate and adapt in unique habitats that many other plants couldn't colonize or survive in. Is this divergent natural selection driving speciation? Or is conservatism reigning supreme?

I intend to investigate the differences in recruitment success of various *Dudleya* taxa, while analyzing the life history trade-off patterns concerning recruitment in a phylogenetic context. Various hypotheses include the following: how does seed size relate to seedling size? How does seed size affect recruitment success in two experimental gardens? Do rare species recruit faster than more common species? Are more common species better at establishing themselves than rare species? Are closely related species very different in their range and habitat dependence? Do closely related species that grow far from each other have similar regeneration niche requirements? Do species planted experimentally have similar reproductive characteristics as well as vegetative structures? How does environmental heterogeneity contribute to differences in the recruitment niche? Can certain species withstand a harsh environment better than others? Do recruits

of closely related species have similar thresholds of tolerance to these varying environments?

Methods

Golden Gate National Recreation area was visited on July 31, 2015. Seeds were collected and mother plant measurements were recorded. Sites in Marin County were: Golden Gate National Recreation Area (37.819°N, -122.531°W and 37.82266°N, -122.532°W).

I sampled 30 individuals of *Dudleya farinosa* and 32 individuals of *Dudleya caespitosa*.

Field Measurements

Dudleya farinosa

On average, inflorescences were about 18.56 ± 0.43 centimeters tall (mean $\pm$ SE, $n=34$), showing about 1.37 ± 0.1 inflorescences per plant. Inflorescences had an average of 24 ± 1.10 fruits. The longest leaf measurements averaged at about 2.31 ± 0.20 centimeters. The average diameter of the rosettes measured were 4.75 ± 0.20 centimeters.

Dudleya caespitosa

On average, inflorescences were about 19.62 ± 1.67 centimeters tall (mean $\pm$ SE, $n=34$), showing about 1.46 ± 0.17 inflorescences per plant. Inflorescences had an average of 17.75 ± 1.91 fruits. The longest leaf measurements averaged at about 2.30 ± 0.13 centimeters. The average diameter of the rosettes measured were 4.0 ± 0.19 centimeters.

I personally observed about 3 different species of spiders on *Dudleya* inflorescences, presumably used as scaffolding, hunting grounds and/or egg/nest protection. The identity of the genera is still being worked on as I have gotten a few conflicting ideas.

Seed Measurements

Seeds were collected from reproductive individuals in the field and taken back to the lab. Each individual's seeds were counted into 6 sets of 5 (30 seeds total), with 5 of those seeds randomly chosen to photograph under the dissecting scope. Photographs were run through ImageJ software to find seed area. See Figures 2 & 5.

Dudleya farinosa seeds were $0.231 \text{ mm}^2 \pm 0.0032$ (N= 120) on average.

Dudleya caespitosa seeds were $0.243 \text{ mm}^2 \pm 0.0043$ (N= 135) on average.

Experimental Gardens

Two experimental gardens have been established. One is on my campus at California State University, Northridge (CSUN) at the Botanic Garden. This is serving as a harsh inland treatment. The other garden is 50 miles west of CSUN at California State University, Channel Islands (CSUCI). This is the cooler/moister coastal treatment.

The germination experiment has been conducted at CSUN in the Greenhouse located within our Botanic Garden. Up to 30 seeds from each individual were planted in sets of 6 pots (5 seeds/pot). All seeds were planted on 21 November 2015 in 3 ¼ inch pots with a California native soil blend that I custom mixed with 40% pumice. Vermiculite was sprinkled on top to aid in moisture containment during the germination phase. Pots were watered daily until 25 December 2015, and since have been watered about every other day. Flats have been rotated along the bench weekly. Pots have been fertilized monthly with a 4x dilute, equal ratio Miracle Grow solution by hand. Germination censuses have been completed monthly and environmental data (temp/ humidity/ dew point) have been recorded by a data logger (HOBO U023) every 15 minutes.

