

## WINTER EPHEMERAL VEGETATION AND SEED BANKS OF FOUR NORTH-FACING SLOPES IN THE SONORAN DESERT

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### ABSTRACT

Variable temperature and precipitation in hot deserts interact to trigger germination of ephemeral plants; however, in the Sonoran Desert, little information is available on how these winter ephemeral plant communities vary among localities and how the seed bank contributes to the above ground diversity. This study quantifies the similarity in seed banks (below ground flora) of winter ephemeral plants among sites and the relationship to the above ground flora. In November 1999, ninety-five soil samples were collected across four Sonoran Desert localities and germinated in a glass house under site temperature and light conditions and were misted daily. In February 2001, when winter rains were sufficient to germinate winter ephemerals *in situ*, the same four localities were revisited and data were taken on the genera present within plots. The Jaccard Similarity Index, Margalef Diversity Index, lists of taxa, and densities of common taxa were compared among sites and between the seed bank and above ground flora. Overall, seed bank similarity of taxa among sites averaged 41% whereas the above and below ground data averaged 49% similarity. Only three of 36 genera were present in the seed bank and above ground flora in all sites: *Pectocarya* DC. ex Meisn. (Boraginaceae), *Eucrypta* Nutt. (Hydrophyllaceae), and *Amsinckia* Lehm. (Boraginaceae); the density of these varied significantly among sites and between above and below ground floras. The Poaceae taxa, *Poa bigelovii* Vasey & Scribn., *Vulpia octoflora* (Walter) Rydb., *Schismus arabicus* Nees, and *Bromus rubens* L., were notably dominant in the seed bank while less dense in the above ground flora. Due to the variability of seed banks and above ground floras, adding seed bank analysis to the above ground vegetation data taken in most studies would enhance our understanding of overall site diversity.

**Key Words:** Winter ephemerals, seed bank, above ground vegetation, Sonoran.

Desert winter ephemeral plant communities are highly structured by fluctuations in precipitation and temperature (Went 1948; Sala and Lauenroth 1982; Venable and Pake 1999). In fact, the interplay between these two factors drives temporal variation of ephemeral plant diversity in the Mojave Desert (Beatley 1974) with specific temperatures and precipitation combinations resulting not only in different winter and summer vegetation, but in different species dominating between winters and between summers (Tevis 1958a, b). Likewise, geographic variability of germination within the same season has been documented for several populations in the Mojave and Sonoran Deserts (Shreve 1951; Epling et al. 1960; Pake and Venable 1996), and other studies have commented on these differences between years (Roberts 1986; Coffin and Lauenroth 1989). Ephemeral plants are here defined as those plants germinating in response to unpredictable seasonal precipitation and temperature cues; they are not considered to be annuals since several years may pass before germination occurs. Few large scale comparisons have been made among the four North American deserts (Guo et al. 1998, 1999) with most studies having focused on

single sites within the same desert (Went 1948; Burk 1982). These studies have examined seed bank dynamics by studying seed distribution, species composition (Tevis 1958a, b; Bowers 1987; Henderson et al. 1988), and germination conditions (Harlan and Went 1945; Juhren et al. 1956). Seed bank dynamics play a large role in maintaining ephemeral plant diversity in arid areas. Not only do they increase the ability for species to persist in arid environments (Epling et al. 1960), but by germinating less than 100% of its seeds each season (Baskin and Baskin 1978), depletion of the seed bank in a given area is unlikely (Venable and Lawlor 1980). Diversity is thus actually greater per unit area since many species are able to coexist in germinated and ungerminated conditions and not simultaneously compete for resources (Pake and Venable 1996).

