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Effect of Pinyon–Juniper Tree Cover on the Soil Seed Bank

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Abstract

As pinyon–juniper (specifically, *Pinus monophylla* and *Juniperus osteosperma*) woodlands in the western United States increase in distribution and density, understory growth declines and the occurrence of crown fires increases, leaving mountainsides open to both soil erosion and invasion by exotic species. We examined if the loss in understory cover that occurred with increasing tree cover was reflected in the density and diversity of the seed bank. Seed banks in stands with low, medium, and high tree cover were measured in late October for 2 yr. Multivariate analyses indicated that cover and diversity of standing vegetation changed as tree cover increased. However, the seed bank did not differ in overall seed density or species diversity because seeds of the 13 species that comprised 86% of the seed bank occurred in similar density across the tree-cover groups. Sixty-three percent of the species that were in the seed bank were absent from the vegetation (mostly annual forbs). In addition, 49% of the species that occurred in the standing vegetation were not in the seed bank (mostly perennial forbs and shrubs). Only *Artemisia tridentata*, *Bromus tectorum*, and *Collinsia parviflora* displayed positive Spearman rank correlations between percent cover in the vegetation and density in the seed bank. Thus, much of the standing vegetation was not represented in the seed bank, and the few species that dominated the seed bank occurred across varying covers of pinyon–juniper.

Resumen

Conforme los bosques de "Pinyon–juniper" (específicamente, *Pinus monophylla* Torr. & Frém. y *Juniperus osteosperma* (Torr.) Little) del oeste de Estados Unidos de América se incrementan en distribución y densidad, el crecimiento del estrato herbáceo disminuye y la ocurrencia de incendios aumenta, dejando las laderas de las montañas expuestas a la erosión del suelo y la invasión de especies exóticas. Examinamos si la pérdida de cobertura herbácea, que ocurre al aumentar la cobertura de los árboles, se reflejó en la densidad y diversidad del banco de semillas del suelo. Durante 2 años, a finales de octubre, se midió el banco de semillas en poblaciones con cobertura de árboles baja, media, y alta. Los análisis multivariados indicaron que la cobertura y diversidad de la población vegetal cambió al incrementarse la cobertura de árboles. Sin embargo, el banco de semillas del suelo no difirió en la densidad y diversidad general de especies, porque las semillas de las 13 especies que constituyeron el 86% del banco de semillas, ocurrieron en densidad similar en los tres niveles de cobertura de árboles. El 63% de las especies que formaban el banco de semilla no estaban presentes en la vegetación (principalmente hierbas anuales). Además, 49% de les especies presentes en la vegetación no estaban en el banco de semilla (principalmente hierbas perennes y arbustos). Solo *Artemisia tridentata* Nutt., *Bromus tectorum* L. y *Collinsia parviflora* Lindl. Mostraron correlaciones de rango Spearman positivas entre el porcentaje de cobertura en la vegetación y la densidad en el banco de semilla. Por lo tanto, buena parte de la vegetación no estuvo representada en el banco de semillas, y las pocas especies que dominaron el banco de semillas ocurrieron en los diferentes niveles de cobertura de "Pinyon–juniper".

Key Words: *Artemisia tridentata*, *Bromus tectorum*, *Collinsia parviflora*, *Poa secunda*, seed density, seed-bank diversity

INTRODUCTION

A prominent feature on midslopes of many mountain ranges in the Great Basin of western North America is the pinyon–juniper woodland belt. However, since 1860, pinyon–juniper woodlands have expanded into adjacent shrub steppe and other communities as well as increased in tree density (Burkhardt and Tisdale 1976; Jameson 1986; Miller and Wigand 1994; Miller and Tausch 2001). As woodlands expand into shrub steppe, major changes in community structure and diversity occur. Cover and diversity of the understory vegetation is reduced, in particular that of shrubs (Naillon et al. 1999). As tree size and density increase in the encroached shrub steppe, the accompanying greater fuel loads and more contiguous tree crowns promote higher-intensity wildfires that destroy both trees and understory vegetation (Tausch 1999; West 1999). Because burned areas are subject to erosion and invasion by exotic species, rapid re-establishment of vegetative cover is highly desirable.

A potentially large component of postdisturbance plant recruitment is from the soil seed bank (Harper 1977). Everett and Ward (1984) suggest that many initial colonizers after fire in pinyon–juniper woodlands are those species found in the seed bank prior to the fire. Therefore, knowledge of the existing seed bank is useful for planning postfire rehabilitation. For example, when a catastrophic fire occurs in pinyon–juniper woodlands, land managers need to know if there is a sufficient seed source for new plants and what species are likely to occur in order to better plan rehabilitation efforts.

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Although not as well studied as the three warm deserts of North America, a few seed-bank studies exist for the Great Basin (Hassan and West 1986; Guo et al. 1998; Humphrey and Schupp 2001; Boudell et al. 2002; Wehking 2002). In general, seed density in Great Basin communities is lower than in other North American deserts, and some evidence suggests that it is less variable because of the predominance of perennial vegetation (Kemp 1989). However, like other deserts, Great Basin seed banks are spatially patchy (Johnson and Fryer 1992; Guo et al. 1998; Boudell et al. 2002) because seed entrapment and seed persistence varies among spatial locations (Fenner 1985; Chambers 2000; Marone et al. 2004). Little is known about seed banks in pinyon–juniper woodlands, especially those in the western portion of the Great Basin, where *Pinus monophylla* and *Juniperus osteosperma* are the overstory trees (hereafter specifically referred to as Pimo–Juos woodland). *Pinus monophylla* most likely forms a transient seed bank because seeds quickly lose viability and hence either germinate the following spring or die (Gilleard 1985; Chambers 2001). The other common tree, *J. osteosperma*, and the most common shrub, *Artemisia tridentata*, produce seeds that remain viable for more than 1 yr, although the latter is relatively short-lived (Hassan and West 1986; Chambers et al. 1999). In contrast, small-seeded annual forbs generally form long-lived persistent seed banks.

Koniak and Everett (1982) conducted the only previously published study of the Pimo–Juos seed bank. Their research focused on microsite differences across a successional gradient. Unfortunately, the generality of their conclusions was limited by an experimental design that included a single study area and only one experimental plot for each successional stage. A broader extrapolation of these study results was further limited as they did not include data describing the proportions of different microsites at the landscape level. A more random sample design and multiyear measurements may be necessary to characterize seed-bank dynamics, as these systems are highly variable in both space and time (Bigwood and Inouye 1988; Gross 1990).