Pots will be randomly split in half and moved outside to each of the experimental gardens in April. There they will be fenced, under shade cloth with data loggers set up above flats. This will be the start of the establishment experiment. Successful establishment will mean that plants survive the summer.

Germination Censuses

Dudleya farinosa

There are 139 pots in the greenhouse currently. Censuses of seedlings for December, January and February have been completed, with total germination percentages being 29%, 57% and 52% respectively. 1 pot has very noticeable post-cotyledonous leaves.

Dudleya caespitosa

There are 96 pots in the greenhouse. Censuses for December, January and February have total germination percentages of 73%, 81%, and 79%.

Findings

The diversity of *Dudleya*'s in Marin County is interesting. The differences between *D. farinosa* and *D. caespitosa* are difficult to discern. They may hybridize or be entirely new/separate species. Figure 1 shows some morphological data for each species sampled. *D. farinosa* seems to have a much taller inflorescence than *D. caespitosa*. Figure 2 shows seed size comparisons for each species. *Caespitosa* seeds are considerably larger than *farinosa*. This is in line with my hypothesis that seed size and mature plant size would be negatively correlated. This trend has been found for

all populations of different species included in my study (20 total). A tradeoff has been seen where inflorescence height has an effect on seed size, where a taller inflorescence will produce smaller seeds. Presumably, this is due to dispersal ability and possibly pollinator preference. So far, no correlation has been found between seed size and germination. It will be interesting to see if seed size is eventually correlated with successful seedling establishment over summer.

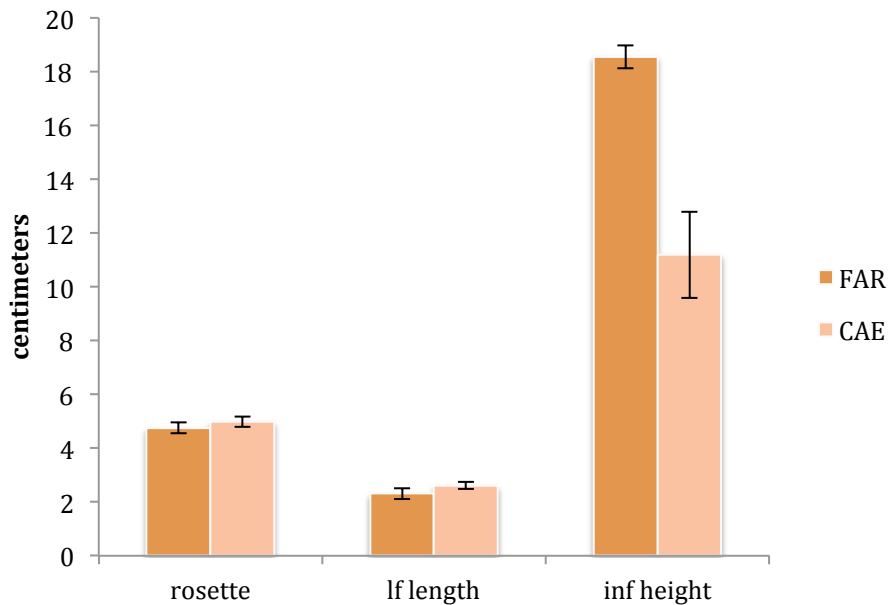


Figure 1: Morphological data for *D. farinosa* and *D. caespitosa* which includes: rosette diameter, longest leaf length and inflorescence height. Bars are means with standard errors.

