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Rainfall Variability in Deserts and the Timing of Seed Release in Chorizanthe rigida, a Serotinous Winter Desert Annual

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Rainfall Variability in Deserts and the Timing of Seed Release in *Chorizanthe rigida*, a Serotinous Winter Desert Annual

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Plant Biology

by

Alejandra Martínez-Berdeja

June 2014

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ABSTRACT OF THE DISSERTATION

Rainfall Variability in Deserts and the Timing of Seed Release in *Chorizanthe rigida,* a Serotinous Winter Desert Annual

by

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Doctor of Philosophy, Graduate Program in Plant Biology
University of California, Riverside, June 2014
Dr. Exequiel Ezcurra, Chairperson

Serotiny and delayed seed dispersal are thought to have evolved to cope with environmental variability. A taxonomic survey of serotinous desert species in the Mojave and Sonoran deserts showed that this strategy is widespread among many families in this arid region. Furthermore, results also showed that similar seed retention syndromes such as those of plants belonging to other world deserts have evolved in North American deserts region. The next three chapters of the dissertation explored both the ecological and evolutionary significance of seed retention using *Chorizanthe rigida* as the study system. First, I explore the small scale distribution pattern of *C. rigida*, a serotinous desert annual, in a shrub-mound-to-desert-pavement gradient. The consequences of seed retention and desert landscape soil and surface features are discussed. By timing seed release after the winter rains *C. rigida*'s seeds are dispersed by run-off into the desert pavements and transition zones where it forms dead seed-retaining structures that persist for years, releasing seeds to subsequent rain events. Predictions regarding environmental variability and unpredictability were tested by analysing geographic-scale rainfall patterns and serotiny in *C. rigida*, a strict winter desert annual that retains its seeds and releases them after rainfall events. Results show that populations living in bi-seasonal environment have higher seed retention and are adapted to avoid releasing seeds to a summer rainfall cue. Biomechanical tests were performed to assess the functionality of propagule attachment structures. Moreover, a strong correlation between propagule size within-individual variance and winter rainfall variability was found, as predicted by bet-hedging theory. These results suggest that seed size variability allows this species to cope with different levels of environmental unpredictability by displaying a diversifying risk strategy. In conclusion, despite the extreme variability and unpredictability of desert ecosystems, seed retention and timing seed release to rain cues allows serotinous desert plants to thrive during brief windows of opportunity and to persist through harsh conditions.

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Introduction

Delayed dispersal after seed maturation is caused by retention of seeds in the mother plant, a process called serotiny. Serotiny has mostly been studied in fire-pulsating ecosystems and is thought to provide seed protection and to allow synchronization of seed release to favorable conditions for seedling establishment. Serotinous species have also evolved in rainfall pulse-driven ecosystems such as deserts and arid environments, where delayed dispersal has been considered a trait allowing the timing of seed release to rainfall events, regulating the number of seeds that germinate in a given year. Thus, seed retention is important in environments where conditions for successful germination and establishment occur as random pulses and where there is a low probability of successfully establishing outside this ephemeral resource pulse. In this context, the general objective of my dissertation is to provide further evidence of the adaptive significance of seed retention and timing of seed release, an important life-history trait of serotinous desert annuals.

The first chapter of my dissertation is an assessment of the serotinous species in the Mojave and Sonoran desert floras, to provide information about serotinous species in North American deserts that is lacking with respect to other desert floras. The taxonomic review consists of a list of species that retain seeds for variable periods of time, and a classification for these species according to their life-cycles and dispersal syndromes. The analysis of the distribution of serotinous species at the small and regional scale allowed me to set a baseline to address questions related to the ecological and evolutionary significance of serotiny in desert species. Timing of seed release is a critical parameter influencing the probability of seedling survival. As such, serotiny plays a crucial role in plant fitness, as it allows timing dispersal to rainfall, the most limiting, variable, and unpredictable factor in deserts. A specific objective of my dissertation is to understand how seed retention allows desert plants to cope with rainfall variability occurring at different temporal and spatial scales. For this purpose, I analyzed how seed retention allows desert plants to cope with two important sources of environmental variability in desert ecosystems: precipitation and its interaction with soil and geomorphological features. I used *Chorizanthe rigida* (Polygonaceae), a serotinous desert species, as my study system to understand the adaptive significance of seed retention and timing of seed release. *C. rigida* is a low winter annual whose dead spiny skeletons persist for several years, releasing involucres (dispersal units) to rainfall events. This species is associated with desert pavements, and thus constitutes a good system to explore the interaction between rainfall variability and desert geomorphological features. My second chapter consists of a study on the small-scale distribution pattern of *C. rigida*, in a shrub-mound to desert-pavement gradient. For this study I characterized the land surface and soil properties of these two contrasting geomorphological features (i.e., desert pavements and shrub mounds), to assess if seed retention allows *C. rigida* to establish outside the canopy of a nurse-shrub, and if so, to understand why is it that desert pavements provide a suitable habitat for this serotinous species.

C. rigida is distributed from the Great Basin, to the Mojave, Colorado, and Sonoran deserts; its broad distribution range allows testing for the evolution of varying dispersal strategies to adapt to different rainfall variability gradients. My third chapter explores the relationship between seed retention and different levels of rainfall variability and unpredictability. For this, I conducted a morphometric study of *C. rigida* involucres (propagules) including individuals from six populations distributed throughout the Mojave and Sonoran deserts. The different *C. rigida* populations experience either a winter or a bi-seasonal (summer and winter) precipitation regime which allowed me to address the following question: Do the winter-spring growing *C. rigida* plants living in sites with a bi-seasonal rainfall pattern display stronger seed retention than the ones living in sites with strict winter rains in order to avoid releasing seeds to an unfavorable summer rain cue? Moreover, deserts vary strongly in their rainfall predictability, as inferred from long-term climate data. Thus, the different *C. rigida* populations also experience a winter-rain unpredictability gradient allowing me to test the following life-history theory question: does *C. rigida* display a diversifying bet-hedging strategy to cope with winter rainfall unpredictability? Finally, for my fourth chapter I explore the functional morphology of *C. rigida*'s involucres. I use a biomechanical approach to analyze seed release in *C. rigida*, to test the prediction that both timing and the amount of seed release in *C. rigida* is mechanically controlled by propagule morphology, rainfall conditions, and weathering of the plant.

Chapter 1

Delayed seed dispersal in North American deserts

Abstract

Serotiny and delayed seed dispersal are thought to have evolved to cope with environmental variability. I conducted a literature search of serotinous desert plants in the Mojave and Sonoran deserts and classified them according to their life-cycle and seed retention syndrome. Serotinous species in North American deserts have coevolved similar seed retention syndromes as those of plants belonging to other world deserts. Seed retention in deserts plants is a common seed dispersal strategy in arid ecosystems that allows plants to cope with environmental variability and unpredictability.

Introduction

Serotiny consists on the retention of mature seeds within the maternal canopy, delaying seed dispersal for varying periods of time (also known as bradychory or delayed dispersal; Thanos 2000, 2004). Serotiny has been described in different pulse-driven ecosystems such as the seasonally dry, fire-prone mediterranean woody scrubs and temperate forests in Australia, South Africa, and North America (Le Maître 1985; Lamont 1991; Lamont and Enright 2000). The adaptive significance of seed retention and delayed dispersal in these environments has been interpreted as providing protection to seeds from predators and burns (Enright et al. 1998a, b); synchronizing seed release in a nutrient rich environment and with decreased competition for light and water, conditions allowing for higher seedling establishment (Lamont 1991); and reducing post-dispersal hazards by swamping the predator populations with high number of seeds (Janzen 1976).

Despite the fact that most of the literature on serotiny gravitates around fire-driven ecosystems, seed retention and delayed dispersal have also evolved in arid environments. In the central Namib Desert, around eleven species, representing ca. 13% of the flora, retain seeds (Günster 1992). About 40 species in Israel and the Sinai have delayed dispersal mechanisms triggered by the onset of rains (Gutterman and Ginot 1994). Clearly, the serotinous retention of seeds seems to be advantageous in environments where conditions for successful germination and establishment pulsate more or less randomly, and where the probability of establishment outside an ephemeral pulse period is relatively low. Environmental pulses are important in fire-driven ecosystems, but —in the form of randomly-varying water availability— are also known to constitute a major factor driving the dynamics of desert communities (Noy-Meir 1973; Loik *et al.* 2004; Reynolds *et al*. 2004).

The objective of this paper is to provide with a comprehensive list of serotinous species in the Mojave and northern Sonoran Desert in California and neighboring states (Arizona, Sonora, and Baja California) floras. I also aimed at classifying seed retaining species according to the different serotinous reproductive structures.

Methods

A literature search in two regional desert floras was performed: *Flora of the Gran Desierto and Río Colorado of Northwestern Mexico* (Felger 2000) and *The Jepson Desert Manual: Vascular plants of southeastern California* (Baldwin *et al*. 2002) looking for indications of serotiny in the botanical descriptions such as “dry dead skeletons remain on the field for several years retaining seeds”, or for terms associated to seed retention, such as “tardily or irregularly dehiscent fruit”, “woody persistent fruits”, "indehiscent fruit" among others. This broad first list was complemented by including other species known to be serotinous, and by eliminating species that, although having lignified structures, do not retain seeds for any significant period of time based both on field notes and by continuous consulting with experts on the California desert flora. These results were verified through a more in-depth literature search, looking for information on the dispersal characteristics, life-cycle, growth season, habitat, and distribution of species with apparent seed retention syndromes in the Sonoran and Mojave deserts. Finally, this information was confirmed using herbarium specimens and looking for evidence of prolonged seed retention on the specimens, to come with a final list of serotinous species in the California desert region.

Plants can be classified according to their life cycle (Gutterman 1993). Serotinous desert plants have been classified according to the type of seed-retaining structure and the period of seed retention (Zohary 1962; van der Pijl 1982; van Rheede van Oudtshoorn and van Rooyen 1999). For instance, plants that release seed after a long delay (i.e., bradyspores) can be divided into two broad groups depending on length of the period of time of seed retention: plants that retain seed only for one year, from one season to the next, and plants that can retain seeds for several years. I classified serotinous species in the Sonoran and Mojave deserts according to their seed retention syndrome and life-history characteristics.

Results

Known seed-retaining plants are only 1.26% of the species listed in the Sonoran and Mojave deserts floras (Appendix 1.A). However, we found that 13 of 114 families (11.4%) belonging to thirteen different orders have at least one serotinous species (Table 1.A). The serotinous species identified are described in the following sections, and a summary table of the list is provided in Appendix 1.B:

1. Ground-level ephemerals (basicarpy)

Basicarpic species are desert ephemeral plants that produce flowers immediately above ground level, and retain their seeds in hard, lignified structures for a long period of time after the mother-plant dies, releasing seeds to rainfall events (Ellner and Shmida 1981). A basicarpic species in the California desert region is *Chorizanthe rigida* (Torr.) Torr. & A.Gray (Polygonaceae), a short (2–15 cm) winter annual whose dead spiny skeletons persist for several years releasing involucres to rainfall events (Fig. 1a; Felger 2000; Baldwin et al. 2002). *C. rigida* is associated with desert pavements (Martínez-Berdeja et al. 2013), and is distributed from the Great Basin, to the Mojave, Colorado, and northern Sonoran deserts. Although Ellner and Shmida (1981) classified this species as basicarpic, it is noteworthy that, while the plant is low (ca. 5 cm) in the Mojave, towards the southern end of its distribution in the Central Desert of Baja California the plant shows a more erect habit and can reach 20 cm in height. Another basicarpic species in this region is *Camissonia palmeri* (S.Watson) P.H.Raven (Onagraceae), a winter annual that grows close to the ground (5–7 mm stalk length) bearing lignified, rigid capsules that have an opening-closing mechanism triggered by wetting (Fig. 1.1b). Old skeletons, at least one year old, have been observed and collected in the field. This species is uncommon and grows in open areas, between shrubs, on desert flats in the Great Basin and Mojave deserts where winter rainfall dominates (Baldwin *et al.* 2002). Within the basicarpic group, some species retain seeds for a shorter-period of time. For instance, *Chorizanthe spinosa* S.Watson (Polygonaceae) is a winter annual that grows spreading across gravelly surfaces, leaving dense stands of dried skeletons from previous years that retain a few involucres. In the field, most of the involucres are released during the following winter season. Its distribution range is restricted to a winter-rain-only region in the Mojave Desert (Baldwin *et al.* 2002).

2. Persistent plants with lignified fruits

Oxystylis lutea Torr. & Frém. (Cleomaceae) is a summer annual that branches from the base (50–150 cm) forming a dry spiny structure with two "fairly spheric, smooth, white to deep purple, stiff, spine-like nutlets" (2.0–2.5 mm) containing one seed each (Fig. 1.2). The reduction of the silique towards a thick and spinescent style, with a short and stout pedicel "enclosing a seed, tightly and permanently, with but a minute pore at their attachment point" has been considered as an adaptation to aridity (Iltis 1957). This species is endemic to Death Valley, forming dry stands in alkaline flats (Baldwin *et al.* 2002). The seeds are retained for long periods, but the final release mechanism and the factors that trigger it are unknown. *Amaranthus crassipes* var. *crassipes* Schltdl. (Amaranthaceae) is a summer-fall annual whose upper fruit clusters fall from the plant, while the lower woody clusters from early flowering, located near the base of the stem, seem to persist on the plant for a much longer period of time, of unknown duration. This species grows in fine-textured vertisols of playas and sandy soils adjacent to alluvial plains and it is distributed in northwestern Sonora and southwestern Arizona (Felger 2000).

3. Gradually opening capsules

This group includes species that exhibit lignified branches or peduncles holding woody capsules that open gradually along a year or even longer. In some species, there is evidence that the opening of the capsule’s sutures is accelerated by moisture, a trait that allows seed to occur preferentially when the capsule is exposed to rainwater (Walck and Hidayati 2007). In the California deserts, this group is represented by two genera, both in the Onagraceae, that tend to inhabit more or less unstable geomorphological surfaces such as sand washes and desert dunes. Simple wetting experiments we have done, both in the field and in the lab, show that capsular opening in these long-term seed retainers is triggered by moisture.

Camissonia boothii (Douglas) P.H.Raven (Onagraceae) is a winter annual species that germinates and forms a basal rosette from which an erect stalk develops (3–35 cm). The stalk bears cylindrical capsules with a narrow tip that are persistent and tardily dehiscent (Fig. 1.3). There are five subspecies in the Western US that vary in the degree of woodiness and their distribution area. The three less woody and less serotinous subspecies are associated with colder deserts with predictable winter rain: *C. boothii* subsp. *boothii*, *C. boothii* subsp. *alyssoides* and *C. boothii* subsp. *intermedia* grow on sandy slopes or flats in the Great Basin Desert and Northwest Arizona. In contrast, the two more woody and more serotinous species are found in the gravelly and sandy soils of desert flats and washes of the southern, hotter, and climatically more unpredictable Mojave and Sonoran deserts: *C. boothii* subsp. *condensata* and *C. boothii* subsp. *desertorum* (Sanders 1997; Felger 2000; Baldwin *et al.* 2002).

The genus *Oenothera* includes desert winter-spring annuals associated to unstabilized sand dunes or low, sandy mounds more or less stabilized by shrubs in desert regions characterized by winter precipitation and dry summers (Munz 1931; Klein 1970). *Oenothera deltoides* Torr. & Frém. has five subspecies, only one of which is a strict desert dweller and is strongly serotinous suggesting that capsule woodiness is a critical factor in its distribution: *O. deltoides* subsp. *deltoides* develops dry, lignified, basketlike skeletons that persist for several years bearing lignified capsules that dehisce with moisture (Felger 2000) (Fig. 1.4). This spring ephemeral grows on moving dunes and rolling sand plains in the Great Basin, Mojave, and Sonoran desert (Munz, 1931; Klein 1970; Felger 2000; Baldwin *et al.* 2002). Hygrochasy allows this species to disperse its seeds after rainfall events when it is at the upper part of the sand dune, thus allowing successful seedling establishment in an unstable and dynamic landscape. *Oenothera primiveris* A.Gray is a winter-spring annual whose dry skeletons consist of part of the taproot and stem, and a cluster of woody capsules, that may persist for several years. *O. primiveris* grows on sand flats, playas, and gravelly-sandy washes, and is absent from sand dunes, thus this species seems to be adapted to less mobile sandy surfaces. It is distributed in the Mojave and Sonoran deserts (Felger 2000; Baldwin *et al.* 2002).

Semelparous plants in the genus *Agave* form rosettes with tough succulent leaves, and at the end of their life cycle they produce a large flowering scape with dry seed-bearing capsules. The seeds remain in the capsules on the scape for one or more years as it gradually opens (Gentry 1982).The dry paniculate scapes of *Agave deserti* Engelm. (Agavaceae) persist for two or more years after the rosette has died, and its capsules gradually open as they weather, releasing seeds into the environment. *A. deserti* grows in rocky slopes, and in washes in desert scrub in the Sonoran Desert, Arizona and Baja California (Felger 2000; Baldwin *et al*. 2002).

The annual *Datura discolor* Bernh. (Solanaceae) has spiny globose capsules that retain seed and gradually turn downwards as the dead plant skeleton dries. It grows in desert plains, dunes, and washes in the Sonoran desert (Felger 2000; Baldwin *et al*. 2002), and the dry stalks with seed-bearing capsules often persist for as much as a year.

4. Reproducive dimorphism (amphicarpy)

Amphicarpic species display a dimorphic bet-hedging strategy producing two different propagule morphs that differ in their dispersal and survival characteristics: one with higher dispersal and less energy reserves and, another with less dispersal ability and higher energy reserves, representing a high- and low-risk reproductive strategy (Barker 2005). *Enneapogon desvauxii* P.Beauv. (Poaceae), a small annual grass, bears cleistogamous spikelets in the lower leaf axils yielding caryopses that eventually germinate *in situ* within their protective sheaths; and chasmogamous spikelets with smaller unprotected caryopses that are immediately dispersed. This species grows in crevices, rocky habitats and rocky-gravelly soils, and is distributed in the

Mojave, Colorado and Sonoran deserts (Felger 2000; Baldwin *et al.* 2002). A similar case of fruit dimorphism is also found in *Muhlenbergia microsperma* Trin. (Poaceae), a clumped annual to short-lived perennial grass that grows among rocks, along arroyos, and also on sand flats and playas in the Great Basin, Mojave and Sonoran deserts (Chase 1918; Felger 2000).

5. Schizocarps with hetero-mericarps (schizocarpy)

Schizocarps are dry fruits developed from multiple carpels that, when mature, split up into mericarps. In some schizocarpic plants the mericarp itself is the dispersal unit, while in others the mericarp forms a small capsule with two or more seeds, which are shed individually. Heterogeneity in the shedding ability of the mericarps may lead to some seeds being retained for relatively long periods of time, while others may become readily detached. The ability of schizocarps to function as seed-retaining structures was recognized by Shreve and Wiggins (1964) when describing the dry schizocarps of the creosote bush (*Larrea tridentata* Coville; Zygophyllaceae), however, mericarp retention in creosote bushes does not last for more than a few months.

The globemallows (*Spheralcea* spp., Malvaceae) fruit is a schizocarp that separates into mericarps which have an upper smooth dehiscent part and a lower reticulate indehiscent part, with a deep notch between the two sections. Mericarps in desert globemallows contain 1–3 reniform dark brown seeds (Head 1968; Welsh 1980), and the size of the dehiscent and the undehiscent portion of the mericarp varies among species (Baldwin et al. 2002) (Fig. 5). Six species in the genus *Sphaeralcea* are found in California deserts (Pendery and Rumbaugh 1993; Shriladda *et al*. 2012). Four of these species (*S. ambigua* A.Gray, *S. angustifolia* G.Don, *S. emoryi* Torr., and *S. rusbyi* A.Gray) show mericarps with 60–75% of the carpel open, while the last two (*S. orcutti* Rose and *S. coulteri* A.Gray) show higher seed retention ability, with only 20–

30% of the mericarp opening. Coincidentally, these last two, more serotinous, species are strictly endemic to the Sonoran Desert, while all the others have wider distributions and have been collected largely outside desert environments. Five of these desert globemallows are herbaceous perennials with the exception of *S. coulteri* that is an annual species (Baldwin *et al.* 2002).

6. Persistent fruits

The desert ragweeds (*Ambrosia* spp., Asteraceae) are monoecious plants with commonly two-flowered pistillate capitula that develop into dry, spiny, bur-like heads capable of retaining seeds for some time (Payne 1962). The white bursage [*A. dumosa* (A.Gray) W.W.Payne] forms small hemispherical shrubs with an intricate maze of young stems, many of which die during the dry season retaining the lignified burs within the plant's canopy, often for more than one year (Shreve and Wiggins 1964). This species is common throughout the driest parts of the Sonoran Desert. The armed ragweed (*A. bryantii*; Fig. 1.6) grows in the central Gulf Coast region, in Baja California, Mexico, an area of highly unpredictable rainfall patterns. It is a small, perennial shrub bearing woody, spiny heads, developed from highly transformed capitula that form hard, resistant, flask-shaped involucre cases bearing 1–2 achenes, with the tips of the phyllaries forming prominent spines. The spiny heads remain attached to the plant through several growing seasons, retaining seeds within the involucres which "serve the function of armature" (Payne 1962).

