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Does *Ferocactus wislizeni* (Cactaceae) have a between-year seed bank?

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Field and laboratory experiments at Tumamoc Hill, Tucson, Arizona, U.S.A., demonstrated that *Ferocactus wislizeni*, a common perennial cactus in the northern Sonoran Desert, has a between-year seed bank. In laboratory studies, *F. wislizeni* seeds lost dormancy during storage at room temperature and had a light requirement for germination. Field experiments suggested that as much as 2% of the annual seed crop might escape post-dispersal predation even when unprotected; where suitable safe sites exist, a higher percentage might escape. Germination of seed recovered monthly from above- and below-ground components of an artificial seed bank showed that seeds can survive at least 18 months in and on the soil. Seed banks enable *F. wislizeni* to take advantage of favorable rains and temperatures throughout the growing season, thus increasing the number of opportunities for germination. Moreover, seed banks enable *F. wislizeni* to respond hugely when the climate seems especially favorable, thus producing the large cohorts necessary to compensate for high seedling mortality.

Keywords: climate; *Ferocactus wislizeni*; seed banks; germination; seed longevity; Arizona, U.S.A.; Sonoran Desert

Introduction

In arid regions, many ephemerals have between-year seed banks as a hedge against climatic uncertainty (Venable & Lawlor, 1980; Venable, 1989), whereas most woody plants supposedly do not (Kemp, 1989). Seeds form a between-year seed bank when they persist in or on the soil for 13 months or longer (Thompson & Grime, 1979) or when they live until the second germination season after maturation (Baskin & Baskin, 1998). Several hypotheses have been offered to explain the difference in seed longevity between annuals and perennials in deserts. For one, the intermittent seed production typical of desert ephemerals would lead to extirpation or extinction if seeds could not survive long gaps between reproductive episodes, whereas the yearly seed production typical of most woody plants obviates any need for long-lived seed (Kemp, 1989). Even if a population of woody plants experiences occasional crop failure, some or most individuals will almost certainly live to reproduce again, thus plant (rather than seed) longevity serves as a buffer against extirpation or extinction.

Seeds that persist in the soil tend to possess certain physiological, morphological, and ecological characteristics. They must be able to remain viable under natural conditions for at least 13 months (Thompson & Grime, 1979; Ellis & Roberts, 1981; Baskin & Baskin, 1998). Some portion of the annual seed crop must be able to escape destruction by predators and pathogens (Ellis & Roberts, 1981; Kemp, 1989; Crist & Friese, 1993). A light requirement for germination is a common mechanism by which between-year seed banks are formed (Pons, 1992). After-ripening (loss of dormancy when stored at room temperature) is also sometimes associated with seed banks (Murdoch & Ellis, 1992). Small and compact seeds are more likely than large seeds to persist in the soil from year to year (Thompson *et al.*, 1993). Finally, some seeds that form between-year seed banks undergo annual cycles of dormancy/non-dormancy in response to particular environmental cues (Baskin & Baskin, 1985; Vleeshouwers *et al.*, 1995; Baskin & Baskin, 1998).

The purpose of this study was to determine whether *Ferocactus wislizeni* (Engelm.) Britton & Rose, a short-columnar cactus common throughout much of the northern Sonoran Desert, has a between-year seed bank. For several reasons, populations of *F. wislizeni* might be able to survive without a reserve of seeds in the soil. Because the low surface:volume ratio of mature plants is a buffer against drought (Cody, 1986), flowers and fruits are produced even in dry years (Bowers, 1998), making crop failure unlikely. Moreover, if seed set is occasionally low or none, the fecundity (30,000 seeds plant^{-1} year^{-1}) (Bowers, 1998) and longevity (maximum of 50 years) (Bowers, unpublished data) of mature plants should compensate for the loss. On the other hand, certain other traits support the idea that *F. wislizeni* has a between-year seed bank. Several *Ferocactus* species require light for germination (Rojas-Arechiga *et al.*, 1997). In addition, increased germination of *F. wislizeni* after dry storage (Zimmer, 1980) suggests after-ripening.

