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Source: Madroño, 62(1):21-32.

Published By: California Botanical Society

DOI: <http://dx.doi.org/10.3120/0024-9637-62.1.21>

URL: <http://www.bioone.org/doi/full/10.3120/0024-9637-62.1.21>

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## DELAYED SEED DISPERSAL IN CALIFORNIA DESERTS

ALEJANDRA MARTÍNEZ-BERDEJA<sup>1</sup>

Department of Botany and Plant Sciences, University of California, Riverside,  
900 University Ave, 2140 Batchelor Hall, Riverside, CA 92521

<sup>1</sup>amart051@ucr.edu

EXEQUIEL EZCURRA

Department of Botany and Plant Sciences, University of California, Riverside,  
900 University Ave, 3324 Olmsted Hall, Riverside, CA 92521

ANDREW C. SANDERS

University of California, Riverside Plant Herbarium, University of California, Riverside,  
900 University Ave, 2140 Batchelor Hall, Riverside, CA 92521

### ABSTRACT

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

### RESUMEN

Se cree que la serotinia y la dispersión retrasada de semillas han evolucionado como un mecanismo que permite a las plantas hacer frente a la variabilidad ambiental. En el presente estudio realizamos una búsqueda en la literatura sobre las plantas serótinas de zonas áridas en los desiertos del Mojave y Sonorense en California. Las plantas encontradas fueron clasificadas de acuerdo al síndrome de retención de semillas. Las especies serótinas de los desiertos de Norte América han evolucionado síndromes de retención de semillas similares a los de las plantas de otros desiertos del mundo. La retención de semillas en plantas de desierto es una estrategia de dispersión común en los ecosistemas áridos que permite a las plantas adaptarse a la variabilidad e impredecibilidad ambiental.

Key Words: Basicarpy, delayed dispersal, desert serotiny, dispersal syndromes, hygrochasy, rain pulses.

Serotiny consists of the retention of mature seeds within the maternal canopy, delaying seed dispersal for varying periods of time (also known as bradychory or delayed dispersal; Lamont 1991; 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 Maitre 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, thus 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 have been shown to retain seeds (Günster 1992). Similarly, about 40 species in Israel and the Sinai have been described as having delayed dispersal mechanisms triggered by the onset of rains (Gutterman and Ginot 1994). Environmental pulses in desert ecosystems—in the form of randomly varying water availability—constitute a major factor driving the dynamics of desert communities (Noy-Meir 1973; Loik et al. 2004; Reynolds et al. 2004). 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.

The objective of this paper is to provide a list of serotinous species in the Mojave and northern Sonoran Desert in the flora of California. We also classify seed retaining species according to their different seed retention syndromes.

METHODS

We did a literature search in two regional desert floras: *Flora of the Gran Desierto and Rio Colorado of Northwestern México* (Felger 2000) and *The Jepson Desert Manual: vascular plants of southeastern California* (Baldwin et al. 2002). Although Felger’s flora deals with México’s Gran Desierto and not strictly with Californian deserts, the region is a natural continuation of the Lower Colorado Valley across the Mexican border, and the book contains very valuable descriptions of plants common to the larger desert region. In both books we looked for indications of serotiny in botanical descriptions such as “dry dead skeletons remain on the field for several years retaining seeds”, or for terms associated with seed retention, such as “tardily or irregularly dehiscent fruit”, “woody persistent fruits”, and “indehiscent fruit” among others.

We narrowed this broad first list by eliminating species that, although having lignified structures, readily release their seeds at the end of the growing season. We did this based on our own field notes and by consulting with experts on the flora of the regional deserts. We then verified our results 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 (references consulted are listed in the following section). Finally, we confirmed our information using herbarium specimens (University of California, Riverside Plant Herbarium [UCR]; <http://www.herbarium.ucr.edu/Herbarium.html>) and looked for evidence of prolonged seed retention on the specimens, to come with a list of serotinous species in the California desert region.