The primary objective of our study was to quantify changes in the seed bank as an *A. tridentata* subsp. *vaseyana* steppe community is converted to Pimo–Juos woodland. We hypothesized that as tree cover increases, understory cover and species diversity will decrease, whereas maximum stand age will increase; proportions of spatial microsites will change, with shrub and interspace microsites decreasing and undertree and litter microsites increasing; and seed-bank density and diversity will decrease due to the decrease of understory species that form the persistent seed bank. In addition, we hypothesized that vegetative cover of a given species would be positively correlated with the abundance of seeds of that species in the seed bank. A last hypothesis was that the majority of species that comprise the long-term persistent seed bank in Pimo–Juos woodlands would be from the understory vegetation, with the exception of *J. osteosperma*.

METHODS

Site Description

Nine circular study plots, each 50 m in diameter, were located on the east side of the Shoshone Mountain Range in central Nevada. Six plots were clustered in two areas just south of the mouth of Bonita Canyon (lat 39°03′N, long 117°31′W) and the other three plots were in an area 1.65 km farther south (lat 39°02′N, long 117°31′W). All plots were at elevations between 2 195 and 2 255 m and had similar soils (coarse loamy frigid typic haploxerolls), slope (7°–15°), and aspect (east of northeast to east facing). The mean daily temperature for Austin, Nevada, which is about 65 km north and at 2 066-m elevation, is 21°C and − 1°C in July and January, respectively, with average annual precipitation of 364 mm, mostly occurring in winter and spring (Western Regional Climate Center 2005). Precipitation in Austin for 1 October 2000 to 30 September 2001, for 1 October 2001 to 30 September 2002, and for 1 October 2002 to 30 September 2003, which were the year before and the 2 yr of the study, were 225 mm, 241 mm, and 253 mm, respectively.

All plots were located where Pimo–Juos woodlands were encroaching upon *A. tridentata* subsp. *vaseyana* steppe. Each of the study areas consisted of a mosaic in which different levels of *Pinus monophylla* and *Juniperus osteosperma* encroachment had occurred within visually-similar shrub/bunchgrass communities that were previously dominated by *A. tridentata* ssp. *vaseyana*. To achieve a range in tree dominance, three plots were selected in each of the three study areas such that each area had plots with high, medium, and low tree dominance, based on ocular estimates of *P. monophylla*–*J. osteosperma* cover. Tree cover was largely dominated by *P. monophylla*. The seven largest *P. monophylla* trees were cored at each plot to estimate maximum stand age. Two perpendicular increment cores were sampled for each tree at 1.07-m height, and the tree's age estimated as the average of the two cores.

Vegetation Assessment

Relative cover of understory and overstory species was recorded during peak biomass in mid-June of 2003 with the use of the line intercept method (Barbour et al. 1999). Three 50-m transects were spaced at even intervals to estimate cover on each plot. The tree overstory species were comprised of only *P. monophylla* and *J. osteosperma*, and projected cover was considered continuous if the gap between foliage was 5 cm or less. For understory shrubs, cover was measured the same as for the overstory trees. To determine the cover of rosette forbs and bunchgrasses, the basal intercept was recorded to the nearest 1 cm. For single-stem understory plants or plants that covered less than 1 cm, the total number of plants were counted along the transect. Each single-stem plant was considered to be 0.5 cm of cover, which is equivalent to 0.0001% cover. We then multiplied the number of single-stem individuals by 0.0001 to estimate total cover for that species. We also measured the spatial cover of the four principal microsites (tree litter, undertree, undershrub, and the interspace between woody plant canopies).

Seed-Bank Sampling

We sampled the seed bank in late October of both 2002 and 2003 when the majority of the seeds were dispersed but the ground was neither frozen nor snow-covered. Fifty seed-bank samples were collected from random locations within each plot. These samples were obtained by hammering a hollow, metal template of 10 × 10 × 5 cm (length × width × depth) into the ground and placing the enclosed soil into a labeled plastic bag. We sampled only to a depth of 5 cm because the majority of seeds occur within the top 5 cm of soil (Roberts 1981). Each sample also was characterized by microsite: tree litter, undertree, undershrub, or within the interspace. The samples were returned to the lab where they were wet to field capacity and then placed in a 3°–4°C refrigerator for cold–wet stratification. The samples remained in the refrigerator for a minimum of 90 d to vernalize the seeds. During the first week of February in 2003 and 2004, the samples were removed for seed-bank determination.

Seed-Bank Determination

The seed bank was determined by the germination method in which the viable seeds in the soil samples are given optimal germinating conditions (Gross 1990). Samples were spread over sterilized sand to an average thickness of 0.8 cm in germination flats of 25 × 25 × 5 cm (length × width × depth) in a greenhouse (Freas and Kemp 1983; Ter Heerdt et al. 1996). Flats were well watered for the first month, with the soil surface kept wet. Flats were given a half-strength dose of 20–20–20 NPK fertilizer about 4 wk into the watering to stimulate seedling growth and possibly induce germination of the seed of some species (Karssen and Hilhorst 1992; Giba et al. 2003). Individual seedlings were identified to species, counted, and removed as soon as the seedlings produced a minimum of one set of true leaves. Unknown seedlings of the same type were assigned a temporary classification, and samples were transferred to a pot containing a mixture of sand and potting soil for species identification at a later growth stage, generally upon flower production. Once the emergence of new seedlings abated, flats were allowed to dry for 2 wk before being watered again; new seedling emergence was recorded. Total time for the two wetting and drying cycles was 3–4 mo. Total number of seedlings that emerged during both wetting cycles was our measure of viable seeds in the seed bank. Seed-bank density was calculated as the number of seedlings divided by the cross-sectional area of the metal sampling template.

As with all seed-bank studies, actual seed density and diversity is likely underestimated. The potential causes of underestimation include undersampling of soil and insufficient methods to break dormancy or meet germination requirements. However, we followed a sampling approach of collecting numerous but small-sized soil samples, as suggested by Bigwood and Inouye (1988) and Gross (1990). In addition, our random sampling of the soil ensured that the inherent variability in the seed bank was captured. Meeting germination requirements and breaking dormancy mechanisms for all species that are potentially in the seed bank is difficult to accomplish. To counteract these obstacles, we tried to simulate the environmental conditions experienced by seeds in the soil through 90 d of wet–cold stratification and subsequent placement in a greenhouse that experienced diurnal temperature fluctuations (17°C) similar to those experienced in the Great Basin.