To determine whether *F. wislizeni* seeds persist in the soil for 13 months or longer, the following questions were investigated in field and laboratory studies: (1) Do the seeds have a light requirement for germination? (2) Do they undergo after-ripening? (3) Are they physically suited for persistence in the soil? (4) Does a proportion of the seed crop survive post-dispersal predation? (5) Under natural conditions, do seeds remain viable for 13 months or longer? (6) Is there any evidence of cyclical germination in response to environmental cues? A positive answer to these questions would strongly suggest that *F. wislizeni* has a between-year seed bank.

Methods

Study area

Tumamoc Hill (32°13′N, 111°05′W), an outlier of the Tucson Mountains, Pima County, Arizona, U.S.A., has a maximum elevation of 948 m above sea level and a basal elevation of 703 m. The rocky, basaltic-andesitic slopes are dominated by *Cercidium microphyllum* (Torr.) Rose & I. M. Johnston, *Carnegiea gigantea* (Engelm.) Britton & Rose, *Ambrosia deltoidea* (A. Gray) Payne, and other woody plants characteristic of the northern Sonoran Desert. The study site, situated on a gently sloping bench with a north-east aspect, was at 814 m on Tumamoc Hill. Between 1978 and 1988, average maximum and minimum temperatures in January, the coldest month, were 19·9°C and 7·9°C. In June, the hottest month, they were 39·8°C and 24·5°C. Rainfall averages 300 mm/year, and almost half of this falls during July, August, and September; most of the remainder comes between November and March.

Seed collection

Seeds for the following experiments were extracted from ripe fruits, air dried, then stored in envelopes at room temperature. Fruits were collected when ripe, generally in October or November, in several different years from eight to ten plants. Unless otherwise noted, all seeds used in any single experiment were harvested at the same time.

Seed morphology

To assess whether *F. wislizeni* seeds are physically suited for persistence in the soil, mean seed variance, an index of seed size and compactness (Thompson *et al.*, 1993), and mean seed weight were determined. Length, width, and depth of 10 randomly selected seeds were measured to the nearest 0·1 mm. The dimensions were transformed by treating length as unity; the transformed values were then used to calculate a variance for each seed (Thompson *et al.*, 1993). Mean seed weight was determined from 500 randomly selected seeds weighed collectively to the nearest 0·1 g. According to Thompson *et al.* (1993), seeds that can persist in the soil for at least 5 years have a mean weight <4·0 mg and mean variance < 0·15.

Germination experiments with stored seeds

To test for a light requirement for germination, four replicates of 15 seeds each were placed on moist paper toweling in covered petri dishes at average daily maximum/minimum room temperatures of 24·5°C/22·2°C. Half the replicates were wrapped in aluminum foil, and the rest were exposed to natural daylight. The number of seedlings was recorded daily, and then the seedlings were discarded. Seeds were 6-months-old at the time of the experiment.

Two experiments assessed after-ripening. In the first, 25-month-old seeds and 1-month-old seeds were germinated in natural daylight at average daily maximum/minimum room temperatures of 27·8°C/25·6°C. For each age group, there were four replicates of 20 seeds. In the second experiment, 3-month-old and 15-month-old seeds were germinated in natural daylight at average daily maximum/minimum room temperatures of 24·6°C/20·0°C. Linear regression was used to model the relation between age and percentage germination.

Establishing an artificial seed bank

To determine seed viability under natural conditions, an artificial seed bank was created by sewing seeds into packets made of fine nylon mesh. The packets were about 8 cm by 7 cm, and each contained 100 3-month-old seeds. On February 20, 1996, the seed packets were placed outdoors, half above ground, half below ground. There were two replicates of each treatment. For each below-ground replicate, a shallow trench about 7 cm deep, 60 cm long, and 12 cm wide was dug under the drip-line of a *Cercidium microphyllum* tree, and 18 packets were placed in a single layer on the bottom of the trench. The trench was filled with soil and marked with flagging tape. For each above-ground replicate, 18 packets were placed in a single layer on the soil surface, again under the drip-line of *C. microphyllum*, and protected from animals with cylindrical covered cages made from narrow-mesh hardware cloth. Every month from March 1996 to August 1997, a packet was removed from each treatment and replicate. The recovered seeds were stored in their packets at room temperature in labeled envelopes. One packet from the above-ground seed bank and two packets from the below-ground seed bank were not found; apparently they were overlooked or carried away by animals.