Serotinous desert plants have been classified according to the period of time of seed retention (Zohary 1962; van der Pijl 1982; van Oudtshoorn and van Rooyen 1999). However, because of the lack of data on seed-retention times within the Sonoran and Mojave deserts, we classified our plants into two types: (a) strongly serotinous species were identified as those that possess tough, strongly lignified seed-retaining structures, and (b) weakly serotinous species were identified as those showing softer, or less rigid seed-retaining structures (suggesting that seed retention occurs for a shorter time period).

RESULTS

In total, we identified 21 strongly serotinous and nine weakly serotinous species. Of the 30 serotinous species, 27 were dicots and only three were monocots. The plants we identified as seed-retaining form 1.1% of the species listed in *The Jepson Desert Manual* (Baldwin et al. 2002) and

TABLE 1. ORDER, FAMILY, AND GENERA OF DESERT SPECIES IN THE MOJAVE AND SONORAN DESERTS.

Order	Family	Genera	Serotinous species
Asparagales	Agavaceae	1	1
Caryophyllales	Amaranthaceae	2	1
Asterales	Asteraceae	121	1
Boraginales	Boraginaceae	11	1
Caryophyllales	Cactaceae	8	4
Celastrales	Celastraceae	1	1
Malvales	Malvaceae	9	2
Myrtales	Onagraceae	6	3
Lamiales	Orobanchaceae	1	1
Poales	Poaceae	74	2
Caryophyllales	Polygonaceae	13	1
Sapindales	Simaroubaceae	1	1
Solanales	Solanaceae	8	2
Zygophyllales	Zygophyllaceae	5	1
Total		261	22

3.7% of those listed in the *Flora of the Gran Desierto* (Felger 2002). This estimate represents a minimum threshold, as other serotinous species may exist that have not been identified with the procedure we followed. The ability to retain seeds seems to be taxonomically widespread: 14 out of 114 families of desert plants (12.3%; two monocot families and 12 dicot families) belonging to 13 different orders have at least one serotinous species (Table 1; a detailed list is provided in Appendix 1). After inspecting the range and type of seed-retaining strategies we found, serotinous species were classified into the following six groups: (1) ground-level ephemerals, (2) persistent plants with lignified fruits, (3) gradually opening capsules, (4) reproductive dimorphism, (5) schizocarps with heteromericarps, and (6) persistent fruits.

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 involucre to rainfall events (Fig. 1a; Felger 2000; Baldwin et al. 2002). *Chorizanthe 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