Shreve (1951) was the first to note the drastic changes in diversity that can occur in a Sonoran Desert winter ephemeral plant community when heavy rains elicit germination of rarer species. These regional germination events are often linked to the El Niño climate cycle which brings above average winter rainfall to the desert when critical temperatures break seed dormancy (Venable and Pake 1999); more often, off-El Niño rainfall triggers localized flowering events every three to four years (Dimmitt 2000; but see Jennings 2001). For

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these smaller, isolated blooms, taxonomic similarity or the contribution of the seed bank has been little explored in the Sonoran Desert. Multi-site seed bank and above ground flora studies are lacking although some anecdotal evidence exists for floristic dissimilarities between proximal sites. For example, Went (1948) noted that in adjacent areas in the Mojave Desert, different populations of ephemeral species existed. In a Chihuahuan Desert study, sites separated by as little as four km differed significantly in plant density and species diversity (Dye 1969, cited in Kemp 1989). By investigating the geographic heterogeneity of ephemeral plant germination as well as the contribution of the seed bank to the above ground flora, a better understanding of Sonoran Desert seed bank dynamics and ephemeral diversity is gained and differences among North American Deserts can be further explored. This study compares the floristic similarity of winter ephemeral plants among four localities and analyzes the contribution of the seed bank to the above ground flora. Data from seed bank and field studies from four Sonoran Desert sites in the Phoenix area are used to make these comparisons.

#### METHODS

**Study sites.** The city of Phoenix, Arizona has preserved 33% of its land in the form of desert mountain preserves (Morrison Institute 2000). All four study sites are located in desert remnants in the metropolitan Phoenix area under the jurisdiction of Phoenix City Parks or the U.S. Military (Fig. 1). All of these areas are relatively undisturbed and are characterized as Sonoran Desert Scrub (Brown and Lowe 1994) and are dominated by *Larrea tridentata* (Sesse & Moc. ex DC.) Coville (Zygophyllaceae), *Parkinsonia microphylla* Torr. (Fabaceae), and *Ambrosia deltoidea* (Torr.) W.W. Payne (Asteraceae). To be consistent in microclimate, north-facing slopes were chosen for all sites. Sites were selected based on winter ephemeral diversity as observed personally or reported by park rangers and local botanists. North Barnes Butte, which was believed to be species poor based on previous fieldwork, was added for comparison since the data was to be collected for another simultaneous project.

The North Barnes Butte (BB) site is located on the Arizona National Guard Papago Park Military Reservation at 33°27'N; 111°57'W. The 157 ha base is bordered on all sides by residential areas and has been fenced since 1909 keeping the area relatively undisturbed. Historical site activity include the foundation of a homestead (ca. 1800's) and probable usage by the Maricopa and Pima peoples (Gart 1996). While military exercises are carried out to the north of the butte, the butte itself is rarely used since it flanks an active firing range. Soil analyses showed that the area is a sandy loam with an average pH of 6.6, organic matter 2.9% and nitrate 23 ppm.

The Shaw Butte (SB) site is located in the North Mountain Recreation Area of the 7000 ha Phoenix Mountains Preserve at 33°35'N and 112°4'W. This site is located near the edge of the preserve, though not adjacent to any designated trail. Soil for this area is loam with a pH of 7.0, 2.7% organic matter, and nitrate 16.5 ppm.

The South Mountain (SM) site is located in South Mountain Park at 33°15'N and 112°5'W. South Mountain Park became a 16,677 ha city park in 1924. The study site was located over a mile from hiking trails, though within site of a residential area. Previous usage of the area includes an abandoned home site (pre-1950's) visible from the collection area. The soil is a sandy loam with a pH of 6.9, 1.9% organic matter, and nitrate 18 ppm.

The Squaw Peak (SQ) site is located in the Squaw Peak Recreation Area in the Phoenix Mountains Preserve at 33°31'N and 112°1'W. The entire Preserve spans 2833 ha and was created in the 1960's with the Squaw Peak portion first set aside in 1910. Verbal reports of previous mining and grazing activities exist for the general area, but not specifically for the study site. Soil at this site is characterized as loam with a pH of 6.05, 2.15% organic matter and 12 ppm nitrate.

**Seed bank sampling.** Soil samples were collected October–December 1999 for soil seed bank germination. Soil was sampled from open areas adjacent to *Parkinsonia microphylla* or *Ferocactus cylindraceus* (Engelm.) Orcutt (Cactaceae) plants at each site, which are widely dispersed across the slopes. Ninety-five total samples were collected, 20–25 samples per site, using a 6.4 cm diameter copper cylinder that was pressed 2 cm into the soil—the average depth of the active soil seed bank (Childs and Goodall 1973). To account for heterogeneity of seed distribution in the soil (Nelson and Chew 1977; Bertiller and Coronato 1994), each of the 20–25 soil samples (128.7 cm<sup>3</sup> per sample) was composed of four pooled sub-samples (Bigwood and Inouye 1988). Across all samples at each site, a surface area of 0.3 m<sup>2</sup> was studied.