Data Analyses

Tree cover was used as both a continuous and discrete variable in the statistical analysis of the vegetation and seed-bank data. To examine trends in vegetation characteristics, tree cover was correlated with shrub, grass, and herbaceous cover; the cover of individual understory species; the total number of species in the vegetation (alpha diversity); and maximum stand age. Overall seed-bank density, seed-bank diversity, and seed-bank density for individual species and life-form groups also were correlated with tree cover to test if increasing tree cover reduced the abundance and diversity of the seed bank. If a species occurred in both the vegetation and in the seed bank, its cover value was tested for correlation with seed density. In addition, overall seed density and tree-litter depth were tested for correlation. All tests of association were performed with the use of PROC CORR in SAS Version 9 and examined by both Pearson product moment correlation (r) and the nonparametric Spearman rank correlation (r_s). Results from the two correlations were always very similar. Because the small number of plots ($n = 9$) made it difficult to test assumptions of normality and equal variance that are required for Pearson product moment correlation, only Spearman rank is reported. Unless otherwise indicated, $P \leq 0.05$ was considered significant.

Data sets with multiple factors were analyzed with tree cover as a discrete variable. The three tree-cover classes (low, medium, and high) that were used as a basis for original plot selection also were used as class variables for analysis of variance (ANOVA). Two-way ANOVA was used to assess the significance of microsite effects as a function of tree-cover class. Treatment effects on seed density and seed-bank diversity were assessed with the use of two-way ANOVA with tree-cover class as fixed effect and year as random effect. The influence of microsite on seed density was examined with the use of three-way ANOVA with tree-cover class and microsite as fixed effects and year as a random effect. Mean comparisons from ANOVA were conducted with the use of Tukey-adjusted least-square means. PROC MIXED in SAS Version 9 was used for all ANOVA tests.

Multivariate analyses were performed on both vegetation and seed-bank data. Differences in the vegetation community across the three tree-cover classes were examined with hierarchical cluster analysis, Bray-Curtis ordination, and multi-response permutation procedures (MRPP). Hierarchical cluster analysis grouped the nine study plots based on species composition similarity and displayed the results in a dendrogram. The distance measure and linkage method applied were Sorensen distance and group average, respectively. Bray-Curtis ordination is different than other ordinations in that the points are arranged with respect to endpoints. The endpoints for axis 1 were chosen based on the range of measured tree-cover values, which is the gradient of interest in this study. The distance measure used was Sorensen. MRPP, a nonparametric method that tests for group differences, yields a test statistic T, a value for the effect size A, and P value (McCune and Grace 2002; Huebner and Vankat 2003). Sorensen distance measure was used, and groups consisted of the three replicate plots in each tree-cover class. For seed-bank analyses, MRPP was used to examine community and life-history–level differences among tree-cover classes. Indicator-species analyses used a Monte Carlo randomization test (2 000 permutations) to discern the potential affinity of seed-bank species to a particular tree-cover class. Czekanowski-similarity-coefficient matrices (Kent and Coker 1992) were created with both individual species and life form used as responses. With the exception of the Czekanowski similarity coefficient, all multivariate analyses of community data used PC-ORD V 4.25 (Gleneden Beach, OR).

Some of the seed-bank data were not included in the analysis due to ambiguities in either their reproductive origin or identity. The perennial forb *Lithophragma tenellum* can reproduce via seeds or underground bulbils. Although this species was common in the first year of seed-bank determination, the number of individuals dramatically increased in the second year. During cold–wet stratification for the second year of seed-bank determination, *L. tenellum* individuals emerged while in cold storage. Individual stems of this species that emerged in clusters were assumed to be vegetatively propagated and were excluded from the seed-bank analyses. We considered *L. tenellum* individuals of the first year and those individuals that developed after hand-removing the vegetative propagules to be seed propagated. Also, tillers of *Poa secunda* vegetatively regenerated in both 2003 and 2004, and these individuals were excluded from the seed-bank analyses. Diversity measures are slightly underestimated, as some unknown seedlings could not be identified because they died or never flowered. Samples that could be identified at the genus, family, or growth-form level were included in the analysis at that level of taxonomic resolution. Sagebrush seedlings were assumed to be *A. tridentata* subsp. *vaseyana* because that was the only variety of sagebrush occurring on the study plots.

RESULTS

Changes in Vegetation Characteristics With Tree Cover

Total grass, herbaceous, and shrub cover significantly decreased as total cover of Pimo–Juos trees increased (Fig. 1, top). Relative cover was also examined because total vegetation cover changed across the study plots, and it showed similar results as total cover (data not shown). Shrub cover decreased the most precipitously with increasing tree cover (Fig. 1). All five of the shrub species decreased with increased tree cover, but only *A. tridentata* subsp. *vaseyana* and *Chrysothamnus viscidiflorus* had significant correlations at the individual species level (Table 1). For species such as *Ephedra nevadensis* with low cover and infrequent occurrence (*E. nevadensis* occurred in only two of nine plots), the lack of a significant correlation is likely due to an insufficient sample size. For other species such as *Purshia tridentata* with relatively high cover and frequent occurrence (five of nine in this case), the lack of a significant correlation indicates that the species did not respond to changes in Pimo–Juos cover. Overall, total grass cover showed a gradual decline with the increase in tree cover (Fig. 1), but only the perennial bunchgrass *Achnatherum thurberianum* significantly decreased at the individual species level (Table 1). The most common grasses in the study, the perennial bunchgrass *P. secunda* and the invasive annual grass *Bromus tectorum*, had similar cover across tree-cover classes. Finally, cover for the majority of individual herbaceous species declined with increased tree cover, although the relationship was significant for only one annual and four perennial forb species. Of these five, two were well-represented in the vegetation: *Astragalus purshii* and *Phlox hoodii*.