Germination of seeds from the artificial seed bank

Germination of recovered seeds was tested on a laboratory bench, where the temperature could not be precisely controlled. To obtain a uniform germination temperature, seeds were tested in a single batch at the end of the 18-month period (August 1997) rather than month by month at the time of recovery. To check results from the first germination trial, a second trial was made in December 1997. For each germination trial, 40 seeds from every recovered packet were placed on moist paper toweling in two covered petri dishes. In the first germination trial, seeds were kept at room temperature (average daily maximum/minimum temperatures = 29·9°C/26·4°C) in natural daylight; because room temperatures at the time of the second trial were considerably cooler, seeds were given bottom heat (average daily maximum/minimum temperatures = 27·1°C/22·3°C), again with natural daylight. The experiments ended when there had been no new seedlings for two consecutive days. Altogether, each experiment comprised 69 petri dishes (two seed-bank components × 18 months × two replicates minus the three unrecovered packets). The number of seedlings was recorded daily, and seedlings were then discarded.

Statistical analysis of seed bank germination trials

Multi-factorial analysis of variance (ANOVA) was used to examine the effects of seed-bank component (above or below ground), climate at the time of recovery (warm or cool season), and germination trial (August or December 1997) on mean monthly percentage germination (square-root transformation). The warm season was defined as April through September, the cool season as October through March.

Post-dispersal seed predation

Predation by granivores, especially ants and rodents, strongly influences seed density and distribution in the Sonoran Desert (Davidson, 1977; Mares & Rosenzweig, 1978; Reichman, 1979; M'Closkey, 1980). According to Kemp (1989), rodent predation is so high that seeds of perennial plants seldom persist from year to year. Post-dispersal predation of *F. wislizeni* seeds over the long term and the short term was assessed by monitoring the disappearance of seeds from depots. For the sake of simplicity, it was assumed that animals ate any seeds they took.

For the long-term study, two seed depots were placed under each of 12 *Cercidium microphyllum* trees on October 30, 1994. The depots, which were steel cans 8·5 cm in diameter and 4 cm in height, were filled nearly to the rim with soil, then 100 seeds were scattered on the surface of each and lightly tamped down. Depots were placed in shallow holes such that the rim of the can was flush with the soil surface. Every month for 1 year, two depots were selected at random and removed from the study site. The contents were sifted through 1·0-mm soil screens to retrieve any remaining seeds. An ANOVA was used to determine the effect of time (in months) on number of seeds remaining.

For the short-term study, 10 depots were placed about 30 cm apart in a five-by-two array among low subshrubs. One hundred *F. wislizeni* seeds were scattered on the soil surface in each depot. Two randomly selected depots were removed every day for 5 days, their contents sieved, and any remaining seeds counted. The effect of time (in days) on number of seeds remaining was examined using an ANOVA.

A third study of seed removal was undertaken to determine whether seed survival varies with type of substrate, used here as a proxy for degree of exposure to potential predators. Fifteen depots, which were shallow aluminum foil pans 25 cm in diameter, were placed in a five-by-three array among low subshrubs and filled with damp sand. One of three treatments was randomly assigned to each depot: sand surface left bare (high seed exposure), sand surface 100% covered with gravel (moderate seed exposure), and sand surface about 95% covered with rocks (low seed exposure). One hundred seeds were scattered over the treated surface in each depot. There were five replications of each treatment. The number of seeds remaining was determined after 5 days. The effect of substrate on number of seeds remaining at the end of the experiment was examined using an ANOVA.

Results

Seed morphology

On average, *F. wislizeni* seeds weighed 3·0 mg. Mean length, width, and depth were, respectively, 2·6 mm (S.E. = 0·06), 1·7 mm (S.E. = 0·08), and 1·1 mm (S.E. = 0·06), yielding a mean seed variance of 0·08. Mean seed variance and weight were within the range of values reported for seeds that can persist for at least 5 years.