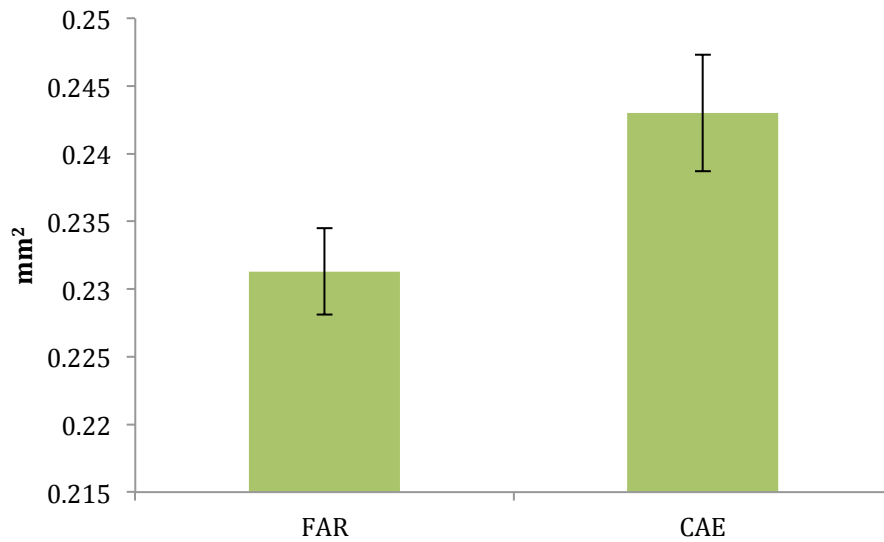


Figure 2: Seed size comparisons for each species

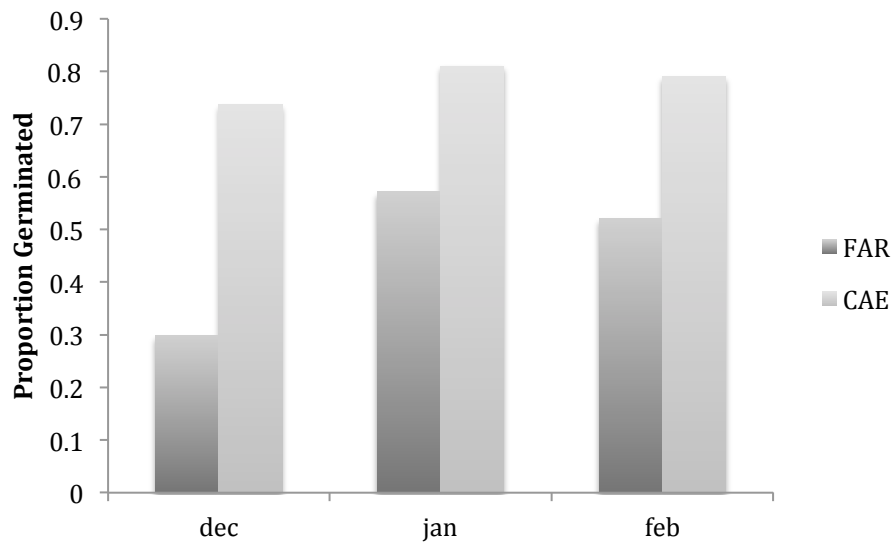


Figure 3: Germination percentages for each species over the first 3 months of the study.

Figure 3 is a comparison of each species' germination percentages for the first 3 months of the study. *D. farinosa* has lower germination than *D. caespitosa* indicating that the seeds of this species may sit in the soil for a longer duration before proceeding through inhibition and germination. *D. caespitosa*'s greater germination

percentage may be due to it having larger seeds. Usually larger seeds are thought to have more nourishment for seedlings. Germination has slightly decreased for the last month on record in all species included in my study. This is likely due to light soil movement when watering which can obscure seedlings. It's also very difficult to see cotyledons on the surface of the soil- especially for species that are showing anthocyanins. They are almost camouflage against the soil/vermiculite mix. This may also be an adaptive trait shielding them from possible predation.

Figure 4 shows a broader finding of my study so far. Mature plant size (rosette diameter) of all populations is negatively correlated with seed size ($r = -0.73$, $P > 0.001$).