Since seeds do not germinate when they are buried greater than 1 cm below the ground (Freas and Kemp 1983), 103 cm<sup>3</sup> of each field soil sample (80%) was spread 1 cm deep over an autoclaved mixture of potting soil and pumice in each of two (10 × 10 cm) pots. These were placed in a randomized block design in a non-heated, evaporatively cooled greenhouse. Trays of the autoclaved soil and pumice mixture were interspersed with the collected soil samples to detect sample cross contamination. Samples were misted with water once a day to maximize germination and to avoid desiccation. Temperatures inside the greenhouse fluctuated like those at the study sites, though being slightly higher or lower on occasion, but met the seasonal germination requirements of most winter ephemerals (Baskin and Baskin 1998). All plants, including any

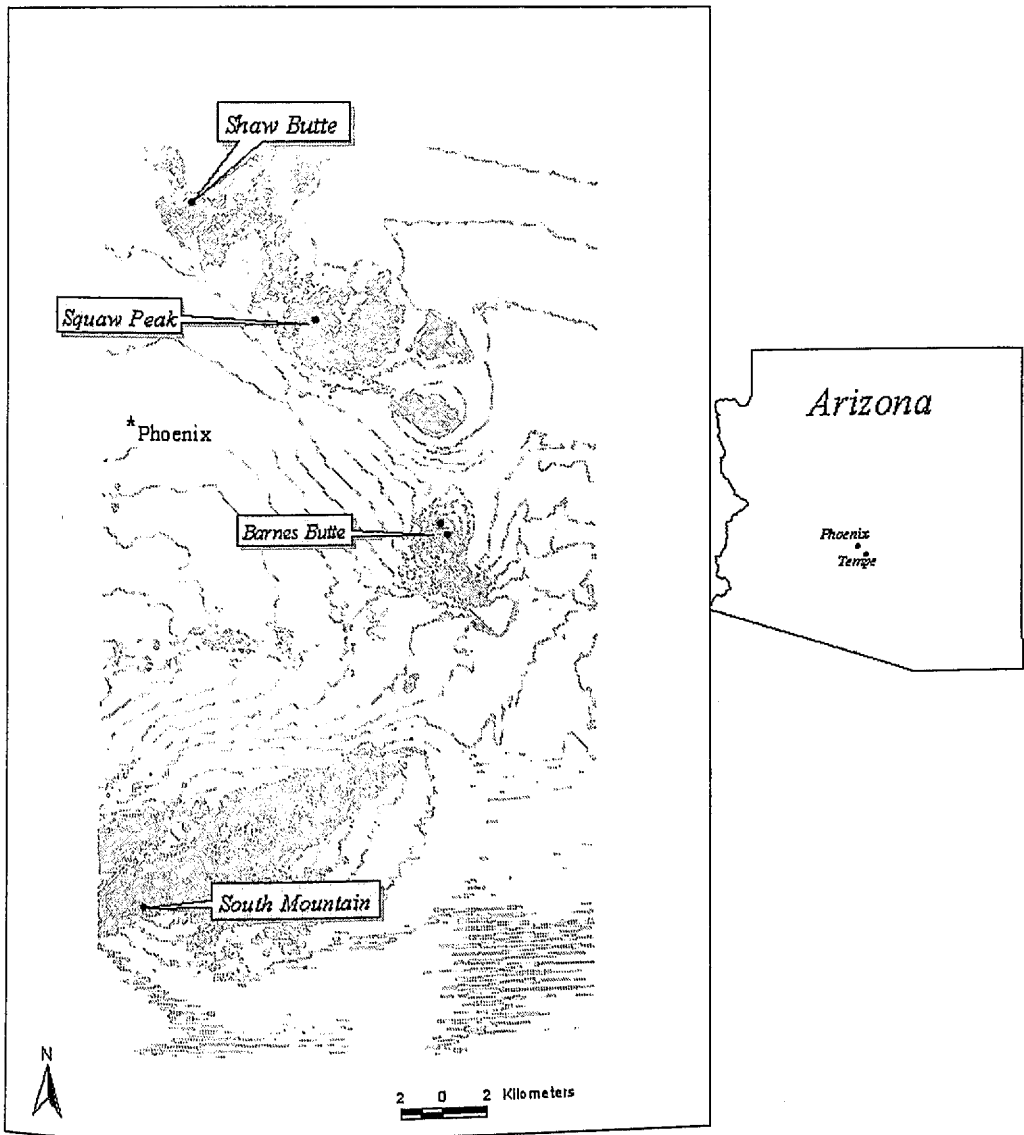


Fig. 1. Study areas located in the Metropolitan Phoenix area, Arizona.

Perennials and grasses, were inventoried weekly from October 1999–March 2000. All taxa were identified to species when possible (some died before flowering) and vouchered at the ASU herbarium with nomenclature following the USDA National Plants Database (2001). To convert greenhouse densities of plants to densities expected in the field, all greenhouse plant densities were divided by 80%, which was the amount of field soil germinated in the greenhouse.

**Field sampling.** Sufficient rain fell in the winter of 2000–2001 for successful in situ germination of winter ephemeral plants. Thus, in February 2001, the same areas where soil samples were taken for the seed bank study were revisited. The same or

adjacent trees were resampled with fifteen 2 × 2 dm vegetative plots each located two paces down slope from each tree. For each plot, the number of individuals per genus were recorded. For each study site, 0.6 m<sup>2</sup> was sampled.

