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Characterizing soil seed banks and relationships to plant communities

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Abstract Estimates of soil seed banks are important to many ecological investigations and plant conservation, yet seed banks are among the most difficult plant community attributes to accurately quantify. To compare extraction and emergence seed bank characterization methods, we collected 0- to 5-cm soil seed bank samples and measured plant community composition in six microsite types (below different perennial plant species and interspaces) at 10 field sites in the Mojave Desert, USA. Extraction detected five times more species sample^{-1} and orders of magnitude greater seed density than emergence, though evaluating viability of extracted seed was not straightforward. Only 13 % of 847 tested seeds from extraction emerged in follow-up assays. Considering all sites, species detection was more similar between methods: 21 taxa for emergence and 28 for extraction. Results suggest that: (i) capturing microsite variation is critical for efficiently estimating site-level desert seed banks; (ii) method comparisons hinged on the scale of analysis for species richness, as differences in species detection between methods diminished when increasing resolution from the sample to the regional scale; (iii) combining data from all seed bank methods provided the strongest correlation with vegetation; and (iv) improving knowledge of seed germinability is important for advancing both seed bank methods, including for extraction to evaluate the proportion of extracted seeds that are viable. Multifactor approaches that balance several effectiveness measures (e.g., both seed density and species detection at multiple scales) and procedural challenges are most likely to accurately represent complexity in tradeoffs for choosing methods to quantify soil seed banks.

Keywords Comparison · Emergence · Extraction · Gypsum · Method · Mojave Desert

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Introduction

Soil seed banks have been part of theories in plant ecology regarding species evolution, traits, and succession since Darwin (1859) noted the presence of seeds stored in soil of pond ecosystems and the

potential of these seeds to facilitate plant recruitment. Today, assessments of seed banks have key relationships with understanding ecological processes and many cornerstone topics of major interest in plant ecology and biological conservation. For example, seed banks are related to propagule pressure and invasiveness in invasion biology (Robertson and Hickman 2012), plant establishment in community assembly and ecological restoration (Richardson et al. 2012), and genetic storage in adaptation to global change (Damschen et al. 2012). Reliable estimates of seed banks have direct practical importance when they are used for such purposes as to evaluate plant regeneration potential, resources available to seed-eating organisms, site history (e.g., evidence of past disturbance), which species in the vegetation form seed banks (van der Valk and Pederson 1989; Bakker et al. 1996; Espeland et al. 2010), and conservation applications such as managing rare species that rely on seed banks or for detecting exotic plant species (Schneider and Allen 2012). Seed banks are clearly important to understanding a plant community, yet are difficult to quantify. An ideal seed bank characterization method would detect all species and accurately estimate viable seed density (only viable seeds are considered part of the living seed bank), while being as easy as possible to implement. Because this ideal has not been attained, comparisons of seed bank methods constitute an active area of plant ecology research (e.g. Ishikawa-Goto and Tsuyuzaki 2004; Bernhardt et al. 2008; Price et al. 2010).

The two main categories of methods for characterizing seeds in soil samples are emergence and extraction (Thompson et al. 1997; Baskin and Baskin 1998). Both have advantages and disadvantages. In the emergence method, soil samples are placed in pots or flats in greenhouses or similar environments. Seedlings emerging from the soil are identified and counted as an estimate of seeds in the seed bank. The advantages of the method are that all seeds detected are known to be viable, a laborious separation of seed from soil is not required, it is generally easier to taxonomically identify plants than seeds, and non-detection bias due to seed size, shape, or color that can occur during extraction is avoided (Roberts 1981). Disadvantages are that not all seeds will germinate under greenhouse conditions, samples must be maintained for multiple months to allow as many seeds as possible to emerge, and greenhouse space and resources (e.g., water) are required to maintain samples. In the extraction method, seeds are separated from soil and other particles by flotation or other techniques, then isolated and identified (Roberts 1981). The principal advantages of the method are that results can be available more quickly than for the emergence method because time for emergence is not necessarily required and seeds varying in germination requirements can be detected (Warr et al. 1993). The major disadvantages are that extraction and seed identification are considered labor-intensive, detectability of seeds is not uniform across species (e.g., detecting small-seeded species is difficult), identifying seeds to species can be challenging (especially for 'weathered' seed), and determining viability of seeds is not always straightforward.

Seed bank estimates obtained by the two methods can sharply differ (Forcella 1992; Ishikawa-Goto and Tsuyuzaki 2004; Bernhardt et al. 2008), and method comparison studies have yielded conflicting results regarding their relative performance. For example, it is often assumed that extraction detects more seeds than emergence, but some studies have found that seed densities and species richness estimated by emergence are similar to or even significantly greater than those estimated by extraction (Gross 1990; Cardina and Sparrow 1996; Price et al. 2010). There is also a need for studies that calibrate the methods against each other to help make studies using different methods more comparable. For instance, species richness estimates between the methods could be correlated (such that richness derived from one method could be estimated for the other method), and suitability of each method for particular species could be identified to understand which species go undetected.

The performance of seed bank characterization methods is poorly known in deserts, a particularly important knowledge gap given that many desert plants rely on seed banks to survive unfavorable conditions and reestablish populations during favorable times in the extreme desert environment (Pake and Venable 1996). In the past, seed bank studies in the Mojave and Sonoran Deserts of the North American Southwest employed only the extraction method (e.g. Nelson and Chew 1977; Pake and Venable 1996; Guo et al. 1998). More recent work embraced the emergence method (Abella et al. 2009; DeFalco et al. 2009; Esque et al. 2010; Schneider and Allen 2012), but there has been no comparison of the two methods in this habitat. The method comparison may be further

complicated in deserts by especially high spatial variation of seed banks within sites (e.g., below perennial plants versus interspaces between plants; Nelson and Chew 1977; Reichman 1984). The objectives of this study were to compare the extraction method with two variations of the emergence method for characterizing seed banks across perennial plant microsites and sites, identify which method best detected rare species of conservation priority, relate the emergence and extraction methods to each other, and evaluate how closely each of the methods corresponded to aboveground vegetation. We conducted the study within a desert landscape of conservation significance containing rare native plant species, where estimates of seed bank composition are desired to help understand regeneration strategies of native species and the presence of exotic species that could threaten indigenous ecosystems.

Methods

Study area

We sampled 10 sites in the eastern Mojave Desert in Lake Mead National Recreation Area and adjacent Bureau of Land Management lands in southern Nevada, southwestern USA (Table 1). We selected these sites because they are long-term sites maintained by the National Park Service for monitoring rare plant habitat and spanned an extent of 59 km with a mean (±SD) distance between sites of 21 ± 17 km. Located at an elevation of 768 m, the Boulder City, Nevada, weather station has recorded the following averages: daily high July temperature of 39 °C, daily low January temperature of 4 °C, and 14 cm year^{-1} of precipitation (1931–2004 records; Western Regional Climate Center, Reno, NV, USA). On average, 73 % of annual precipitation is received during the September through April growing season for winter annual plants, with peak blooms typically occurring in March–May depending on adequate timing and amounts of rainfall beginning the previous September (Beatley 1974). Elevations of sample sites ranged from 383 to 634 m, and topography was flat to undulating with slope gradients <10 %. Soils were on or associated with gypsum parent material and were classified as Petrogypsids, Haplocalcids, Haplogypsids, and Calciargids (Lato 2006). Physiognomy was typical of Mojave Desert communities: scattered perennial plants separated by interspaces containing mostly bare soil or annual plants in moist years (Meyer 1986). Annual plants overall were most abundant in "fertile island" microsites below canopies of perennial plants (Meyer 1986). Two rare perennial species (*Arctomecon californica* and *Anulocaulis leiosolenus*), protected under a regional conservation plan, occupied some sites (Table 1). As a short-lived (<10 years) herbaceous species, *Arctomecon* is considered reliant on soil seed banks to maintain populations (Megill et al. 2011).