In a remarkable case of evolutionary convergence, the Sonoran Desert crucifixion thorns, three spiny, leafless woody trees with “retamoid” morphology (Shmida 1981), show persistent fruits that dry out while still attached to the plant, and can remain fixed for long periods of time (Felger et al. 2001). *Castela emoryi* (A.Gray) Moran & Felger (Simaroubaceae) is an intricately branched, leafless shrub with large thorns and very hard and twisted wood. Its fruit is a oneseeded dry and woody drupe (6 mm) with a flat top and a rounded base, organized in clusters resembling a seven carpel star-like structure that persists for several years in the outer branches (Shreve and Wiggins 1964; Sanders 1998). It is endemic to the Sonoran Desert where summer rainfall is common or predominant, but extends sparsely into the eastern Mojave (Sanders 1998). Similarly, *Canotia holacantha* Torr. (Celastraceae) has persistent fruits, fleshy at first "but soon becoming woody capsules with 5 carpels splitting apically into awned valves, each with several seeds" (Felger et al. 2001). In the field, capsules produced in previous years can be easily identified because of their differential weathering. This species is found in the Sonoran Desert and the eastern Mojave. Lastly, *Koeberlinia spinosa* Zucc. (Koeberliniaceae) has two-chambered berries that dry "capsule-like" (Felger *et al.* 2001). There is no information about the long-term persistence of the fruits, and the plant's status as a serotinous species is doubtful. It has a wide distribution in the Chihuahuan Desert, the Mexican central drylands, and in the thorn forests of Southern Sonora and Sinaloa.

Other desert plants within the family Solanaceae develop berries that become dry and capsule-like, and are able to retain seed for some time. *Solanum elaeagnifolium* Cav., an introduced weedy herbaceous perennial that multiplies by rhizomes and root fragments, has bright orange, often persistent dry berries (1.0–1.5 cm) that commonly remain attached to the dead plants. The plants sometimes break off at the base of the stem and blow in the wind like tumbleweeds. It is a successful dry-land ruderal and it is distributed from California to South America (Boyd *et al*. 1984; Baldwin *et al.* 2002). A related species, *Solanum hindsianum* Benth., is a sparsely branched perennial shrub with round dark and light green fruits (2 cm) that dry out in the plant and persist for an unknown period. It grows in arroyos and washes in the southern Sonoran Desert (Felger 2000).

In the cactus family, seed retention seems to be a common phenomenon in many desert genera. Many species of columnar and barrel cacti in different tribes develop spiny-wooly structures called cephalia where the fruits can be retained for a long time, often to be released or exposed to fruit dispersers at the onset of the following rain period (Britton and Rose 1923; Bravo-Hollis and Sánchez-Mejorada 1991). In the Californian deserts *Echinocactus polycephalus* Engelm. & J.M.Bigelow (Cactaceae) forms clusters containing 6–50 globose-cylindrical stems (23–30 cm in diameter each). The tips of the stems harbor densely tomentose fruits that dry after maturation. As the fruit dries the apical tip opens gradually, allowing dispersal of seeds (Chamberland 1997; Felger 2000; Baldwin et al. 2002). Serotiny is also common in small, tuberculate cacti, many in the genus *Mammillaria*, but also in other genera (Bravo-Hollis and Sánchez-Mejorada 1991; Anderson 2001). Many *Mammillaria* species can retain fruits for long periods, sunken deep within the stem tissue in the axils of the tubercles, protected by the spines of the areoles, and release them when moisture conditions in the environment are favorable (Rodríguez-Ortega et al. 2006; Peters et al. 2009). Although there are no studies of fruit retention in Californian *Mammillaria* species, extrusion of mature fruits from past flowering events in *Mammillaria dioica* K.Brandegee indicate that the fruits have resided sunken in the stems for 1–3 years.

Discussion

The adaptive significance of seed retention in desert plants has been discussed by Ellner and Shmida (1981) and van Rheede and van Rooyen (1999). Other, more specific, studies have attributed different adaptive meaning to serotiny in deserts as allowing to: (a) synchronize seed dispersal to water availability by releasing seeds to rainfall cues (Gutterman and Ginot 1994; Hegazy et al. 2006); (b) adaptively regulate the amount of seeds dispersed depending on the within-season amount and frequency of rainfall (Friedman et al. 1978; Ellner and Shmida 1981; Peters et al. 2009); (c) produce an above-ground seedbank with fractional seed release allowing to spread the risk of germination over several years (Ellner and Shmida 1981; Günster 1994; Gutterman and Ginot 1994; Narita 1998; Rodríguez-Ortega 2006; Peters et al. 2009); (d) keep seeds enclosed in dispersal-restricting seed containers protecting them from predation (Ellner and Shmida 1981; Narita and Wada 1998) and; (e) retain the parental site, a proven microhabitat for successful establishment (Friedman and Stein 1980; Ellner and Shmida 1981; Günster, 1992, 1993; Hegazy and Kabiel 2007).

Within this general context, the results of this study underscore that serotinous species occur in most deserts of the world, and there is a striking convergence of dispersal syndromes. Common seed retention syndromes in serotinous species of the Sonoran and Mojave deserts, such as basicarpy, amphicarpy, and hygrochastic capsules, have also evolved in other deserts around the world. There seems to be an association between basicarpy and winter rains, and between "persistent plants with lignified fruits" and summer rains, as all of the basicarps in the floras reviewed are distributed mostly in the Mojave and northern Sonoran deserts, where rain falls predominantly during winter. While both groups retain seeds in lignified structures, winter-spring seed retainers produce their fruits near ground level while summer seed retainers show high stems and erect growth. Furthermore, different dispersal syndromes seem to be related to particular geomorphological desert features. For instance, *Chorizanthe rigida*, the most common basicarpic winter annual in the Mojave and northern Sonoran deserts, grows mainly in desert pavements. Coincidentally, other basicarpic plants in different world deserts and in different families such as Acanthaceae, Asteraceae, and Brassicaceae also seem to establish preferentially in pavements (Friedman et al. 1978; Ellner and Shmida 1981; Gutterman and Ginot 1994; Narita and Wada 1998; van Rheede and van Rooyen 1999). Similarly, the lignified basket-like structures of the

Onagraceae in mobile sand dunes of the Mojave and Sonoran deserts is remarkably convergent with the growth morphology of *Artemisia* species (Asteraceae) in desert dunes in China (Ma et al. 2010). In conclusion, seed retention constitutes a common strategy to cope with desert environmental variability, as shown by the similarity of seed retention syndromes that have evolved in different deserts, including those in North America. Timing of seed release and having an adaptive seed release response are traits that allow desert serotinous species to cope with rainfall variability.

Literature Cited

Anderson, E. R. 2001. *The Cactus Family*. Timber Press, Portland, Oregon, USA.

Baldwin, B. G., Boyd, S., Ertter, B. J., Patterson, R. W., Rosatti, T. J., and Wilken, D. H. (eds.). 2002. *The Jepson Desert Manual. Vascular plants of Southeastern California.* University of California Press, Canada.

Barker, N. P. 2005. A review and survey of amphicarpy, basicarpy and geocarpy in the African and Madagascan flora. *Annals of the Missouri Botanic Garden* 92, 445–462.

Boyd, J. W., Murray, D. S., and Tyrl, R. J. 1984. Silverleaf nightshade, *Solanum elaeagnifolium*, origin, distribution and relation to man. *Economic Botany* 38, 210–217.

Bravo-Hollis, H., and Sánchez-Mejorada, H. 1991. *Las cactáceas de México*. Vol. III. Universidad Nacional Autónoma de México, Mexico City.

Britton, N. L., and Rose, J. N. 1923. *The Cactaceae*. Dover Publications. Inc., New York, USA.
Chamberland, M. 1997. Systematics of the *Echinocactus polycephalus* Complex (Cactaceae). *Systematic Botany* 22, 303–313.

Chase, A. 1918. Axillary cleistogenes in some American grasses. American Journal of Botany 5, 254-258.

Ellner, S. and Shmida, A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* 51: 133–144.

Enright, N. J., Marsula, R., Lamont, B. B., and Wissel. C. 1998a. The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs. *Journal of Ecology* 86, 946–959.

Enright, N.J., Marsula, R., Lamont, B. B., and Wissel, C. 1998b. The ecological significance of canopy seed storage in fire-prone environments: a model for re-sprouting shrubs. *Journal of Ecology* 86, 960–973.

Felger, R. S. 2000. *Flora of the Gran Desierto and Río Colorado of Northwestern Mexico*. The University of Arizona Press. USA.

Felger, R. S., Johnson, M. B., and Wilson, M. F. 2001. *The Trees of Sonora, Mexico*. Oxford University Press.

Friedman, J. and Stein, Z. 1980. The influence of seed-dispersal mechanisms on the dispersion of *Anastatica hierochuntica* (Cruciferae) in the Negev Desert, Israel. *Journal of Ecology* 68, 43–50.

Friedman, J., Gundermann, N., and Ellis, N. 1978. Water response of the hygrochastic skeletons of the true Rose of Jericho (*Anastatica hierochuntica* L.). *Oecologia* 32, 289–301.

Gentry, H. S. 1982. *Agaves of Continental North America.* The University of Arizona Press, Tucson, Arizona.

Günster, A. 1992. Aerial Seed Banks in the Central Namib: distribution of serotinous plants in relation to climate and habitat. *Journal of Biogeography* 19, 563–572.

Günster, A. 1993. Microhabitat differentiation of serotinous plants in the Namib Desert. *Journal of Vegetation Science* 4, 585–590.

Günster, A. 1994. Seed bank dynamics — longevity, viability and predation of seeds of serotinous plants in the central Namib Desert. *Journal of Arid Environments* 28, 195–205.

Gutterman, T. 1993. *Seed Germination in Desert Plants*. Adaptations of Desert Organisms. Springer, Berlin.

Gutterman, Y., and Ginott, S. 1994. Long-term protected "seed bank" in dry inflorescences of *Asteriscus pygmaeus*, achene dispersal mechanism and germination. *Journal of Arid Environments* 26, 149–163.

Head, J. M. 1968. The genus *Sphaeralcea*, subgenus *Eusphaeralcea* (Malvaceae) in Texas, New Mexico and Arizona: A taxonomic study. B.S. Thesis in Botany. Texas Technological College, TX.

Hegazy, A. K., and Kabiel, H. F. 2007. Significance of microhabitat heterogeneity in the spatial pattern and size-class structure of *Anastatica hierochuntica* L. *Acta Oecologica* 31, 332–342.

Hegazy, A. K., Barakat, H. N., and Kabiel, H. F. 2006. Anatomical significance of the hygrochastic movement in *Anastatica hierochuntica*. *Annals of Botany* 97, 47–55.

Iltis, H. H. 1957. Studies in the Capparidaceae. III. Evolution and phylogeny of the Western North American Cleomoideae. *Annals of the Missouri Botanical Garden* 44, 77–118.

Janzen, D. H. 1976. Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics* 7, 347–391.

Klein, W. M. 1970. The evolution of three diploid species of *Oenothera* Subgenus *Anogra* (Onagraceae). *Evolution* 24, 578–597.

Lamont, B. B. 1991. Canopy seed storage and release - what's in a name? *Oikos* 60: 266–268.

Lamont, B. B. and N. J. Enright. 2000. Adaptive advantages of aerial seedbanks. *Plant species biology* 15, 157–166.

Le Maître, D. C. 1985. Current interpretations of the term serotiny. *South African Journal of Science* 81, 289–290.

Loik, M. E., Brashears, D. D., Lauenroth, W. K., and Belnap, J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141, 269–281.

Ma, J., Liu, Z., Zeng, D., and Liu, B. 2010. Aerial seed bank in Artemisia species: how it responds to sand mobility. *Trees* 24, 435–441.

Martínez-Berdeja, A., Pietrasiak, N., Tamase, A., Ezcurra, E., and Allen, E. B. 2013. Living where others dare not: Microhabitat distribution in *Chorizanthe rigida*, a serotinous desert annual. *Journal of Arid Environments* 97, 120–126.

Munz, P. A. 1931. Studies in Onagraceae VI. The subgenus *Anogra* of the genus *Oenothera*. *American Journal of Botany* 18, 309–327.

Narita, K. 1998. Effects of seed release timing on plant life-history and seed production in a population of a desert annual, *Blepharis sindica* (Acanthaceae). *Plant Ecology* 136, 195–203.

Narita, K. and Wada, N. 1998. Ecological significance of the aerial seed pool of a desert lignified annual, *Blepharis sindica* (Acanthaceae). *Plant Ecology* 135, 177–184.

Noy-Meir, I. 1973. Desert ecosystems: environments and producers. *Annual Review of Ecology and Systematics* 4, 25–41.

Payne, W. W. 1962. The unique morphology of the spines of an armed ragweed *Ambrosia bryantii* (Compositae). *Madroño* 16, 233–236.

Pendery, B. M. and Rumbaugh, M. D. 1993. Globemallows. *Rangelands* 15, 127–130.

Peters, E. M., Martorell, C., and Ezcurra, E. 2008. Nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti (*Mammillaria*) in the Tehuacán Valley, Mexico. *Journal of Arid Environments* 72, 593–607.

Reynolds, J. F., Kemp, P. R., Ogle, K., and Fernández, R. J. 2004. Modifying the ‘pulse-reserve’ paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141, 194–210.

Rodríguez-Ortega, C., Franco, M., and Mandujano, M. C. 2006. Serotiny and seed germination in three threatened species of *Mammillaria* (Cactaceae). *Basic and Applied Ecology* 7: 533–544.

Sanders, A. 1997. Clarification of three *Camissonia boothii* subspecies distributions in California. *Madroño* 44, 106–109.

Sanders, A. 1998. Crucifixion thorn. *Castela emoryi* (Gray) Moran and Felger [*Holacantha emoryi* Gray].

Shmida, A. 1981. Mediterranean vegetation in California and Israel: similarities and differences. *Israel Journal of Botany* 30, 105–123.

Shreve, F. and Wiggins, I. L. 1964. *Vegetation and flora of the Sonoran Desert*. (Two volumes). Stanford University Press, Stanford, California.

Shriladda, C., Kratsch, H. A., and Larson, S. R.. 2012. Morphological and genetic variation among four high desert *Sphaeralcea* species. *HortScience* 47, 715–720.

Thanos, C. A. 2000. Ecophysiology of seed germination in *Pinus halepensis* and *P. brutia*. In Ne'eman, G., and Trabaud, L. (eds.), Ecology, biogeography and management *Pinus halepensis* and *P. brutia* forest ecosystems in the Mediterranean Basin. Backhuys Publishers, Leiden, The Netherlands, pp. 37–50.

Thanos, C. A. 2004. Bradychory – The coining of a new term. In Arianoutsou, M. and Papanastasis, V. P. (eds.), *Ecology, conservation and management of Mediterranean Climate Ecosystems.* Millpress, Rotterdam, pp. 1–6.

van der Pijl, L. 1982. *Principles of dispersal in higher plants*. 3rd revised and expanded edition. Springer-Verlag. Germany.

van Rheede van Oudtshoorn, K. and M. W. van Rooyen. 1999. *Dispersal Biology of Desert Plants*. Adaptations of Desert Organisms. Springer, Berlin.

Walck, J. L., and Hidayati, S. N. 2007. Ombrohydrochory and its relationship to seed dispersal and germination strategies in two temperate North American *Oenothera* species (Onagraceae). *Journal of Plant Sciences* 168: 1279–1290.

Welsh, S. L. 1980. Utah Flora: Malvaceae. *Great Basin Naturalist* 40, 27–37.

Zohary, M. 1962. *Plant life of Palestine. Israel and Jordan*. The Ronald Press Company, New York.

Tables

Table 1.1. Order, family and genera of desert species in the Mojave and Sonoran deserts. The column labeled "serotinous genera" refers to genera that have at least one serotinous species.

Order	**Family**	**Genera**	**Serotinous genera**
Asparagales	Agavaceae	1	1
Caryophyllales	Amaranthaceae	2	1
Asterales	Asteraceae	121	1
Caryophyllales	Cactaceae	8	2
Brassicales	Capparaceae	5	1
Celastrales	Celastraceae	1	1
Malvales	Malvaceae	9	1
Myrtales	Onagraceae	6	2
Poales	Poaceae	74	2
Caryophyllales	Polygonaceae	13	1
Sapindales	Simaroubaceae	1	1
Solanales	Solanaceae	8	2
Zygophyllales	Zygophyllaceae	5	1
Total		**254**	**17**

Appendices

Appendix 1.A

Family, species and serotinous species in the Mojave and Sonoran deserts included in *The Jepson Desert Manual. Vascular Plants of Southeastern California* (Baldwin et al. 2002).

Family	**Species**	**Serotinous species**
Acanthaceae	2	0
Aceraceae	1	0
Agavaceae	1	1
Aizoaceae	2	0
Alismataceae	2	0
Amaranthaceae*	11	1
Anacardiaceae	2	0
Apiaceae	42	0
Apocynaceae	5	0
Araceae	1	0
Arecaceae	2	0
Asclepiadaceae	16	0
Asteraceae*	342	2
Berberidaceae	3	0
Betulaceae	2	0
Bignoniaceae	1	0
Boraginaceae	75	0
Brassicaceae	118	0
Buddlejaceae	1	0
Burseraceae	1	0
Cactaceae*	25	2
Callitrichaceae	1	0
Campanulaceae	12	0
Capparaceae*	9	1
Caprifoliaceae	5	0
Caryophyllaceae	25	0
Celastraceae*	1	1
Ceratophyllaceae	1	0
Chenopodiaceae	57	0
Convolvulaceae	5	0
Cornaceae	1	0
Crassulaceae	7	0

Crossosomataceae	3	0
Cucurbitaceae	7	0
Cuscutaceae	5	0
Cymodoceaceae	1	0
Cyperaceae	67	0
Datiscaceae	1	0
Elaeagnaceae	2	0
Elatinaceae	2	0
Ericaceae	4	0
Euphorbiaceae	39	0
Fabaceae	145	0
Fagaceae	5	0
Fouquieriaceae	1	0
Frankeniaceae	1	0
Garryaceae	1	0
Gentianaceae	11	0
Geraniaceae	3	0
Grossulariaceae	6	0
Haloragaceae	1	0
Hippocastanaceae	1	0
Hydrocharitaceae	6	0
Hydrophyllaceae	65	0
Hypericaceae	1	0
Iridaceae	5	0
Juncaceae	24	0
Juncaginaceae	3	0
Koeberliniaceae	1	0
Krameriaceae	2	0
Lamiaceae	36	0
Lemnaceae	7	0
Lennoaceae	2	0
Lentibulariaceae	1	0
Liliaceae	35	0
Linaceae	2	0
Loasaceae	28	0
Lythraceae	3	0
Malvaceae*	22	6
Martyniaceae	2	0
Molluginaceae	2	0
Nyctaginaceae	23	0

Oleaceae	6	0
Onagraceae*	49	4
Orchidaceae	5	0
Orobanchaceae	5	0
Oxalidaceae	1	0
Papaveraceae	10	0
Philadelphaceae	3	0
Plantaginaceae	4	0
Platanaceae	1	0
Poaceae*	201	2
Polemoniaceae	80	0
Polygalaceae	3	0
Polygonaceae*	96	2
Portulacaceae	18	0
Potamogetonaceae	9	0
Primulaceae	6	0
Rafflesiaceae	1	0
Ranunculaceae	25	0
Resedaceae	1	0
Rhamnaceae	10	0
Rosaceae	43	0
Rubiaceae	16	0
Rutaceae	1	0
Salicaceae	19	0
Santalaceae	1	0
Saururaceae	1	0
Saxifragaceae	4	0
Scrophulariaceae	95	0
Simaroubaceae*	1	1
Simmondsiaceae	1	0
Solanaceae*	29	3
Sterculiaceae	1	0
Tamaricaceae	5	0
Typhaceae	2	0
Ulmaceae	2	0
Urticaceae	3	0
Valerianaceae	1	0
Verbenaceae	6	0
Violaceae	3	0
Viscaceae	6	0

Vitaceae	2	0
Zannichelliaceae	1	0
Zygophyllaceae*	8	1
Total	**2140**	**27**

Appendix 1.B

Family, dispersal syndrome and life-cycle of serotinous species in the Mojave and Sonoran deserts.