**Climatic measurements.** In 1999–2000, Greenhouse temperatures were monitored every two days for high and low temperatures. These were compared with outside greenhouse temperatures also monitored on site to ensure that the greenhouse was within range of normal outside temperatures. Monthly field temperatures and precipitation for 2000 were secured from the National Weather Service in Phoenix, Arizona (National Weather Service 2001).

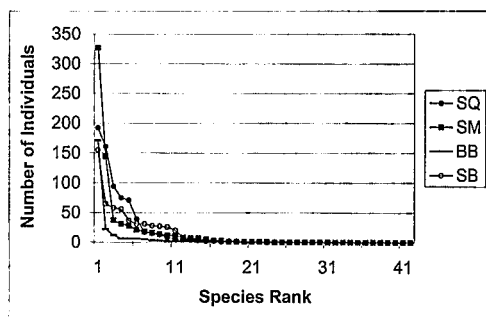


FIG. 2. Rank abundance curves for four sites showing that most sites were characterized by a few dominants and numerous rare species.

**Statistics and indices.** The following indices and measures were calculated: number of taxa, density, the Margalef index (Magurran 1988), Jaccard Similarity Index (Magurran 1988), average density and average diversity per unit area. These were chosen because they are common measures in other studies; in addition, the Margalef combines density and diversity into a single number that facilitates comparisons between data sets. Higher scores indicate higher diversity. The Margalef was calculated as follows:

$$D_{Mg} = \frac{(S - 1)}{\ln N}$$

where  $S$  equals the number of taxa recorded and  $N$  is the number of individuals summed over all taxa in the sample. ANOVAs were conducted on square-root transformed Margalef Index scores of the seed bank data. Scheffé tests were applied to determine significant differences in diversity among sites.

To compare changes in taxa that were dominant at all sites, the seed bank data were used. Due to the many zeros in the data set, averages of plants/sample were compared with the Wilcoxon ( $W$ ) test in SAS 8.1 (2000). For comparison of the above and below ground floras for the most common genera, both data from the greenhouse (below ground/seed bank) and the field (above ground) were used. Genera were used due to a plant identification error of the two *Amsinckia* species in the seed bank study; therefore all *Amsinckia* determinations were lumped into the genus. Because these methods used different plot dimensions, all numbers were converted to individuals per square decimeter before conducting Wilcoxon tests. Ancillary graphs were created using Microsoft Excel 2000.