Seed bank sampling

We conducted sampling in March 2007 to quantify the persistent seed bank (Baskin and Baskin 1998). This was a dry year, with only 49 % of average precipitation for September through March prior to sampling (Las Vegas, NV weather station, 1937–2010 records; Western Regional Climate Center, Reno, NV, USA). As a result, there had been little to no plant emergence at the study sites, which also helped to isolate the persistent seed bank. Within an area of 1 ha centered at each site, we established a 50-m transect. Along transects, we collected seed bank samples from three individuals each of six microsite types: below the perennials *Ambrosia dumosa*, *Anulocaulis leiosolenus*, *Arctomecon californica*, *Ephedra torreyana*, and *Psorothamnus fremontii*, and in interspaces (≥1 m from the nearest perennial plant). We sampled these microsites because they were most common among sites and this approach stratified sampling to represent below perennial and interspace microsites that can influence desert seed banks (Reichman 1984). We selected the largest perennial plants and interspaces for sampling that were within 5 m of either side of transects. We collected samples from three points equally spaced around each perennial plant halfway between the main stem and canopy drip line. In interspaces, we collected samples from three equally spaced points within an area of 1 m^2. We collected samples as cores, 7 cm in diameter, from a depth of 0–5 cm (200 cm^3), which could include litter (typically <0.5 cm thick, if present). Guo et al. (1998) reported that the 0–5 cm depth contained 97 % of seeds in Mojave Desert seed banks. We composited samples from each individual microsite and further combined these samples by microsite type at each site,

Table 1 Characteristics of study sites for seed bank sampling in the Mojave Desert, USA

	Site									
	1	2	3	4	5	6	7	8	9	10
Geography										
UTM-*x* (m)[a]	730433	731351	725083	709067	720723	732470	731489	731984	683973	722515
UTM-*y* (m)	4029759	4032711	4020333	4010099	4013458	4028535	4033178	4035767	4001684	4019182
Elevation (m)	456	424	465	546	634	383	431	425	598	544
Slope gradient (%)	3	4	6	3	0	12	2	1	0	4
Soil (0–5 cm)[b]										
Texture	SL	L	SL	SL	L	SL	SL	SL	L	L
pH (1:1 soil:water)	7.6	8	7.5	7.7	7.4	7.7	7.7	7.7	7.6	7.5
P (mg kg^{-1}, Olsen method)	9.6	4.0	<0.1	<0.1	<0.1	2.4	4.1	4.3	1.3	4.0
Total C (%)	1.3	1.5	1.6	4.1	3.9	2.7	1.0	1.2	3.5	1.7
Total N (%)	0.029	<0.01	<0.01	<0.01	0.038	<0.01	0.012	<0.01	<0.01	<0.01
Total S (%)	3.2	2.1	5.7	2.4	4.3	1.0	2.6	2.1	2.0	3.5
Plant density (ha^{-1})[c]										
Ambrosia dumosa	300	600	0	<20	<20	100	60	200	<20	0
Anulocaulis leiosolenus	0	0	500	0	300	<20	0	0	200	100
Arctomecon californica	100	100	<20	300	900	<20	100	500	300	200
Ephedra torreyana	20	25	100	200	100	100	200	300	100	25
Psorothamnus fremontii	500	100	600	0	200	600	400	500	200	200

SL sandy loam, *L* loam

[a] Universal Transverse Mercator, North American Datum, Zone 11

[b] Sampling was conducted in interspaces between perennial plants

[c] Perennial species below which soil seed bank samples were collected

for a sample volume of 1,800 cm^3. Thus, there were 6 total composite samples (one for each microsite type) that were analyzed at each of the 10 sites and served as the units for analysis in the seed bank assay and statistical analyses.

Seed bank assay

We assayed the seed bank using three different procedures. For emergence method 1, within one week of sample collection, we placed 360 cm^3 of seed bank soil in a 2-cm thick layer on top of potting soil (Black Gold cactus mix, Sun Gro Horticulture Distribution, Inc., Bellevue, WA, USA) in a 4-L, 15-cm diameter pot for each microsite type at each site. We randomly arranged pots on a bench in an unheated greenhouse with natural lighting. Samples received 1.5 cm of water day^{-1} from an automated misting system. Over 9 months, we checked samples at least every 2 days and counted and pulled identified seedlings every 2 weeks.

For emergence method 2, we placed 360 cm^3 of soil from each microsite in a nylon mesh bag and stored the samples outdoors within a fenced greenhouse complex. Samples were stored on a wooden shelf raised 10 cm above the ground and covered with a 1-m^2 wooden roof so the samples were not exposed to rainfall. After storing the samples for 12 months, we established them in the greenhouse using the same methods as for emergence method 1.

In separate samples, seeds were extracted from soil (360 cm^3 $sample^{-1}$) using a water flotation technique (e.g. Gross 1990; Pake and Venable 1996; Bernhardt et al. 2008) combined with sieving samples through progressively finer sieves (Thompson et al. 1997). Each soil sample was placed in a beaker, water was added, and the suspension filtered through stainless steel sieves with the smallest having openings 0.18 mm in diameter. After the suspension air dried, seeds were visually separated from other material under microscopes with $\geq 10\times$ magnification. We identified extracted seeds to the finest taxonomic level possible (species for 76 % of 41 taxa, genus for 20 %, and family or higher for 4 %) using Baldwin et al. (2002), comparing to local seed collections (e.g. Lake Mead National Recreation Area plant nursery, Boulder City, NV, USA) or seeds on plants at study sites, or germinating seeds and identifying seedlings. We weighed and photographed extracted seeds (Online Resource 1). We sought to estimate viability using procedures of previous seed bank studies in deserts (Pake and Venable 1996), and other ecosystems (Price et al. 2010), by visually examining or poking seeds and recording them as viable if an embryo was fleshy and intact. Not all seeds are amenable to tetrazolium testing for viability because of their small size, dormancy stage, or other factors (Pake and Venable 1996), so instead, we further assessed germinability by sowing seeds in pots established in the same manner as for emergence methods. Because of uncertainty in the viability and germinability assay detailed in the results section, we report seed density and species richness based on the total extracted seeds without consideration to viability.

Vegetation sampling

To elucidate how closely seed bank composition correlated with vegetation present during the growing season following seed bank sampling, we measured vascular plant species in May 2008 at each microsite where seed bank samples were collected. This was considered an average year for annual plants, with >68 % of average September through April precipitation (Las Vegas, NV weather station; Western Regional Climate Center, Reno, NV, USA). Sampling was conducted using a 1 × 1 m quadrat centered on the perennial plant or interspace for each microsite. Using Peet et al. (1998) cover classes, we visually categorized areal cover of each plant species (including of the focal perennial plant in perennial microsites) rooted in each quadrat. Nomenclature follows NRCS (2013).

Data analysis

Seed density, species composition, and species richness 360 cm^3 $sample^{-1}$ were analyzed in a linear mixed model as a partially hierarchical design containing the fixed effects of microsite (tested over the interaction between microsite and site), method (tested over the residual), and the interaction between microsite and method (tested over the residual term). Random effects included site, soil sample, and their two-way interactions with microsite and method. Seed density (due to highly non-normal residuals) and species composition (based on relative seed density, calculated as $species_i$/sum all species) were analyzed using permutational multivariate analysis of variance in DISTLM software (Anderson 2001). The distance matrix was based on the Sørensen index and p values

and post-hoc contrasts were determined from 999 permutations by soil sample for the microsite effect and soil sample by method for the method effect. Species richness was Poisson distributed and was analyzed using a general linear model (GLM) assuming a Poisson distribution with PROC GLIMMIX in SAS version 9.2 (SAS Institute 2009).

To compare site-level seed bank species richness (based on the total species detected across microsites within a site) among methods, we used a GLM with Poisson error and one fixed effect (method, tested over the residual) and one random effect (site). Post-hoc permutation tests were conducted for significant terms. We related seed density and species richness at microsite and site scales between seed bank methods using Pearson correlation. We graphically displayed species composition (relative seed density) among methods with non-metric multidimensional scaling ordination using PC-ORD's "slow and thorough" autopilot setting and Sørensen distance (McCune and Mefford 1999).