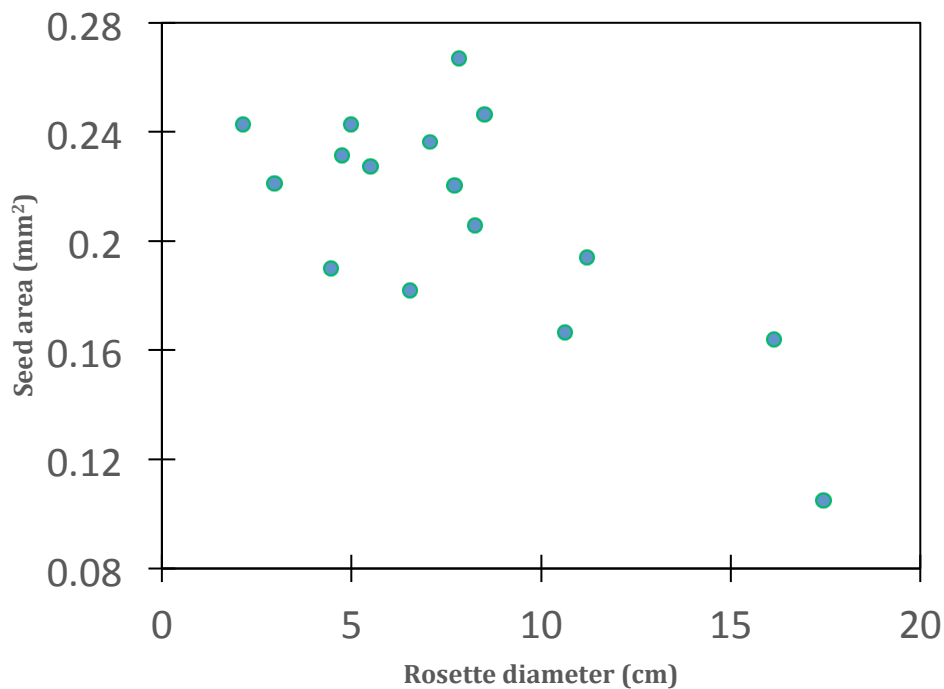


Figure 4: Seed area and rosette diameter are negatively correlated for all populations sampled.

When considering all species sampled, there is a significant effect of mature plant size on seed size. It seems that larger bodied species have the smallest seeds, and small species having the largest. Figure 5 shows the seed size relationships between all species sampled.