Rank abundance curves were calculated for each site by ordering all taxa per site from most to least abundant (based on number of individuals) and then plotting them in that order versus the number of individuals for that taxa. This allows one to examine the distribution of taxa as being predominantly rare or common for a given area. For ex-

TABLE 1. DIFFERENCES IN NUMBERS OF SPECIES ( $S$ ), THE MARGALEF INDEX ( $D_{Mg}$ ) AND DENSITY AMONG STUDY SITES. Higher Margalef scores indicate higher diversity and density.

	$S$	$D_{Mg}$	Density individuals/m <sup>2</sup>
N. Barnes Butte (BB)	19	3.26	820.4
Shaw Butte (SB)	26	3.94	1392.8
South Mountain (SM)	23	3.36	1949.6
Squaw Peak (SQ)	22	3.20	2102.3

ample, *Pectocarya* was ranked first at SM, numbering nearly 350 individuals (see Fig. 2).

## RESULTS

**Among site comparisons of below ground flora.** Based on seed bank data alone, there were 34 winter ephemeral genera and 43 species (Appendix A). *Crassula erecta* (Hook. & Arn.) A. Berger (Crasulaceae) was excluded from the analysis due to its prolific seed production, self sowing, and re-germination that would have augmented seedling counts. Sites ranged from 19–26 species with an average of 22.5 species per site. Densities ranged from 820–2102 individuals/m<sup>2</sup> (Table 1).

Sixteen of these taxa (37%) were found at only one site; 10 taxa (23%) were common to two sites; 10 taxa (23%) were common to three sites; and only six taxa (14%) were found at all four sites, namely *Schismus arabicus*, *Pectocarya recurvata* I.M. Johnst., *Amsinckia* spp., *Poa bigelovii*, *Vulpia octoflora*, and *Eucrypta micrantha* (Torr.) A. Heller. Most taxa were rare in occurrence with only a few, such as the above, being numerous (Fig. 2). Using the Margalef index to indicate highest diversity across sites, all sites were similar in species richness with only Barnes Butte and Shaw Butte being significantly different ( $F_{3,05} = 3.87$ ,  $P = 0.0117$ ) (Fig. 3). Generic Jaccard similarity indices among sites averaged 41%. SB and BB were the least similar in composition with 24% similarity of species richness whereas BB and SQ received the highest Jaccard Similarity Index of 58%. Other sites fell in

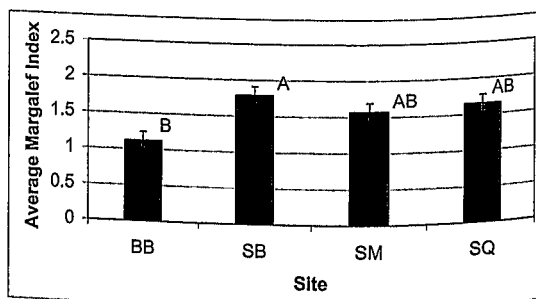


FIG. 3. Average Margalef diversity index scores of seed banks. Sites with different letters are significantly different and higher scores indicate higher diversity.

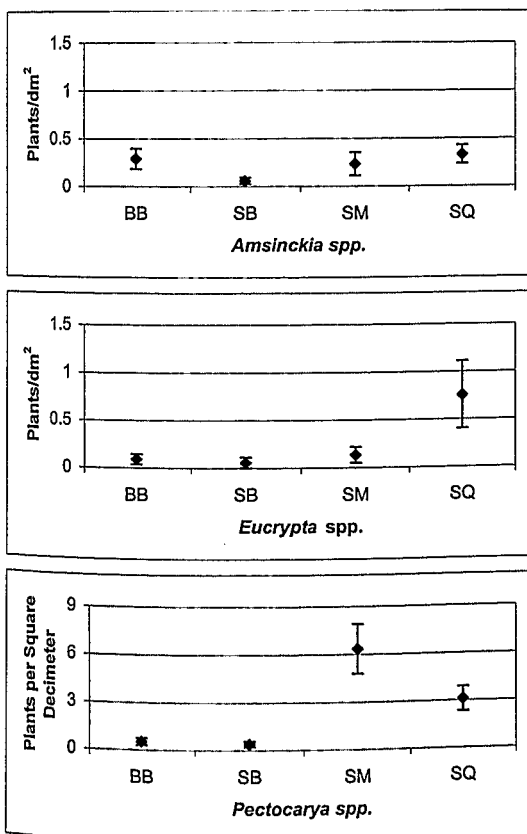


FIG. 4. A comparison of taxa density among the seed banks of the four study sites. Note scale change for *Pectocarya*. Bars denote standard error.

between these ranges with SM having 34% of its species in common with BB and 48% similarity with SB. SQ was least similar to SM (39%) and next most similar to SB (41%).