We related seed bank and vegetation species richness at the microsite and site scales using Pearson correlation. To evaluate congruence in species composition between seed bank methods (and all methods combined) and vegetation at microsite and site scales, we used Mantel tests (Mantel 1967), with 999 permutations, on species presence/absence matrices converted to Jaccard distances. We derived the combined estimates (both emergence techniques, and both emergence techniques + extraction) by summing seeds across methods for each species and expressing density as seeds m^{-2} using the total volume of soil sample analyzed by the methods. We ran the Mantel tests with the "vegan" package in R (version 2.8.1, R Foundation for Statistical Computing, Vienna, Austria).

Results

Seed density

Overall, extraction detected orders of magnitude greater seed densities than either emergence method and most of the differences between methods were statistically significant across microsites (Table 2; Fig. 1). Microsite also affected seed density estimates and interacted with method. None of the microsites differed from each other within the extraction method, but some microsites statistically differed from each other for the emergence methods (Fig. 1). *Ambrosia dumosa* microsites contained significantly greater seed densities than *Anulocaulis leiosolenus* microsites in emergence method 1, and in emergence method 2, *Ambrosia dumosa* and *Ephedra torreyana* microsites had significantly more seeds than open microsites. In relating methods to each other, the emergence methods were more strongly correlated to each other than they were to extraction (Table 3).

Species richness

There were also significant differences among methods in estimating seed bank species richness $sample^{-1}$, and these patterns were consistent across microsites (Table 2). At the site scale with all microsites combined, method significantly affected estimated richness $site^{-1}$ ($F_{2,\ 18} = 25.8$, $p < 0.001$). The same pattern of multiple comparisons occurred at both the sample and the site scales: richness did not differ between emergence methods and extraction detected more species than either emergence method (Fig. 2). A total of 41 taxa were detected in all seed bank samples, with detection ranging from 13 taxa in

Table 2 Statistical results for the influences of microsite (five perennial plant species and interspaces), seed bank characterization method (two types of emergence and extraction), and their interaction on characteristics of soil seed bank samples of the Mojave Desert, USA

	Species richness			Density			Species composition		
Effect	*df*[a]	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Microsite	5,47	3.3	0.013	5,10	1.9	0.060	5,45	1.8	0.006
Method	2,94	58.3	<0.001	2,104	20.7	0.001	2,104	12.5	0.001
Microsite × method	10,94	0.7	0.751	10,104	1.8	0.016	10,104	1.05	0.010

[a] Numerator, denominator degrees of freedom

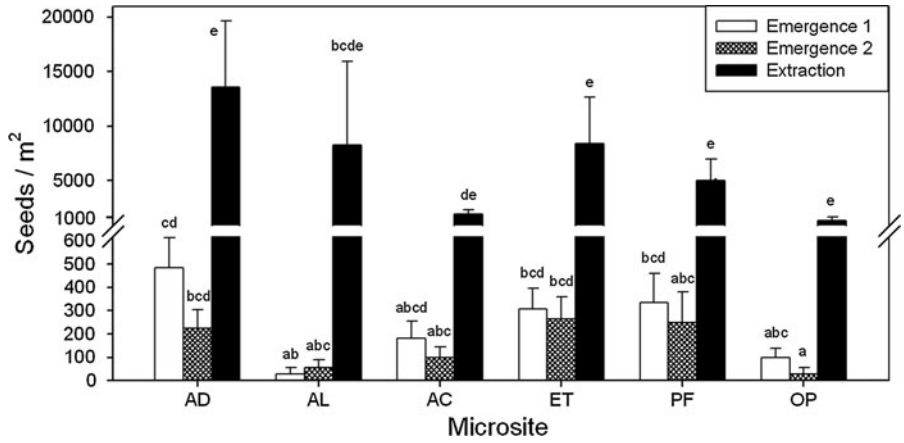

Fig. 1 Mean seed density by seed bank characterization method and sampling microsite in the Mojave Desert, USA. Means without shared letters differ at $p < 0.05$ and *error bars* are standard errors of means. Microsites include interspace (OP, openings between perennial plants) and below the canopy of the perennial plants *Ambrosia dumosa* (AD), *Anulocaulis leiosolenus* (AL), *Arctomecon californica* (AC), *Ephedra torreyana* (ET), and *Psorothamnus fremontii* (PF)

Table 3 Relationships between seed bank methods and vegetation in the Mojave Desert, USA

	Comparing seed bank methods					
	Seeds m^{-2}			Site species richness		
	m	*b*	*r*	*m*	*b*	*r*
Emergence 1: emergence 2	0.63	6	0.77	0.51	1	0.48
Emergence 1: extraction	11.06	2959	0.40	0.82	7	0.42
Emergence 2: extraction	19.62	2760	0.57	0.82	7	0.45
	Comparing seed bank and vegetation richness					
	Microsite scale			Site scale		
Emergence 1: vegetation	0.74	2	0.33	0.39	9	0.14
Emergence 2: vegetation	1.16	2	0.51	1.05	8	0.39
Extraction: vegetation	0.50	1	0.47	0.68	4	0.46
All combined: vegetation	0.49	1	0.54	0.59	4	0.50

The intercept (*b*), slope (*m*) and coefficient of correlation (*r*) are reported

emergence 1, to 28 in extraction (Table 4). In relating methods to each other, all methods were similarly correlated ($r = 0.42$–0.48) for estimates of richness $site^{-1}$ (Table 3).

Species composition

The effect of seed bank method on recorded species composition of the sample depended on microsite (Table 2). The ordination further revealed a clear separation in species composition between emergence and extraction methods and similarity in composition between emergence methods (Fig. 3). *Typha* was detected by both emergence and extraction but was a dominant species in emergence, displaying a strong correlation to emergence methods in the ordination. In contrast, several species, such as *Ambrosia dumosa* and *Arctomecon californica*, displayed correlations with the extraction method because the species were not observed using emergence methods (Table 4).

Extraction detected 20 taxa that were not detected by emergence, compared to 4 taxa which were unique to emergence 1 and 7 taxa unique to emergence 2. There were six general categories of taxa: (i) detected by all methods and also occurring in the vegetation (5 species), (ii) detected only by emergence and also in

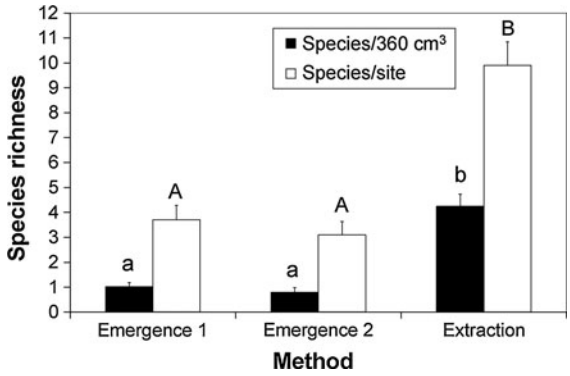

Fig. 2 Mean species richness at two scales compared across characterization method for soil seed banks of the Mojave Desert, USA. Means within a scale (differentiated by *uppercase* and *lowercase letters*) without shared letters differ at $p < 0.05$. *Error bars* are standard errors of means

vegetation (2 species), (iii) detected only by extraction and also in vegetation (9 species), (iv) only in the seed bank and not in vegetation at the sites (12 species), (v) only in vegetation and not detected in the seed bank (8 species), and (vi) rare, detected only once (5 species). The three exotic taxa (*Bromus rubens*, *Malcolmia africana*, and *Schismus* spp.) were detected both by emergence and extraction. For the two rare species with conservation status, *Arctomecon californica* was detected only by extraction, while *Anulocaulis leiosolenus* was not detected in the seed bank.

Considering plant growth forms, the major difference between emergence and extraction was that extraction detected shrubs, whereas emergence did not (Table 4). The two emergence methods combined detected 15 forb (71 % of the 21 total taxa detected by emergence), 6 graminoid (29 %), and 0 shrub taxa. Extraction detected 17 forb (61 % of the 28 total taxa detected), 5 graminoid (18 %), and 6 shrub taxa (21 %). This difference translated into extraction detecting a larger percentage of perennial taxa than emergence: 33 % perennial (including annual–perennial and biennial–perennial life spans), or 7 taxa, for emergence compared to 61 % perennial, or 17 taxa, for extraction.