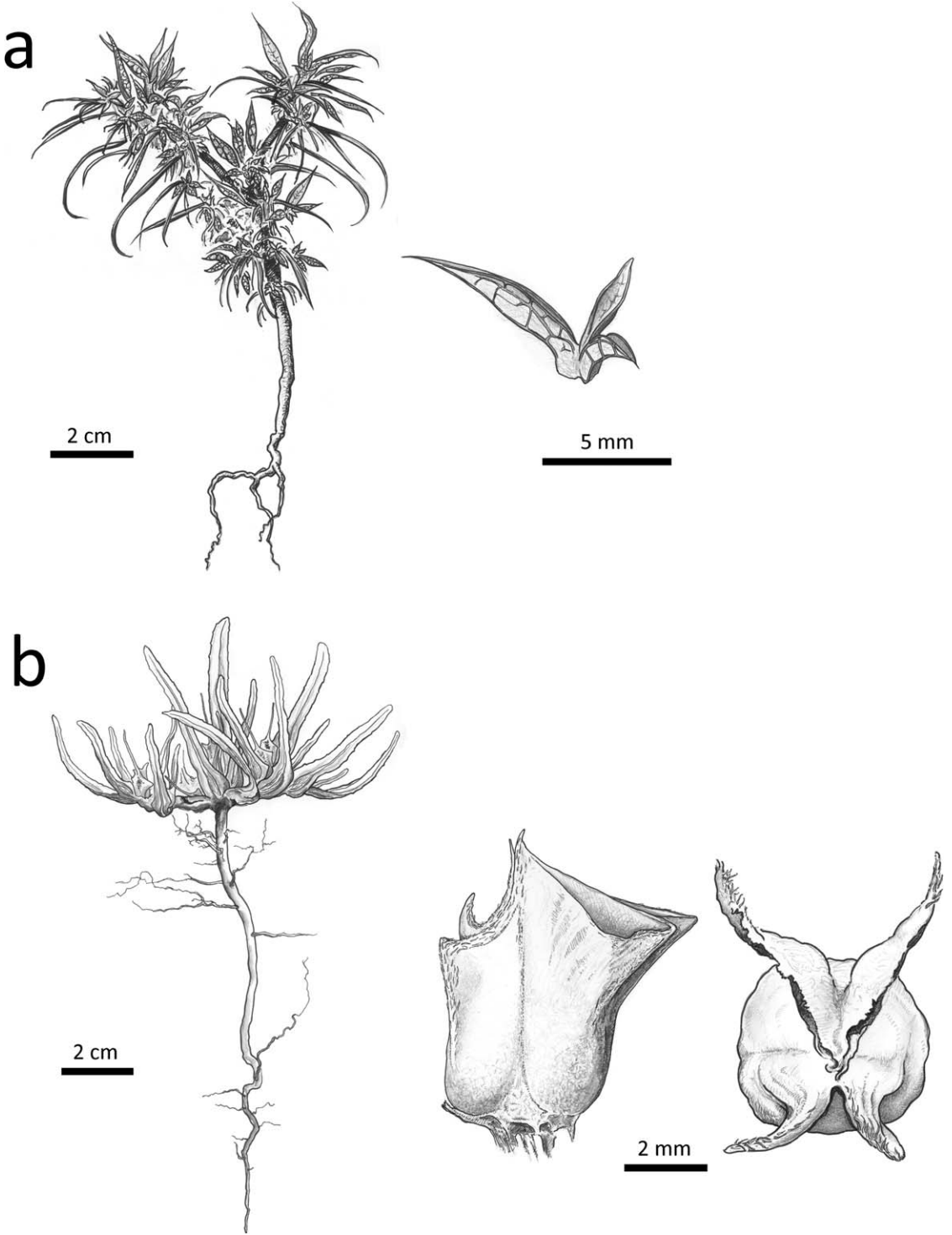


FIG. 1. Ground-level ephemerals (basicarpy): (a) dry dead skeleton and involucre of *Chorizanthe rigida*, and (b) whole individual, side and top view of the hydrochastic lignified capsule of *Tetrapteron palmeri*.

Desert of Baja California the plant shows a more erect habit and can reach 15 cm in height. Another basicarpic species in this region is *Tetrapteron palmeri* (S. Watson) W. L. Wagner & Hoch (Onagraceae), a winter annual that grows close to the ground (5–7 mm stalk length) bearing lignified, rigid capsules with hygrochastic opening and closing (Fig. 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 Desert 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 involucre. In the field, most of the involucre 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. (Capparaceae) 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” containing one seed each (Fig. 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, p. 83). 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* Schlttdl. var. *crassipes* (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 capsular sutures is accelerated by moisture, a trait known as