When the six taxa common to all sites were ex-

amined for density among sites, not all species were represented equally; furthermore, half of these dominants were grasses, including the naturalized exotic, *Schismus*. When *Eucrypta* density was examined, there was a significant difference among sites ( $W_{3,05} = 16.4022$ ,  $P = 0.0009$ ); *Pectocarya* exhibited the same trend ( $W_{3,05} = 37.3922$ ,  $P < 0.0001$ ). However, for *Amsinckia* ( $W_{3,05} = 6.6909$ ,  $P = 0.0824$ ), there was no significant difference in density among sites (Fig. 4).

**Below ground and above ground comparisons.** When the data for the seed bank and above ground flora studies were combined at the generic level, 36 genera were present at all sites. There was an average 49% taxonomic similarity between above and below ground floras with SQ having 46% similarity, SB with 48%, and both BB and SM having a 50% similarity between above and below ground floras at those sites. Three grass species were dominant in all sites in the seed bank, though scarcely present in the above ground flora. However, despite the changes in the presence or absence of rarer plants, three genera were always present at all sites in the seed bank and the above ground flora, although not always in the same proportions. *Eucrypta* was significantly denser in the field ( $W_{3,05} = 5571$ ,  $P < 0.0003$ ); however, *Pectocarya* ( $W_{3,05} = 4835.5$ ,  $P = 0.56$ ) and *Amsinckia* ( $W_{3,05} = 4488$ ,  $P = 0.36$ ) were not (Fig. 5).

**Temperature and precipitation comparison between field and greenhouse.** Greenhouse temperatures were 5–19°F higher in the day and 4–8°F cooler at night thus potentially allowing for more germination cues to be met. Greenhouse plants were misted for 10 minutes per day while Phoenix sites received 0–3.17 inches of rain per month. Seed bank germination occurred primarily during the first two weeks of irrigation with limited germination thereafter.

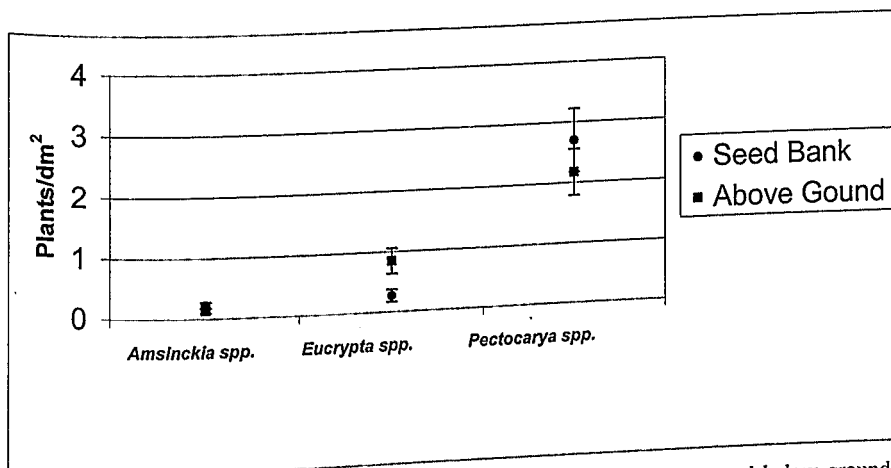


FIG. 5. A comparison of the density of the three genera common in both the above and below ground floras. Bars denote standard error.