Extracted seed germinability and viability assessment

Of 847 extracted seeds in the extraction method assessed for germinability through emergence, 114 (13 %) emerged. Few perennial taxa, including shrubs, emerged, making it difficult to interpret whether the greater detection of shrub and perennial taxa in extraction compared to emergence noted above resulted from extraction detecting non-viable seeds that are not considered part of the live soil seed bank. For example, no seeds emerged of the perennial forb *Arctomecon californica* (50 seeds tested), the shrubs *Atriplex* spp. (72 seeds), and the shrub *Ephedra torreyana* (9 seeds). Among the species that did emerge capable of perennial life spans, the annual–perennial forb *Cryptantha holoptera* displayed 21 % emergence (3 of 14 tested seeds), the perennial forb *Enceliopsis argophylla* 43 % (3 of 7 seeds), and the biennial–perennial forb *Mentzelia pterosperma* 30 % (6 of 20 seeds). Because of the weathered nature or small size of many seeds, we also had difficulty assessing potential viability through visually examining or poking seeds. Some extracted seeds of annual taxa were germinable, such as 6 % (5 of 85 seeds) for the forbs *Mimulus* spp., 7 % (11 of 162) for the forb *Phacelia pulchella*, 15 % (4 of 26) for the forb *Plantago ovata*, 17 % (14 of 84) for the grass *Vulpia octoflora*, 22 % (48 of 216) for the exotic grasses *Schismus* spp., and 42 % (10 of 24) for the forb *Phacelia pulchella*.

Seed bank:vegetation relationships

The correlation coefficients (r) between seed bank and vegetation species richness for individual seed bank methods ranged from 0.33 to 0.51 at the microsite scale and from 0.14 to 0.46 at the site scale (Table 3). There were no consistent patterns for higher or lower correlations with respect to seed bank methods, and combining species richness from all methods provided the strongest correlations with vegetation richness at both scales. The trend for species composition was similar, in that no particular seed bank method was consistently correlated with the vegetation, whereas combining all seed bank methods into one compositional estimate resulted in significant Mantel tests at both scales (Table 5).

Discussion

Species patterns and germination requirements

A general model for identifying species detectable by one or the other seed bank method could help reconcile differences between methods and help understand

Table 4 Comparison of individual taxa detected by three seed bank methods and in the vegetation aboveground at 10 sites in the Mojave Desert, USA

Species[a]	GF[b]	Emergence 1	Emergence 2	Extraction	Vegetation
Seed bank and vegetation					
*Bromus rubens**	aG	2[c]	3	2	4
Phacelia palmeri	aF	5	2	7	1
Plantago ovata	aF	4	1	6	6
Schismus spp.*	aG	6	5	10	5
Vulpia octoflora	aG	4	2	7	2
Emergence and vegetation					
Dasyochloa pulchella	pG	–	1	–	1
Mentzelia albicaulis	aF	–	1	–	2
Extraction and vegetation					
Ambrosia dumosa	S	–	–	7	8
Arctomecon californica	pF	–	–	9	9
Atriplex confertifolia	S	–	–	1	4
Cryptantha utahensis	aF	–	–	1	2
Enceliopsis argophylla	pF	–	–	4	3
Ephedra torreyana	S	–	–	1	10
Lepidium fremontii	S	–	–	1	1
Phacelia spp.	aF	–	–	1	1
Sphaeralcea ambigua	pF	–	–	3	2
Seed bank only					
Atriplex canescens	S	–	–	2	–
Atriplex elegans	apF	–	–	2	–
Atriplex spp.	–	–	–	2	–
Camissonia claviformis	aF	1	1	–	–
Chenopodium spp.	aF	–	–	2	–
Cryptantha holoptera	apF	–	1	2	–
Lesquerella tenella	aF	–	–	2	–
*Malcolmia africana**	aF	1	–	1	–
Mentzelia pterosperma	bpF	–	–	3	–
Mimulus spp.	–	–	–	4	–
Phacelia pulchella	aF	1	–	9	–
Typha spp.	pG	9	9	8	–
Vegetation only					
Anulocaulis leiosolenus	pF	–	–	–	5
Camissonia multijuga	abF	–	–	–	3
Cryptantha nevadensis	aF	–	–	–	3
Eriogonum inflatum	apF	–	–	–	6
Eriogonum maculatum	aF	–	–	–	2
Phacelia crenulata	aF	–	–	–	2
Plantago patagonica	aF	–	–	–	2
Psorothamnus fremontii	S	–	–	–	10
Rare					
Various species		4 species	6 species	5 species	14 species
Total taxa		13	15	28	38

Species are organized by their detection in the seed bank and vegetation

[a] * Exotic taxa

[b] Growth form: *aF* annual forb, *abF* annual–biennial forb, *apF* annual–perennial forb, *bp* biennial–perennial forb, *pF* perennial forb, *aG* annual graminoid, *pG* perennial graminoid, and *S* shrub (NRCS 2013)

[c] Values are the number out of ten sites in which a taxon was detected, except in the rare and total taxa categories at the bottom of the table which represent numbers of taxa. Dashes denote absences

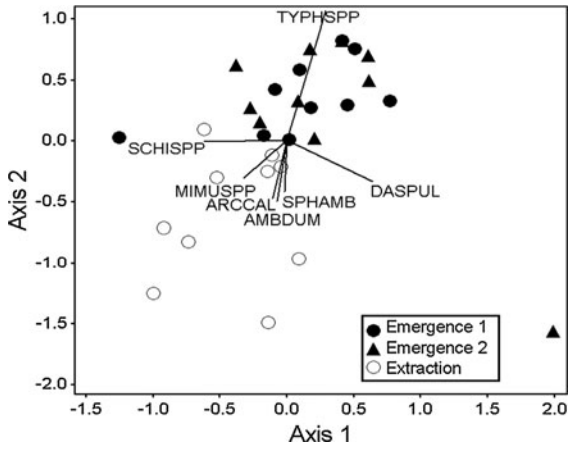

Fig. 3 Non-metric multidimensional scaling ordination of species composition (relative seed density) among seed bank characterization methods for 10 sites in the Mojave Desert, USA. Vectors display species that have $r^2 \geq 0.25$ with axes and are abbreviated as: AMBDUM, *Ambrosia dumosa*; ARCCAL, *Arctomecon californica*; DASPUL, *Dasyochloa pulchella*; MIMUSPP, *Mimulus* spp.; SCHISPP, *Schismus* spp.; SPHAMB, *Sphaeralcea ambigua*; and TYPHSPP, *Typha* spp.

Table 5 Relationships of species composition between seed bank methods and vegetation aboveground at microsite (five perennial plant species and interspaces) and site scales (all microsites combined) in the Mojave Desert, USA

Seed bank method	Microsite scale	Site scale
Emergence 1	0.14 (0.227)	−0.15 (0.764)
Emergence 2	−0.01 (0.400)	−0.20 (0.846)
Emergence 1 + 2	0.09 (0.267)	−0.15 (0.770)
Extraction	*0.19 (0.003)*	0.18 (0.167)
All combined[a]	*0.22 (0.002)*	*0.43 (0.005)*

Values are r (p value) from Mantel tests italicized for tests significant at $p < 0.05$

[a] Cumulative seed bank composition from all methods

which species go undetected by a particular method but that are likely in seed banks. Seed size is a useful characteristic in some ecosystems, as especially small seeds can be difficult to detect via extraction (Thompson et al. 1993). However, our data revealed no clear overall trend with seed size and detectability, as some small- (<1 mg) and large-seeded (≥1 mg) species were detected by both extraction and emergence. For example, small-seeded *Typha* (0.04 mg) and *Schismus* spp. (0.1 mg) were detected by both methods, similar to the large-seeded *Plantago ovata* (1.1 mg) and *Bromus rubens* (2.9 mg). Some important large-seeded species in the vegetation were only detected by extraction (e.g., 7.0 mg *Ambrosia dumosa*, 1.6 mg *Arctomecon californica*), implying that seeds were not viable or emergence techniques did not meet germination requirements of these species (Megill et al. 2011).