Serotinous species			
Family	**Species**	**Syndromes**	**Life-cycle**
Polygonaceae	*Chorizanthe rigida*	basicarpy	winter ephemeral
Polygonaceae	*Chorizanthe spinosa*	basicarpy	winter ephemeral
Onagraceae	*Camissonia palmeri*	basicarpy	winter ephemeral
Capparidaceae	*Oxystylis lutea*	lignified fruits	summer ephemeral
Amaranthaceae	*Amaranthus crassipes*	Lignified fruits	summer ephemeral
Onagraceae	*Camissonia boothii*	hygrochasy	winter ephemeral
Onagraceae	*Oenothera deltoides*	hygrochasy	winter ephemeral
Onagraceae	*Oenothera primiveris*	hygrochasy	winter ephemeral
Solanaceae	*Datura discolor*	hygrochasy	summer ephemeral
Agavaceae	*Agave deserti*	hygrochasy	semelparous
Poaceae	*Enneapogon desvauxii*	amphicarpy	iteroparous
Poaceae	*Muhlenbergia microsperma*	amphicarpy	non-seasonal ephemeral
Malvaceae	*Sphaeralcea orcuttii*	hetero-mericarps	iteroparous
Malvaceae	*Sphaeralcea coulteri*	hetero-mericarps	winter ephemeral
Simaroubaceae	*Castela emoryi*	persistent dry fruits	iteroparous
Celastraceae	*Canotia holacantha*	persistent dry fruits	iteroparous
Cactaceae	*Echinocactus polycephalus*	persistent dry fruits	iteroparous
Cactaceae	*Mammillaria dioica*	persistent dry fruits	iteroparous
Asteraceae	*Ambrosia dumosa*	persistent dry fruits	iteroparous
Asteraceae	*Ambrosia bryantii*	persistent dry fruits	iteroparous
Short-term serotinous species			
Family	**Species**	**Syndromes**	**Life-cycle**
Zygophyllaceae	*Larrea tridentata*	hetero-mericarps	iteroparous
Malvaceae	*Sphaeralcea ambigua*	hetero-mericarps	iteroparous
Malvaceae	*Sphaeralcea angustifolia*	hetero-mericarps	iteroparous
Malvaceae	*Sphaeralcea rusbyi*	hetero-mericarps	iteroparous
Malvaceae	*Sphaeralcea emoryi*	hetero-mericarps	iteroparous
Solanaceae	*Solanum elaeagnifolium*	persistent dry fruits	iteroparous
Solanaceae	*Solanum hindsianum*	persistent dry fruits	iteroparous

Figures

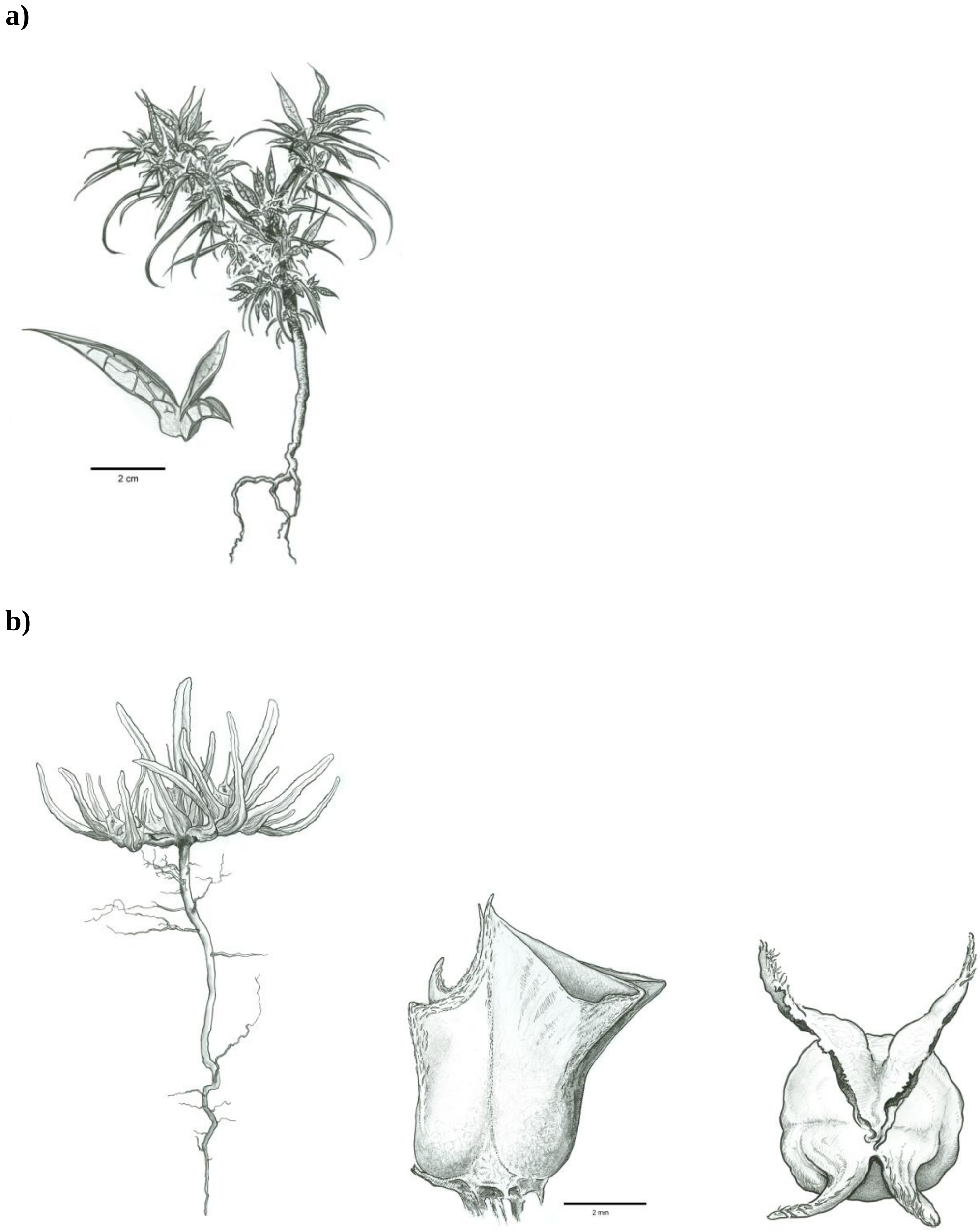

Figure 1.1. Ground-level ephemerals (basicarpy): (a) dry dead skeleton and involucre of *Chorizanthe rigida*, and (b) whole individual, side and top view of the hygrochastic lignified capsule of *Camissonia palmeri*.

Figure 1.2. Erect plant with sclerocarpic fruits in *Oxystylis lutea*.

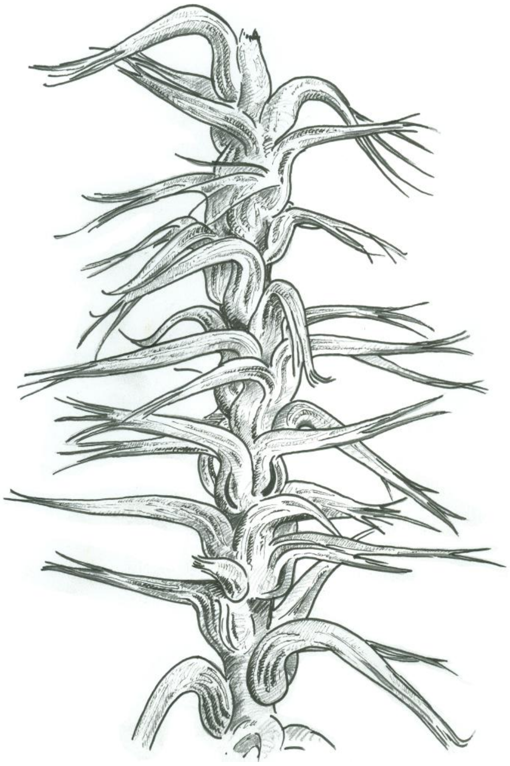

Figure 1.3. Lignified stem and hygrocastic capsules of *Camissonia boothii boothii*.

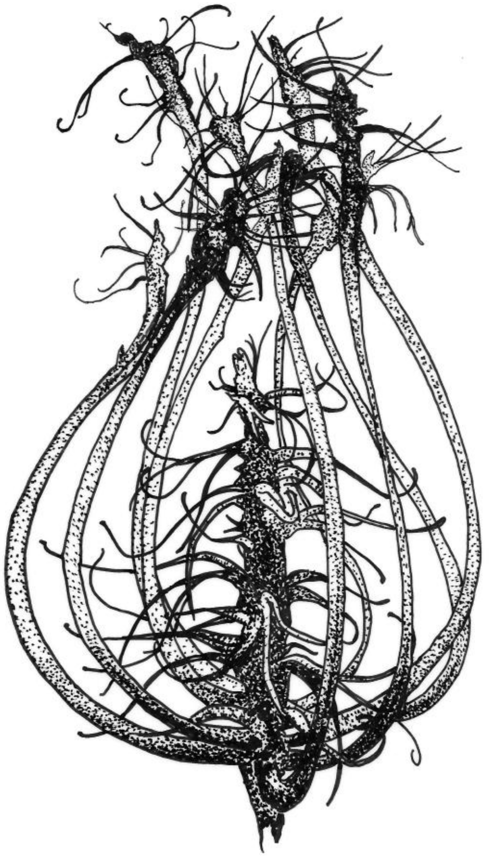

Figure 1.4. Lignified stem and hygrocastic capsules of *Oenothera deltoides* (by A. Turner after drawing by H. R. Mockel).

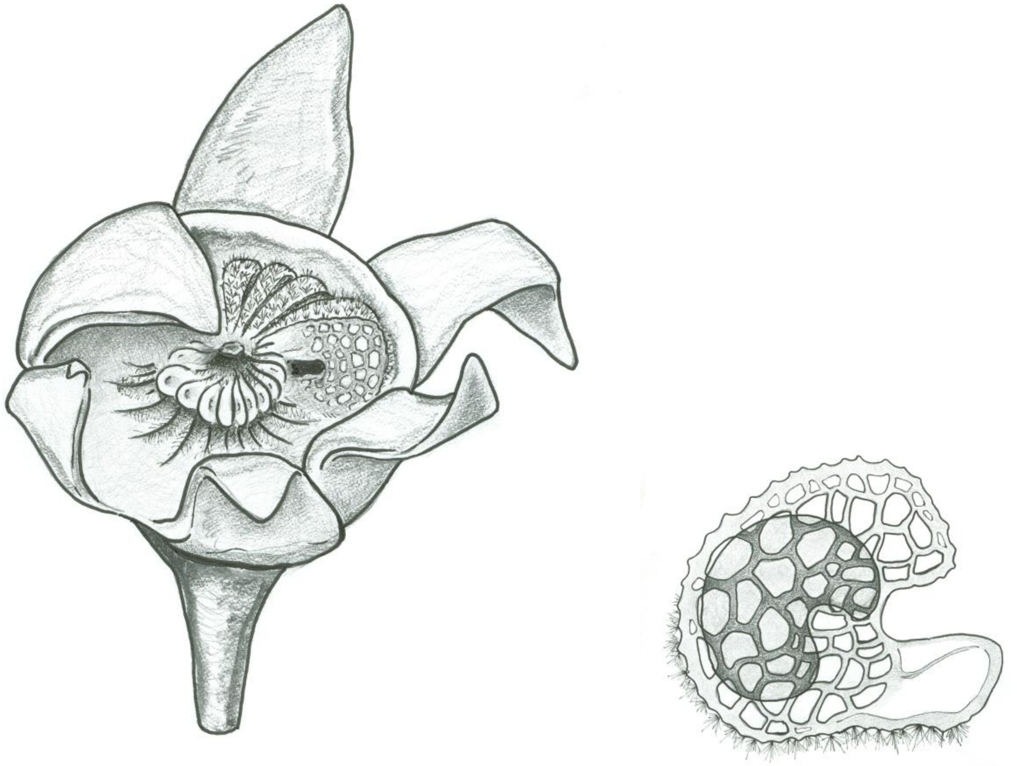

Figure 1.5. Schizocarp and mericarp of *Sphaeralcea coulteri*, showing the reticulate portion holding one persistent seed.

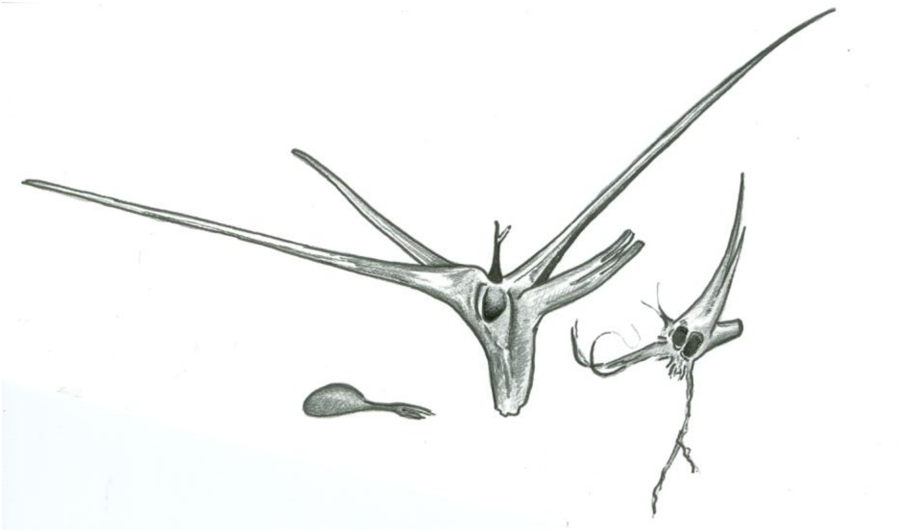

Figure 1.6. Persistent lignified fruit and seed in *Ambrosia bryantii*.

Chapter 2

Living where others dare not: Microhabitat distribution in *Chorizanthe rigida*, a serotinous desert annual

Abstract

I studied the small scale distribution pattern of *Chorizanthe rigida*, a serotinous desert annual, in a shrub-mound-to-desert-pavement gradient. Two sites were established in the Mojave Desert and two sites where established in the Sonoran Desert. Transects were placed along a soil surface gradient from shrub mounds to desert pavements to measure land surface properties, soil characteristics, and *C. rigida*'s small scale distribution. A Principal Components Analysis was done on the resulting site × soil variables matrix. *Chorizanthe rigida* established preferentially in desert pavements outside shrub canopies. Pavements showed finer soil textures and higher electrical conductivities, while shrub mounds had sandy textures, low surface rockiness, higher nitrogen, and higher cover of annuals. I discuss a probable relationship between seed retention and the establishment on desert pavements: timing seed release allows this species to avoid wind- or animal-induced seed dispersal into shrub mounds and establish outside the nurse mounds, where most annual plants concentrate. The seeds encased in the serotinous involucres, released after rains, are dispersed by run-off into the desert pavements and transition zones where, once developed, the dead seed-retaining structures of adult *C. rigida* plants persist for years releasing seeds to subsequent rain events.

Introduction

The distribution of plants across landscapes results from life history traits interacting with environmental conditions at a local scale. In deserts, dispersal and establishment play a major role in plant distribution and in the clumped structure of desert communities (Shmida and Whittaker 1981; Yeaton and Romero Manzanares 1986; Silvertown and Wilson 1994). Although most desert plants germinate and establish below the protective shade of "nurse" shrubs (Valiente-Banuet et al. 2006), some species are able to establish successfully in open spaces. For example, the globose cactus *Mammillaria pectinifera* is able to colonize gravelly surfaces in the arid Tehuacán Valley in Mexico through its ability to (a) retain seeds in specialized serotinous fruits and release them after strong rains, and (b) to germinate and establish in the microhabitat provided by the protective shade of pavement rocks (Peters et al. 2008). Similarly, in the Sonoran and Mojave deserts most annual plants establish under the protective shade of shrubs, but some species seem to preferentially establish in open pavements. One of the most common cases of these non-nursed species are serotinous annual plants of "basicarpic" morphology: small ephemeral plants that produce flowers and seeds near ground level and retain them for long periods in hard, lignified, structures (Ellner and Shmida 1981). Basicarpic plants with delayed seed dispersal occur in many deserts throughout the world and in different families. Some examples are *Anastatica hierochuntica* (Brassicaceae, "rose of Jericho") and *Anthemis melampodina* (Asteraceae, "Negev chamomile") in Israel, *Torularia torulosa* (Brassicaceae, "torularia") in Pakistan, *Plantago coronopus* (Plantaginaceae, "minutina") throughout Eurasian deserts, *Glossonema boveanum* (Apocynaceae) in the Sahara (Steinberger et al. 1990), as well as *Blepharis grossa* (Acanthaceae, "desert thistle"), and *Geigeria alata* and *G. ornativa* (Asteraceae) in the Namib (Günster 1992). Most of these species seem to prosper well in open pavements, and do not seem to need the protective shade of nurse shrubs in order to survive harsh desert conditions (Gutterman 1994, 2002).

In the Sonoran and Mojave deserts the most common basicarpic plant is *Chorizanthe rigida* (Polygonaceae), a serotinous winter desert annual distributed from the southern Great Basin Region to the Mojave, Sonoran, and Baja Californian Deserts (Felger 2000; Baldwin *et al*. 2002). *Chorizanthe rigida*'s dead spiny plants persist for several years firmly anchored to the ground by their deep tap roots. The species' dispersal units (i.e., the seed-bearing involucres) remain attached to the dried mother plant, which thus retains seeds after maturation and death. The dry involucres become loose at their base when the plant is rehydrated by rain and can get detached from it. This process is followed by tissue dehydration causing unreleased involucres to re-attach to the mother plant for months to years until another rain event occurs. Like in many other basicarpic desert annuals, the seed-retention system of *C. rigida* demands the allocation of sizeable amounts of the plant's photosynthetic budget towards the construction of the plant's rigid, lignified structures. The adaptive significance of this dispersal syndrome seems related to the ability to retain an above-ground seed bank in the dry maternal tissues, instead of releasing the seeds to the ground at the end of the life cycle.

Desert landscapes are often formed by a spatial mosaic composed of a matrix of barren pavements and mounds with shrubs growing on them (Musick 1975; Evenari 1985). Open pavements and shrub mounds differ in soil texture and surface rockiness, which result in varying micro-topographic properties (Wood *et al*. 2002). Desert pavements develop on flat, gently sloping, landforms and are covered by coarse gravel and cobble-sized clasts (Musick 1975). The tightly-packed clasts trap fine particles and, consequently, the rocky surface overlays fine textured soils with low infiltration rates, resulting in salt accumulation in the upper horizons

(Wood *et al.* 2005). In contrast, the adjacent shrub mounds show more bare soil (Wood *et al.* 2002) and low surface rockiness formed by sparse and heterogeneous clasts. The microtopography of mounds and the occurrence of associated shrubs promote eolian sand deposition (Parsons *et al.* 1992; Abrahams *et al.* 1995). These sandy soil patches have high infiltration rates and deep leaching of salts, which resulting in ameliorated growth conditions for annual plants compared to the adjacent, generally barren, desert pavements (Musick 1975; Wood *et al.* 2005).

The preference of basicarpic plants for pavements, an unfavorable environment avoided by most other annual plants, is intriguing. Shrubs enhance water infiltration (Berndtsson and Larson 1987; Schlesinger and Pilmanis 1998) while their canopy shading decreases evaporation and reduces high soil surface temperatures (Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991), which results in higher water availability and more suitable growth conditions under nurses. Decomposition of plant litter is carried out under shrubs by bacterial activity while in open pavements it is mostly caused by photodegradation (Montaña *et al.* 1988). Hence, shrubs also increase soil nutrient content from organic decomposition in the soil (García-Moya and McKell 1970; Lajtha and Schlesinger 1986). Granivorous rodents preferentially dig their burrows under shrubs, further contributing to water infiltration and the incorporation of organic matter into the soil profile (Whitford and Kay 1999; Neave and Abrahams 2001).

As part of a broader study on the functional ecology of serotiny and delayed dispersal in desert plants, in this study I explore the hypothesis that *Chorizanthe rigida*, like other lignified basicarpic plants, is able to colonize desert pavements, occupying a micro-niche contrastingly different from that of the most common, nurse-dependent annual desert plants. To test this hypothesis, I analyzed the small-scale distribution pattern of *C. rigida* along the pavement-to-shrub-mound desert gradient, and characterized soil properties along these microhabitats.

Methods

Study species

Chorizanthe rigida is a short, erect desert annual, normally 2–10 cm high. It has a single main taproot and stout stems covered by stiff, spiny bracts. As the stem grows, the soft, long-petioled basal leaves are shed, and give place to linear, rigid bracts (or cauline leaves) armed with a terminal spiny awn that becomes hard and thorn-like in age. The single flowers, with a diminutive yellow perianth, are subtended by a 3-segmented involucre with hard spiny bracts. The fruit is an achene that matures inside the involucre.

Study sites

Field work was conducted at desert pavement and bare-ground mosaic landscapes (*sensu* Wood, Graham, and Wells 2002) where *C. rigida* populations occur. All sites had creosote (*Larrea tridentate*) shrub associations. The creosote bush was the dominant shrub occupying the desert mounds, and well-developed desert pavements were found between mounds. In order to cover the distributional and environmental range of the species, two sites were established in the colder, winter-rain fed Mojave Desert, and two in the bi-seasonal Sonoran Desert, which receives both winter Pacific fronts and summer monsoon rains. Because the surface characteristics of desert pavements may vary according to geologic age, clast lithology, and local geomorphology (Al-Farraj and Harvey 2000), four sites were selected in order to cover as much variation as possible in micro-topographic pavement traits that could be relevant in explaining the small-scale distribution pattern of *C. rigida*. Two sites were established at the Mojave Desert National Preserve, California; the first one was located on an alluvial fan skirt with dolomite limestone deposits located in the Clark Mountains Wilderness Area (35° 31' 32" N / 115° 35' 19" W, 1065 m elevation, 144 mm mean annual precipitation, and 24.8°C mean annual temperature, NOAA, Mojave, CA Weather Station), and the second one was established on volcanic lava deposits located in the Cima Volcanic Field (35° 12' 0.4" N / 115° 52' 11.6" W, 700 m elevation, reported annual precipitation and temperature of 70 mm and 17°C respectively; Wood, Graham and Wells 2002). A third site was established on rhyolitic alluvial deposits located in the Arizona Upland portion of the Sonoran Desert in Organ Pipe National Monument, Arizona (32° 07' 49.4" N / 112° 45' 56.4" W, 550 m elevation, 240 mm mean annual precipitation and 20.3°C mean annual temperature, NOAA, Organ Pipe Cactus National Monument, AZ, Weather Station), and, finally, a fourth site was located near the southeastern edge of the plant’s distribution, on volcanic lava deposits in the Lower Colorado Valley portion of the Sonoran Desert, in the Pinacate Biosphere Reserve, Sonora, Mexico (31° 51' 48.8" N / 113° 26' 45.8" W, 322 m elevation, 140 mm mean annual precipitation and 21°C mean annual temperature (Ezcurra and Rodrigues 1986; Coll-Hurtado 2007).