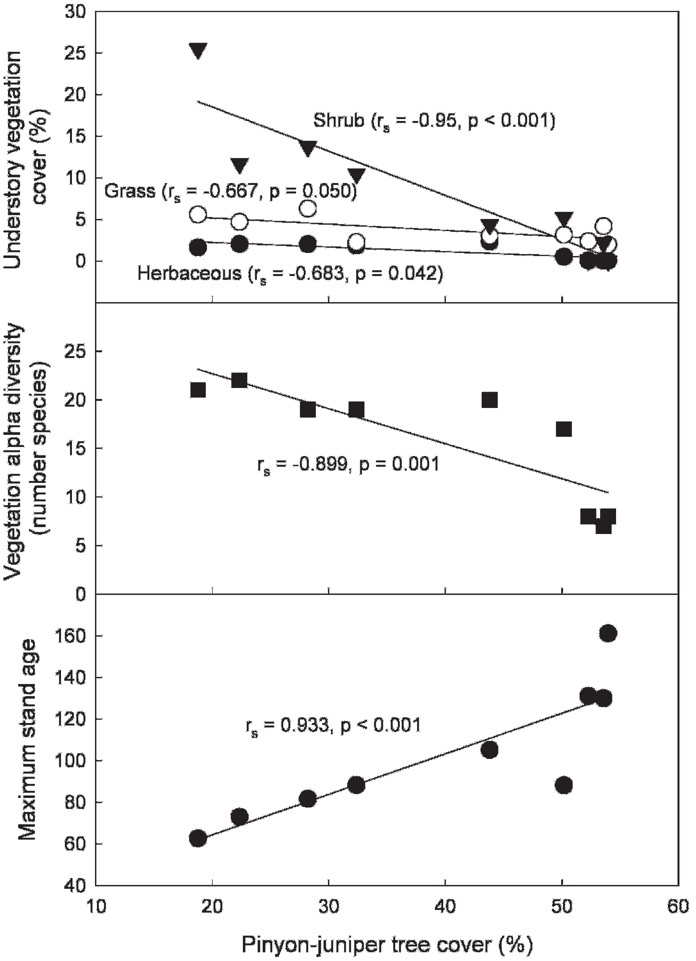

Figure 1. Relationship between *Pinus monophylla–Juniperus osteosperma* (pinyon–juniper) tree cover and (top panel) understory cover of shrub (inverted triangle), grass (open circles), and herbaceous (solid circles) plants; (middle panel) alpha diversity of the vegetation (i.e., number of species) at each study plot; and (bottom panel) maximum stand age determined from seven largest *P. monophylla* trees in each plot. Spearman rank correlation (r_s) and its *P* value are shown for individual data sets.

As tree cover increased, the study plots contained fewer species. The combined total of species across all nine study plots was 37 (including the two tree species), but the number of species in the vegetation for low and medium cover plots averaged more than twice that for high-cover plots (Fig. 1, middle panel). Twenty-four species were restricted to the low and medium cover plots, and no species were unique to the high-cover plots (Table 1). Of the species that only occurred at low and medium cover, most were negatively associated with tree cover. Tree cover and tree age were positively and significantly correlated with each other (Fig. 1, bottom panel). Therefore, changes in vegetation characteristics with tree cover as well as changes in seed-bank characteristics with tree cover that are noted in the text could be due to changes in tree cover or to changes in stand age. Although we recognize this potentially confounding effect of tree cover and stand age, we focus our analyses and interpretations on tree cover primarily because cover is easier and quicker to determine.

Our original placement of study plots into low, medium, and high tree-cover classes was supported by multivariate analyses

Table 1. Average percentage cover in the standing vegetation across all plots for each species, Spearman rank correlation (r_s), and its P value between percent cover by species and total *Pinus monophylla* and *Juniperus osteosperma* tree cover ($N = 9$), and number of plots (of three) that each species was present for each tree-cover class. Species are sorted by life form, then alphabetically by species name.

		Correlation between species cover and tree cover		No. of plots species present in tree-cover class		
Understory species	Average percent cover	r_s	P	High	Med	Low
Shrubs						
Artemisia tridentata Nutt. subsp. *vaseyana*	6.05	−0.904	<0.001	1	3	3
Chrysothamnus viscidiflorus (Hook.) Nutt.	0.30	−0.809	0.008	0	2	3
Ephedra nevadensis S. Wats.	0.06	−0.274	0.476	1	0	1
Purshia tridentata (Pursh) DC.	1.70	−0.496	0.174	1	2	2
Tetradymia canescens DC.	0.05	−0.644	0.061	0	1	2
Grasses—annual						
Bromus tectorum L.	0.39	−0.251	0.515	3	2	3
Grasses—perennial						
Achnatherum hymenoides (Roemer & J. A. Schultes) Barkworth	<0.01	−0.137	0.725	0	1	0
Achnatherum thurberianum (Piper) Barkworth	0.28	−0.712	0.031	0	3	3
Elymus elymoides (Raf.) Swezey	0.08	−0.564	0.113	1	0	2
Poa secunda J. Presl	2.96	−0.517	0.150	3	3	3
Pseudoroegneria spicata (Pursh) A. Löve	0.02	−0.274	0.476	0	0	1
Forbs—annual						
Collinsia parviflora Lindl.	0.05	0.000	1.000	2	1	1
Cryptantha circumscissa (Hook. & Arn.) I. M. Johnston	<0.01	0.299	0.435	1	2	0
Eriastrum sparsiflorum (Eastw.) Mason	<0.01	−0.456	0.217	0	1	1
Gayophytum diffusum Torr. & Gray	<0.01	−0.428	0.250	0	3	2
Leptosiphon harknessii (Curran) J. M. Porter & L. A. Johnson	<0.01	−0.802	0.009	0	1	3
Microsteris gracilis var. *gracilis* (Hook.) Greene	<0.01	−0.337	0.376	0	2	1
Forbs—perennial						
Agoseris glauca (Pursh) Raf.	<0.01	−0.337	0.376	0	1	2
Allium atrorubens S. Wats.	<0.01	0.000	1.000	0	1	0
Antennaria dimorpha (Nutt.) Torr. & Gray	<0.01	0.000	1.000	0	1	0
Arabis holboellii Hornem. var. *retrofracta*	<0.01	0.539	0.135	3	2	2
Astragalus filipes Torr. Ex Gray	<0.01	0.000	1.000	0	1	0
Astragalus purshii Dougl. Ex Hook.	0.10	−0.765	0.016	2	2	3
Crepis acuminate Nutt.	0.02	−0.772	0.015	0	1	2
Cryptantha flavoculata (A. Nels.) Payson	0.02	−0.436	0.241	0	1	2
Cymopterus ibapensis M. E. Jones	0.08	−0.566	0.112	0	2	2
Erigeron aphanactis (Gray) Greene	<0.01	−0.388	0.302	0	1	1
Eriogonum elatum Dougl. Ex Benth.	0.07	−0.840	0.005	0	1	3
Eriogonum microthecum Nutt.	<0.01	−0.411	0.272	0	0	1
Lithophragma tenellum Nutt.	<0.01	0.137	0.725	0	1	0
Lupinus caudatus Kellogg subsp. *caudatus*	0.05	−0.402	0.284	0	2	2
Penstemon watsonii Gray	0.01	0.000	1.000	0	1	0
Phlox hoodii Richards	0.68	−0.728	0.026	1	3	3
Phlox longifolia Nutt.	<0.01	−0.455	0.219	0	3	2
Pleiacanthus spinosus (Nutt.) Rydb.	0.03	−0.137	0.725	0	1	1