Accuracy of both methods could be enhanced by increasing our understanding of germination requirements of species to help detect seeds through emergence and estimate germinability/viability of extracted seeds. This is especially important in ecosystems such as deserts where germination ecology is not well understood nor is viability testing (such as tetrazolium assays) well developed for species exhibiting specialized dormancies for desert climates (Pake and Venable 1996). It is important to recognize that germination of freshly collected seed or seed stored in the lab is not necessarily the same as for seeds that have resided in soil seed banks (Baskin and Baskin 1998). Similarly, the process of extraction could change seed dormancy in ways that are poorly understood, complicating germinability and viability estimates that should be part of the extraction method. Our study found no advantage of storing soils in outdoor conditions to increase emergence, as stored samples exhibited lower seed densities than samples that were analyzed immediately. Testing other treatments for increasing seed detection through emergence could be valuable (Espeland et al. 2010). For example, treating soils of semi-arid USA *Pinus ponderosa* forests with liquid smoke increased seed detection by 21 % (Abella et al. 2007), and different water regimes influenced estimates of species composition in the Great Basin Desert (Espeland et al. 2010). Treatments increase labor, materials, and time required to assay samples, but developing effective treatment regimes is needed for emergence seed assays to detect species that have no known protocol for inducing germination. This applies to both emergence and extraction methods, because it remains unclear what proportion of extracted seed was viable and hence truly part of the living soil seed bank. The same limitation—not meeting germination requirements of species—that affects the emergence method also affects the extraction method when other procedures for evaluating seed viability are not well developed.

Microsite influences

"Fertile island" microsites, displaying ameliorated microclimates and nutrient-rich soil below perennial plants, are key ecological features structuring spatial patterns and functions of desert ecosystems (Reichman 1984). Our finding of greater seed densities below perennial plants, especially of larger perennial species, is consistent with studies in other arid environments (Guo et al. 1998). Several mechanisms might explain the observed greater seed densities below perennial plants, such as: seed production of the perennial itself; microclimate amelioration and increased soil fertility below the perennial, in turn fostering annual plant communities and increasing their seed production; trapping of seeds via wind deposition of dust or surface movement of soil; soils of low bulk density below perennials facilitating seed penetration into the soil; the presence of surface litter able to trap seeds; and greater animal activity near perennial plants (Reichman 1984). While perennial plant microsites occupy small portions of desert landscapes, they contain disproportionately high seed density and are, therefore, a source of variation important to capture for efficient site-level seed bank sampling.

Vegetation

Many studies have compared seed bank with vegetation composition (e.g. Olano et al. 2005), but few studies have examined how different seed bank methods correspond to vegetation (Cardina and Sparrow 1996). The practical value of accurately estimating seed bank:vegetation relationships includes understanding seed bank potential for regenerating current aboveground species versus new species (van der Valk and Pederson 1989; Schneider and Allen 2012). Seed bank formation by species of current vegetation promotes high seed bank:vegetation similarity, whereas seed persistence from past vegetation, seed bank formation from off-site seed dispersal of different species, and lack of seed bank formation by current on-site vegetation all promote low seed bank:vegetation similarity. Because some species were present in the seed bank but not vegetation and vice versa, which varied by seed bank methods, we did not find that a particular seed bank method was consistently most strongly correlated with vegetation. In fact, combining data from all seed bank methods resulted in the strongest correlation with vegetation. Both methods also detected *Typha*, a major genus in seed banks but not present in vegetation (reducing seed bank:vegetation similarity). *Typha* spp. are wetland plants not known to occur in vegetation of upland gypsum soils (Meyer 1986), and seeds likely wind dispersed from moister areas or the nearby Lake Mead shoreline.

Conclusion

This study revealed several specific considerations about seed bank methods depending on the purpose of the characterization. For example, detecting exotic species could be an important purpose of seed bank assays, especially when the species are annuals or short-lived perennials that may not be evident in the vegetation for several years (Pake and Venable 1996). The three main exotics within the study area—*Schismus* spp., *Bromus rubens*, and *Malcolmia africana*—were detectable by all methods. Detection of native species of conservation priority, in contrast, was more challenging. Only extraction can detect *Arctomecon californica*, unless improving knowledge of its germination ecology can enhance effectiveness of the emergence method, and it also remains unclear what proportion of extracted seeds were viable because none germinated. When comparing seed banks to vegetation is a goal, combining data from both extraction and emergence methods provided the strongest correlation with vegetation. If a general inventory of the seed bank is desired, results suggested that extraction detects more seeds and species than emergence. It is important to recognize, however, that assessing seed viability/germinability in extraction was not straightforward and emergence detected some species extraction did not.

Results may also offer more general insight into strategies for assessing soil seed banks. Findings suggested that one seed bank characterization method (extraction or emergence) could not be considered "better" overall than the other. A multi-variable perspective revealed that different soil seed bank characterization methods could be strong in certain areas (e.g., maximizing species detection) but weak in other areas, and both extraction and emergence methods have inherent logistical tradeoffs (e.g., laborious seed extraction procedures versus required

greenhouse space). For meeting many seed bank characterization purposes, extraction and emergence were not necessarily that dissimilar. For example, exotic species were detected by both extraction and emergence, and overall species detection (21 for emergence and 28 for extraction) was not that divergent. In fact, employing both extraction and emergence likely provides the most comprehensive estimate of seed bank composition, and when constraints limit a study to using only one of the methods, approaches such as those used in this study to reconcile differences between the methods might be valuable. When choices must be made to optimize seed bank characterization for a variety of purposes and level of effort, results suggest that a multivariate perspective including several seed bank measures (e.g. detectability of exotic species) is needed to accurately evaluate tradeoffs among methods. Enhancing knowledge of seed and seed bank germination requirements will likely be linked with future improvements to seed bank characterization methods, because extraction also is subject to the same limitation (not meeting germination requirements) as emergence when other procedures for determining viability of extracted seeds are not well developed.

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Characterizing soil seed banks and relationships to plant communities
Plant Ecology

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Online Resource 1 Photos of seeds extracted from soil seed bank samples and of selected fresh seeds collected from plants within the study area of the eastern Mojave Desert, USA. Divisions in the scale are 1 mm. Photos, descriptions, and scales on photos are not available for all species. Species are organized by family

Asteraceae

Ambrosia dumosa

Fruit: bur 4–9 mm, ± spheric, golden to purple or brown, puberulent; spines 12–35, 2–4 mm, spiraled, flat, straight, sharp (Baldwin et al. 2012).

Seed bank

Harvested from plant

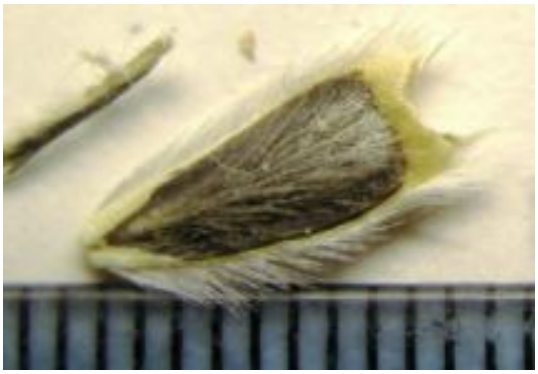
Enceliopsis argophylla

Cypselae: 9–13 × 4–5 mm, hirsute; **pappi:** usually of 2 awns 1–2 mm (plus minute scales or teeth), sometimes 0 (FNA 2012).

Fruit: ± 10 mm, 6.5 mm wide, glabrous or puberulent; pappus awns ± 1 mm, smooth (Baldwin et al. 2012).