Sampling

Three 5 m × 1 m transects were set up parallel to each other at three identified land surface mosaics: desert pavement zone, bare-ground shrub mounds and the transition zone between those two surfaces (Figs. 2.1 and 2.2). These transect triads were replicated five times at each site, totaling 15 transects per site, except for El Pinacate, which had three replicates and hence only 9 transects total. Transects were subdivided into ten subplots, 0.5 m × 1 m in size. Soil and land surface variables were sampled on the even-numbered subplots; the number of dry, seed-bearing individuals of *C. rigida* was recorded in each transect on the odd-numbered subplots (total sub-lot area per transect = 2.5 m^2). Changes in plant tissue color caused by weathering allowed for identification of plants belonging to 2011, 2010, and previous years.

Land surface properties were characterized by measuring surface roughness, surface cover, and surface clast dimensions. Surface roughness was obtained by placing a 1 m bicycle chain on the ground and measuring its shortened length (L.) and comparing it to the original length (L_0 = 100 cm). A roughness index (*RI*) was calculated using the following formula (RI = 100 (1 - L_s/L_0); Saleh 1993). Surface cover was characterized by placing a grid with 36 intersections on five of the 0.5 m × 1 m subplots along the transects of each land mosaic. The ground surface below each intersection was categorized according to their soil surface as bare soil, gravel (2-6 mm), and rocks (>6 mm), and according to their biological cover as soil crust, annuals (forbs and grasses) and shrubs. A 1 m tape was placed on three even numbered 0.5 × 1 m plots, and all of the clasts intersecting the meter were collected and measured to obtain projected area, and SE was calculated as a measure of clast size heterogeneity (Wood et al. 2002).

A total of 54 composite soil samples were obtained by taking five 6-cm-deep core soil samples from each transect. Soil samples were air dried and sieved to remove coarse fragments (>2 mm). Percentages of gravel and finer soil particles were calculated gravimetrically. Particle-size distribution was determined through the Bouvoucos hydrometer method (Gee and Bauder 1986). Surface soil aggregates were collected for soil bulk density determination by the paraffin-coated clod method corrected for gravel content (Hirmas and Furquim 2006). Electrical conductivity and pH values were recorded from a 1 : 1 soil/water extract (Rhoades 1982). Total carbon and nitrogen of the composite soils were obtained by the combustion method using a CE Elantech Nirogen Carbon Analyzer (Nelson and Sommers 1996).

Statistical analyses

Log-linear contingency table analysis model with χ^2 deviance were used to study the effect of site (Pinacate, OPNM, Cima and Clark) and landscape mosaic (pavement, transition, shrub zone) on the number of individuals of *C. rigida*. In order to reduce the dimensionality of the soil surface data and to simplify the effect of correlated variables, a Principal Components Analysis (PCA) was performed on the soil data, using the following 18 environmental variables as descriptors of the transect soils: (1-6) soil cover (% bare soil, gravel, rock, biological soil crusts, annual plants, and shrubs), (7) surface roughness, (8) mean clast area, (9) SE of mean clast area, (10) soil bulk density, (11-14) soil texture (% gravel, sand, silt, and clay), (15) electrical conductivity, (16) pH, (17) total carbon and (18) total nitrogen. Variables were standardized prior to analysis given that they are measured in different units. I used a Varimax rotation on the PCA results (following Noy-Meir and Whittaker 1977) to maximize the association between our axes and external environmental factors such as site or position along the landscape mosaic gradient, thus rendering the data more directly interpretable ecologically without losing any of the variance extracted by the component axes. The broken stick test was used to select the principal components axes that explained more variance than could be expected under a random null model. Because in a standardized-data PCA the loadings of the variables on each axis are correlation to coefficients, we identified the soil variables that were significantly associated with each axis at $P = 0.01$. The variables that had highest PCA scores (roughness, clast area, SE of clast area, % rock cover, and soil bulk density) were analyzed with a two-way ANOVA to test their differences among sites and among transects, or the interaction of both factors.

Finally, a response function model was fitted to the abundance data of *C. rigida* along PC1 to model the species distributional niche along the environmental micro-topographic gradient and to identify the preferred soil microhabitat for the species. Given that abundances are measured in number of individuals (a frequency count), in order to model the species response to the multivariate soil gradient, we fitted a bell-shaped, quadratic log-linear model with Poisson error using Generalized Linear Models, taking PC1 as the independent predictor and species abundance in each transect as the dependent variable. For each modeled response curve the predicted point of maximum abundance along the gradient (x_{max}) was calculated using the first derivative of the fitted model and solving it for the point that makes the slope equal to zero (the function's maximum).

Results

The number of individuals of *C. rigida* significantly differed as a result of the effect of site (χ^2 = 10.41, df = 3, P = 0.015), landscape mosaic (χ^2 = 14.24, df = 2, P = 0.0008), and their interaction (χ^2 = 55.69, df = 6, P < 0.0001, Table 1). In most sites (Clark, OPNM, and Pinacate), *C. rigida* established preferentially in the transition zone. In the Cima site, however, maximum counts were observed in the open pavements (Fig. 2.3).

Only two PCA axes for soil variables differed from the random expectation of the broken stick model. These two principal components jointly explained 50.8% of the soil variation in the data (PC1 = 25.8%, PC2 = 25.0%). PC1 was negatively associated with % sand, cover of annuals, total nitrogen, and the presence of bare soil, and positively associated with electrical conductivity and finer soil particles (% clay and % silt). PC2 was negatively associated with surface gravel, and positively associated with bulk density, rockiness, clast area, clast variance, and surface roughness (Table 2.2, Fig. 2.4a). Clearly, PC1 depicts the land surface gradient: bare ground areas with shrub mounds are distributed on the left hand of the axis while desert pavements appear at the right hand of the axis. PC2, on the other hand, separated our plots into two groups: Pinacate, OPNM and Clark, all of which have gravelly pavements, are on the negative side of this axis, while, in contrast, the transects from Cima, which have a much higher rockiness, larger clasts, and a rougher ground surface, appear on the positive side of PC2 (Fig. 2.4b). This visual interpretation was statistically confirmed by a simple ANOVA on each axis: 69% of the variance in PC1 was explained by the position of the plot along the topographic gradient ($F_{2,51} = 105.6$, $P < 0.0001$), while the effect of sites only explained 6% of the variance on this axis ($F_{3,50} = 6.6$, $P = 0.001$). Variance in PC2 was largely (81%) explained by the effect of sites ($F_{3,50} = 82.3$, $P < 0.0001$) while the effect of the topographic gradient was non-significant on this axis.

In all sites had a bell-shaped response function to the multivariate soil gradient as measured by PC1 (Fig. 2.5). The fit for the Pinacate site was only marginally significant ($P = 0.04$), possibly due to the lower number of transect units. In all other sites, the model fit was highly significant ($P < 0.01$) but the optimum of the distribution varied according to the site: While the modeled abundance of *C. rigida* peaked near the center or the left of PC1 in Pinacate, OPNM, or Clark (where the function's maximum $x_{\max}$ was, respectively, 0.09, -0.02, and -0.21), in Cima it peaked towards the right of PC1 ($x_{\max} = 0.35$). In short, the response-function model replicated the results of the first analysis: *Chorizanthe rigida* shows maximum densities in the transition zone between shrubs and pavements, but in the more rocky environments of the Cima volcanic field it establishes better in full pavements.

All selected soil variables (roughness, clast area, SE of clast area, rock cover, and bulk density) varied significantly between sites. As a general rule, in the ANOVAs the Cima site showed significantly ($P < 0.0001$) higher surface roughness, and larger and more variable clasts, as well as higher rock cover and bulk densities, while the other three sites did not differ significantly among themselves (Table 3). On the other hand, only two variables —% rock cover, and soil bulk density— showed significant ($P < 0.0001$) differences among transects: rock cover was lowest under shrubs, highest in pavements, and intermediate in the transition areas, while bulk density was significantly lower under shrubs and did not differ between pavements and transition areas.

Discussion

Chorizanthe rigida establishes preferentially in the transition zones along the shrub-to-pavement micro-topographic gradient. However, in surfaces with a high degree of rockiness and large clast size, as in the Cima site, it is also able to colonize open pavements. The establishment of *C. rigida* seems to be associated with a combination of surface roughness and rock cover, as captured in the PCA axes: In three of our studied sites (Pinacate, OPNM, and Clark) pavements are relatively homogeneous, formed mostly by densely-packed small rocks and gravel, while the transition zones maintain a high surface roughness but show a lower rock and gravel cover, leaving small patches of exposed soil between clasts (Table 2.3). In Cima, in contrast, the pavement is formed by larger rocks, and the maximum degree of roughness was found in the pavements, where the large surface rocks leave small patches of bare soil between them. Thus, in all sites *C. rigida* established preferentially on those surfaces that had rocks and gravel combined with open soil spaces. These micro-topographic traits seem to play an important role in the establishment and distribution of *C. rigida,* possibly because a higher number of runoff-dispersed propagules get trapped in surfaces with higher roughness (Harper *et al.* 1964; Chambers and MacMahon 1994). In agreement with these results, it has been well reported that the aggregation patterns of basicarpic species in other deserts depend on rainfall and runoff conditions (Friedman and Stein 1980; Günster 1992, 1993; Hegazy and Kabiel 2007).

The distribution of *C. rigida* is negatively correlated to the cover of other annual forbs and grasses. This highlights the fact that, while most desert annuals tend to establish preferentially under shrub canopies, as the nurse-shrub paradigm predicts, *C. rigida* is consistently using a microhabitat markedly different from that of most other annuals; it established chiefly in rocky transition zones and desert pavements, two microenvironments that are more saline, less fertile, and more impermeable than the mounds. This distinct microhabitat differs from that used by other desert annuals, which release their seeds at the end of the growing season and are dispersed by faunal activity and wind into shrub mounds where they form a soil seed bank (Pake and Venable 1996; Venable 2007). In contrast with most desert ephemerals, *C. rigida* delays seed dispersal retaining the achenes in its lignified stems, timing release with incoming rains and allowing seeds to reach the ground at a time when run-off accumulates on flat desert pavements (Turk and Graham 2011). By preferentially establishing on stable geomorphic surfaces, such as desert pavements, where underlying highly aggregated soils provide a suitable substrate for long-term anchoring, *C. rigida* seems to achieve the persistence necessary to release seeds during several rain events, in contrast with dynamic shrub mound areas with low soil aggregation and high bioturbation activity (Ellner and Shmida 1981). Furthermore, as in the previously discussed case of *Mammillaria pectinifera* (Peters *et al.* 2008), in *C. rigida* surface rocks seem to provide seedling protection during establishment. This study provides microhabitat data in support of the hypothesis that the ecological significance of serotiny in desert annuals lies in allowing the seed-retaining, lignified plant skeletons, to repeatedly release seeds after rain events, at an adequate time to establish and develop in normally inhospitable desert pavements.

Literature cited

Abrahams, A. D., Parsons, A. J., and Wainwright, J. 1995. Effects of vegetation change on interrill runoff and erosion, Walnut Gulch, Southern Arizona. *Geomorphology* 13, 37–48.

Al-Farraj, A., and Harvey, A. M. 2000. Desert pavement characteristics on wadi terrace and alluvial fan surfaces: Wadi Al-Bih, U. A. E. and Oman. *Geomorphology* 35, 279–297.

Baldwin, B. G., Boyd, S., Ertter, B. J., Patterson, R. W., Rosatti, T. J., and Wilken, D. H. (Eds.), 2002. *The Jepson Desert Manual. Vascular plants of Southeastern California*. University of California Press, Canada.

Berndtsson, R., and Larson, M. 1987. Spatial variability of infiltration in a semi-arid environment. *Journal of Hydrology* 90, 117–133.

Chambers, J. C., and MacMahon, J. A. 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* 25, 263–292.

Coll-Hurtado, A. (Ed.), 2007. *Nuevo Atlas Nacional de México*. Universidad Nacional Autónoma de México, Instituto de Geografía. Mexico.

Ellner, S., and Shmida, A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* 51, 133–144.

Evenari, M. 1985. *The desert environment. Ecosystems of the World. Hot Deserts and Arid Shrublands*. Part 12A. Elsevier Science Publishing Company, New York. pp. 1–22.

Ezcurra, E., and Rodrigues, V. 1986. Rainfall patterns in the Gran Desierto, Sonora, Mexico. *Journal of Arid Environments* 10, 13–28.

Felger, R. S. 2000. *Flora of the Gran Desierto and Río Colorado of Northwestern Mexico*. University of Arizona Press, USA, pp. 398–400, 403.

Franco, A. C., and Nobel, P. S. 1989. Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology* 77, 870–886.

Friedman, J., and Stein, Z. 1980. The influence of seed-dispersal mechanisms on the dispersion of *Anastatica hierochuntica* (Cruciferae) in the Negev Desert, Israel. *Journal of Ecology* 68, 43–50.

Garcia-Moya, E., and McKell, C. M. 1970. Contributions of shrubs to the nitrogen economy of a desert wash plant community. *Ecology* 51, 81–88.

Gee, G. W., and Bauder, J. W. 1986. *Particle Size Analysis. Methods of soil analysis: Physical methods*, Part 2 SSSA Book Series 5 (Ed. A. Klute). SSSA and ASA, Madison, WI, pp. 383–411.

Günster, A. 1992. Aerial seed banks of the central Namib: the distribution of serotinous plants in relation to climate and habitat. *Journal of Biogeography* 19, 563–572.

Günster, A. 1993. Microhabitat differentiation of serotinous plants in the Namib Desert. *Journal of Vegetation Science* 4, 585–590.

Gutterman, Y. 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. *The Botanical Review* 60, 373–425.

Gutterman, Y. 2002. *Survival strategies of annual desert plants*. Springer Verlag, Berlin, Germany.

Harper, J. L. Williams, J. T., and Sagar, G. R. 1964. The behavior of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *Journal of Ecology* 53, 273–286.

Hegazy, A. K., and Kabiel, H. F. 2007. Significance of microhabitat heterogeneity in the spatial pattern and size-class structure of *Anastatica hierochuntica* L. *Acta Oecologica* 31, 332–342.

Hirmas, D. R., and Furquim, S. A. 2006. Simple modification of the clod method for determining bulk density of very gravelly soils. *Communications in Soil Science and Plant Analysis* 37, 899–906.

Lajtha, K., and Schlesinger, W. H. 1986. Plant response to variations in nitrogen availability in a desert shrubland community. *Biogeochemistry* 2, 29–37.

Musick, H. B. 1975. Barrenness of desert pavement in Yuma County, Arizona. *Arizona-Nevada Academy of Sciences Journal* 10, 24–28.

Neave, M., and Abrahams, A. D. 2001. Impact of small mammal disturbances on sediment yield from grassland and shrubland ecosystems in the Chihuahuan Desert. *Catena* 44, 285–303.

Nelson, D. W., and Sommers, L. E. 1996. *Total Carbon, organic carbon and organic matter. Methods of soil analysis: Chemical methods.* Part 3 SSSA Book Series 5 (Eds. D.L. Sparks), SSSA and ASA, Madison, WI, pp. 961–1010.

Noy-Meir, I., and Whittaker, R. 1977. Continuous multivariate methods in community analysis: some problems and developments. *Vegetatio* 33, 79–98.

Pake, C. E., and Venable, D. L. 1996. Seed Banks in Desert Annuals: Implications for Persistence and Coexistence in Variable Environments. *Ecology* 77, 1427–1435.

Parsons, A. J., Abrahams, A. D., and Simanton, J. R. 1992. Microtopography and soil-surface materials on semi-arid hillslopes, *Southern Arizona. Journal of Arid Environments* 22, 107–115.

Peters, E. M., Martorell, C., and Ezcurra, E. 2008. Nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti (*Mammillaria*) in the Tehuacán Valley, Mexico. *Journal of Arid Environments 72, 593–607*.

Rhoades, J. D. 1982. *Soluble salts. Methods of soil analysis*. Part 2. 2nd ed. Agronomy Monograph 9 (Eds. A. L. Page, R. H. Miller & D. R. Keeney). ASA, Madison, WI. pp. 167-179.

Saleh, A. 1993. Soil roughness measurement: chain method. *Journal of Soil and Water Conservation* 48, 527–529.

Schlesinger, W. H., and Pilmanis, A. M. 1998. Plant-soil interactions in deserts. *Biogeochemistry* 42, 169–187.

Shmida, A., and Whittaker, R. H. 1981. Pattern and biological microsite effects in two shrub communities, *Southern California. Ecology* 62, 234–251.

Silvertown, J., and Wilson, J. B. 1994. Community Structure in a Desert Perennial Community. *Ecology* 75, 409–417.

Turk, J. K., and Graham, R. C. 2011. Distribution and properties of vesicular horizons in the Western United States. *Soil Science Society of America Journal*, 75, 1449–1461.

Valiente-Banuet, A., and Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *Journal of Ecology 79, 961–970*.

Valiente-Banuet, A., Vital-Rumebe, A., Verdu, M., and Callaway, R. M. 2006. Modern Quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages. *Proceedings of the National Academy of Sciences* 103, 16812–16817.

Venable, D. L. 2007. Bet hedging in a guild of desert annuals. *Ecology* 5, 1086–1090.

Whitford, W. G., and Kay, F. R. 1999. Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments* 41, 203–230.

Wood, Y. A., Graham, R. C., and Wells, S. G. 2002. Surface mosaic map unit development for a desert pavement surface. *Journal of Arid Environments* 52, 305–317.

Wood, Y. A., Graham, R. C., and Wells, S. G. 2005. Surface control of desert pavement pedologic process and landscape function, Cima Volcanic field, Mojave Desert, California. *Catena* 59, 205–230.

Yeaton, R. I., and Manzanares, A. R. 1986. Organization of vegetation mosaics in the *Acaciaa schafftri-Opuntia streptacantha* association, southern Chihuahuan Desert, Mexico. *Journal of Ecology* 74, 211–217.

Tables

Table 2.1. Log-linear contingency-table analysis for the effect of site (Pinacate, OPNM, Cima and Clark), gradient (desert pavement, transition, shrub zone) and the interaction on the number of individuals of *C. rigida* (see Fig. 3 for the corresponding plot).

Source	X^2 deviance	*df*	*P*	r^2
site	10.41	3	**0.0150**	0.08
gradient	14.24	2	**0.0008**	0.11
site × gradient	55.69	6	**<0.0001**	0.41
error	53.96	42		
total model	134.29	53		0.60

Table 2.2. Principal Component Analysis of soil traits: (a) Eigenvalues, percent of variance, and cumulative percent of variance explained by PC1 and PC2. (b) Loadings/correlation coefficients for each environmental variable in each eigenvector. Bold numbers indicate significant ($P < 0.01$) loading values.

	PC 1	*PC 2*
a) Axis values		
Eigenvalue	4.65	4.51
Percentage	25.81	25.04
Cumulative %	25.81	50.85
b) Environmental variables		
roughness	0.106	**0.818**
bare soil	**-0.627**	-0.109
gravel	0.577	-0.709
rock	0.498	**0.731**
crust	-0.539	0.319
annuals	**-0.710**	0.292
shrub	-0.285	-0.063
clast area	0.330	**0.792**
SE(area)	0.049	**0.785**
bulk_density	0.376	**0.646**
pH	0.539	0.480
EC	**0.591**	0.529
%TN	**-0.629**	-0.285
%TC	-0.133	-0.381
% gravel	0.247	-0.434
% sand	**-0.789**	-0.057
% clay	**0.595**	-0.096
% silt	**0.668**	0.044

Table 2.3. Roughness and clast values for each land surface mosaic for each site (mean ±SE).