of vegetation data, although the absolute tree cover varied within the low- and medium-cover classes. The final join between entities in hierarchical cluster analysis occurred between the three high plots as one entity and the three low and three medium plots as the other entity (Fig. 2), indicating that all three high tree-cover replicates were more alike to each other than to the six low and medium plots. Bray-Curtis ordination (not shown) showed distinct groupings along axis 1 by tree-cover class. MRPP computed a test statistic of $T = -3.307$ ($P = 0.006$), indicating that the likelihood of differences among tree-cover classes was high. Further mean comparisons revealed that all three tree-cover classes were compositionally different from each other.

The relative ground area taken up by interspace, undershrub, tree-litter, and under tree microsites varied with tree-cover class (Table 2; Fig. 3). In agreement with our second hypothesis, the

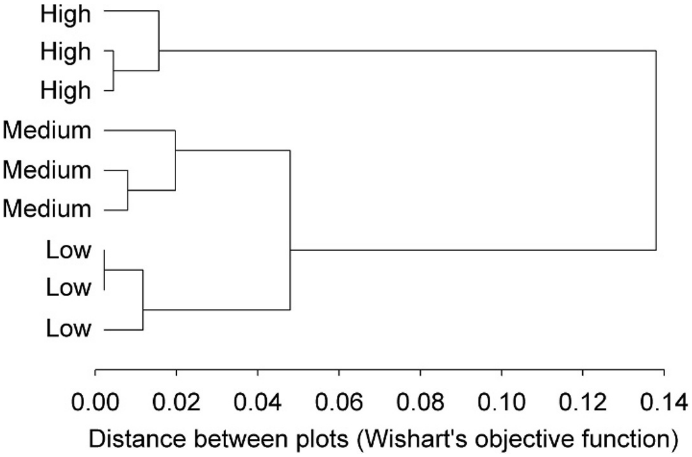

Figure 2. Cluster analysis dendrogram based on arc-sine transformed vegetation cover for high, medium, and low tree-cover plots.

proportions of interspace and undershrub microsites in the low- and medium-cover classes were greater than those in the high-cover class, whereas those for both tree-litter and undertree microsites were lower. Although the 3-way interaction of tree-cover class × microsite × year was also significant, the ordering of the tree-cover classes within each microsite was the same for each year, although the statistical groupings differed within year. Thus, the mean comparisons shown in Figure 3 are not contradicted by those for the 3-way interaction.

Table 2. ANOVA table for proportion of microsites (top) and seed density (bottom) with the use of tree-cover class (TCC) and microsite (MS) as fixed effects and year as a random effect. Proportion of different microsites (tree litter, undertree, undershrub, and interspace) among three different tree-cover classes (low, medium, and high) determined during collection of randomly placed seed-bank samples in each plot during 2 yr of seed-bank sampling. Seed density of four microsites among three tree-cover classes for seed-bank samples collected during 2 yr.

Effect	Num df	Den df	F value	$P > F$
Proportion of microsites				
TCC	2	24	< 0.01	1.000
MS	3	24	24.96	< 0.001
TCC * MS	6	24	12.66	< 0.001
Year	1	24	< 0.01	0.965
Year * TCC	2	24	< 0.01	0.998
Year * MS	3	24	1.71	0.191
Year * TCC * MS	6	24	3.37	0.015
Seed density				
TCC	2	6	0.03	0.971
MS	3	39	5.55	0.003
TCC * MS	6	39	2.98	0.017
Year	1	39	2.13	0.152
Year * TCC	2	39	0.78	0.465
Year * MS	3	39	0.40	0.752
Year * TCC * MS	5	39	0.17	0.973

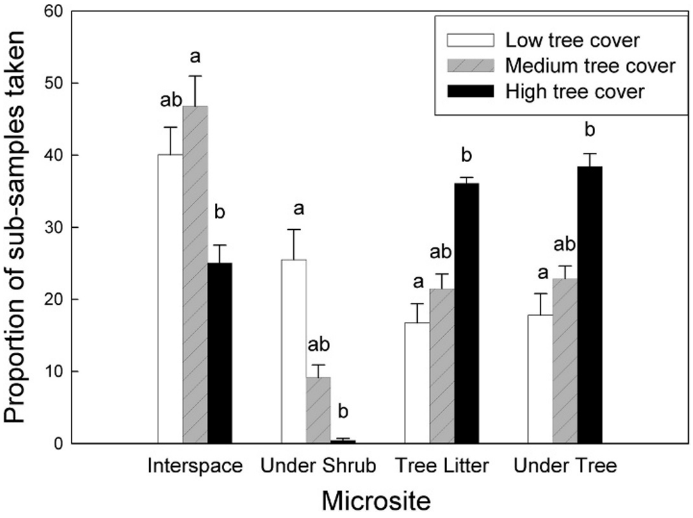

Figure 3. Proportion of soil subsamples taken from a microsite for each tree-cover class. Values are mean ± SE ($N = 50$) at each plot. Lowercase letters above the bars indicate significant differences among tree-cover classes within a microsite.

Changes in Seed-Bank Characteristics With Tree Cover

Contrary to the third hypothesis, total seed density and species diversity in the seed bank did not significantly change as Pimo–Juos tree cover increased (Fig. 4). Seed density by life-form groups also was not correlated with tree cover (data not shown). Furthermore, the seed-bank community as a whole did not differ between tree-cover classes using either seed density by species or by life-form groups as responses in MRPP ($T = -0.0468$, $P = 0.437$ and $T = -0.050$, $P = 0.434$, respectively). However, shrub seed densities of high and medium tree-cover classes did differ from low tree-cover classes using MRPP ($T = -1.826$, $P = 0.054$). Finally, Czekanowski similarity coefficients did not display any patterns in relation to changes in tree cover.