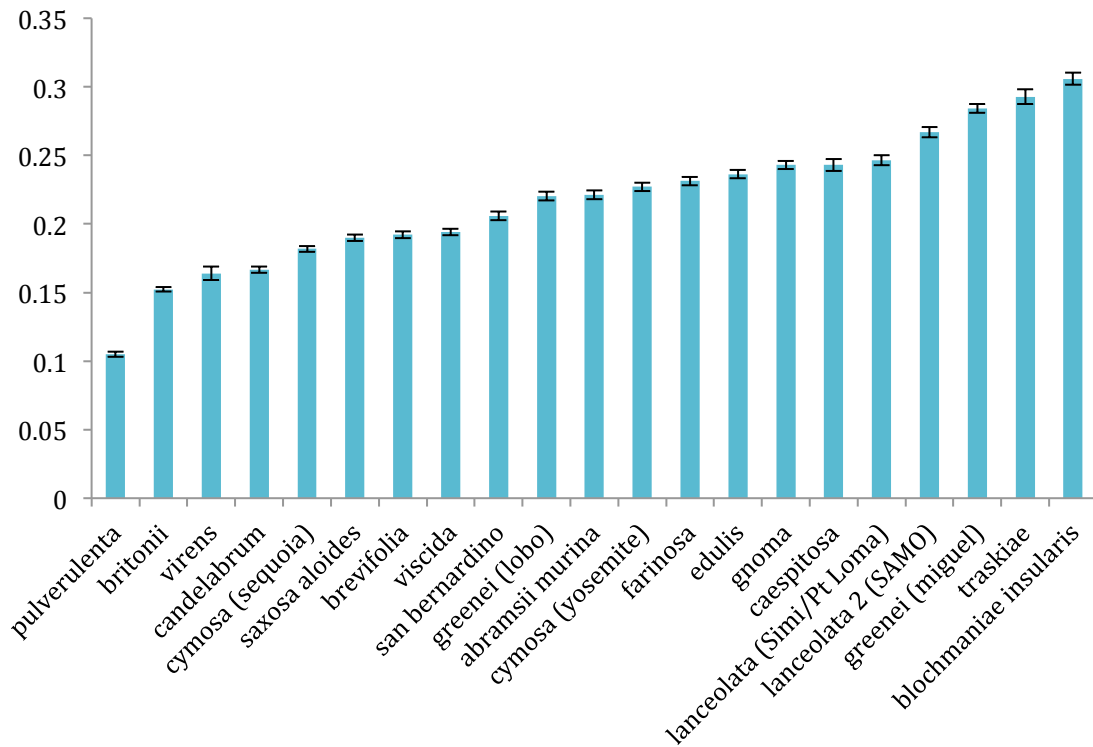


Figure 5: Average seed size for all populations sampled. Bars are SE of the mean.

Conclusion

The previous study on *Dudleya* (Dorsey & Wilson 2011) raised questions about whether seed size might be part of a life-history correlation affecting geographic range size. My early data argues against such a relationship. Seed size was not correlated with germination or range size. I also failed to find a relationship between mature plant size and range size. Unlike mature plant size, germination percentage, range size and even seed size seem not to be phylogenetically conservative. Eventually, phylogenetic independent contrasts will be used to help parse out the possibility of correlated evolution versus phylogenetic conservatism.

References

- Bailey, Tanya G, Davidson, Neil J, Close, Dugald C. 2012. Understanding the regeneration niche: Microsite attributes and recruitment of eucalypts in dry forests. *Forest Ecology and Management* 269: 229-238.
- Cervera, J Carlos, Andrade JL, Sima JL and Graham, EA. 2006. Microhabitats, germination, and establishment for *Mammillaria gaumeri* (Cactaceae), a rare species from Yucatán. *International Journal of Plant Science* 167(2):311-319.
- Clarke, Peter J, and Davison, Elizabeth A. 2004. Emergence and survival of herbaceous seedlings in temperate grassy woodlands: Recruitment limitations and regeneration niche. *Austral Ecology*, Vol. 29, 320-331.
- Dlamini, Cliff S. 2011. Provenance and family variation in seed mass and fruit composition *Sclerocarya birrea* sub-species *caffra*. *Journal of Horticulture and Forestry*, Vol. 3 (9), pp. 286-293.
- Dodd, Geraldine L, and Donovan, Lisa A. 1999. Water potential and ionic effects on germination and seedling growth of two cold desert shrubs. *American Journal of Botany*, Vol. 86, pp. 1146-1153.
- Donath, TW and Eckstein, RL, 2010. Effects of bryophytes and grass litter on seedling emergence vary by vertical seed position and seed size. *Plant Ecology* 207: 257-268.
- Dorsey, Ann and Wilson, Paul S. 2011. Rarity as a life-history correlate in *Dudleya* (Crassulaceae). *American Journal of Botany* 98(7): 1104-1112.
- Ellison, AM. 2001. Interspecific and intraspecific variation in seed size and germination requirements of *Sarcocolla*. *American Journal of Botany* 88: 429-437.
- Felsenstein, Joseph. 1985. Phylogenies and the Comparative Method. *The American Naturalist*, Vol. 125, No. 1, pp. 1-15.
- Grinnell, Joesph. 1917. The niche-relationships of the California Thrasher. Contribution from the Museum of Vertebrate Zoology of the University of California. October. Vol. XXXIV. Pp. 427-433.
- Grubb, PJ. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* 52, pp. 107-145.
- Hickman, JC. 1993. The Jepson Manual: Higher plants of California. University of California Press, Berkeley, California, USA.