		Roughness Index (%)	**Clast area (mm^2)**	**SE Clast area**	**Rock (% cover)**	**Bulk density (g/cm^3)**
Desert	Pinacate	2.00 ± 0.4	262.7 ± 55.1	28.2 ± 8.0	9.26 ± 4.0	1.20 ± 0.1
Pavement	OPNM	1.16 ± 0.2	232.4 ± 29.3	22.8 ± 4.3	7.44 ± 1.3	1.23 ± 0.1
	Cima	4.16 ± 1.0	504.3 ± 51.7	82.3 ± 11.1	53.78 ± 5.1	1.59 ± 0.0
	Clark	0.68 ± 0.1	165.7 ± 23.3	13.4 ± 1.6	5.37 ± 2.0	1.45 ± 0.1
Transition	Pinacate	2.45 ± 0.6	237.7 ± 90.4	27.1 ± 11.2	8.02 ± 4.3	1.08 ± 0.2
	OPNM	1.57 ± 0.4	199.5 ± 24.1	23.0 ± 4.5	7.33 ± 3.0	1.16 ± 0.0
	Cima	3.66 ± 0.6	507.3 ± 19.9	103.5 ± 41.3	27.56 ± 6.8	1.56 ± 0.0
	Clark	1.58 ± 0.3	143.8 ± 15.2	12.9 ± 1.2	1.67 ± 0.6	1.19 ± 0.1
Shrub Zone	Pinacate	1.49 ± 0.4	113.8 ± 20.6	57.8 ± 42.7	2.78 ± 1.4	1.05 ± 0.0
	OPNM	1.50 ± 0.4	192.9 ± 27.7	21.8 ± 3.5	4.00 ± 1.4	1.08 ± 0.0
	Cima	3.08 ± 0.6	253.0 ± 63.8	47.0 ± 11.7	8.22 ± 5.7	1.31 ± 0.0
	Clark	1.34 ± 0.2	155.4 ± 28.3	18.9 ± 3.1	2.87 ± 1.4	1.12 ± 0.0

Figures

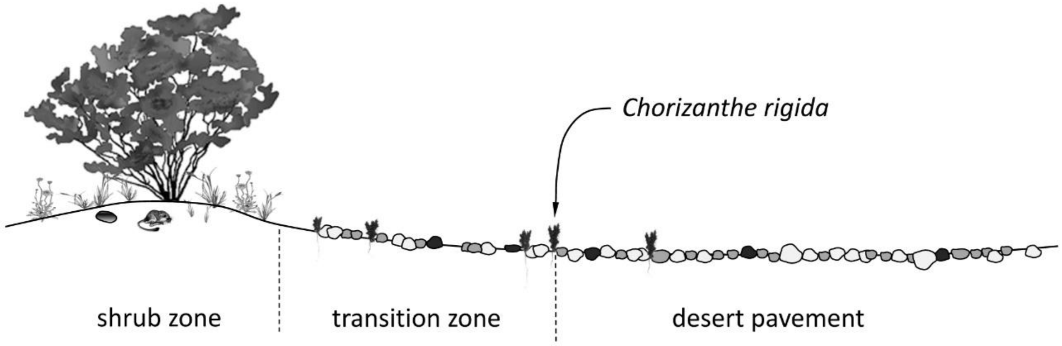

Figure 2.1. Profile diagram of the desert plain microhabitats: desert pavement, transition area, and shrub mound.

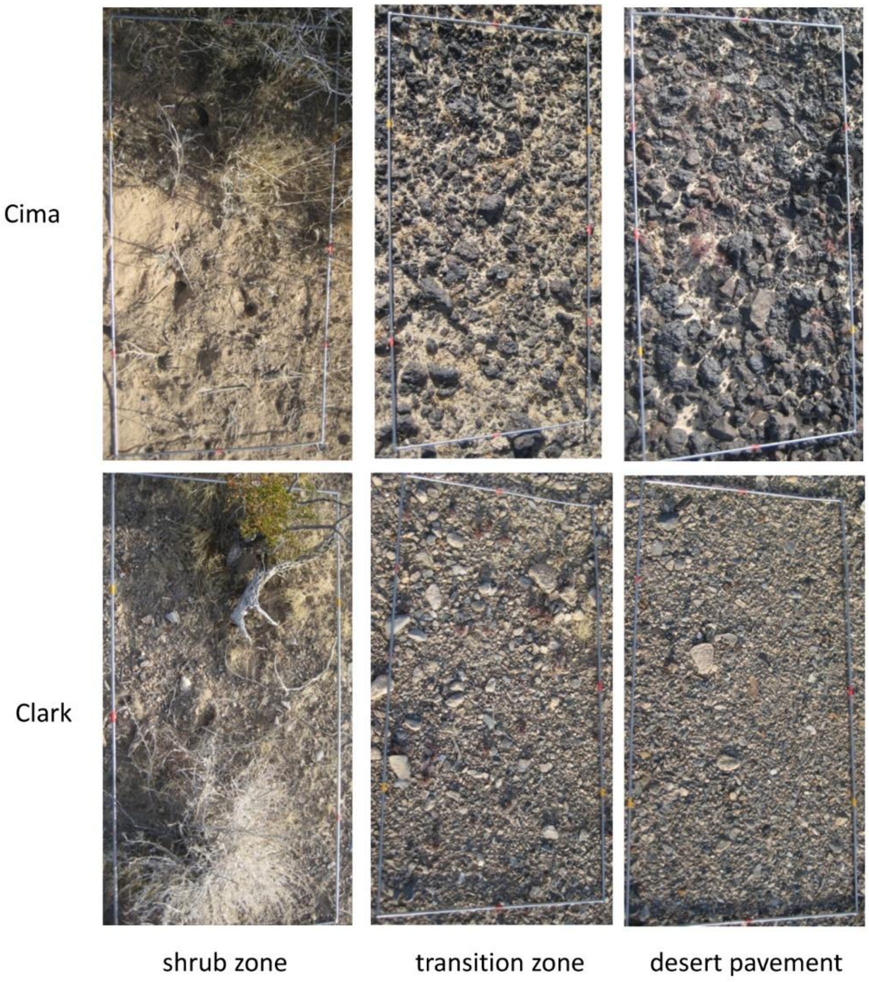

Figure 2.2. Photographs of the three land surface mosaics in two of the sites located in the Mojave Desert. Field of view of each photograph is approximately 100 cm × 50 cm.

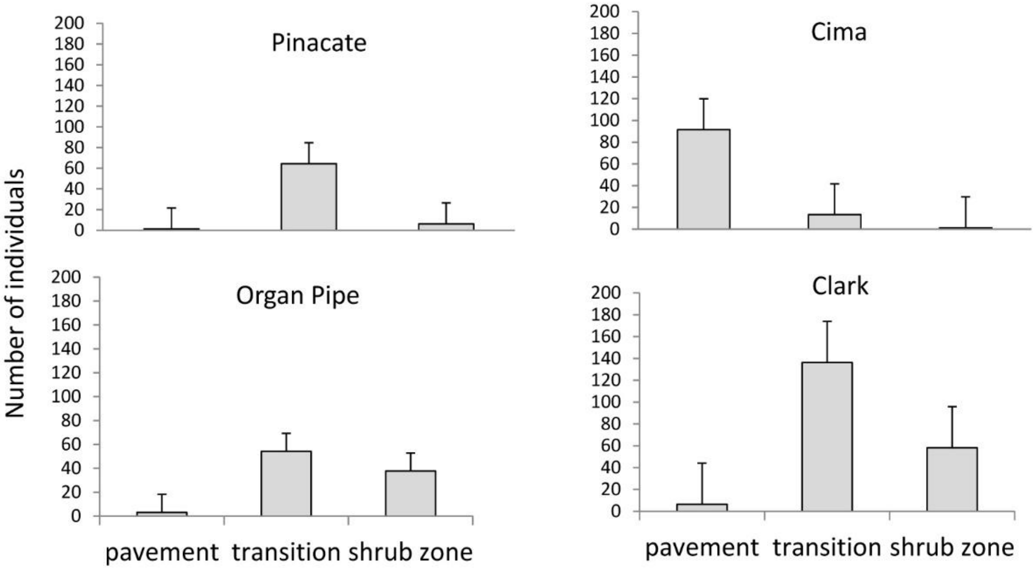

Figure 2.3. Total number of individuals (mean ±s.e.) of *C. rigida* on the land surface (pavement, transition, and shrub zone) in each site (El Pinacate, OPNM, Cima and Clark). A highly significant interaction term ($P<0.0001$) was found in the corresponding log-linear model (Table 2.1), highlighting the fact that while the highest densities in the Cima site were found in open pavements, in all other sites the highest densities occurred in transition areas.

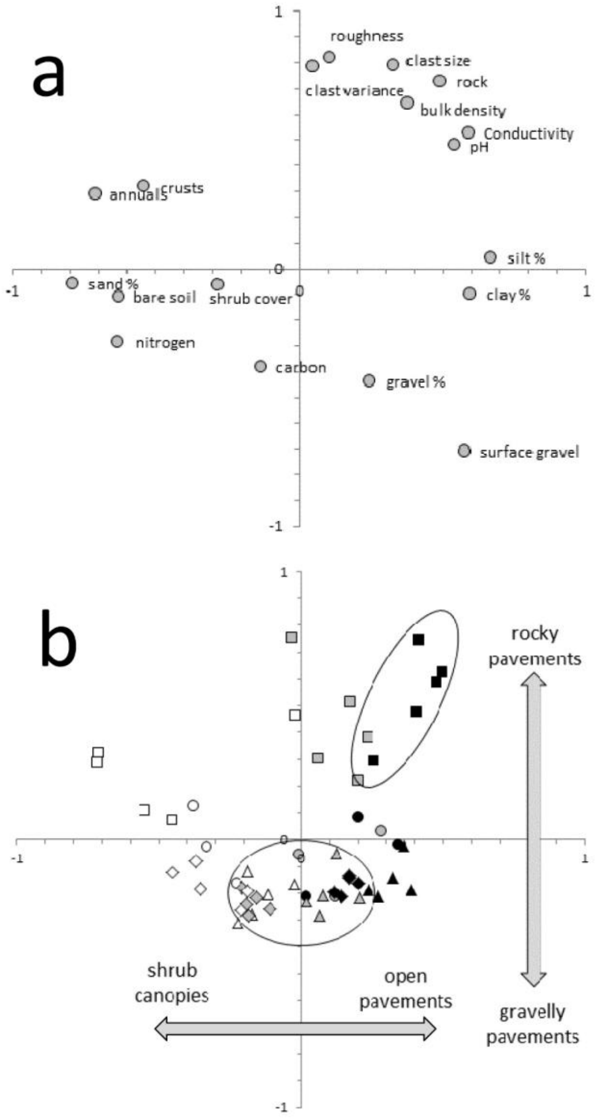

Figure 2.4. PCA bi-plot showing (a) the loadings of environmental variables along PC1 and PC2, and (b) the site scores on PC1 and PC2. Sites are shape coded as follows: Pinacate ○, OPNM △, Cima □, and Clark ◇. Sample points are color coded as follows: black – desert pavement, grey – transition, white – shrub zone. Ellipses around the symbols encircle replicate sets in which *C. rigida* is distributed.

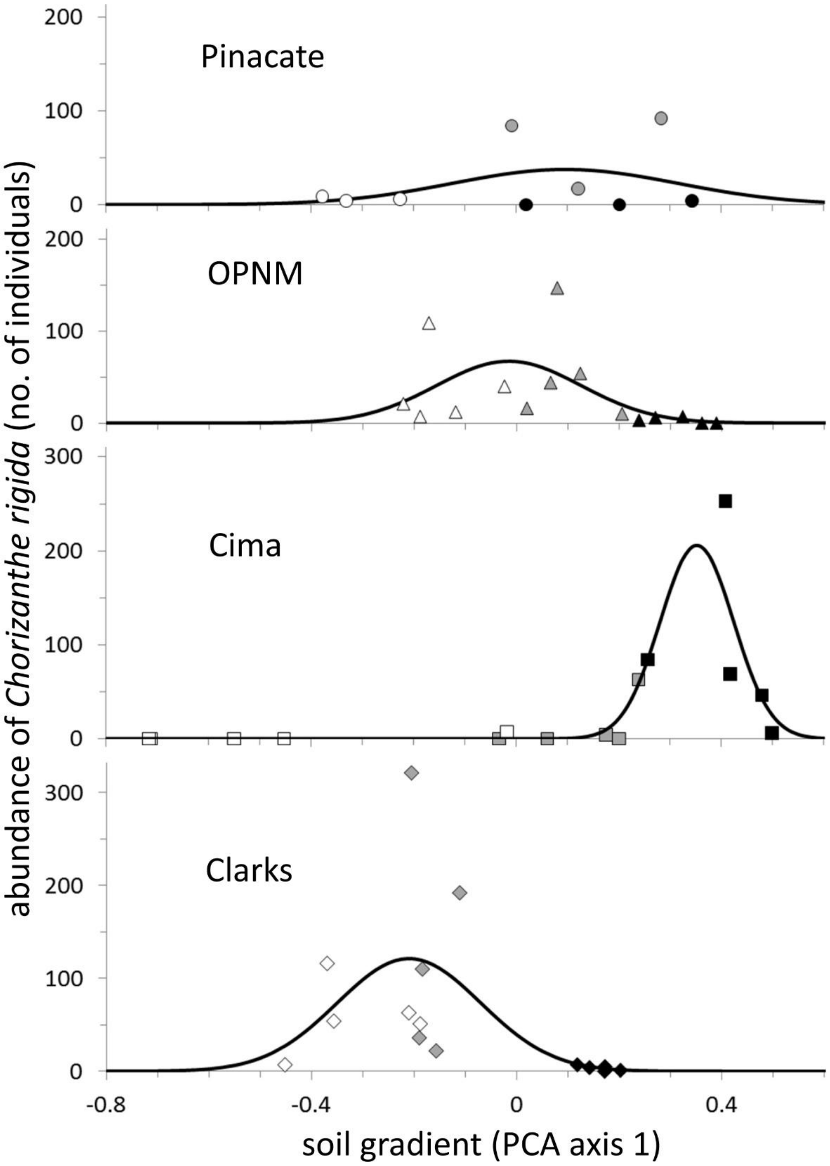

Figure 2.5. Distribution of *C. rigida* along the composite soil axis (PC1). Data points coded as in Fig. 2.3. The bell-shaped lines show the functional response model of species density against the soil axis.

Chapter 3

The biogeography of bet-hedging: Morphological variability in propagules of a desert annual as a function of rainfall unpredictability.

Abstract

Two predictions regarding environmental variability were tested by analysing geographic-scale patterns of seed retention (serotiny) in *Chorizanthe rigida*, a strict winter desert annual that retains its seeds and releases them after rainfall events: (a) that organisms adapt to systematic environmental cues with changes in their morphology, and (b) that they display bet-hedging strategies as a response to environmental unpredictability. I quantified morphological variation in *C. rigida* propagules (involucres) from six populations distributed throughout the Mojave and Sonoran deserts covering: (a) a systematic, West-to-East, winter-to-bi-seasonal (summer and winter) precipitation gradient, and (b) a winter-rain predictability gradient inferred from long-term climatic data. Biomechanical tests were performed to assess the functionality of propagule attachment structures.

The propagule retention structure (i.e., base area) of *C. rigida* individuals experiencing a bi-seasonal rainfall doubled the size of those that have evolved under a strict winter rainfall regime. These results, along with the biomechanical tests, indicate that: (a) seed release is triggered by rainfall, (b) *C. rigida* has an adaptive seed release response depending on the amount of rainfall and, (c) populations living in bi-seasonal environments have higher seed retention and are adapted to avoid releasing seeds to a summer rainfall cue. A strong correlation between propagule variance (within-individual heteromorphism) and winter rainfall variability was found,

as predicted by bet-hedging theory. These results suggest that seed heteromorphism allows this species to cope with different levels of environmental unpredictability by displaying a diversifying risk strategy. In conclusion, *C. rigida* propagules show consistently larger bases in deserts with summer rainfall, which allow the avoidance of seed release during summer rainfall cues, and display seed heteromorphism associated with rainfall unpredictability, which allows them to spread risks in highly variable environments. This study provides evidence of local adaptation of desert annual populations to cope with both random and systematic rainfall variation.

Introduction

In a seminal paper on the reproduction of desert ephemerals in randomly varying environments, Cohen (1966) showed that, in order to maximize long-term fitness, the seed fraction that germinates every year should be proportional to the probability of reproducing successfully and that the seed fraction that does not germinate should be directly related to the probability of total or near total failure. Indeed, the seeds of desert annual plants face the problem of successfully completing their life cycle within a short and relatively unpredictable growing season. On the one hand, in order to take advantage of the short growing period, selective pressures favor early germination, that is, the ability to sprout immediately after the first good rain. However, if the first rain event is not followed by sufficient rainfall, the plant will die before setting seed. Cohen demonstrated that one way to survive and reproduce in a risky environment is to spread the risk so that one failed season will not be irreversibly harmful for the individual. Spreading the risk of germination, also known in ecology as “bet-hedging” means that the seeds produced by one parent will not germinate all at the same time even if they experience the same environmental conditions, but rather spread out their germination over many seasons (Seger and Brockman 1987; Philippi and Seger 1989). Although the mathematics behind Cohen's model can be complex, the concept and the conclusions are clear. First, in highly unpredictable environments natural selection should favor the evolution of a high variability in seed germination response. Second, not all seeds from a single parent should react equally to the same environmental cue. Instead, they should show a heterogeneous germination response (Philippi 1993; Simons and Johnston 2006). Third, the more unpredictable the environment, the greater the fraction of seeds that should not germinate. Fourth, the stronger the moisture cue, the more seeds that should germinate (Philippi 1993; Pake and Venable 1996; Clauss and Venable 2000; Sadeh *et al*. 2009).

In desert annuals, bet-hedging is accomplished by a variety of mechanisms involving parentally-induced morphological or developmental heterogeneity in the offspring (Gutterman 1993; Shem-Tov and Gozlan 1998). Among this wide array of strategies, some desert ephemerals retain seeds in their dry skeleton after they die, releasing a fraction of seeds each time it rains (Evenari *et al.* 1971). The retention of mature seeds within the maternal plant —a phenomenon called serotiny or delayed dispersal— is a syndrome of adaptive significance in randomly fluctuating arid ecosystems (Ellner and Schmida 1981; Kamenetsky and Gutterman 1994; van Oudtshoorn and van Rooyen 1999) that reduces risks by spreading seed dispersal over time (Cohen 1966, Venable and Lawlor 1980). In serotinous desert plants, seed retention and delayed dispersal take the place of delayed germination in the soil seed bank of other desert annuals (Venable and Lawlor 1980; Philippi 1993; Clauss and Venable 2000; Venable 2007). Normally, the seed-retaining structures (e.g., capsules or dry involucres) will gradually release a few seeds into the environment, providing an effective risk-hedging strategy during harsh years by only exposing a few embryos at a time. However, in most serotinous plants the seed-retaining structures can also release more seeds as a response to environmental cues (i.e., higher moisture) thus allowing plants to adaptively increase the fraction of embryos released for immediate germination (Friedman *et al*. 1978; Peters *et al.* 2009) providing an important opportunity for successful establishment. Empirical evidence on the adaptive value of bet-hedging traits has mostly focused on plants forming seed banks in the soil, but less is known about above-ground seed banking in serotinous desert annuals.

The adaptive significance of serotiny may vary according to particular weather patterns. Deserts, due to their low and sporadic rainfall, are inherently variable and unpredictable environments (Noy-Meir 1973). However, deserts are not perfectly random environments; there is a systematic component and a random component to precipitation patterns: Desert regions have different annual, seasonal and intra-seasonal precipitation patterns (Reynolds *et al*. 2004). For example, in North America, the Mojave Desert has mostly winter precipitation while precipitation in the Sonoran Desert has a bimodal distribution with precipitation peaks in both winter and summer (Sheppard *et al*. 2002; Reynolds *et al*. 2004). Even within a region, strong variation may exist in intra-seasonal rainfall timing and intensity. In some desert sites winter precipitation is more variable, and hence less reliable, than in others (Ezcurra and Rodrigues 1986).

Desert annuals have adaptations to cope with seasonal rainfall patterns and avoid germinating in the wrong season (Loik *et al*. 2004; Lytle and Poff 2004). Winter and summer annuals have different germination requirements, phenology, life history traits, growth form, and physiology, and each group is adapted to conditions associated to the two major precipitation seasons in deserts (Shreve and Wiggins 1964; Mulroy and Rundel 1977; Ehleringer 1983; Venable and Brown 1988; Guo and Brown 1996; Guo *et al.* 2002). For instance, winter desert annuals respond to thermo or photoperiods that indicate the beginning of the winter growth season, and thus allow them to time germination to a season when they can successfully grow and establish (Baskin *et al*. 1993; Gutterman 1993, 2002; Childs et al. 2010; Reed *et al*. 2010). Widely distributed serotinous plants that prosper in deserts with different degrees of climatic uncertainty provide an excellent opportunity to test the ideas behind bet-hedging models and adaptations to environmental cues. Serotinous plants have an above-ground seed bank that lies within the maternal tissues in the plant's dry skeleton, a trait that makes them a good model organism to test Cohen's predictions that within-plant seed variability should increase with increasing rainfall unpredictability. *Chorizanthe rigida,* a winter desert annual found across the Sonoran and Mojave Deserts of North America, forms an above-ground seed bank by retaining seeds on its lignified dead skeletons for several years. Seed dispersal in this plant is triggered by rainfall events: Involucres (i.e., dispersal structure formed by three-bracts holding one achene) are held on to the branch by a hygrochastic-tissue base that swells and softens when wet, allowing seed detachment caused by the pounding of raindrops (Fig. 3.1). Undispersed involucres remain attached to the plant as the lignified tissues re-dry (Ellner and Shmida 1981; van Rheede van Oudtshoorn and van Rooyen 1999).

According to Cohen's model, the same species should show varying seed-retaining and seed-release mechanisms in different deserts, as an adaptation to seasonal rain variability and the predictability of winter rainfall pulses in each particular site. In sites that receive monsoon rains, *C. rigida* must face the challenge of retaining seed when the summer showers arrive, systematically evading a seed-release response to the false summer cue. Once the following winter arrives, however, plants should release seed according to the tenets of bet-hedging theory: The more unpredictable the winter rains, the more variable the seeds should be in their size, morphology, or germination response within the progeny of each individual. In this study I test this prediction by analyzing the geographic trends and patterns in the involucre morphology of this serotinous desert annual. The leading hypotheses were that (a) plants growing in deserts with summer-rain pulses should show a consistently different involucre morphology leading to a lower ease of release when facing a single summer rain shower, and (b) that within-individual variance in propagule traits associated with successful establishment should increase with the unpredictability of winter rainfall.