The most abundant species in the seed bank were the perennial grass *P. secunda* and two annual forbs, *Gayophytum diffusum* and *Collinsia parviflora* (Table 3). For seven of the nine species that comprised 2% or more of the seed bank (*P. secunda*, *G. diffusum*, *C. parvilfora*, *L. tenellum*, *Arabis* spp., *B. tectorum*, and *Mimulus suksdorfii*), seed-bank densities were not correlated with tree cover. Most of these species occurred in more than half the plots, indicating that seed density did not respond to tree cover. Only two species exhibited a significant correlation between seed density and tree cover. The annual forb *Microsteris gracilis* var. *gracilis* exhibited a significant ($P = 0.009$) increase in density from medium to high tree cover, and *A. tridentata* exhibited a significant decrease in seed density as tree cover increased ($P = 0.032$).

Most species did not have significantly greater seed-bank densities at any single tree-cover class. Seventy-one percent of the species found in the seed bank (34 of 48) were present in either one or two tree-cover classes, but not all three. Most of these species had only 1–5 individuals emerge during the two wetting cycles of the germination trials. However, *Descurainia pinnata* and *Epilobium ciliatum* were indicators of high tree cover (indicator value [IV] = 80, $P = 0.08$ and IV = 100, $P = 0.04$, respectively).

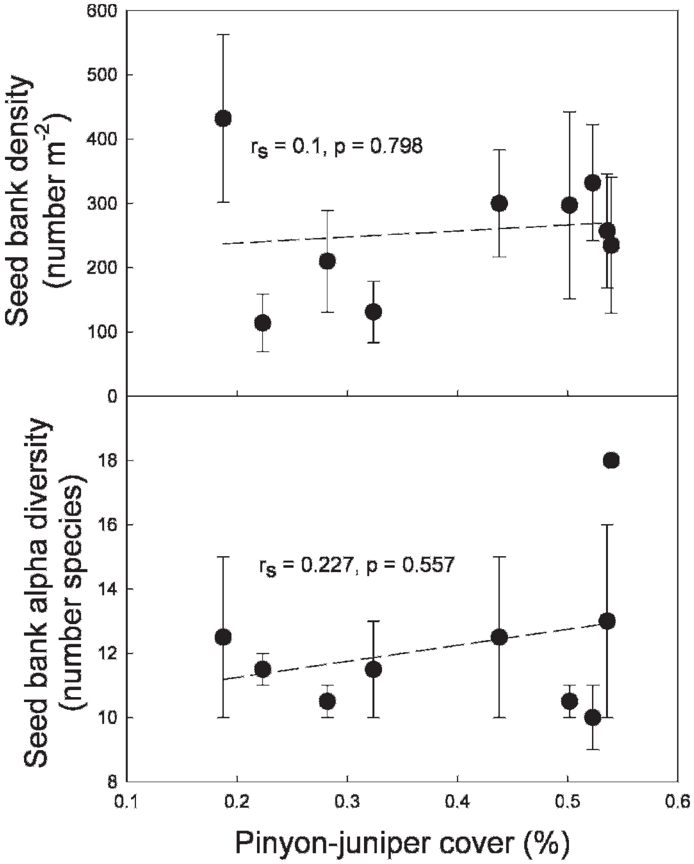

Figure 4. Top panel, Spearman rank correlation between mean seed density and *Pinus monophylla–Juniperus osteosperma* (pinyon–juniper) tree cover. Values are mean ± SE averaged over both field seasons, for each plot. Bottom panel, Spearman rank correlation between total number of species in the seed bank (alpha diversity) and tree cover. Values are total species ± SE averaged over both field seasons, for each plot.

Year-to-year variation was low for total seed density but high for species diversity. Mean seed densities across all plots in 2003 and 2004 were 272 (SE = 37) and 244 (SE = 44) seed · m^{-2}, respectively. Both sampling years yielded the same number of species in the seed bank (36), but because each year had species that were unique to that year, the total species over both years was 48. Sixty-seven percent of the species were common to both years.

Seed density was not significantly different among tree-cover classes within a given microsite (Table 2; Fig. 5). Across all tree-cover classes, the descending order of seed density was undershrub, interspace, undertree, and tree litter. However, note that statistical differences by tree-cover class within the undershrub microsite were not estimable because no shrub microsites occurred in the random sample of seed-bank locations in high tree-cover plots during the second sampling year. Because we were curious about whether tree-litter depth may influence seed banks, we recorded litter depth, which varied from 0.2 to 13.8 cm (mean = 4 cm), but litter depth was not significantly related to seed density (data not shown).

Relationship Between the Seed Bank and the Vegetation

The correspondence between presence of a species as mature vegetation and presence of that species in the seed bank was consistently low. Thirty of 48 species in the seed bank did not occur in the vegetation, and 18 of the 37 species in the standing vegetation were not detected in the seed bank. Those species present in the seed bank but absent from the vegetation were mostly annual forbs (Table 4A), whereas those species in the standing vegetation but not in the seed bank were perennial forbs and shrubs (Table 4B). A total of 18 species occurred in both the seed bank and in the vegetation, but only three of these species (*A. tridentata*, *B. tectorum*, and *C. parviflora*) had a significant, positive correlation between their seed density and their cover in the vegetation (Table 4C).

Low species diversity in the high tree-cover class was reflected both in the aboveground vegetation and in the seed bank. Of the 24 species that only occur in the standing vegetation of low or medium plots, only six occur in the seed bank of high tree-cover plots (Table 5). The 13 species that occur in the vegetation of the high tree-cover plots are also found in the vegetation of the low and medium plots. Of these species, only *J. osteosperma*, *E. nevadensis*, and *P. hoodii* were not found in the seed bank of low and medium tree-cover plots.

DISCUSSION

Changes in Vegetation and Seed-Bank Characteristics With Tree Cover

As hypothesized, both understory cover and diversity decreased as tree cover increased (Figure 1; Table 1). In addition, changes in microsite composition followed the expected pattern of decreasing shrub microsites and increasing tree and tree-litter microsites as tree cover increased (Fig. 3). However, the changes in seed-bank characteristics were unexpected (Tables 3 and 4; Fig. 4). We hypothesized that increased tree cover reduces or eliminates understory species, which in turn reduces their contribution to the persistent seed bank. Contrary to this hypothesis, the 13 species that comprised 86% of the total seed bank occurred in all three tree-cover classes, and their seed density did not change significantly with change in tree cover. Furthermore, four species (*P. secunda*, *C. parviflora*, *Arabis* spp., and *B. tectorum*), which account for 52% of the seed bank, had similar vegetation cover and seed density in all tree-cover classes. Therefore, the species that are most abundant in the seed bank, and hence drive the overall seed density response, have similar seed densities across the tree-cover gradient.