## DISCUSSION

Quantities of light and water determine which areas are suitable for germination in a particular season. This combination is never the same: as each species varies slightly in its germination requirements, the mix of germinating species in a locality can change from year to year (Grubb 1977). For example, in Went's early studies of *Pectocarya*, *Plantago* L. (Plantaginaceae), and *Schismus*, different precipitation and temperature conditions resulted in domination of different taxa (Went 1948, 1949). In my Sonoran Desert study sites, there was a 49% taxonomic similarity between the above and below ground floras despite differences in dominants and rarer taxa. In keeping with Shreve's observations of changes in dominant taxa between years, although *Eucrypta* accounted for approximately 40% of all individuals at SB in the above ground vegetation, below ground it accounted for only 5%. Similarly, in a six-year Mojave Desert field study, 34 of the 62 study species occurred every year and only eight occurred in a single year (Bowers 1987). However, not all taxa shifted drastically in dominance above and below ground. At SM, for instance, *Pectocarya* was dominant in both above and below ground floras. Grasses, however, had the greatest response, with *Poa*, *Schismus*, and *Vulpia* dominating the seed bank but not the above ground flora.

The change in dominance of grasses between the seed bank and the above ground flora yields evidence of the environmental triggers for the germination of this guild. The difference probably lies in the greater water availability in the greenhouse while the field received only 16 cm of rain. *Schismus* responds well to high water availability (Szarek et al. 1982) often outranking *Plantago* in mesic conditions; however, *Bromus rubens*, another exotic grass, dominated the seed bank of SQ but was absent in the above ground flora despite dominating local riparian areas that same spring (Boudell personal communication). Nonetheless, grasses can change from rare to common in the above ground flora as evidenced by the Chihuahuan Desert study where the density of *Vulpia octoflora* significantly increased over the course of 15 years (Guo et al. 2000).

Species dominance also varies among localities in the seed bank. Among the seed bank floras of the four sites, there was a 41% overlap among taxa with most taxa being represented by few individuals. There was less similarity among seed banks than between each sites seed bank and above ground flora. Of the 42 species, 38% were only found in a single site and only 14% were found at all sites. Likewise in a desert grassland study 21 of the 45 were species restricted to less than five percent of all samples (Henderson et al. 1988). These results suggest that there is a different plant assem-

blage and high turnover at each location despite similar aspect, soil, and woody vegetation.

In this study, only six taxa were common to all sites. Of these, I evaluated the three non-Poaceae taxa. These were the only genera common at all sites in both the seed bank and above ground flora, although their densities varied. Only *Eucrypta* was significantly different between above and below ground floras while *Pectocarya* and *Amsinckia* were not. These common desert plants, while fluctuating themselves, are surrounded by many other taxa that appear and disappear from the above ground flora while remaining in the seed bank.

Data from this study are based on field-sampled quadrats and greenhouse-germinated soil samples that potentially underestimate plant diversity: two years of data are not enough to fully comprehend the temporal variability of these winter ephemeral assemblages. Above ground data were based on one month's study not allowing for plants blooming outside of that window to be included (see Jennings 2001). When compared to the below ground data, six months of continuous monitoring, as well as a wider range of temperatures, potentially allowed for more taxa to be represented in the seed bank. Furthermore, the above data were collected 14 months after the soil samples when winter rains were next sufficient to induce germination; the interim months may have allowed granivory to occur (Price and Reichman 1987). However, whether one compares methods or years, the conclusion is still the same: different environmental conditions result in the germination of different taxa contributing to the variability between above ground and seed bank floras.

The combination of species with different germination requirements promotes species coexistence within a small scale (Pake and Venable 1996). However, this study suggests that plants also coexist on a larger scale. Variable weather patterns coupled with unique dormancy requirements and limited dispersal creates a potential mosaic of winter ephemeral diversity that varies greatly from area to area as well as above and below ground. This influences our concepts of rarity and commonness, which in the desert take on a spatial and temporal component: what may be locally rare one year might be very abundant the following year. The diversity stored in the seed bank is not often considered in the formation of these concepts. If both dormant and germinated seeds were used to characterize the plant species diversity of an area, it is possible that taxa that were once thought to be rare may actually be quite common, awaiting a temporal germination niche seasonally and unpredictably realized.

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# APPENDIX A. WINTER EPHEMERAL PLANT SPECIES GERMINATED DURING SEED BANK STUDY.