Seed bank

Harvested from plant

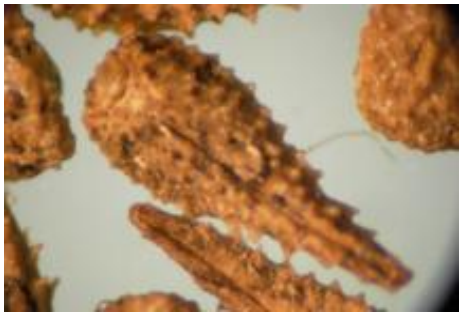


Boraginaceae

Cryptantha utahensis

Fruit: nutlet, 1.7–2.5 mm, lanceolate to lance-ovate, white-grainy papillate to minute-spiny, ± dull, margin distally a ± flat inward bent narrow rim to basally sharp-angled, base rounded, tip ± acute; abaxially low-rounded; adaxially occasionally smooth, biconvex, attachment scar edges ± narrow-gapped, triangular-flare-gapped at base; axis generally to nutlet(s) (Baldwin et al. 2012).

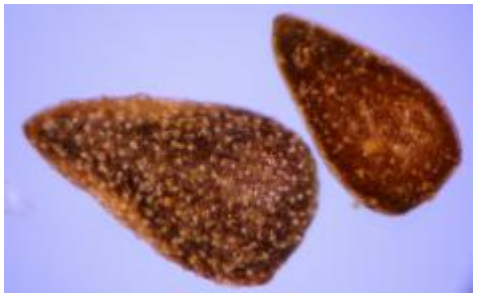
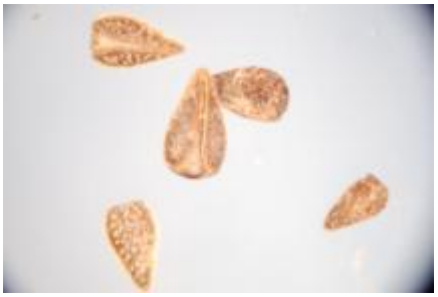
Seed bank



Cryptantha holoptera

Fruit: nutlets 4, (1.5)1.8–2.5 mm, ovate to triangular, dark with pale tubercles, ± dull, margin a ± flat narrow to wide non-papery wing; abaxially low-rounded, ridge 0; adaxially biconvex, attachment scar edges raised, abutted near tip, wide-triangular-flare-gapped at base; axis beyond nutlets (Baldwin et al. 2012).

Seed bank

Cryptantha dumetorum

Fruit: nutlets 4, 1.5–2.5 mm (1 > others), larger 1 wide-lanceolate, ± rough, persistent, smaller 3 ± lanceolate, deciduous, generally white-sharp-grainy, dull; abaxially rounded, ridge 0, adaxially ± rounded, attachment scar edges not raised, ± wide-gapped entire length, not flared or forked at base; axis generally to nutlet tips (Baldwin et al. 2012).

Seed bank


Brassicaceae

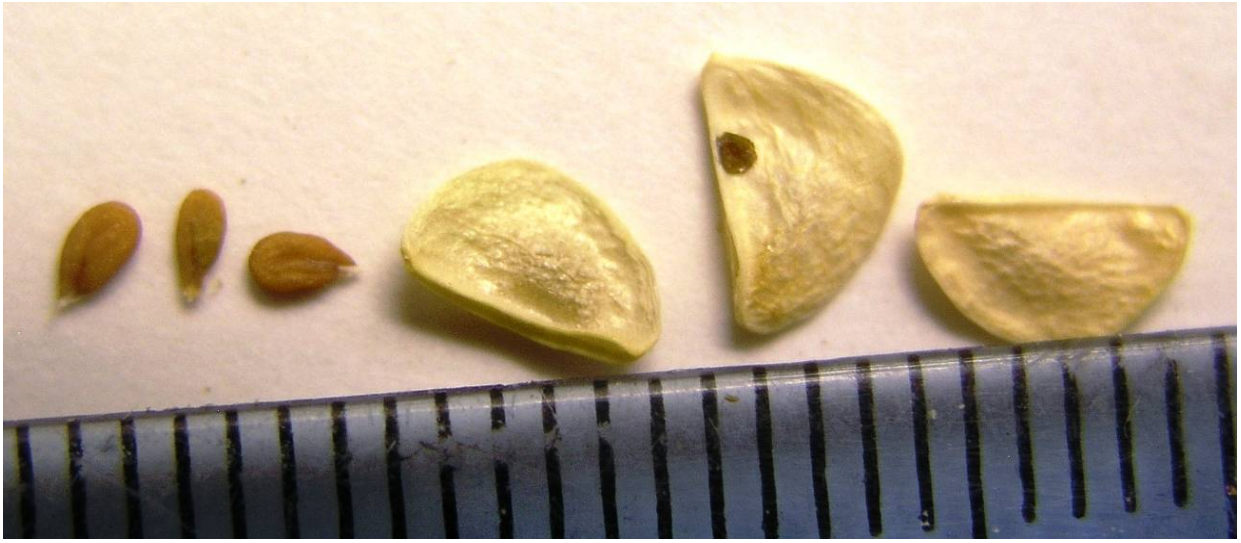
Lepidium fremontii

Fruit: (4)4.5–7(8) mm, 4.2–7(8) mm wide, obovate to round, flat, tip winged, notch (0.1)0.2–0.5 mm; valves glabrous, not veined; style 0.2–0.8(1) mm, exserted beyond notch; pedicel spreading, (3.5)4.3–7.6(8.5) mm, cylindric, glabrous.

Seed: 1.6–2.1 mm, ovate (Baldwin et al. 2012).

Seed bank

Harvested from plant

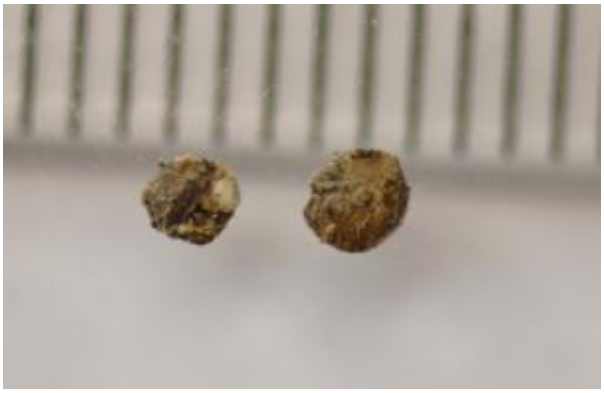


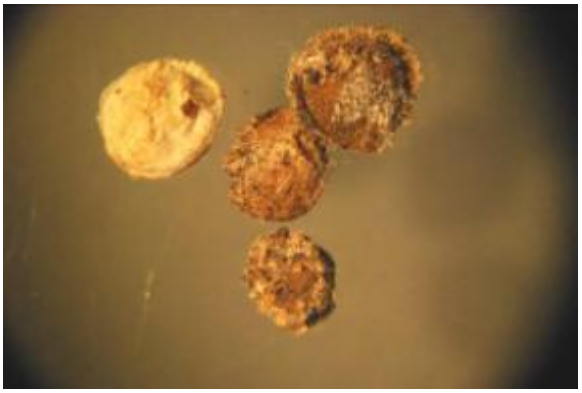
Lesquerella tenella

Fruit: (3.5)4–6 mm, spheric to obovoid, generally ± compressed, sparsely hairy outside, densely hairy inside; style 2–4.5 mm; pedicel 5–15 mm.

Seed: 4–12, flattened, margined (Baldwin et al. 2012).

Seed bank





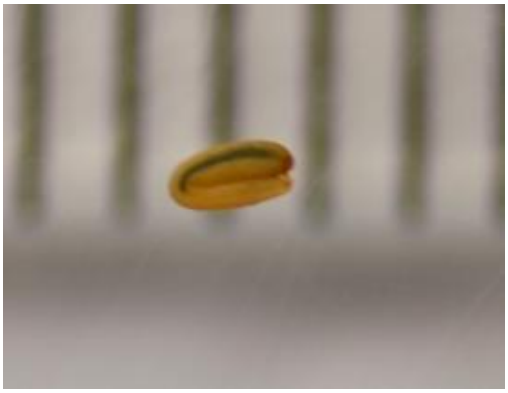
Malcolmia africana

Fruit: ascending, (2.5)3.5–5.5(7) cm, 1–1.3 mm wide; style 0; pedicel 0.5–2(4) mm.