Germination experiments with stored seeds

Seeds of *F. wislizeni* require light for germination. There was no germination in the dark treatment, whereas germination of seeds exposed to light was 70% (S.E. = 16·70). Fifty per cent germination was reached on the 14th day.

Germination increased linearly with seed age ($R^2 = 0{\cdot}99$, $p < 0{\cdot}005$). One-month-old seeds did not germinate. Mean germination of seeds aged 3, 15, and 25 months was, respectively, 10·0% (S.E. = 2·04), 28·8% (S.E. = 2·39), and 51·3% (S.E. = 2·18). It appears that *F. wislizeni* seeds have an afterripening requirement and that freshly dispersed seeds are dormant.

Germination of seeds recovered from the artificial seed bank

In the multi-factorial analysis of seed-bank germination, the only main effect was trial ($F = 28{\cdot}86$, $p < 0{\cdot}005$) (Table 1). Mean percentage germination across all 18 months was 45·2% (S.E. = 2·90) in the second trial, and 26·0% (S.E. = 2·28) in the first. Unfortunately, the experimental variables of storage time (95 days longer in the second trial) and average daily germination temperature (4·2°C lower in the second trial) were confounded, thus higher germination in the second trial could have been a function of storage time, germination temperature, or both.

There was also a season × component interaction ($F = 4{\cdot}69$, $p < 0{\cdot}05$) (Table 1). Within the above-ground component, mean percentage germination across all 18

Table 1. *Effect of seed-bank component, season at the time of recovery, and germination trial on mean monthly percentage germination of* Ferocactus wislizeni: *results of multi-factorial ANOVA. Seeds from above-ground and below-ground components of an artificial seed bank were recovered monthly from March 1996 to August 1997 and germinated in two trials (August 1997 and December 1997). Season, a surrogate for climate at the time of recovery, was used to group warm months (April to September) and cool months (October to March)*

Source	SS	df.	F	p
Component	60·659	1	16·24	<0·005
Season	30·572	1	8·18	<0·01
Trial	107·797	1	28·86	<0·005
Component × season	17·531	1	4·69	<0·05

months was higher for seeds recovered in the warm than in the cool season (warm season = 50·1%, S.E. = 3·34; cool season = 31·7%, S.E. = 4·06). It appears that germination of seeds on the soil surface was influenced by seasonal climate at the time of recovery. Within the below-ground component, however, there was virtually no difference between seasons (warm season = 27·6%, S.E. = 3·43; cool season = 27·3%, S.E. = 3·95).

Despite the confounding of storage time and germination temperature, it is clear that monthly peaks and troughs in germination followed the same general pattern in both trials (Fig. 1(a, b)). These cycles of relatively high and low germination appeared to be roughly correlated with monthly temperature (Fig. 1(c)), especially in the above-ground seed bank, but in the absence of soil-temperature data knowledge of precise climatic effects on seeds in the seed bank must await further study.

Post-dispersal seed predation

In the short-term seed-removal experiment, the mean number of seeds dropped rapidly in the first 3 days (93·5, 51·0, 6·5), then leveled off in the last 2 days (1·5, 3·5). In the long-term experiment, there was no statistically significant difference among months in the number of seeds left ($F = 1{\cdot}41$, $p > 0{\cdot}30$). An average of 1% of seeds remained per month, showing that predators do not necessarily remove all exposed seeds, even when given ample time to do so. Type of substrate, that is, degree of exposure to predators, strongly influenced the proportion of seeds removed (and presumably consumed) over 5 days. Average seed survival was 30·2% (S.E. = 2·35) for rock-covered surfaces (low exposure of seeds), 4·0% (S.E. = 1·00) for gravel-covered surfaces (moderate exposure of seeds), and only 0·4% (S.E. = 0·24) for bare sand surfaces (high exposure of seeds). The differences were highly significant ($F = 132{\cdot}95$, $p < 0{\cdot}001$). It appears that seeds can escape predation if they are adequately hidden.