hygrochastic dehiscence (e.g., Walck and Hidayati 2007) that allows seeds to be released preferentially when the capsule is exposed to rainwater. Hygrochastic dispersal mechanisms allow for seed dispersal through the movement of plant organs or the softening of tissues when wet. These mechanisms rely on the biomechanical properties of some plant tissues, which may have compounds that allow them to soften or expand as they absorb water, triggering the release of seeds (van Oudtshoorn and van Rooyen, 1999; Hegazy et al. 2006; Pufal et al. 2010). 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. *Eremothera boothii* (Douglas) W.L. Wagner & Hoch (Onagraceae) is a winter annual 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. 3). This species has two different seed morphs coexisting within the same plant: pale brown seeds, minutely pitted in rows, and coarsely papillate dark brown seeds. 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: *Eremothera boothii* subsp. *boothii*, *E. boothii* subsp. *alyssoides* (Hook. & Arn.) W.L. Wagner & Hoch, and *E. boothii* subsp. *intermedia* (Munz) W.L. Wagner & Hoch 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: *Eremothera boothii* subsp. *condensata* (Munz) W.L. Wagner & Hoch and *E. boothii* subsp. *desertorum* (Munz) W.L. Wagner & Hoch (White and Sanders 1997; Felger 2000; Baldwin et al. 2002).