Methods

Study system

Chorizanthe rigida (rigid spineflower, Polygonaceae) is a short, erect desert annual, 2–10 cm of height. It has a single main taproot and stout stems covered by stiff, spiny bracts. As the stem grows, the soft, long-petioled basal leaves are shed, and give place to linear, rigid bracts (or cauline leaves) armed with a terminal spiny awn that becomes hard and thorn-like with age. The single flowers, with a diminutive yellow perianth, are subtended by a 3-segmented involucre with hard spiny bracts (Fig. 3.1). The fruit is a single achene, or "seed", that matures inside the involucre. Its flowering season lasts from March to May and plants mature and produce seeds at the end of the spring season (April–May). Seeds germinate inside the involucre and seedlings emerge in the winter season (December–February). This plant has a 1300-km-wide latitudinal span, ranging from Baja California's Central Desert (lat. 29°N) to the Great Basin in Nevada (lat. 40°N) and is common in the Mojave and Sonoran deserts, especially in desert pavements (Felger 2000; Baldwin *et al*. 2002).

Sampling

Individuals were collected from six populations distributed along two precipitation gradients: a West-to-East precipitation gradient, going from winter-rain to bi-seasonal (summer and winter) deserts; and a winter precipitation gradient with varying predictability. One population was sampled in the eastern Mojave Desert at the Mojave Desert National Preserve, California, located in the Clark Mountains Wilderness Area. Five populations were sampled in the Sonoran Desert: one was located in the Arizona Upland subdivision of the Sonoran Desert in Organ Pipe National Monument, Arizona, while the other four populations were sampled in the Lower Colorado Valley subdivision of the Sonoran Desert in Ocotillo Wells State Vehicular Recreation Area, the Pinacate Biosphere Reserve in Sonora, Mexico, Valle de Las Tinajas in Baja California, Mexico, and in Calamajué, Baja California, Mexico (Fig. 3.2, Table 3.1). Plants belonging to the 2009 growth season were collected right at the end of the growth season (summer 2010) to avoid tissue weathering and decomposition.

Morphometric measurements

Because the predictions of bet-hedging theory apply to the seed traits in the progeny of each single individual, in all our morphometric measurements and subsequent analyses the identity of the parental individuals were maintained. Sixty *C. rigida* individuals (10 per population) were soaked in water for 10 min to facilitate detachment of the involucres. Involucre sampling design was as follows: within an individual plant, three to four involucres were obtained from nodes of the different branches (i.e., tertiary, secondary and central), and this sampling was repeated at three plant levels (level 1 being the closest to the root and level 3 the one closest to the plant’s tip). The individual plant, branch position, and level from which each involucre was collected were recorded; a total of 27–36 involucres were collected from each individual plant. Involucre images (frontal and base views, Fig. 3.1) were obtained using a dissecting scope and a digital camera. The following morphometric variables were measured from the involucre images: (1) the size of the seed receptacle in the involucre (referred hereafter as “involucre size”), measured as the projected area of the involucre’s central “belly”; (2) involucre length, measured from the top of the central bract of the involucre to the base; and (3) involucre base area. Areas were defined with points marked using a custom program made in Matlab 7.5 with Image Processing Toolbox 6.0 (MathWorks, Natick, MA).

Climatological analysis

Long-term precipitation and temperature data were obtained from the weather stations (from NOAA in the US and from SMN (*Servicio Meteorológico Nacional*) in Mexico) nearest to the sampled *C. rigida* populations. Weather stations were located in the following sites: Mojave, California; Borrego Desert Park, California; San Felipe, Baja California; Chapala, Baja California; Organ Pipe Cactus National Monument, Arizona; Sonoyta, Sonora (Table 3.1).

Because of the species’ long latitudinal span, temperatures—and hence evaporative demand—can differ considerably from one site to another. In order to correct for different evaporative demands, we divided each monthly precipitation value by Walter's Evapotranspiration (PET) estimate for that month ($PET = 2\ T$, where T is the monthly mean temperature; Walter 1968), in order to get a measure of effective moisture reaching the plants. That is, an effective precipitation value of, say, 0.3 for a given month indicates that the precipitation that fell during that month covered only 30% of the plant’s theoretical water demand. Before doing this transformation, we validated Walter’s model regressing tank evaporation data, as a proxy of PET, against Walter's estimated PET for four different weather stations within the study region (Sonoyta r^2=0.88; San Agustín: r^2=0.89; San Felipe: r^2=0.92; and San Luis Gonzaga: r^2=0.81; $p < 0.0001$ in all cases).

When the altitude of the weather station differed from that of the site, mean temperature values were previously corrected by elevation, assuming an adiabatic gradient of 0.8°C for each 100 m. Sites that had $\leq$ 5% effective summer rain (Clark and Las Tinajas) were classified as winter rain locations, while all other sites were classified as having a bi-seasonal rainfall distribution. In particular, the Las Tinajas site is located northwest of the San Felipe weather station, in the rainshadow of Las Tinajas range, where the summer monsoon coming from the southeast rarely reaches. Summer precipitation in the San Felipe weather station, exposed to the Gulf of California, is 7%, so we can safely assume that in our sample site it is considerably lower. Finally, in order to get an estimate of the unpredictability of winter rainfall in each site, we calculated the inter-annual coefficient of variation (*cv* = *st.dev./annual winter mean*) of total winter effective precipitation.

Statistical analyses

Involucre morphometric data was analyzed with linear regression using step-wise variable addition that included the effect of precipitation pattern (a factor with two levels: winter vs. bi-seasonal precipitation), and three covariates: plant canopy width, branch hierarchy where each involucre was found (central, tertiary, secondary), and, when appropriate, involucre length. Because the branching pattern of these plants is determinate, there was no difference between sites in the proportion of involucres produced within different branches. The model also included the effects of interactions, the effect of site nested within the precipitation pattern, and of individuals nested within sites. The analysis was performed on four dependent variables: base area (mm^2), involucre size (mm^2), involucre length (mm), and estimated propagule biomass (mg). A subsample ($n = 160$) of seed-bearing involucres for which we had morphometric data was weighed to estimate whole propagule biomass. A multiple regression model using involucre size and involucre length as quantitative predictors and site as a co-variate factor were used to estimate biomass for all propagules ($r^2 = 0.845$; $F = 118.4$; df = 7, 152; $P < 0.0001$). The total number of involucres sampled was 1921 (Las Tinajas, 316; Clark, 336; Organ Pipe, 317; Ocotillo Wells, 321: Calamajué, 314; and Pinacate, 317). Variables were log-transformed before the analysis, on the one hand, to meet the normality assumptions of statistical tests and, on the other, to linearize the power-function relationships that often crop-up in morphometric and allometric studies (Gould 1966; West *et al*. 1997). In all analyses we performed Bartlett's Test to verify homogeneity of variances.

Results

There was a significant effect of precipitation pattern (winter vs. bi-seasonal) on involucre base area (Table 3.2): Populations experiencing almost exclusively winter precipitation had a significantly ($P < 0.0001$) smaller base than those under a bi-modal rainfall distribution pattern (Fig. 3.3, Table 3.2). Two within-individual covariates (branch hierarchy and involucre length) were also strongly related with the area of the involucre base (Table 3.2). There was also a significant, but quantitatively small ($r^2 = 0.004$), effect of the plant's canopy width as a covariate of involucre base area (Table 3.2). Similarly, some interaction terms were also significant, but their contribution was quantitatively negligible ($r^2 < 0.001$ in all cases, Table 2). The final model included the effect of precipitation and the two main covariates branch hierarchy and involucre length ($r^2 = 0.80$). The variances of the involucre bases were quite similar among sites, and did not differ significantly between them with one exception: Calamajué, a site on the southern edge of the species' distribution whose variation in base area is significantly larger than the rest.

In the case of the other three morphological variables, involucre size, length, and mass, significant differences in the variances between sites were found (Bartlett's $K^2 = 180.6$, df = 5, $P < 0.0001$ for involucre size; $K^2 = 61.9$, df = 5, $P < 0.0001$ for length; $K^2 = 98.70$, df = 5, $P < 0.0001$ for mass). The lack of homogeneity of variances violates the basic assumptions of the ANOVA model and hinders the testing of hypothesis regarding differences between the means. However, the variances of morphological traits can be themselves informative: After separating the variances of traits into between-individuals and within-individuals variances using a nested ANOVA (the effect of individuals was nested within sites), significant positive correlations were found between the coefficient of variation of winter effective precipitation and the site-specific within-individual mean variances of involucre size ($r = 0.90$, $P = 0.0004$; Fig. 4), propagule mass ($r = 0.83$, $P = 0.003$), and involucre length ($r = 0.77$, $P = 0.009$; the nested ANOVAs used to calculate within-individual variation are shown in the Appendix A). No significant correlation was found between winter effective precipitation and the within-individual variances of involucre base ($r = 0.01$, $P = 0.98$).

Additionally, because much of this study is based on the assumption that seed release in *C. rigida* strongly depends on the cross-section area of the hygrochastic tissue at the base of the involucre, a comprehensive biomechanics experiment was done to confirm this assumption. A detailed description of this supporting experiment is given in Chapter 4.

Discussion

The summer monsoon: Adaptation to bi-seasonal rainfall patterns

The smaller the base cross-section, the easier it is for propagules to be released by a rain event, as bigger cross-areas require more force for the breakage or detachment of biological parts (Vogel 2003). Monsoon rains reach the Sonoran Desert from the south, following the low-pressure centres that form along the Pacific coasts of Mexico in summer, and may bring brief, but intense, showers to the desert (Caso *et al.* 2007). For topographic and latitudinal reasons, in two of our study sites summer rains rarely, if ever, occur; but in the four sites exposed to the arrival of monsoon rains the false cue of a summer rainstorm can potentially trigger the release of seeds into the environment at a time when high temperatures and evapotranspiration rates would not allow *Chorizanthe rigida*, a strict winter annual, to establish successfully. When the winter rains arrive the following year, the involucres in the strict winter-rain deserts undergo wetting for the first time, while the ones in bi-seasonal deserts have already undergone one or more wetting events. Biomechanical measurements performed in the lab showed that repeated wetting and weathering lowers the involucres' breaking force (see Chapter 4). In agreement with this, the base area of involucres in plants growing in sites with frequent monsoon influence was significantly larger than that of plants exposed solely to winter rains. The two-fold difference in base areas from the Mojave and Las Tinajas sites compared to the ones in Ocotillo Wells, Organ Pipe, Pinacate, and Calamajué, strongly suggests that different populations of *C. rigida* have evolved biomechanical characteristics adapted to local rainfall seasonality patterns.

Winter rains: Adaptation to within-season variability

The biomechanical tests showed that (a) seed release is triggered by wetting of the involucre bases, or involucral pedicels, that soften under soaking conditions, and (b) that, given similar involucre bases, the longer the soaking time the lower the breakage force needed for seed release. Thus, *C. rigida* has a well-defined seed dispersal mechanism: The dry plant is able to release the achenes formed during the previous reproductive seasons, and the amount of seeds released depends on the amount and timing of precipitation (Evenari *et al.* 1971; Noy-Meir 1973). Cohen (1968) showed that a strategy in which only a fraction of seeds germinate and the rest remain dormant maximizes fitness in environments where the probability of successful establishment is low and randomly variable. In *C. rigida* fruit retention may effectively take the place of delayed germination in other annual plants that form true soil seed banks (Venable and Lawlor 1980). In seasons with high moisture availability, the repeated wetting of the involucral pedicels allows plants to adaptively increase the fraction of seeds released for immediate germination. Thus, the moisture-dependent capacity for active release of achenes during precipitation pulses seems to provide an important opportunity for successful establishment.

Seed size and environmental unpredictability

Demonstrating that variance in a morphological trait may be part of an adaptive bet-hedging strategy requires: (a) quantifying trait diversification and (b) a positive correlation between trait variance and a measure of environmental heterogeneity (Sadeh *et al*. 2009; Simons 2009, 2011). Bet-hedging traits are expected to evolve under highly variable environmental conditions, when natural selection favours reducing the risk of demographic extinction across generations (i.e., maximizing the geometric mean fitness; Sadeh *et al*. 2009; Simons 2009; Childs *et al*. 2010, but see Simons 2002). Under such conditions, selection is expected to act on variation rather than on the mean of bet-hedging traits (Simons and Johnston 2006). Although several studies have attempted to provide evidence of adaptive bet-hedging in germination fractions in species experiencing different levels of environmental variability, results have not been conclusive (Pake and Venable 1996; Clauss and Venable 2000). In this study, and in agreement with the predictions of bet-hedging theory, a significant positive correlation was found between the unpredictability of winter rainfall and within-individual variability of involucre size and propagule biomass. This study provides evidence that the within-individual variance of seed size increases significantly as rainfall unpredictability increases.

Seed heteromorphism—variation in seed size—has important effects on fitness (survival and fecundity), and can be in itself a successful bet-hedging mechanism (Venable and Lawlor 1980; Venable and Brown 1988; Simons and Johnston 2006; Volis and Bohrer 2012), as seeds of different sizes differ in their ecological behaviour (Imbert 2002; Volis and Bohrer 2012 and references therein). More importantly, seed size in desert environments has been demonstrated to be associated with survival probability, as larger seeds are endowed with more endosperm and can survive longer after germination waiting for the next rain (Jurado and Westoby 1992; Leishman and Westoby 1994; Lloret *et al.* 1999; Moles and Westoby 2004). Thus, larger seeds have an obvious advantage in seasons when moisture pulses are set apart. Smaller seeds, on the other hand, demand lower maternal investment in biomass, and can be produced in larger numbers, giving the parent plant an adaptive advantage during wetter years when the embryo can successfully germinate and establish with less maternal endowment. Finally, it has been suggested that propagule size variability in basicarpic annuals may also allow for higher variability in seed release, a trait that is adaptive to unpredictable rain (Friedman et al. 1978).

Conclusions: The ecological significance of serotiny in Chorizanthe rigida

Serotinous desert annuals have above-ground seed banks within their dead lignified structures, which remain in the field releasing seeds for several years, spreading the risk posed by inter-annual rainfall variation. Increased levels of environmental variability have been associated with a higher degree of seed retention in desert serotinous plants (Friedman and Stein 1980; Gutterman 1993, 2002; van Rheede and van Rooyen 1999; Peters *et al*. 2009). Confirming this, I found that areas with higher probability of a false environmental cue (the summer monsoon) had significantly larger cross-areas of retention tissue, which help to retain the seeds during the summer rains until the next winter, when the repeated wetting of the pedicels will have decreased their breakage threshold. I also found that involucre bases soften proportionally to the amount of soaking that the plant has undergone, promoting the active release of achenes during precipitation pulses. Furthermore, bet-hedging theory predicts that seed heteromorphism should increase with increasing environmental unpredictability. In agreement with this, these results show that *C. rigida*'s seed and involucre sizes are significantly more variable in desert regions with higher variation in effective winter precipitation, and hence in environmental unpredictability. Predictable environmental cues and unpredictable variability occurring at different times and spatial scales constitute selective factors that shape the life history evolution and morphological diversity of organisms (Roff 2002; Simons 2011). This study provides evidence that different scales of rainfall variation influence and shape the propagule morphology of the serotinous *Chorizanthe rigida*, allowing it to cope with both systematic and random drivers of rainfall variation.

Literature cited

Baldwin, B. G., Boyd, S., Ertter, B. J., Patterson, R. W., Rosatti, T. J. and Wilken, D. H.eds. 2002. *The Jepson Desert Manual. Vascular plants of Southeastern California*. University of California Press, Canada.

Baskin, C. C., Chesson, P. L. and Baskin, J. M. 1993. Annual seed dormancy cycles in two desert winter annuals. *Journal of Ecology* 82, 551–556.

Caso, M., González-Abraham, C. and Ezcurra, E. 2007. Divergent ecological effects of oceanographic anomalies on terrestrial ecosystems of the Mexican Pacific coast. *Proceedings of the National Academy of Sciences of the USA* 104, 10530–10535.

Childs, D. Z., Metcalf, C. J. E. and Rees, M. 2010. Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B* 277, 3055–3064.

Clauss, M. J. and Venable, D. L. 2000. Seed germination in desert annuals: an empirical test of adaptive bet hedging. *American Naturalist* 155, 168–186.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 16, 1–14.

Ehleringer, J. 1983. Ecophysiology of *Amaranthus palmeri*, a Sonoran Desert summer annual. *Oecologia* 57, 197–112.

Ellner, S., and Shmida, A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* 51, 133–144.

Evenari M., Shanan L. and Tadmor, N. 1971. *The Negev—the challenge of a desert*. Harvard University Press, Cambridge.

Ezcurra, E. and Rodrigues, V. 1986. Rainfall patterns in the Gran Desierto, Sonora, Mexico. *Journal of Arid Environments* 10, 13–28.

Felger, R. S. 2000. *Flora of the Gran Desierto and Río Colorado of Northwestern Mexico.* The University of Arizona Press, United States of America.

Friedman, J. and Stein, Z. 1980. The influence of seed-dispersal mechanisms on the dispersion of *Anastatica hierochuntica* (Cruciferae) in the Negev Desert, Israel. *Journal of Ecology* 68, 43–50.

Friedman, J., Gundermann, N. and Elli, N. 1978. Water response of the hygrochastic skeletons of the true Rose of Jericho. *Oecologia* 32, 298–301.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Review* 41**,** 587–640.

Guo, Q., and Brown, J. H. 1996. Temporal fluctuations and experimental effects in desert plant communities. *Oecologia* 107, 568–577.

Guo, Q., Brown, J. H. and Valone, T. J. 2002. Long-term dynamics of winter and summer annual communities in the Chihuahuan Desert. *Journal of Vegetation Science* 13, 575–584.

Gutterman, T. 1993. *Seed Germination in Desert Plants.* Adaptations of Desert Organisms. Springer, Berlin.

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., Shem-Tov, S. and Gozlan, S. 1998. The effect of post maturation temperatures and duration on seed germinability of *Plantago coronopus* occurring in natural populations in the Negev Desert highlands. *Journal of Arid Environments* 38, 451–463.

Imbert, E. 2002. Ecological consequences and ontogeny of seed heteromorphism. *Perspectives in Plant Ecology, Evolution and Systematics* 5, 13–36.

Jurado, E. and Westoby, M. 1992. Seedling growth in relation to seed size among species of arid Australia. *Journal of Ecology* 80, 407–416.

Kamenetsky, R., and Gutterman, Y. 1994. Life cycles and delay of seed dispersal in some geophytes inhabiting the Negev Desert highlands of Israel. *Journal of Arid Environments* 27, 337–345.

Leishman, M. R. and Westoby, M. 1994. The role of seed size in seedling establishment in dry soil conditions - experimental evidence from semi-arid species. *Journal of Ecology* 82, 249–258.

Lloret, F., Casanovas, C. and Peñuelas, J. 1999. Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Functional Ecology* 13, 210–216.

Loik, M. E., Brashears, D. D., Lauenroth, W. K. and Belnap, J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141, 269–281.

Lytle, D.A., and Poff, N.L. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19, 94–100.
Moles, A. T. and Westoby, M. 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92, 372–383.

Mulroy, W. T., and Rundel, P. W. 1977. Annual plants: adaptations to desert environments. *BioScience* 27, 109–114.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 25–41.

Pake, C. E., and Venable, D. L. 1996. Seed banks in desert annuals implication for persistence and coexistence in viable environments. *Ecology* 77, 1427–1435.

Peters, E. M., Martorell, C. and Ezcurra, E. 2009. The adaptive value of cued seed dispersal in desert plants: seed retention and release in *Mammillaria pectinifera* (Cactaceae), a small globose cactus. *American Journal of Botany* 96, 537–541.

Philippi, T. 1993. Bet-hedging germination of desert annuals: beyond the first year. *American Naturalist* 142, 474–487.

Philippi, T., and Seger, J. 1989. Hedging one's evolutionary bets, revisited. *Trends in Ecology and Evolution* 4, 41–44.

Reed, T. E., Waples, R. S., Schindler, D. E., Hard, J. J. and Kinnison, M. T. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. *Proceedings of the Royal Society B*. doi: 10.1098/rspb.2010.0771

Reynolds, J. F., Kemp, P. R. Ogle, K. and Fernández, R. J. 2004. Modifying the ‘pulse-reserve’ paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141, 194–210.

Roff, D. A. 2002. *Life History Evolution*. Sinauer Associates, Inc., Massachusetts.

Sadeh, A., Guterman, H., Mordechai, G. and Ovadia, O. 2009. Plastic bet-hedging in an amphicarpic annual: an integrated strategy under variable conditions. *Evolutionary Ecology* 23, 373–388.

Seger, J., and Brockman, H. J. 1987. What is bet-hedging? *Oxford Surveys in Evolutionary Biology* 4, 182–211.

Sheppard, P. R., Comrie, A. C., Packin, G. D., Angersbach, K. and Hughes, M. K. 2002. The climate of the US Southwest. *Climate Research* 21, 219–238.

Shreve, F. and Wiggins, I. L. 1964. *Vegetation and Flora of the Sonoran Desert.* Stanford University Press.

Simons, A. M. 2002. The continuity of microevolution and macroevolution. *Journal of Evolutionary Biology* 15, 688–701.

Simons, A. M. 2009. Fluctuating natural selection accounts for the evolution of diversification bet hedging. *Proceedings of the Royal Society B.* doi: 10.1098/srpb.2008.1920

Simons, A. M., and Johnston, M. O. 2006. Environmental and genetic sources of diversification in the timing of seed germination: implications for the evolution of bet hedging. *Evolution* 60, 2280–2292.