Discussion

The results indicate that *F. wislizeni* seeds can persist in the soil for at least 18 months, and, if not consumed by predators, can form a between-year seed bank. Considerable evidence supports this conclusion. The seeds are small and compact, therefore readily buried, a common trait of seeds that can persist a year or more in the soil (Thompson & Grime, 1979; Thompson *et al.*, 1993). In addition, the seeds require light for germination, another trait often associated with between-year seed banks (Pons, 1992). Germination of stored *F. wislizeni* increased from none for one-month-old seeds to 51·3% for 25-month-old seeds; the increase suggests that seeds are dormant upon dispersal and after-ripen during dry storage, conditions that are often associated with seed banks (Baskin & Baskin, 1989; Murdoch & Ellis, 1992). Zimmer (1980) also found that germination of *F. wislizeni* increased during storage. In this study, daily maximum and minimum germination temperatures were within the range of tolerance (17 to 36°C) (Zimmer, 1980), and the daily average was generally close to the optimum (25°C) (Zimmer, 1980). Even under these favorable conditions, germination of stored and recovered seed was often < 50%; this is of interest because less-than-total germination suggests that a fraction of seeds can persist in the soil (Baskin & Baskin, 1989; Venable, 1989).

Having a particular set of germination traits does not guarantee formation of a seed bank, however, especially in the Sonoran Desert, where levels of post-disperal seed predation are high (Davidson, 1977; Mares & Rosenzweig, 1978; Reichman, 1979; M'Closkey, 1980; Kemp, 1989). In this study, seeds were most likely to escape