The genus *Oenothera* L. 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: *Oenothera deltoides* subsp. *deltoides* develops dry, lignified, basketlike skeletons that persist for several years bearing lignified capsules that dehisce with moisture (Felger 2000). This spring ephemeral



FIG. 2. Erect plant with sclerocarpic fruits in *Oxystylis lutea*.

grows on moving dunes and rolling sand plains in the Great Basin, Mojave, and Sonoran deserts (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 long, slender woody capsules, that may persist for several years. *Oenothera 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* L. form rosettes with tough succulent leaves, and at the

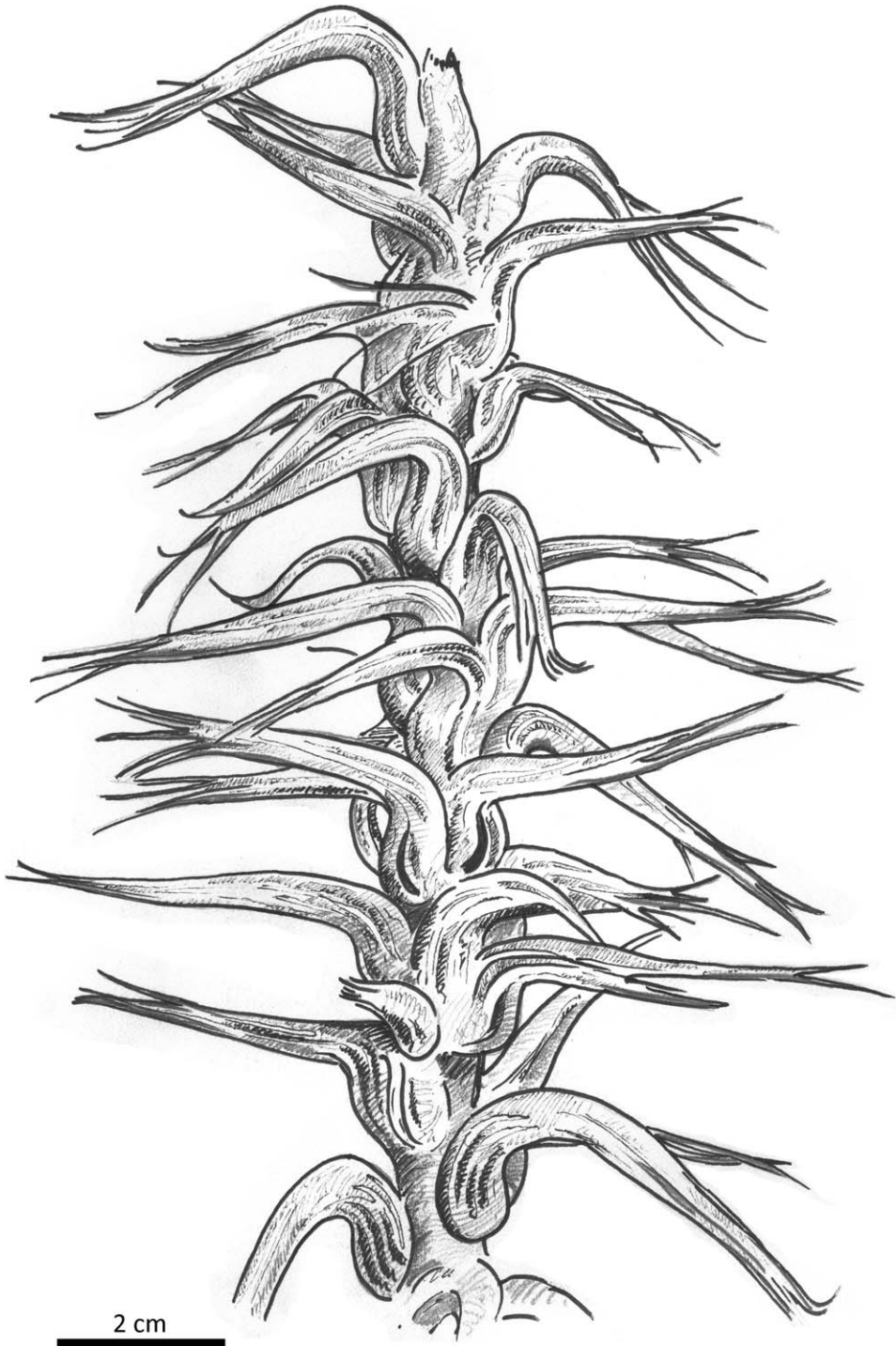


FIG. 3. Lignified stem and hygrocastic capsules of *Eremothera boothii* subsp. *boothii*.

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. *Agave 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 seeds 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. Reproductive Dimorphism (amphicarp)

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, and is also found in coastal sage scrub of southern California (Chase 1918; Felger 2000). Although amphicarpic grasses can be found in the Mojave and Sonoran deserts, reproductive dimorphism in the Poaceae also occurs frequently outside arid ecosystems (Campbell et al. 1983).

#### 5. Schizocarps with Heteromericarps (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). In our fieldwork throughout North American deserts, however, we have not observed mericarp retention in creosote bushes lasting for more than a few months.

The globemallows (*Sphaeralcea* 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 indehiscent portion of the mericarp varies among species (Baldwin et al. 2002) (Fig. 4). 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. orcuttii* 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*, which is an annual species (Baldwin et al. 2002).

Similarly, Felger (2000) describes differentially opening mericarps in the desert mallow *Horsfordia alata* (S. Watson) A. Gray (Malvaceae). The mericarps in this plant have a lower indehiscent chamber that retains seeds until they are dispersed with the entire mericarp, and a dehiscent upper chamber with one or two loose seeds that disperse when the wings of the dry mericarp split (Felger 2000). This species is distributed in rocky slopes, canyons, and arroyos in the Sonoran Desert and Baja California.

#### 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. 5) grows in the central Gulf Coast region in Baja California, México, an area of highly unpredictable rainfall patterns. It is a small,