- Jakobsson, Anna and Eriksson, Ove. 2000. A comparative study of seed number, seed size, and seedling size and recruitment in grassland plants. *Oikos* 88: 494-502.
- James, Jeremy J., Svejcar, Tony J., Rinella, Matthew J., 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology* 48: 961-969.
- Kuniyal, C.P., Purohit, V., Butola, JS, Sundriyal RC. 2013. Seed size correlates seedling emergence in *Terminalia bellerica*. *South African Journal of Botany*, Vol. 87: 92-94.
- Lopez, Blanca R. Yoav Bashan, Marcario Bacilio and Gustavo De la Cruz-Aguero. 2009. Rock-colonizing plants: abundance of the endemic cactus *Mammillaria fraileana* related to rock type in the southern Sonoran Desert. *Plant Ecology* 201: 575-588.
- Martínez-Villegas, JA; Orozco-Segovia, A; Sánchez-Coronado, ME; Pisanty-Baruch, Irene. 2012. Germination of *Sedum oxypetalum* (Crassulaceae) in a primary lava-field shrubland. *Plant Ecology* 213: 871-881.
- McCabe, S. 2012. Crassulaceae: *Dudleya*. Pp. 666-673. In *The Jepson manual of higher plants in California*, 2: Berkeley, California: University of California Press.
- Miller-Struttmann, Nicole. 2013. Rarity and reproductive biology: habitat specialists reveal a complex relationship. *Botany* 91: 349-359.
- Moles, Angela T. and Westoby, Mark, 2004. What do seedlings die from and what are the implications for evolution of seed size? *Oikos* 106:1.
- Moran, RV. 1951a. A revision of *Dudleya* (Crassulaceae). Ph. D. Dissertation. Berkeley, California: University of California.
- Moran, RV. 1951b. Natural hybrids between *Dudleya* and *Hasseanthus*. *The Bulletin of the Southern California Academy of Sciences* 50: 57-67.
- Moran, RV. 1960. "*Dudleya*". Pp. 344-359 in *A Handbook of succulent plants*, 1 ed. H. Jacobsen. Blandford Press, London.
- Ryti, RT. 1984. Perennials on rock island: testing for patterns of colonization and competition. *Oecologia* 64:184-190.
- Uhl, CH, and Moran, RV. 1953. The cytotaxonomy of *Dudleya* and *Hasseanthus*. *American Journal of Botany* 40: 492-502.

- Venable DL. 1992. Size-number trade-offs and the variation of seed size with plant resource status. *American Naturalist* 140: 287-304.
- Warren, Robert J, Bradford, Mark A. 2011. The shape of things to come: woodland herb niche contraction begins during recruitment in mesic forest microhabitat. *Proceedings of the Royal Society B* 278: 1390-1398.
- Watt, AS. 1971. Factors controlling the floristic composition of some plant communities in Breckland. *The Scientific Management of Animal and Plant Communities for Conservation. Symposia of the British Ecological Society* II, 137-152.
- Weekley, CW, Zaya, DN, Menges, ES, and Faivre, AE. 2010. Multiple causes of seedling rarity in scrub plum, *Prunus geniculata* (Rosaceae), an endangered shrub of the Florida scrub. *American Journal of Botany* 97(1): 144-155.
- Westoby, M, Leishmann MR, and Lord, J. 1996. Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society, London, Series B* 351, pp. 1309-1318.
- Wiens, John J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*, Vol. 58:1, pp. 193-197.
- Yost, JM, Bontrager, M, McCabe, SW, Burton, D, Simpson, MG, Kay, KM, and Ritter, M. 2013. Phylogenetic relationships and evolution in *Dudleya* (Crassulaceae)" *Systematic Botany*, 38(4): pp. 1096-1104