Taxon	Family	Site			
		BB	SB	SM	SQ
<i>Amsinckia</i> spp.	Boraginaceae	x	x	x	x
<i>Astragalus nuttallianus</i> DC.	Fabaceae		x	x	
<i>Bowlesia incana</i> Ruiz & Pav.	Apiaceae	x		x	x
<i>Bromus carinatus</i> Hook. & Arn.	Poaceae		x		
<i>Bromus rubens</i> L.	Poaceae		x	x	
<i>Calandrinia ciliata</i> (Ruiz & Pav.) DC.	Portulacaceae		x		
<i>Calycoseris wrightii</i> A. Gray	Asteraceae			x	
<i>Comissonia californica</i> (Nutt. ex Torr. & A. Gray) P.H. Raven	Onagraceae		x		
<i>Caulanthus lasiophyllus</i> (Hook. & Arn.) Payson	Brassicaceae				x
<i>Crassula erecta</i> (Hook. & Arn.) A. Berger	Crassulaceae	x	x	x	x
<i>Cryptantha barbigera</i> (A. Gray) Greene	Boraginaceae		x		
<i>Cryptantha decipiens</i> (M.E. Jones) A. Heller	Boraginaceae	x			
<i>Cryptantha maritima</i> (Greene) Greene	Boraginaceae	x	x		x
<i>Cryptantha pterocarya</i> (Torr.) Greene	Boraginaceae			x	
<i>Daucus pusillus</i> Michx.	Apiaceae		x		
<i>Dichelostemma pulchellum</i> (Salisb.) A. Heller	Liliaceae			x	
<i>Draba cuneifolia</i> Nutt. ex Torr. & A. Gray	Brassicaceae	x		x	x
<i>Erodium cicutarium</i> (L.) L'Her. ex Aiton	Geraniaceae		x		x
<i>Eschscholzia californica</i> Cham.	Papaveraceae		x	x	x
<i>Eucrypta micrantha</i> (Torr.) A. Heller	Hydrophyllaceae	x	x	x	x
<i>Filago arizonica</i> A. Gray	Asteraceae	x		x	x
<i>Gilia</i> Ruiz & Pav. sp.	Polemoniaceae				x
<i>Lepidium lasiocarpum</i> Nutt. ex Torr. & A. Gray	Brassicaceae		x	x	x
<i>Lesquerella gordonii</i> (A. Gray) S. Watson	Brassicaceae		x		
<i>Linanthus</i> Benth. sp.	Polemoniaceae		x	x	
<i>Lotus</i> sp.	Fabaceae		x	x	
<i>Lupinus sparsiflorus</i> Benth.	Fabaceae		x	x	
<i>Monolepis nuttalliana</i> (Schult.) Greene	Chenopodiaceae	x			x
<i>Muhlenbergia microsperma</i> (DC.) Kunth	Poaceae		x		x
<i>Parietaria hespera</i> B.D. Hinton	Urticaceae	x			x
<i>Pectocarya heterocarpa</i> (I.M. Johnst.) I.M. Johnst.	Boraginaceae			x	
<i>Pectocarya platycarpa</i> (Munz & I.M. Johnst.) Munz & I.M. Johnst.	Boraginaceae	x		x	x
<i>Pectocarya recurvata</i> I.M. Johnst.	Boraginaceae	x	x	x	x
<i>Perityle emoryi</i> Torr.	Asteraceae	x		x	
<i>Phacelia distans</i> Benth.	Hydrophyllaceae	x	x		x
<i>Plagiobothrys arizonicus</i> (A. Gray) Greene ex A. Gray	Boraginaceae			x	
<i>Plantago ovata</i> Forssk.	Plantaginaceae	x	x	x	
<i>Plantago patagonica</i> Jacq.	Plantaginaceae	x	x		x
<i>Poa bigelovii</i> Vasey & Scribn.	Poaceae	x	x	x	x
<i>Schismus arabicus</i> Nees.	Poaceae	x	x	x	x
<i>Silene antirrhina</i> L.	Caryophyllaceae		x		
<i>Sisymbrium irio</i> L.	Brassicaceae				x
<i>Vulpia octoflora</i> (Walt.) Rydb.	Poaceae	x	x	x	x