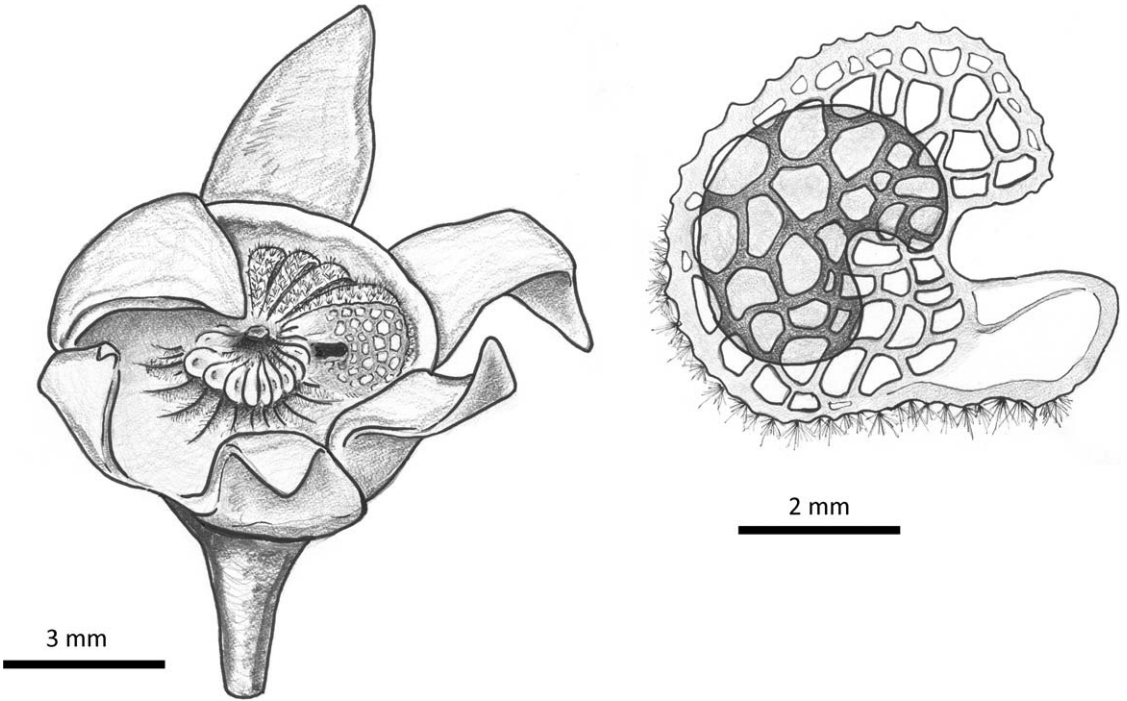


FIG. 4. Schizocarp and mericarp of *Sphaeralcea coulteri*, showing the reticulate portion holding one persistent seed.

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 involucre, which “serve the function of armature” (Payne 1962).

In a remarkable case of evolutionary convergence, the Sonoran Desert crucifixion thorns, two 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 one-seeded 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 five 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.

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, whose berries often persist as dry fruits (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 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).

Some desert root-parasites have dry capsules that can retain seeds for a season or more. In the dunes of the Lower Colorado Valley, the desert sandfood *Pholisma sonorae* (A. Gray) Yatsk. (Boraginaceae) forms stem-pads with many circumscissile capsules that dry out gradually releasing their numerous seeds. Similarly, the inflorescences of the desert broomrape (*Oro-*



FIG. 5. Persistent lignified fruit and seed in *Ambrosia bryantii*.

*banche cooperi* [A. Gray] A. Heller; Orobanchaceae) emerge from the sandy desert plains and rapidly dry out, leaving behind a stalk with dry, two-valve capsules that gradually open from the apex slowly releasing their numerous small seeds.

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). *Ferocactus* Britton & Rose species in the Sonoran Desert often retain fruits. Some chollas, such as *Cylindropuntia cholla* (F. A. C. Weber) F. M. Knuth distributed in Baja California and *Cylindropuntia fulgida* (Engelm.) F. M. Knuth form chained fruits and the ones from previous years retain viable seeds.

Serotiny is also common in small, tuberculate cacti, mostly in the genus *Mammillaria* Haw., but also in other genera (Bravo-Hollis and Sánchez-

Mejorada 1991; Anderson 2001). These globose cacti often have two modes of seed release: (a) they 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, gradually releasing seeds into the environment, or (b) during rainy years they can extrude some of the fruits, which ripen and turn bright red offering their seed content to dispersers (Rodríguez-Ortega et al. 2006; Peters et al. 2008). Although there are no studies of fruit retention in Californian *Mammillaria* species, field observations suggest that these two modes of seed dispersal (fruit retention and gradual seed release vs. fruit extrusion and cued release) are common in some local species such as *M. dioica* K. Brandegee or *M. tetrandra* Engelm.

#### DISCUSSION

The adaptive significance of seed retention in desert plants has been discussed by Ellner and Shmida (1981) and van Oudtshoorn and van Rooyen (1999). Other, 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. 2008); (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. 2008); (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 Kabiell 2007).

Serotinous species occur in different deserts of the world (e.g., Günster 1992 for the Namib and Gutterman and Ginot 1994 for Israel) where common seed retention syndromes observed in serotinous species of the Sonoran and Mojave deserts, such as basicarpy, amphicarpy, and hydrochastic capsules, have also evolved. These 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 Oudtshoorn and van Rooyen 1999). Similarly, the lignified basket-like structures or "bird-cages" of the Onagraceae in mobile sand dunes of the Mojave and Sonoran deserts is remarkably convergent with the growth morphology of *Artemisia* L. species (Asteraceae) in desert dunes in China (Ma et al. 2010).