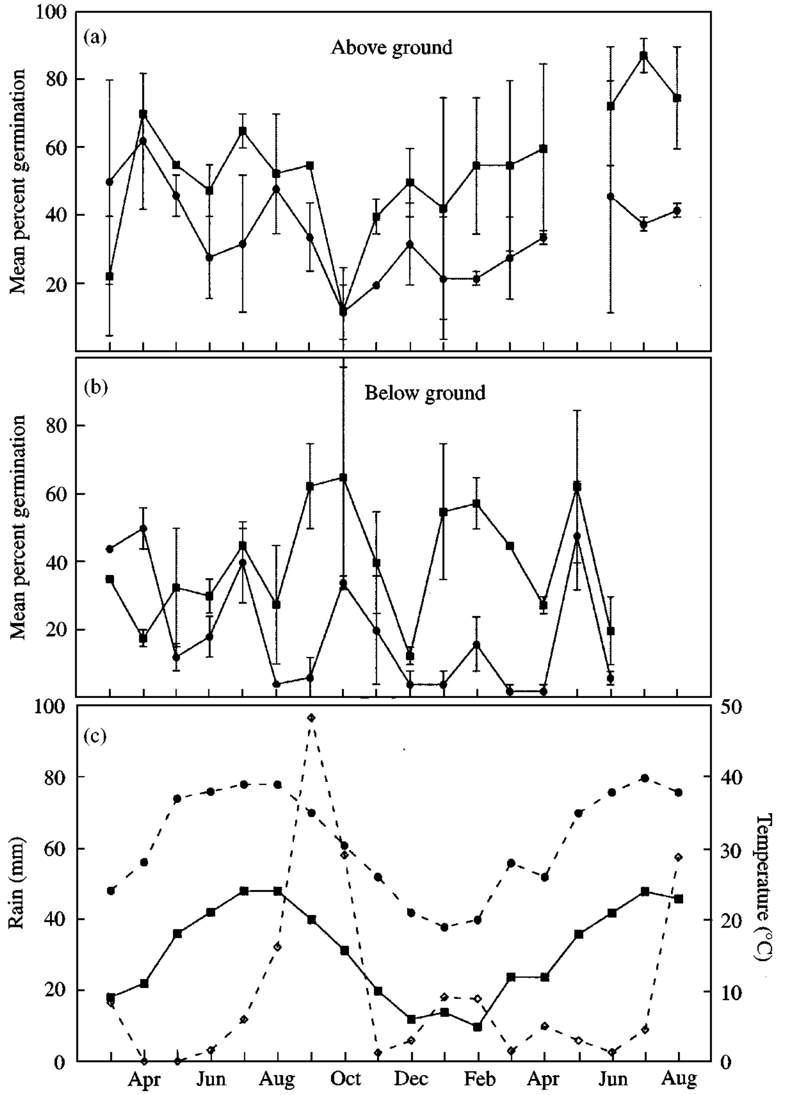

Figure 1. (a) Mean percentage germination of *Ferocactus wislizeni* seeds recovered monthly from the above-ground component of an artificial seed bank and germinated in August 1997 (●) or December 1977 (■). Missing points represent replicates that could not be recovered. (b) Mean percentage germination of *Ferocactus wislizeni* seeds recovered monthly from the below-ground component of an artificial seed bank and germinated in August 1997 (●) or December 1977 (■). Missing points represent replicates that could not be recovered. (c) Average daily maximum and minimum temperatures in the month before recovery (●, ■) and total rain in the week before recovery (-----).

predation when hidden among rocks. In a natural setting, removal of a ripe fruit from a plant makes a hole in the base of the fruit through which seeds readily spill. Those that spill among rocks are presumably better hidden than those that fall on open ground. As this study shows, even exposed seeds might not be entirely removed by predators, possibly because density becomes too low to recompense foraging effort (Reichman, 1979). Exactly what proportion of the *F. wislizeni* seed crop is not consumed by granivores is difficult to calculate precisely; a conservative estimate is that up to 2% of seeds remain in or on the soil each year.

Several mechanisms allow *F. wislizeni* seeds to accumulate in the soil from year to year. Their compactness allows seeds to become easily hidden and thus escape the attention of predators. The light requirement ensures that buried seeds will not germinate. The relatively long time for 50% germination (about 14 days) keeps them from responding to rains that are too light to sustain seedling growth. In addition, climate apparently affects the proportion of seeds that germinate (Fig. 1, Table 1), producing germination cycles that seem akin to predictive germination, defined as 'modification of the … fraction of seeds germinating in response to environmental cues' (Venable, 1989: 73). By promoting germination when the likelihood of seedling survival is good and reducing it when the prospects are poor, predictive germination allows seeds to accumulate in the soil.

Seeds given adequate light, moisture, and heat fail to germinate for reasons other than dormancy, including loss of viability as a result of aging (Ellis & Roberts, 1981) and attack by soil-borne pathogens (Crist & Friese, 1993). Soil-borne pathogens were probably responsible for little if any loss in viability of *F. wislizeni* seed on the soil surface; after 17 months in the above ground seed bank, seed germinated extremely well (87·5%). Buried seeds might have been infected, however; by June of the second year, germination had fallen to 20%. Seed wastage can also occur when buried seeds germinate too deeply for seedlings to emerge. Because *F. wislizeni* requires light for germination, no seeds below ground were expected to germinate while in the seed bank, and none did. No seeds germinated in situ above ground either, perhaps because the largest single rain during the study, 26·2 mm, was too small to serve as a trigger.

Circumstantial evidence suggests that *F. wislizeni* seeds do indeed survive in the soil for a year or longer. From 1987 to 1993, a permanent plot (Area A) on Tumamoc Hill was repeatedly surveyed for seedlings of perennial plants (Raymond M. Turner, unpublished data). Seven *F. wislizeni* seedlings found on October 17, 1987, had probably germinated in response to rains totaling 84·3 mm on September 4 to 6, 1987. Because *F. wislizeni* fruits are seldom ripe by early September, the seedlings were almost certainly not from the 1987 seed crop but had been in or on the soil for at least 13 months.

The usefulness of a between-year seed bank for woody plants has not been extensively discussed in ecological literature, probably because the assumption is that most long-lived perennials do not need one. For several reasons, however, woody plants in general and *F. wislizeni* in particular might benefit from between-year seed banks. First, seed banks can be powerful buffers against seed predation (Crawley, 1992). Moreover, in a region where climate is highly variable within and between years, a reserve of non-dormant seed should enable *F. wislizeni* to respond whenever favorable conditions prevail, thus maximizing opportunities for germination. Finally, predictive germination should enable a high proportion of the seed bank to respond when the climate seems especially favorable for establishment, thus producing the large cohorts necessary to compensate for the high seedling mortality characteristic of woody desert plants.

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