Simons, A. M. 2011. Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proceedings of the Royal Society B.* doi: 10.1098/rsbp.2011.0176.

van Rheede van Oudtshoorn, K., and van Rooyen, M. W. 1999. Dispersal *Biology of Desert Plants.* Adaptations of Desert Organisms. Springer, Berlin.

Venable, D. L. 2007. Bet hedging in a guild of desert annuals. *Ecology* 88, 1086–1090.

Venable, D. L. and Lawlor, L. 1980. Delayed germination and dispersal in desert annuals: Escape in space and time. *Oecologia* 46, 272–282.

Venable, D. L. and Brown, J. S. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* 131, 360–384.

Vogel, S. 2003. *Comparative Biomechanics. Life's Physical World.* Princeton.

Volis, S., and Bohrer, G. 2012. Joint evolution of seed traits along an aridity gradient: seed size and dormancy are not two substitutable evolutionary traits in temporally heterogeneous environment. *New Phytologist*. doi: 1111/nph.12024

West, G. B., Brown, J. H. and Enquist, B. J. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276, 122–126.

Tables

Table 3.1. Field locations of collection sites for *Chorizanthe rigida*, and nearest weather stations used for the analysis.

collection sites	**coords.**	**elev. (m)**	**weather stations and dates**	**coords.**	**elev. (m)**	**total precip. (mm; mean±se)**	**% winter eff. precip.**
Clark Mountains Wilderness Area	35°31'32"N / 115°35'19"W	1065	Mojave, CA 1948–2001	35°03'N / 118°10'W	834	144.2 ± 14	91.52
Organ Pipe Cactus National Monument	32°07'49"N / 112°45'56" W	550	Organ Pipe Cactus N.M., AZ 1949–2009	31°57'N / 112°48'W	512	240.5 ± 11	60.82
Ocotillo Wells State Vehicular Recreation Area	33°09'14"N / 116°09'40"W	156	Borrego Desert Park, CA 1949–1975	33°14'N / 116°25'W	245	122.7 ± 10	78.63
Las Tinajas, Baja California	31°49’48”N / 115°11’29”W	21	San Felipe, BC 1949-2010	31°02’N / 114°50’W	20	54.58 ± 9	63.75
Pinacate Biosphere Reserve, Sonora	31°51'49"N / 113°26'46"W	322	Sonoyta, Sonora 1949–2011	31°52’N / 112°51’W	398	188.4 ± 4	70.17
Calamajué, Baja California	29°29’11”N / 114°17’18”W	480	Chapala, BC 1971–2000	29°29’N / 114°22’W	640	113.9 ± 9	74.15

Table 3.2. ANOVA table showing the effects of different factors on involucre base areas.

Source	d.f.	sum sq.	mean sq.	*F*	*P*	r^2	cumul.
precipitation pattern	1	208.32	208.32	1385.0	< 0.0001	0.152	0.152
branch hierarchy	2	633.32	316.66	2105.2	< 0.0001	0.461	0.613
log-involucre length	1	205.88	205.88	1368.7	< 0.0001	0.150	0.763
precip × branch	2	14.71	7.35	48.9	< 0.0001	0.011	0.773
precip:site	4	11.01	2.75	18.3	< 0.0001	0.008	0.781
precip:site:ind	54	21.31	0.39	2.6	< 0.0001	0.016	0.797
Residuals	1856	279.17	0.15				
Total	1920	1373.72					

Appendix 3.A

Within and among-individuals analysis of variance

ANOVA tables showing that the contribution of within individual variance is higher than the variance among individuals in the four morphometric variables (i.e., 54% of involucre size variation is explained within individuals and only 6% among individuals).

Table B1. Involucre base area ANOVA table

Source	Df	sum sq.	mean sq.	*F* value	*P*(>*F*)	r^2
Site	5	211.62	42.32	69.71	<0.0001	0.15
indiv.-within-sites	54	32.26	0.6	0.98	0.51	0.02
within individuals	1861	1129.85	0.61			0.82
Total	1920	1373.73				

Table B2. Involucre size ANOVA table

source	Df	sum sq.	mean sq.	*F* value	*P*(>*F*)	r^2
Site	5	175.41	35.08	282.93	<0.0001	0.41
indiv.-within-sites	54	23.65	0.44	3.53	<0.0001	0.06
within individuals	1861	230.76	0.124			0.54
Total	1920	429.82				

Table B3. Involucre length ANOVA table

source	Df	sum sq.	mean sq.	*F* value	*P*(>*F*)	r^2
Site	5	135.19	27.04	110.02	<0.0001	0.22
indiv.-within-sites	54	9.98	0.18	0.75	0.91	0.02
within individuals	1861	457.32	0.25			0.76
Total	1920	602.49				

Table B4. Propagule biomass ANOVA table

source	Df	sum sq.	mean sq.	*F* value	*P*(>*F*)	r^2
Site	5	22.07	4.41	10.89	<0.0001	0.03
indiv.-within-sites	54	22.94	0.42	1.05	0.38	0.03
within individuals	1861	754.47	0.41			0.94
Total	1920	799.48				

Figures

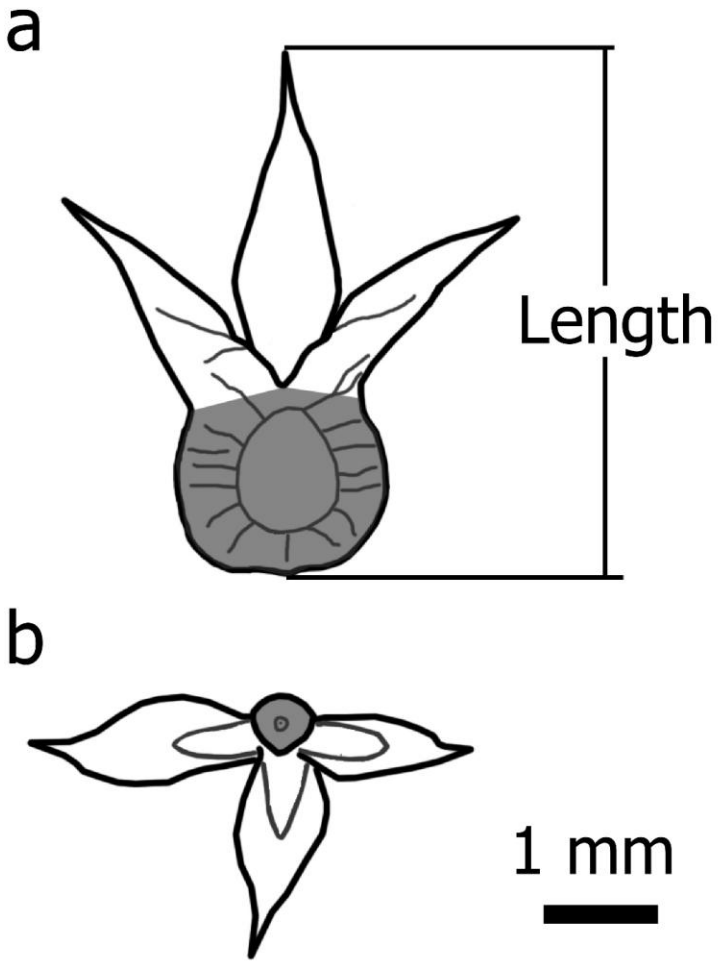

Figure 3.1. Frontal (a) and ventral (b) views of *Chorizanthe rigida*'s involucres. Frontal view showing involucre size (mm^2, in gray) and involucre length (mm). Ventral view showing base area (mm^2, in gray).

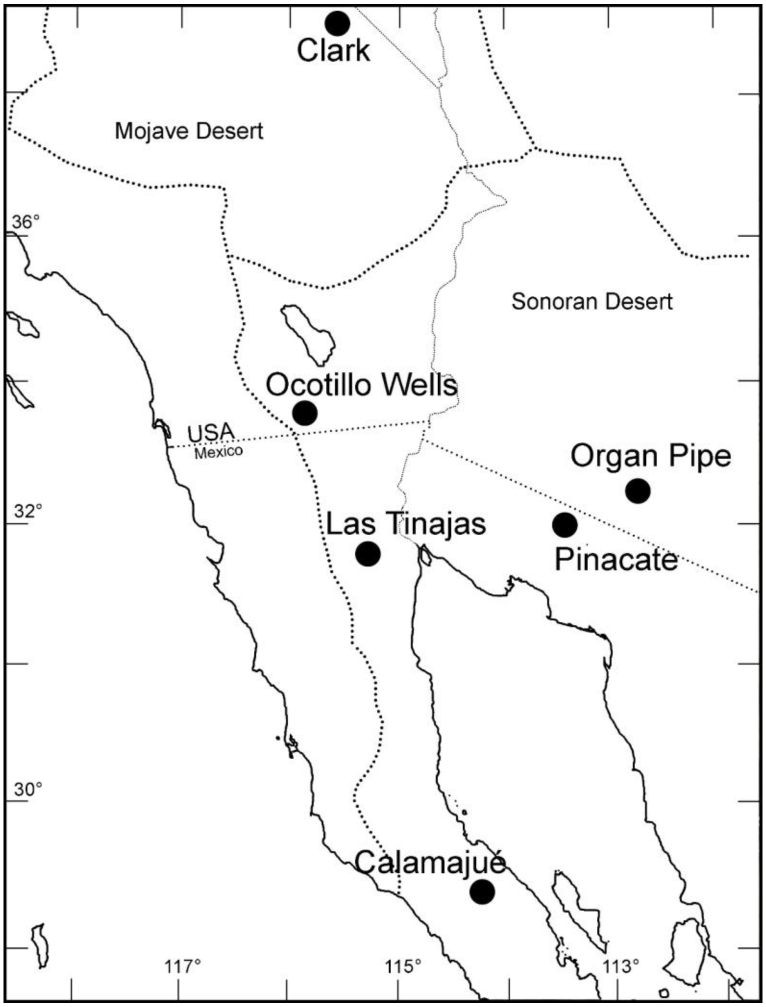

Figure 3.2. Collection sites of *Chorizanthe rigida* populations in the Sonoran and Mojave desert regions (see Table 1 for location details).

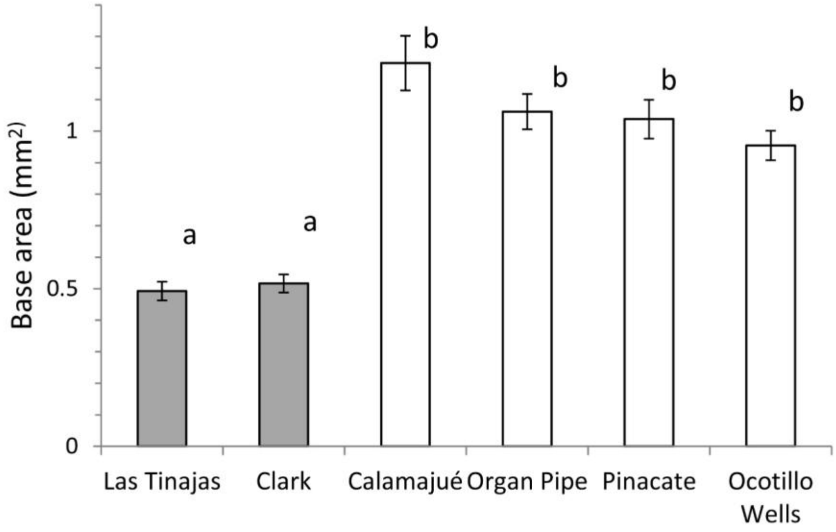

Figure 3.3. Involucre base area (mm^2, $\bar{x} \pm se$) in each study site. Same letters above bars indicate sites that do not differ significantly. Sites with winter rains only (Las Tinajas and Clark; gray bars) have significantly smaller involucre bases than bi-seasonal sites with summer showers (Calamajué, Organ Pipe, Pinacate, and Ocotillo Wells; white bars).

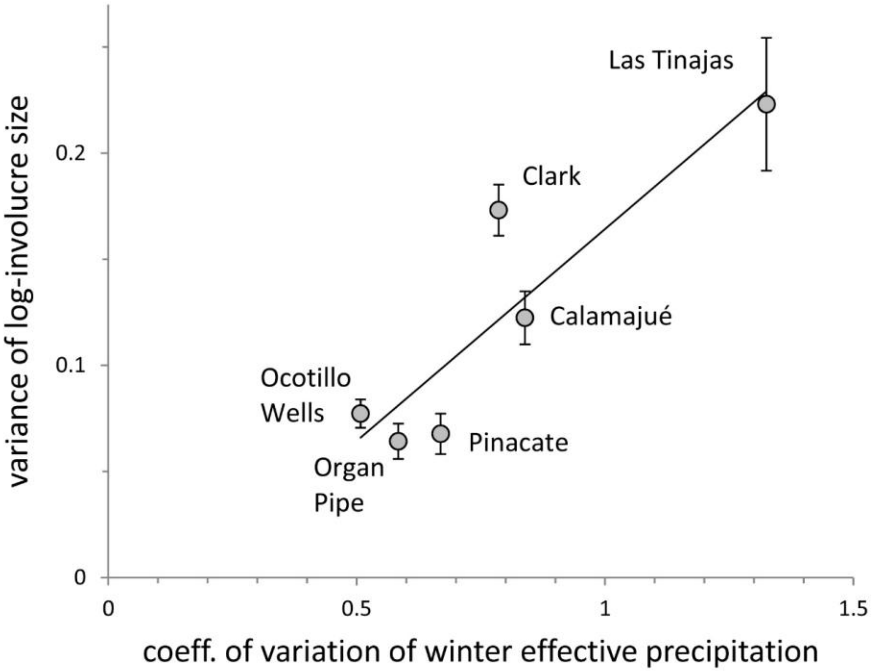

Figure 3.4. Correlation between the variance of log-involucre size and precipitation variability (measured as the coefficient of variation of winter effective precipitation) for the six study sites (*r* = 0.90, *P* = 0.0004).

Chapter 4

Hydration history and attachment morphology regulate seed release in *Chorizanthe rigida* (Polygonaceae), a serotinous desert annual

Abstract

Timing of seed release is a critical parameter influencing the probability of seedling survival. I used a biomechanical approach to analyze seed release in *Chorizanthe rigida*, a seed retaining (serotinous) desert annual, to understand the adaptive significance of seed retention in this species. Pull-to-break tests were performed on individual propagules (i.e., involucres and achene) from new and weathered plants, under dry and wetting conditions, and recorded the breaking force. Involucre base area was measured using digital images and image processing software. A positive correlation was found between the force required to detach an involucre and the size of its base area. The force required to detach involucres from soaked and weathered plants was lower than that for dry and new plants. This pattern provides a mechanism for the plant to control the number of involucres released in different rain events. In conclusion, seed release in *C. rigida* is controlled by the propagule morphology, rainfall conditions, and weathering of the plant. These factors allow this species to cope with desert environmental variability by influencing both timing and the amount of seed release.

Introduction

In pulse-driven ecosystems, such as deserts, where rains are infrequent and unpredictable, the timing of seed release is crucial, as low soil moisture limits germination and seedling survival (Noy-Meir 1973). Seed release is triggered by rainfall in some desert plants, a hygrochastic seed dispersal mechanism that allows them to synchronize seed release to 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 seed germination can increase the probability of survival by allowing only a portion of the seed bank to germinate while the rest stays behind to germinate during later water pulses, as a bet-hedging strategy (Philippi 1993; Gutterman 2002). Although this aspect has received less attention, delayed seed dispersal may also contribute to seed germination variability in serotinous desert plants, which form aboveground seed banks by retaining seeds on the mother plant and release fractions of them after a rainfall event for several years depending on the amount and frequency of rainfall (Friedman *et al.* 1978; Gutterman and Ginot 1994).

Biomechanics has been used to investigate how leaves (Edwards *et al*. 2000; Read and Sanson 2003; Read and Stokes 2006; Peeters *et al*. 2007; Onoda *et al*. 2011) and fruits (Wang and Mai 1995a, 1995b; Seidel *et al.*, 2009; Martone *et al.*, 2010) are protected from predation or adverse environmental conditions. Biomechanics has also 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 (Witztum 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); (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 (Beisman *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 controlled. 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 (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 on successful establishment. 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 found across the Sonoran and Mojave Deserts of North America. It forms an aboveground seed bank by retaining seeds in its lignified dead skeletons for several years (Fig. 4.1a). Its seed dispersal is triggered by rainfall events. The seeds, contained in involucres formed by three bracts holding one central achene (Fig. 4.1b), 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 (Figs. 4.1c and 4.1d). Undispersed involucres remain attached to the plant as the lignified tissues re-dry (Ellner and Shmida 1981; van Rheede van Oudtshoorn and van Rooyen 1999). *C. rigida*'s involucres and their hygrochastic dehiscive tissue vary in size within individuals and among populations (Felger 2000). Given that the base of the involucre controls seed release, variation in this propagule characteristic can have important consequences for both the timing of seed release and the amount of propagules released in response to environmental conditions.

Here I explore the relationship between the basal cross-sectional area of involucre pedicels of *C. rigida* and their ease of release. I test 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. A biomechanical approach was used to measure the strength needed to detach propagules. My prediction was that the force needed to detach involucres with larger base areas will be higher than that used for involucres with smaller base areas. I also predicted that wet involucres would detach more easily than dry involucres, and that the force needed to detach involucres from weathered plants (i.e., plants from past years) would be lower than that needed for new plants.

Methods

Study species

Chorizanthe rigida (rigid spineflower, Polygonaceae) is a short, erect desert annual, 2–10 cm high. It has a single taproot and stout stems covered by stiff, spiny bracts. As the stem grows, the soft, long-petioled basal leaves are shed, and give place to linear, rigid bracts (or cauline leaves) armed with a terminal spiny awn that becomes hard and thorn-like with age (Fig. 4.1a). The single flowers, with a diminutive yellow perianth, are subtended by a 3-segmented involucre with hard spiny bracts. The fruit is a single achene, or “seed” that matures inside the involucre (Fig. 4.1b). The base of the involucre has hygrochastic dehiscent tissue formed by cells with walls that shrink when dehydrated, preventing involucre detachment, and, expand and soften when hydrated, allowing for seed release (Fig. 4.1c and d). The flowering season lasts from March to May and plants mature and produce seeds at the end of the spring season (April–May). Seeds germinate inside the involucre during the winter season (December–February). This species is distributed from Baja California’s Central Desert to the Great Basin in Nevada and is common in the Mojave and Sonoran deserts, especially in desert pavements (Felger 2000; Baldwin et al. 2002).

Sampling

Individuals 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, collections were made on individuals that showed visible signs of weathering, indicating they had established at least one year 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). Either a Pesola Micro-Line Spring Scale (capacity: 100 g, division 1 g) or a Pesola Medio-Line Spring Scale (capacity: 300 g, division: 2 g) was used depending on the size of the involucre. A drag pointer for Pesola Medio-Line Scales was used in the medium scale to mark the breaking force, while for the micro-scale, the breaking force was recorded visually. A mini surgical hemostatic clamp (Mini Bulldog Serrefines, with a serrated jaw of 6 × 22 mm dimensions) was attached to the crocodile clamp at the end of the scale, and was used on small involucres; the crocodile clamp was used directly on larger involucres (Fig. 4.2).

During measurements, each individual was tightly secured on a vice from its taproot at the base of the plant, and the mini 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. Afterwards, 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 minutes after soaking, the medium size involucres were tested after ca. 15 minutes, and the largest involucres were given 30 minutes 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 was recorded (f_b).

Morphometric 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 area and (2) the size 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, MA).

Statistical model and analyses

Two separate analyses were performed. First, the breaking force estimates for a total of 221 involucres from new plants subject to soaking was analyzed (the data from involucres that did not detach during the tensile test was not included). This data was tested for a linear relationship between the breaking force measured experimentally and the pedicel base cross-sectional area with an intercept of zero. The effect of involucre size as a covariate in a linear model was tested to analyze the possible additive effect of involucre size on the breaking force. For the second analysis, a test was performed to analyze 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 involucres, and the interactions between base area and wetting, base area and weathering, and hydration and weathering. The effect of wetting, weathering, and their interaction on the area-specific breaking force (force divided by the base area) was also tested. A total of 253 involucres were examined in this second analysis, including new and weathered plants, tested under dry and wet conditions, and excluding those involucres that did not detached under the maximum tensile force of our equipment.

Results

A significant positive linear relationship was found 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 in the new plants analysis (Fig. 4.3). The mean squares regression slope, an indication of the average tensile strength of the tissue, was 6.1 ± 0.9 (s.e.) mN/mm^2 (millinewton per squared millimeter). There was no correlation between breaking stress in (mN/mm^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 ($r^2 = 0.01$; $F_{1,219} = 2.7$; $P = 0.1$), supporting the hypothesis that base area resistance is independent of propagule size.

A significant effect of base area, hydration, weathering, and the interaction between base area and hydration, base area and weathering, and hydration and weathering were found in the second analyses. However, quantitatively, most of the variation was explained by base area and hydration (Fig. 4.4; Table 4.1). In agreement with these results, there was a significant effect of hydration, weathering and the interaction between hydration and weathering on breaking stress, with a quantitatively larger effect of hydration (Table 4.2).