Seed: 1–1.2 mm, oblong (Baldwin et al. 2012).

Seed bank

Harvested from plant



Chenopodiaceae

Atriplex canescens

Seed: 1.5–2.5 mm. Varieties intergrade (Baldwin et al. 2012).

Seed bank

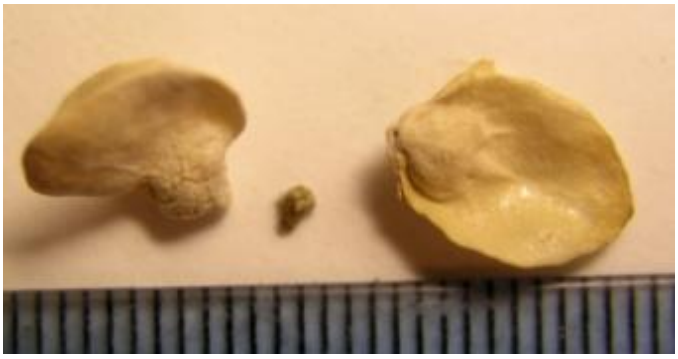
Harvested from plant

Atriplex confertifolia

Seed: 1.5–2 mm (Baldwin et al. 2012).

Seed bank

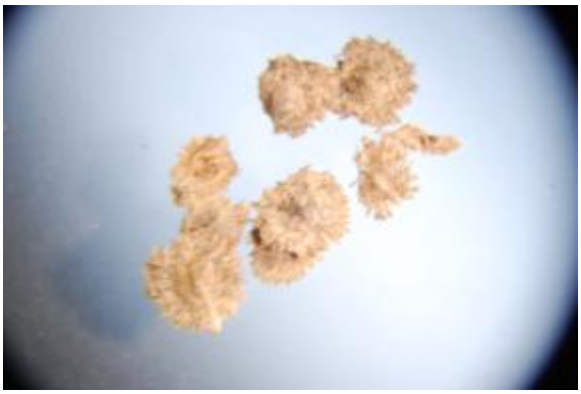
Harvested from plant



Atriplex elegans

Seed: 1–1.5 mm (Baldwin et al. 2012).

Seed bank

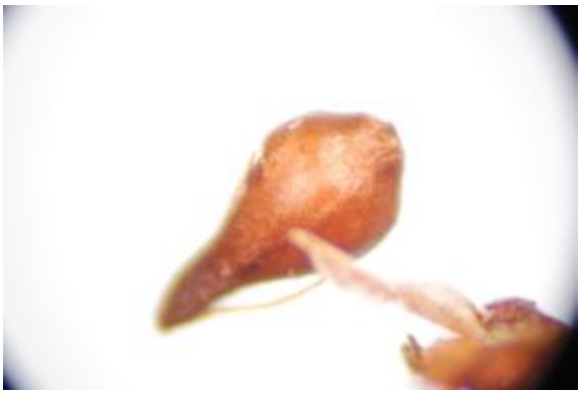


Cyperaceae

Carex sp.

Achenes: Biconvex, plano-convex, or trigonous, rarely 4-angled (FNA 2012).

Seed bank



Ephedraceae

Ephedra torreyana

Seed cones: 1-several at node, ovoid, 9-15 mm, sessile; bracts in 5 or 6 whorls of 3, obovate, 6-9 × 6-10 mm, papery, translucent with orange-yellow to greenish yellow center and base, base clawed, margins minutely dentate, undulate.

Seed: 1-2(-3), ellipsoid, 7-10 × 1.5-3 mm, light brown to yellowish green, scabrous (FNA 2012).

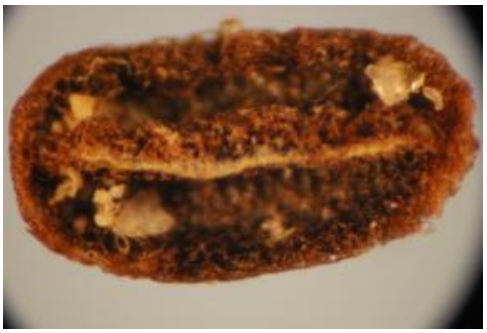
Seed bank

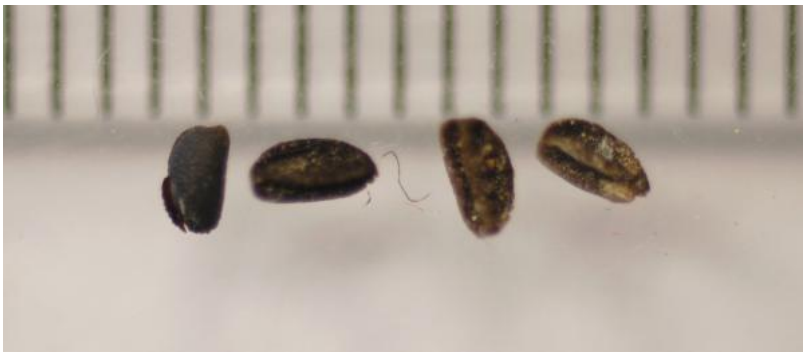
Harvested from plant

Hydrophyllaceae

Phacelia palmeri

Seed bank





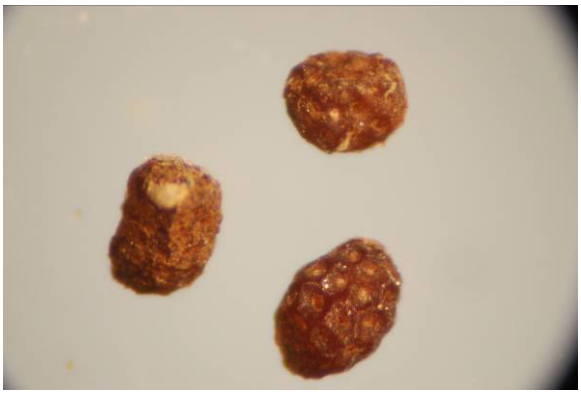
Harvested from plant

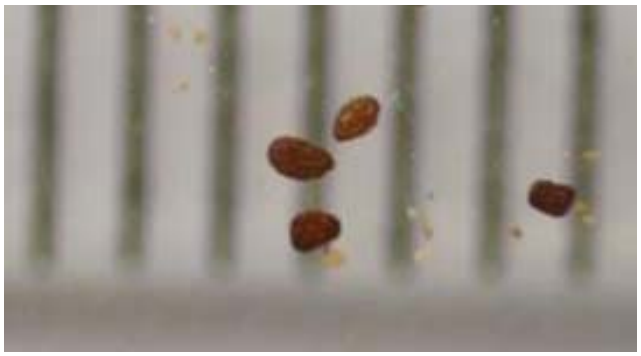
Phacelia pulchella

Fruit: 3–5 mm, ± oblong, short-hairy.

Seed: ± 0.5 mm, pitted (Baldwin et al. 2012).