Although the overall pattern had no relationship between increased tree cover and both seed density and seed-bank diversity, four species showed significant relationships between tree cover and seed density. *Microsteris gracilis* var. *gracilis*, *Descurainia pinnata*, and *Epilobium ciliatum*, which are three small-seeded annuals, had positive relationships with tree cover and were indicator species of the high tree-cover class. In contrast, *A. tridentata* was the only species for which seed density was negatively associated with tree cover. This result is consistent with previous studies (Koniak and Everett 1982) and is likely due to a combination of 1) the density of *A. tridentata* adults decreases with increasing tree cover; 2) 90% of its small, wind-dispersed seeds fall within 9 m of the parent plant (Frischnecht 1978); and 3) the bulk of *A. tridentata* seeds lose viability within 1 yr of dispersal (Hassan and West 1986; Chambers et al. 1999).

Table 3. Percent composition of the seed bank for all species that averaged $\geq$ 0.2% over all tree-cover classes and over both sampling years, Spearman rank correlation (r_s), and its *P* value between seed density and tree cover, and number of plots (of three) that each species was present in the seed bank for each tree-cover class. Percent composition of all other species is noted for reference.

Species	Average percent of seed bank	Correlation between seed density and tree cover		No. of plots that seed was present in tree-cover class		
		r_s	*P* value	High	Medium	Low
Shrubs						
Artemisia tridentata	2.0	−0.710	0.032	1	2	3
Ribes L. species	0.3	0.119	0.760	1	2	1
Grasses—annual						
Bromus tectorum	3.5	−0.221	0.567	3	3	2
Grasses—perennial						
Poa secunda	26.9	0.293	0.444	3	3	3
Forbs—annual						
Collinsia parviflora	15.7	0.126	0.748	3	3	2
Cryptantha circumscissa	0.4	0.199	0.607	1	1	1
Cryptantha torreyana (Gray) Greene	1.9	0.349	0.357	3	2	3
Gayophytum diffusum	19.7	0.167	0.668	3	3	3
Gnaphalium palustre Nutt.	0.3	0.373	0.323	2	1	1
Microsteris gracilis var. *gracilis*	4.1	0.803	0.009	3	1	0
Mimulus suksdorfii Gray	2.0	0.465	0.207	1	2	0
Forbs—perennial						
Allium L. species	0.2	0.120	0.759	1	1	1
Arabis L. species	6.0	0.267	0.488	3	3	3
Erigeron aphanactis	1.4	0.034	0.931	1	3	2
Lithophragma tenellum	9.1	0.018	0.963	1	1	2
Unknown forb	0.7	0.487	0.183	2	3	2
All other seed-bank species	5.7					

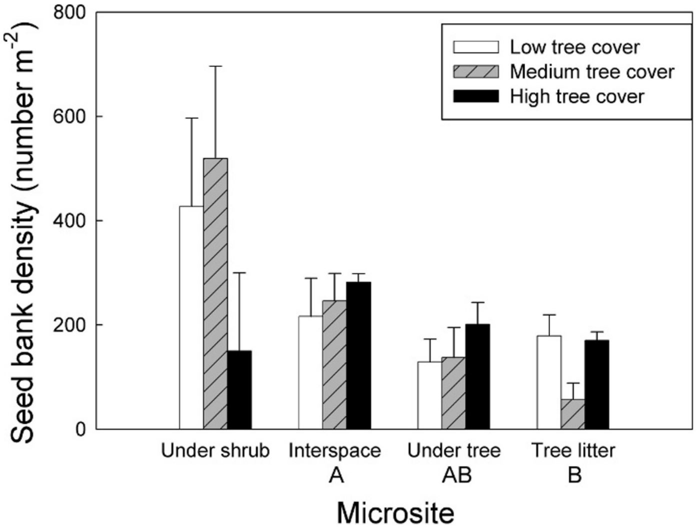

Figure 5. Seed-bank density by microsite and tree-cover class. Values are mean ± SE ($N = 150$) for each tree-cover class. No significant differences occurred among tree-cover classes within each interspace, undertree, and tree-litter microsite. Note that differences among tree-cover classes within the undershrub microsite could not be determined because shrub microsites did not occur in the random sampling of plots during the second year in the high tree-cover group. Uppercase letters below the *x* axis indicate significant differences among microsite.

Relationship Between the Seed Bank and the Standing Vegetation

The presence of a species in the vegetation did not ensure that a seed bank was also present for that species. Although 81% of the vegetation was perennial species, only 43% of the total perennial species in the standing vegetation were represented in the seed bank, whereas 86% of the annual species occurred in the seed bank. Fifteen of 18 perennial species that were present in the vegetation but absent from the seed bank primarily occurred in low and medium tree-cover classes. Potential reasons for the absence of species in the seed bank include low seed production, short seed longevity, and seed predation.

Of those species that occurred in both the vegetation and in the seed bank, seed-bank density of an individual species was correlated with its vegetative cover only for *A. tridentata*, *B. tectorum*, and *C. parviflora*. A positive correlation between vegetation cover and seed-bank density for *A. tridentata* was observed in other Great Basin studies (Koniak and Everett 1982; Hassan and West 1986; Marlette and Anderson 1986).

Perhaps of greater interest are the species that were found in the seed bank but were under-represented in the standing vegetation. For example, nine species, which comprised 34% of the seed bank, had similar seed-bank abundance across the tree-cover classes, but were rare or not present at all in the standing vegetation. One possible explanation for this in-

Table 4. Co-occurrence of species in the seed bank and standing vegetation.

(A) Species present in the seed bank but absent from standing vegetation

Shrubs
- *Ribes* species

Forbs—annual
- *Aster* L. species
- *Cryptantha torreyana*
- *Cryptantha watsonii* (Gray) Greene
- *Descurainia pinnata* (Walt.) Britt.
- *Gilia* Ruiz & Pavón spp.
- *Gnaphalium palustre*
- *Lappula occidentalis* (S. Wats.) Greene var. *occidentalis*
- *Lactuca serriola* L.
- *Mimulus densus* A. L. Grant
- *Mimulus suksdorfii*
- *Nicotiana attenuate* Torr. Ex S. Wats.
- *Pseudognaphalium stramineum* (Kunth) A. Anderb.
- *Veronica peregrine* L.