Discussion

The force needed to detach the involucres and the base area of the involucres were positively correlated in new plants subject to soaking, indicating that thicker pedicels tend to retain seeds more strongly than thinner ones. Also, there was a significant effect of wetting and weathering on the force needed to detach the involucre, thus, given similar bases, wet and older involucres release seed more easily than dry or the ones that have not been subject to weathering. Collectively, these results indicate that seed release in *C. rigida* is under biomechanical control. As expected, there was no correlation between the tensile strength and the involucres cross-sectional area. This means that the mechanical properties of involucral 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), 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 the way 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 perpendicularly to the orientation of cellulose microfibrils (Fahn and Werker 1972; Ellner and Shmida 1981; Gutterman and Ginott 1994; 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, it has swelling tissue at the base of its involucres that become soft 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, as it allows the plant to release or retain propagules through changes on through changes in the hydration of the swelling tissue at the base of the involucre (Fig. 4.1). Furthermore, decreased tensile strength of weathered involucres belonging to old plants is likely caused by changes in the composition and structure of the cell wall. Weathering of cellulosic materials causes lignin degradation and cellulose depolymerisation (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 can have important ecological implications. A hygrochastic seed dispersal mechanism allows this species to synchronize seed release to rainfall events, as it has been reported in other desert annual species (Friedman *et al.* 1978; Gutterman and Ginot 1994; van Oudtshoorn and van Rooyen 1999). Furthermore, *C. rigida* is distributed in desert areas with winter and bi-seasonal (winter and summer) rainfall patterns.

Involucres with larger base areas could be more strongly held to the plant, preventing seed release to false rain cues, such as a sparse winter rainfall event or a summer storm when high temperatures would not allow for the 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). Intra-individual variation in modular structures can play a major role in the way a given plant copes with environmental variation by giving different survival ability to different parts of the plant. These results showed that there is variability in the breaking force needed to detach the involucres. Plants may release more or fewer involucres from their aboveground seed-bank according to a rainfall threshold, as an adaptive bet-hedging dispersal strategy to cope with rain unpredictability. Although these experiments do not simulate the exact conditions for seed release as experimented by this plant in the field, the approach allows for a biomechanical assessment of which involucres are more likely to be dislodged. The obtained data may underestimate the true magnitude of biomechanical variation in propagule ease of release because the tensile strength of both the smaller and the larger involucres could not be adequately measured, which would have added additional variation to the extremes of the data range. After initial wetting, many of the smaller propagules became so loose that they were released as they were attached to the mini-clamp, and before any tensile strength could be applied. Conversely, some of the larger involucres failed to detach within the force range of our tensometer. The basal cross-area of these recalcitrant involucres was significantly larger than that of the experimentally detached ones (1.32 ± 0.09 mm^2 vs. 0.86 ± 0.03 mm^2; $t = 4.67$; d.f. = 53; $P < 0.0001$). As shown by these results, weathering also increases the ease of seed release, thus variation in involucre dispersal increases with the age of the plants' cohorts as plants belonging to different years show varying degrees of weathering.

In conclusion, seed dispersal in *C. rigida* is controlled by involucre base area, wetting, and weathering of the propagules. The biomechanical properties of involucre release and dispersal in *C. rigida* are ecologically and evolutionary relevant, as survival and establishment depend on the correct timing of seed release to a favorable winter rainfall.

Literature Cited

Austin, A. T., and Vivanco, L.. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature Letters* 442, 555–558.

Baldwin, B.G., Boyd, S., Ertter, B. J., Patterson, R. W., Rosatti, T. J., and Wilken, D. H. [eds.], 2002. *The Jepson Desert Manual. Vascular plants of Southeastern California.* University of California Press, Canada.

Beismann, H., Wilhelmi, H., Bailleres, H., Spatz, H. C., Bogenrieder, A., and Speck, T. 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 Nobel, P. S. 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 Physiological Biochemistry* 38, 81–96.

Burgert, I. and Fratzl, P. 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.

Chanliaud, E., Burrows, K. M., Jeronimidis, G., and Gidley, M. J. 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. *The Plant Cell* 9, 1031–1041.

Cosgrove, D. J., and Jarvis, M. C. 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.

Edwards, C., Read, J., and Sanson, G. 2000. Characterizing sclerophylly: some mechanical properties of leaves from heath and forest. *Oecologia* 123, 158–167.

Ellner, S., and Shmida, A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* 51, 133–144.

Endo, Y., Sakamoto, J., Kashiwano, Y., Yokota, H., Nakamura, S., and Kinoshita, E. 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., Hotton, S., and Dumais, J. 2011. The mechanics of explosive dispersal and self-burial in the seeds of the filaree, *Erodium cicutarium* (Geraniaceae). *The Journal of Experimental Biology* 214, 521–529.

Fahn, A., and Werker, E. 1972. Anatomical mechanisms of seed dispersal. In T. T. Kozlowski [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*. The University of Arizona Press. United States of America, 398–400, 403–403.

Friedman, J., Gundermann, N., and Ellis, N. 1978. Water response of the hygrochastic skeletons of the true Rose of Jericho. *Oecologia* 32, 298–301.

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 Johnson, E. A. 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 Ginott, S. 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., Gerry, S. P., and Ellerby, D. J. 2010. The seed dispersal catapult of *Cardamine parviflora* (Brassicaceae) is efficient but unreliable. *American Journal of Botany* 97, 1595–1601.

Hegazy, A. K., Barakat, H. N., and Kabiel, H. F. 2006. Anatomical significance of the hygrochastic movement in *Anastatica hierochuntica*. *Annals of Botany* 97, 47–55.

Jones L, Ennos, A. R., and Turner, S. R.. 2001. Cloning and characterization of *irregularxylem4* (*irx4*): a severely lignin deficient mutant of *Arabidopsis*. *Plant Journal* 26, 205–16.

Marchetto, K. M., Williams, M. B., Jongejans, E., Auhl, R., and Shea, K. 2010. Applications of particle image velocimetry for seed release studies. *Ecology* 91, 2485–2492.

Martone, P. T., Boller, M., Burgert, I., Dumais, J., Edwards, J., Mach, K., Rowe, N., Rueggeberg, M., Seidel, R., and Speck, T. 2010. Mechanics without muscle: biomechanical inspiration from the plant world. *Integrative and Comparative Biology* 50, 888–907.

Montaña, C., Ezcurra, E., Carrillo, A., and Delhoume, J. P. 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 Ellison, A. M. 1998. Seed dispersal characteristics of *Brassavola nodosa* (Orchidaceae). *American Journal of Botany* 85, 675–680.

Niklas, K. J. 1992. Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago, Illinois, USA. pp. 48–125, 234–242, 261–270.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecological Systems* 4, 25–41.

Onoda, Y., Westoby, M., Adler, P. B., Choong, A. M. F., Clissold, F. J., Cornelissen, J. H. C., Díaz, S., Dominy, N. J., Elgart, A., Enrico, A. L., Fine, P. V. A., Howard, J. J., Jalili, A., Kaoru, K., Kurokawa, H., McArthur, C., Lucas, P. W., Markesteijn, L., Pérez-Harguindeguy, N., Poorter, N., Richards, L., Santiago, L. S., Sosinski, E. E., Van Bael, S. A., Warton, D. I., Wright, I. J., Wright, S. J., and Yamashita, N. 2011. Global patterns of leaf mechanical properties. *Ecology Letters* 14, 301–312.

Peeters, P. J., Sanson, G., and Read, J. 2007. Leaf biomechanical properties and the densities of herbivorous insect guilds. *Functional Ecology* 21, 246–255

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 Neale, D. 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., Ryan, K. G., and Garnock-Jones, P. 2010. Hygrochastic capsule dehiscence in New Zealand alpine *Veronica* (Plantaginaceae). *American Journal of Botany* 97, 1413–1423.

Read, J. and Stokes, A. 2006. Plant biomechanics in an ecological context. *American Journal of Botany* 93, 1546–1565.

Ryden, P., Sugimoto-Shirasu, K., Smith, A. C., Findlay, K., Reiter, W., and McCann, M. C. 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.

Seidel R., Buhrig-Polaczek, A., Fleck, C., and Speck, T. 2009. Impact resistance of hierarchically structured fruit walls and nut shells in view of biomimetic applications. In: Thibaut, B. [ed.], *Proceedings of the 6th Plant Biomechanics Conference*. *French Guyana*, *France*, ECOFOG, Cayenne, 406–11.

Sperry, J. 2003. Evolution of water transport and xylem structure. *International Journal of Plant Science* 164, 115–127.

Taylor, P. E., Card, G., House, J., Dickinson, M. H., and Flagan, R. C. 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

Vogel, S. 2003. *Comparative Biomechanics. Life's Physical World*. Princeton, 301–341.

Wang, C. and Mai, Y. 1995a. Deformation and fracture of Macadamia nuts. Part 1: Deformation analysis of 'nut-in-shell'. *International Journal of Fracture* 69, 51–65.

Wang, C. and Mai, Y. 1995b. Deformation and fracture of Macadamia nuts. Part: II Microstructure and fracture mechanics analysis of nutshell. *International Journal of Fracture* 69, 67–85.

Weinkamer, R., and Fratzl, R. 2011. Mechanical adaptation of biological materials – The examples of bone and wood. *Materials Science and Engineering C* 31: 11664–1173.

Whitney, S. E. C., Gothard, M. G. E., Mitchell, J. T., and Gidley, M. J. 1999. Roles of cellulose and xyloglucan in determining the mechanical properties of primary plant cell walls. *Plant Physiology* 121, 657–663.

Witztum, A. and Schulgasser, K. 1995. The mechanics of seed expulsion in Acanthaceae. *Journal of Theoretical Biology* 176, 531–542.

Tables

Table 4.1. ANOVA table showing the effect of base area, hydration, weathering and the interactions on the force needed to detach the involucres.

	df	*F*	r^2	*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			

Table 4.2. ANOVA table showing the effect of hydration and weathering on the breakage force.

	df	*F*	r^2	*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			

Figures

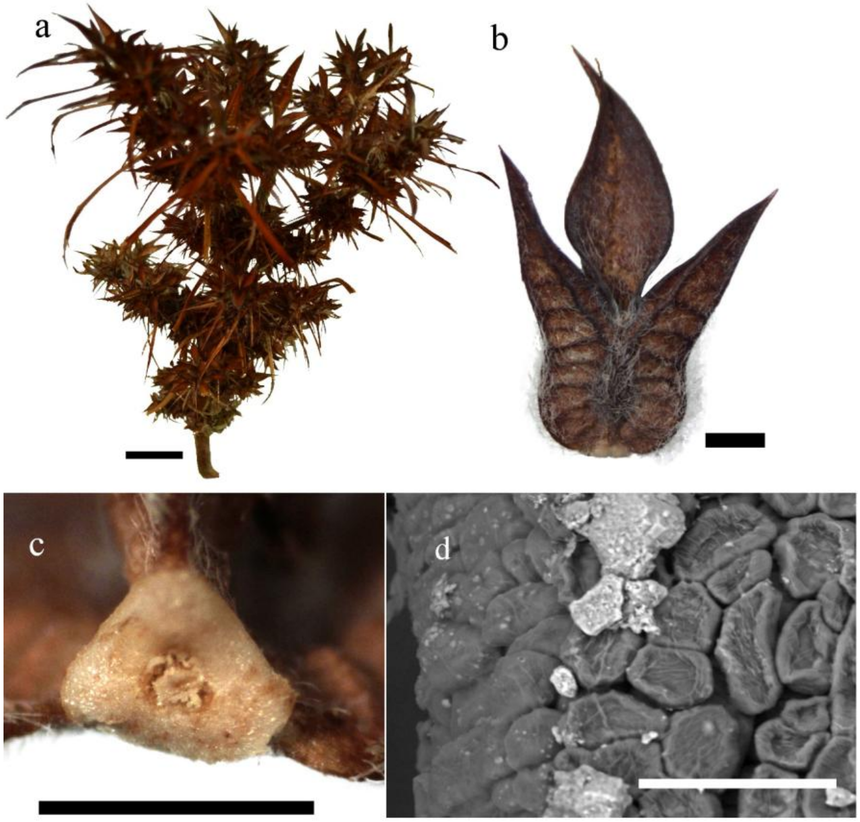

Figure 4.1. (a) *Chorizanthe rigida* whole dry plant, **(b)** involucre, **(c)** involucre base and, **(d)** **e**lectron-microscope image (1500×) of dehydrated cells of the dehiscent tissue at the base of the involucre.

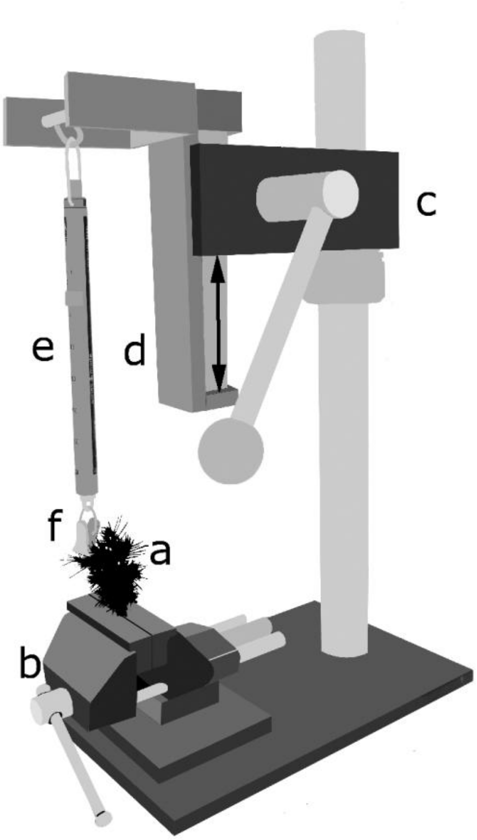

Figure 4.2. Tensometer setup consisting of a) *Chorizanthe rigida* individual, b) clamp, c) stand, d) mobile gauge-holding device, e) force gauge and mini-clamp. The gauge holding device is activated mechanically: it is placed at the lowest end of its mobility range by turning the lever counter-clockwise. Releasing the lever causes the gauge holding device to move upward and thus apply a tensile force to the clamped propagule.

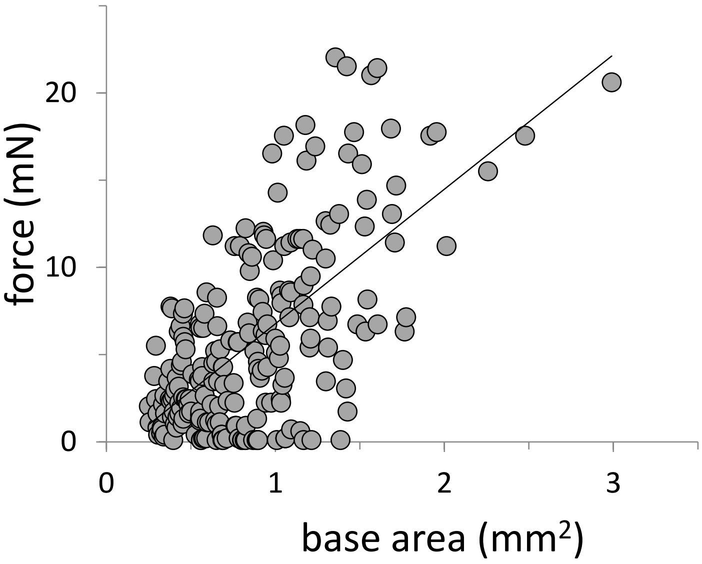

Figure 4.3. Correlation between involucre base area and the force (*F*) necessary for involucre detachment ($r^2 = 0.42$; $F_{1,219}$ 156.6; $P < 0.0001$). The slope of the fitted line defines the area-tensile breaking force (F_b) (6.1 ±0.9 mN/mm^2).

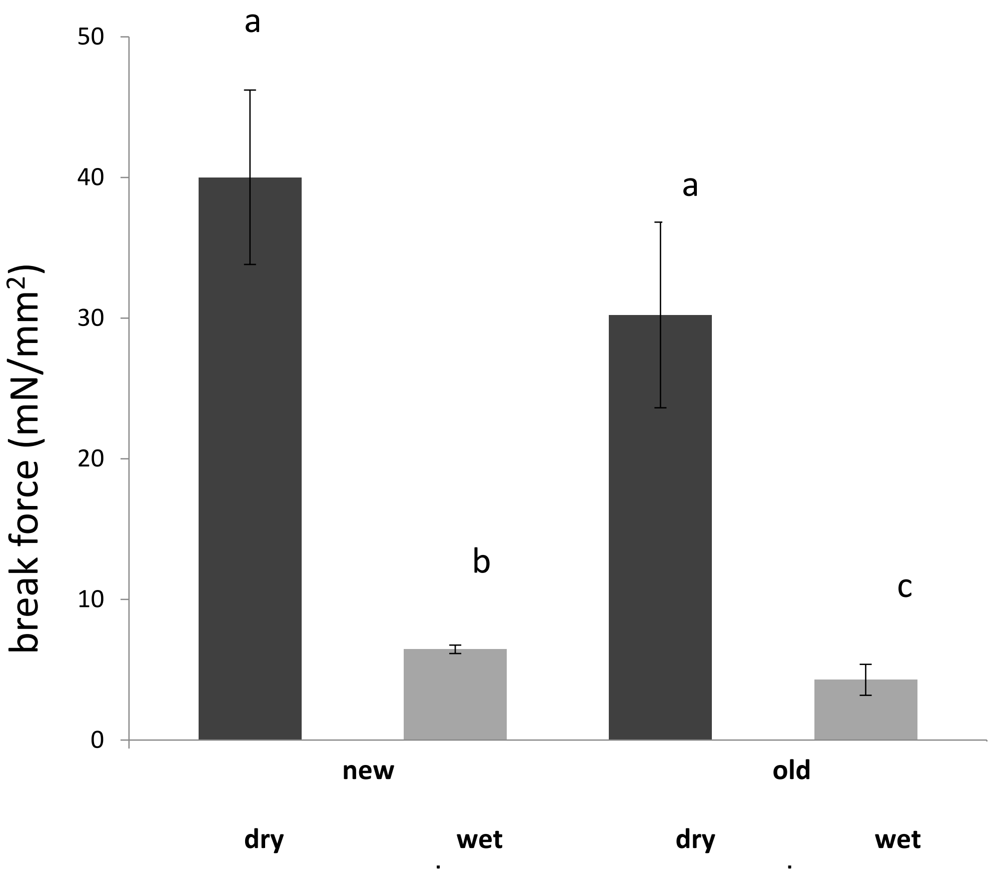

Figure 4.4. Effects of plant age and pedicel wetting on the involucre breaking force (mean ± s.e.; *n* equals 3 for recent plants with dry pedicels, 221 for recent wet, 6 for old plants with dry pedicels, and 26 for old wet). Different letters indicate significantly different ($P < 0.05$) means for a *t*-test with unequal sample sizes.

Conclusions

The adaptive significance of serotiny in desert species has been considered as allowing: (a) to synchronize germination to favorable environmental conditions by dispersing seeds as a response to rainfall cues; (b) to regulate the amount of seeds dispersed depending on the amount and frequency of rainfall events; (c) to display a bet-hedging strategy by having an above-ground seed bank with fractional seed release allowing the spreading of germination risk over several years; and (d) to protect seeds from predation by keeping them enclosed in the mother plant's canopy. My dissertation provides further evidence of the adaptive significance of seed retention and timing of seed release. Moreover, the serotinous species of North American deserts provide important evidence of the evolutionary convergence of dispersal syndromes in arid environments. My taxonomic review of the occurrence of serotiny across taxa opens important questions for further studies aimed at understanding the selective forces that shape the evolution of these convergent seed retention syndromes.

The analysis of the small scale distribution pattern of *C. rigida*, in a shrub-mound to desert-pavement gradient shows how the different land surface and soil characteristics of these two geomorphological features are important drivers of the microhabitat distribution of desert annuals, favoring either soil-seed banking or above-ground seed banking species in mounds and pavements, respectively. I provide evidence in favor of the prediction that seed retention and timing seed release to winter rainfall events allows this species to establish on desert pavements, a fairly stable surface that favors long-term persistence in the field and the use of rainfall run-off as a dispersal agent. By retaining its seeds and releasing them to rain events, *C. rigida* avoids having its seeds dispersed by wind or animals into the shrub mounds, characterized by high bioturbation and competition for establishment with other desert annuals. My microhabitat study also shows that, by regulating the timing of seed release, serotiny in annual plants can have an important effect on the seed dispersal agent (e.g., wind and granivory in non-serotinous species, and water dispersal in rain-cued serotinous plants), and, as a consequence, on the evolution of niche and habitat preference.

Multiple studies on desert annuals have addressed life-history theory predictions on germination traits. However, there is still a lack of solid evidence in favor of bet-hedging strategies in desert annuals because of the difficulties of following the fate of seeds once they get incorporated into the soil. By studying multiple populations of seed-retaining serotinous annual plants distributed across a wide geographic range of desert environments, where the predictability of rainfall varies strongly, I provide evidence in favor of two life-history theory predictions. Firstly, my data shows that *C. rigida* ecotypes experiencing a bi-seasonal rainfall regime are more strongly serotinous to avoid releasing seed to a false summer rainfall cue. Secondly, there is a positive correlation between within-individual propagule diversification in seed traits and the variability of winter rainfall, a fact that strongly suggests that this desert annual displays a diversifying bet-hedging strategy to cope with environmental unpredictability. Testing the generality of these results into soil seed-banking species within this large desert region could further our understanding of other seasonally-cued and bet-hedging traits, such as germination.

In conclusion, by studying the relationship between serotiny and two of the most important sources of environmental variability in desert ecosystems: precipitation and its interaction with temperature, soil and geomorphological features, my dissertation provides a deeper understanding of the adaptive significance of seed retention and timing of seed release in serotinous desert plants.