Seed bank





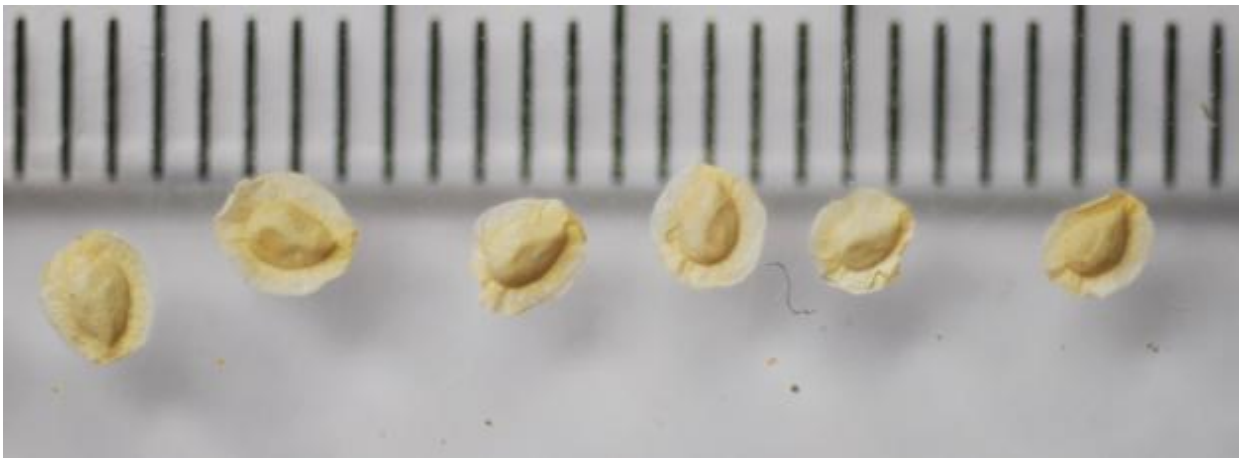
Loaseae

Mentzelia pterosperma

Fruit: erect, 8–14 mm, 5–10 mm wide, cup-shaped to cylindric.

Seed: ± 2.5–4 mm, ± 3 mm wide, lenticular, winged, white (Baldwin et al. 2012).

Seed bank



Malvaceae

Sphaeralcea ambigua

Fruit: segments 9–13, < 6 mm, < 3.5 mm wide, truncate-cylindric, dehiscent part < 3.5 mm, 60–75% of segment.

Seed: 2 per segment, brown, glabrous to hairy (Baldwin et al. 2012).

Seed bank

Harvested from plant

Onagraceae

Oenothera deltoides

Fruit: 20–60(80) mm, cylindric, generally curved, ± twisted (Baldwin et al. 2012).

Seed bank

Papaveraceae

Arctomecon california

Fruit: ovate to oblong, dehiscent from tip.

Capsules persistent, obconic, 1-2.5 cm, dehiscing not more than 1/4 length (FNA 2012). Wrinkled, withered appearance.

Seed bank

Plantaginaceae

Plantago ovata

Seed: 2–2.5 mm (Baldwin et al. 2012). Gelatinous when wet.

Seed bank

Harvested from plant

Poaceae

Bromus rubens

Spikelet: 20–50 mm, not strongly flattened; glumes glabrous to hairy, lower 3.5–13.5 mm, 1-veined, upper 6–20 mm, 3-veined; lemma 12–25 mm, back rounded, glabrous or hairy, teeth 1.5–3 mm, awn 10–25 mm, straight (Baldwin et al. 2012).

Seed bank

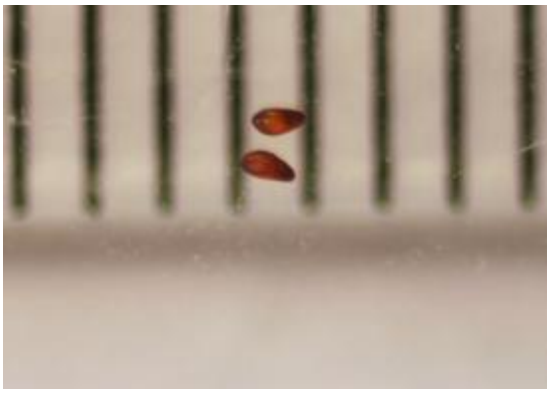


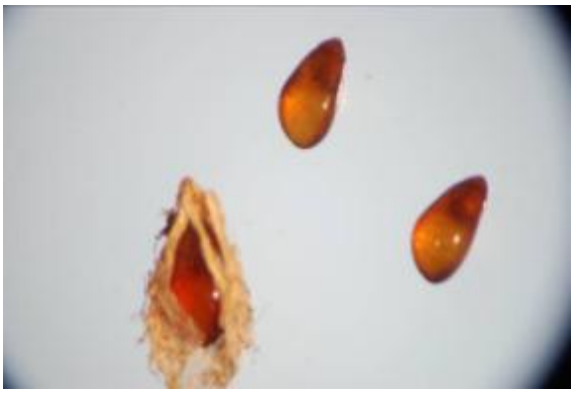
Schismus sp., either *Schismus arabicus* or *Schismus barbatus*

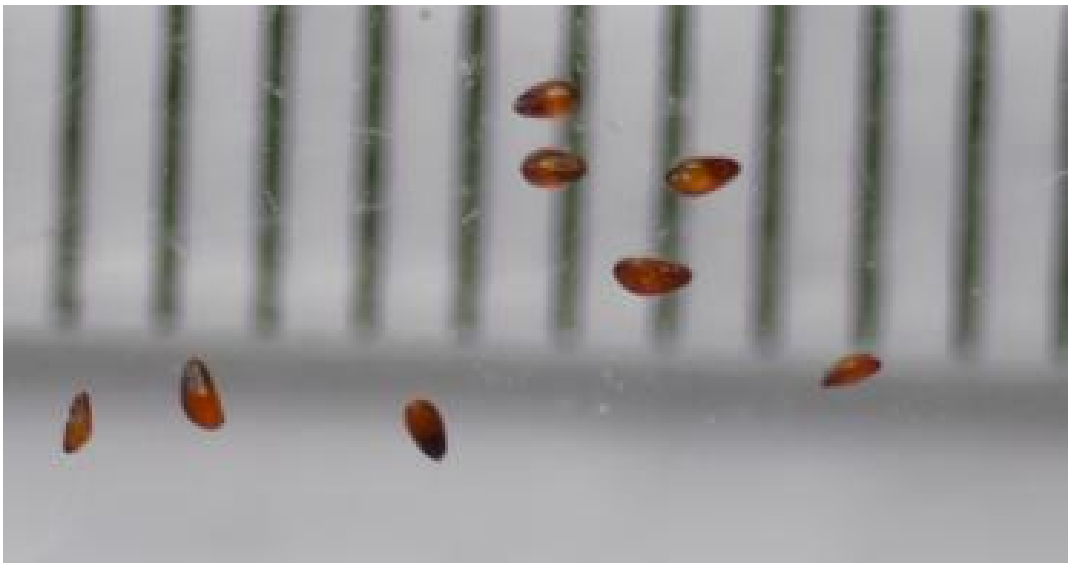
Spikelet (*S. arabicus***):** glumes 4.5–6.5 mm; lemma 2.5–4 mm, teeth ± 0.3 × lemma; palea 2–3 mm

Spikelet (*S. barbatus***):** glume 4–5 mm; lemma 2–2.5 mm, teeth ± < 0.2 × lemma; palea 1.5–2.5 mm (Baldwin et al. 2012).

Seed bank







Vulpia octoflora

Spikelet: 4.5–10 mm; lower glume ± 2–4.5 mm, upper ± 2.5–7 mm; florets (5)7–12; lemma ± 3–5 mm; awns 0.5–5 mm.

Fruit: 2–3.5 mm (Baldwin et al. 2012).

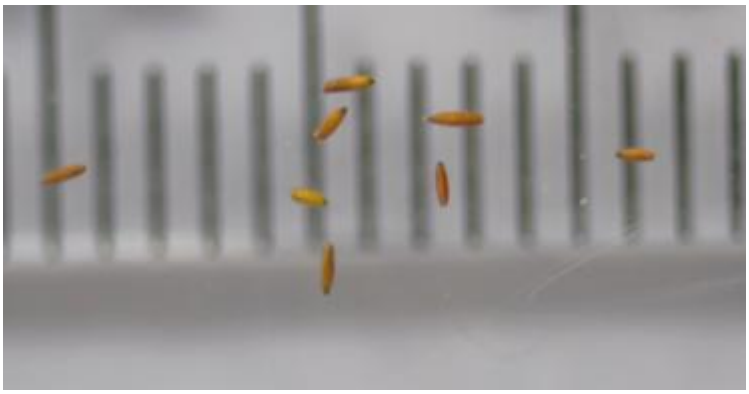
Seed bank

Typhaceae

Typha sp.

Fruit: fusiform, thin-walled, yellow-brown, wind-dispersed (Baldwin et al. 2012).

Seed bank



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