Forbs—perennial
- *Arenaria* L. spp.
- *Epilobium ciliatum* Raf. subsp. *ciliatum*
- *Opuntia* P. Mill. spp.
- *Packera multilobata* (Torr. & Gray ex Gray) W. A. Weber & A. Löve
- *Urtica dioica* L.
- Unknown forb 1
- Unknown forb 2

Ten unknown taxa

(B) Species present in standing vegetation but absent from seed bank

Trees
- *Juniperus osteosperma* (Torr.) Little

Shrubs
- *Chrysothamnus viscidiflorus*
- *Ephedra nevadensis*
- *Tetradymia canescens*

Grasses—perennial
- *Pseudoroegneria spicata*

Forbs—annual
- *Eriastrum sparsiflorum*

Forbs—perennial
- *Agoseris glauca*
- *Antennaria dimorpha*
- *Astragalus filipes*
- *Crepis acuminata*
- *Cryptantha flavoculata*
- *Cymopterus ibapensis*
- *Eriogonum elatum*
- *Eriogonum microthecum*
- *Lupinus caudatus* subsp. *caudatus*
- *Penstemon watsonii*
- *Phlox hoodii*
- *Phlox longifolia*
- *Pleiacanthus spinosus*

Table 4. Continued.

(C) Species present in both seed bank and standing vegetation, along with the Spearman rank correlation (r_s) and its *P* value between seed density (averaged over both sampling years) and vegetative cover for each species

Species	Correlation between seed density and plant cover	
	r_s	*P* value
Trees		
Pinus monophylla Torr. & Frém.	0.428	0.250
Shrubs		
Artemisia tridentata	0.841	0.005
Purshia tridentata	0.572	0.108
Grasses—annual		
Bromus tectorum	0.829	0.006
Grasses—perennial		
Achnatherum hymenoides	− 0.244	0.527
Achnatherum thurberianum	0.000	1.000
Elymus elymoides	0.307	0.421
Poa secunda	0.301	0.431
Forbs—annual		
Collinsia parviflora	0.715	0.030
Cryptantha circumscissa	− 0.006	0.988
Gayophytum diffusum	− 0.507	0.164
Leptosiphon harknessii	0.172	0.659
Microsteris gracilis var. *gracilis*	− 0.228	0.556
Forbs—perennial		
Allium atrorubens	0.573	0.107
Arabis species	0.496	0.175
Astragalus purshii	0.396	0.292
Erigeron aphanactis	0.464	0.208
Lithophragma tenellum	0.600	0.088

congruent result is that the species was present in the plot but simply not on any vegetation transect. However, we compiled a complete list of all species in each plot, including those not on the vegetation transects, and thus likely observed all perennial species present during the study. A second potential explanation is that some annual species do not appear in the vegetation each year (Nowak et al. 1994), and we may have missed them with only 1 yr of vegetation sampling. Finally, the presence of a species in the seed bank that was absent from the aboveground vegetation could be a consequence of seed dispersal from adjacent areas or seed persistence in the soil after the death of an adult plant. Because seed dispersal mechanisms and longevity are poorly understood for many plants in pinyon–juniper woodlands, detailed explanations of patterns in the seed bank can be made for only a few species. For example, *Ribes* spp. was in the seed bank at all tree-cover classes, but not in the vegetation. The red berries of this shrub are dispersed by birds and mammals, and a small population of this species that was along an ephemeral stream about 50 m from the plots may be the source of seeds in our study plots.

Table 5. List of species that only occur in the vegetation of low or medium tree-cover classes and their corresponding occurrence in the seed bank of the high tree-cover class.

Vegetation—species present in low-/medium-cover classes	Seed bank presence/absence in high-cover class
Shrubs	
Chrysothamnus viscidiflorus	–
Tetradymia canescens	–
Grasses—perennial	
Achnatherum hymenoides	+
Achnatherum thurberianum	–
Pseudoroegneria spicata	–
Forbs—annual	
Eriastrum sparsiflorum	–
Gayophytum diffusum	+
Leptosiphon harknessii	–
Microsteris gracilis var. *gracilis*	+
Forbs—perennial	
Agoseris glauca	–
Allium atrorubens	+
Antennaria dimorpha	–
Astragalus filipes	–
Crepis acuminata	–
Cryptantha flavoculata	–
Cymopterus ibapensis	–
Erigeron aphanactis	+
Eriogonum elatum	–
Eriogonum microthecum	–
Lithophragma tenellum	+
Lupinus caudatus subsp. *caudatus*	–
Penstemon watsonii	–
Phlox longifolia	–
Pleiacanthus spinosus	–

Variations in Seed Density and Diversity Among Spatial Microsites

Microsite patchiness in seed density distribution in our study is similar to other seed-bank studies in desert ecosystems. In particular, high seed density under shrubs versus other microsites has been observed in North American deserts (Nelson and Chew 1977; Reichman 1984; Hassan and West 1986; Guo et al. 1998) and in Argentina (Marone et al. 1998). The higher seed density in shrub microsites is because 1) shrubs act as a barrier to abiotic seed dispersal, effectively slowing the seed's velocity and depositing it (Johnson and Fryer 1992); 2) there is a higher occurrence of forbs and grasses under the shrub canopy; and 3) there is potentially greater seed longevity at this microsite. The same pattern of ordering by microsite in our study was also seen by Koniak and Everett (1982).

MANAGEMENT IMPLICATIONS

Our data revealed some surprising but relevant information for land managers to consider as they formulate reseeding and other rehabilitation plans for disturbed Pimo–Juos woodlands. First, the dominant species in the vegetation, with the exception of *P. secunda*, were not well represented in the seed bank. *P. secunda* was consistently represented in both the standing vegetation and the seed bank over a relatively wide range of tree cover. Second, species associated with early successional stages, such as the annual forbs *G. diffusum* and *C. parviflora* and the perennial grass *P. secunda*, were relatively abundant over a wide range of tree cover. Thus, initiation of natural successional processes is likely after fire or other disturbance. Third, of special concern is the positive relation between *B. tectorum* cover and its seed density. Although *B. tectorum* seeds do not survive fire well, the number of seeds that do survive often are sufficient to disrupt natural succession and transform a burned site into a *B. tectorum* monoculture in just a few years postfire (Hassan and West 1986; Humphrey and Schupp 2001). Fourth, this study revealed low seed densities for some of the more desirable perennial grasses and shrubs. Thus, managers generally cannot rely upon recruitment from the natural seed bank to quickly re-establish these species after disturbance.

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