Moreover, there seems to be an association between the low-lying basicarp plants and winter rains, and between taller and erect plants with lignified fruits and summer rains. All of the basicarpic plants in the floras we reviewed are distributed mostly in the Mojave and northern Sonoran deserts, where rain falls predominantly during winter, while the taller seed retaining annuals occur largely in the eastern and southern Sonoran Desert outside California, where summer monsoon rains are important.

In conclusion, there is a striking convergence of dispersal syndromes in distant deserts that are, to a large extent, taxonomically unrelated (e.g., Ellner and Shmida 1981 and van Oudtshoorn and van Rooyen 1999). In the same way as the pulses of wildfires have selected seed-retaining plants in fire-driven ecosystems, the unpredictable pulses of water abundance against a background of extreme water scarcity seem to have played an important role in the evolution of serotinous desert plants. Retaining seeds well protected within the lignified maternal tissues, to release

them later in synchrony with rainfall pulses, can be highly advantageous for plants depending on rare and erratic pulses of water for their survival.

#### ACKNOWLEDGMENTS

We thank Mitch Province for the illustrations for this publication. Sula Vanderplank, Benjamin Wilder, and Richard Felger helped us revise the list of serotinous species. This article is based on the first chapter of the first author's dissertation.

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APPENDIX 1

SEROTINOUS SPECIES IN THE MOJAVE AND SONORAN DESERTS OF CALIFORNIA CLASSIFIED ACCORDING TO THEIR DISPERSAL SYNDROME. Information on the family and life-cycle of each species is also provided. Because of the lack of data on seed-retention times, species were classified into strongly and weakly serotinous according to the toughness and lignification of seed-retaining structures. \* In the case of *E. boothii* the two subspecies that display highly lignified capsules are *E. boothii* subsp. *condensata* and *E. boothii* subsp. *desertorum*.

Syndrome	Family	Taxon	Life cycle
Strongly serotinous species	basicarpy	<i>Chorizanthe rigida</i>	winter ephemeral
		<i>Chorizanthe spinosa</i>	winter ephemeral
	lignified fruits	<i>Tetrapteron palmeri</i>	winter ephemeral
		<i>Amaranthus crassipes</i>	summer ephemeral
	hygrochasy	<i>Oxystylis lutea</i>	summer ephemeral
		<i>Eremothera boothii</i> *	winter ephemeral
		<i>Oenothera deltoides</i>	winter ephemeral
		<i>Oenothera primiveris</i>	winter ephemeral
		<i>Datura discolor</i>	summer ephemeral
	amphicarpy	<i>Agave deserti</i>	semelparous
		<i>Enneapogon desvauxii</i>	iteroparous
		<i>Muhlenbergia microsperma</i>	non-seasonal ephemeral
	heteromericarps	<i>Sphaeralcea orcuttii</i>	iteroparous
	persistent dry fruits	<i>Sphaeralcea coulteri</i>	winter ephemeral
		<i>Horsfordia alata</i>	winter ephemeral
<i>Castela emoryi</i>		iteroparous	
<i>Canotia holacantha</i>		iteroparous	
<i>Echinocactus polycephalus</i>		iteroparous	
<i>Mammillaria dioica</i>		iteroparous	
<i>Ambrosia dumosa</i>		iteroparous	
<i>Ambrosia bryantii</i>	iteroparous		
Weakly serotinous species	heteromericarps	<i>Larrea tridentata</i>	iteroparous
		<i>Sphaeralcea ambigua</i>	iteroparous
	persistent dry fruits	<i>Sphaeralcea angustifolia</i>	iteroparous
		<i>Sphaeralcea rusbyi</i>	iteroparous
		<i>Sphaeralcea emoryi</i>	iteroparous
		<i>Solanum elaeagnifolium</i>	iteroparous
		<i>Solanum hindsianum</i>	iteroparous
		<i>Borlisma sonora</i>	iteroparous
		<i>Orobanchaceae</i>	iteroparous
		<i>Orobancha cooperi</i>	iteroparous