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Estimating Soil Seed Bank Characteristics in Ponderosa Pine Forests Using Vegetation and Forest-Floor Data

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Abstract—Soil seed banks are important for vegetation management because they contain propagules of species that may be considered desirable or undesirable for site colonization after management and disturbance events. Knowledge of seed bank size and composition before planning management activities facilitates proactive management by providing early alerts of exotic species presence and of abilities of seed banks to promote colonization by desirable species. We developed models in ponderosa pine (*Pinus ponderosa*) forests in northern Arizona to estimate the size and richness of mineral soil seed banks using readily observable vegetation and forest-floor characteristics. Regression models using three or fewer predictors explained 41 to 59 percent of the variance in 0- to 2-inch (0- to 5-cm) seed densities of total and native perennial seed banks. Key predictors included aboveground plant species richness/10.8 ft^2 (1 m^2), litter weight and thickness, and tree canopy type (open or closed). Both total and native perennial seed banks were larger and richer in plots containing: (1) species-rich understories, (2) sparse litter, and (3) tree canopy openings. A regression tree model estimated that seed bank density of native perennials is 14-fold greater if aboveground plant richness exceeds eight species/10.8 ft^2, forest-floor leaf litter is < 1 inch (2.5 cm) thick, and tree canopies are open.

Introduction

For the purpose of vegetation management, soil seed banks are viable seeds stored in litter (Oi horizon), duff (Oe+a horizon), or mineral soil that can germinate when germination requirements are met (Bakker and others 1996, Thompson 1987). Seed banks provide propagules that may influence plant community changes after disturbance events and management activities (van der Valk and Pederson 1989). Not all plant species form large and persistent soil seed banks. Species that are short-lived aboveground and associated with disturbance often develop the largest and most persistent seed banks (Koniak and Everett 1982; Roberts 1981; Wienk and others 2004). For example, the native biennial spreading fleabane (*Erigeron divergens*) and the non-native biennial common mullein (*Verbascum thapsus*) are abundant in seed banks of ponderosa pine (*Pinus ponderosa*) forests near Flagstaff, Arizona (Abella and others 2007, Korb and others 2005). However, some native perennials, such as White Mountain sedge (*Carex geophila*), mountain muhly (*Muhlenbergia montana*), and muttongrass (*Poa fendleriana*), also occur in these seed banks.

Soil seed banks are important for vegetation management in ponderosa pine forests in at least four ways. First, seed banks may provide on-site seed sources for species considered undesirable (for example, exotic species) for site colonization after management activities such as tree thinning. Second, they may provide seed sources for early successional species and species considered desirable (for example, perennial grasses) that hasten vegetation recovery after disturbance. Third, seed banks can provide seedlings for the establishment and maintenance of some aboveground plant populations in the absence of major disturbance. Fourth, seed banks lacking desirable species may indicate that seeding or other treatments are necessary to meet management objectives for understory vegetation. Locally calibrated estimates of seed bank size and composition could assist resource managers in determining possible understory responses to management activities. Knowledge of these seed bank characteristics could be used to predict which exotic species could become management concerns or for deciding whether to seed native species based on their abundance in seed banks (Glass 1989). Although on- or off-site seed dispersal from existing vegetation is also important (Wienk and others 2004), several studies have found partial correlations between seed bank composition and species colonizing sites after disturbance (Korb and others 2005, Springer and Hastings 2004).

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Our objective was to develop a first approximation of models to estimate seed bank density and species richness using soil and aboveground vegetation variables that are more easily measured in the field than the seed bank characteristics themselves. Our models were developed for ponderosa pine forests in a local study area. Thus, the models require more extensive testing before extrapolation to other ponderosa pine forests that potentially differ from our study area in species pools and in other factors affecting seed banks.

Methods

Study Area

We conducted this study on forty-five, 82 × 66 ft (25 × 20 m), 0.12-acre (0.05-ha) plots in the southern half of the Northern Arizona University Centennial Forest. The Centennial Forest consists of 640-acre (259-ha) sections that alternate with U.S. Forest Service sections within the Coconino National Forest, about 5 to 15 mi (8 to 24 km) southwest of the city of Flagstaff in northern Arizona. The maximum distance between plots was 10 mi (16 km). Forests in the study area are pure ponderosa pine with occasional Gambel oak (*Quercus gambelii*). Understory vegetation is dominated by grasses, sedges, and forbs. Plot elevations ranged from 7,072 to 7,472 ft (2,156 to 2,278 m), with slope gradients less than 10 percent. Plots were located and stratified by a terrestrial ecosystem classification following methods in Abella and others (2007). Five plots were located within each of three randomly selected mapping units of each of the 536, 570, and 585 terrestrial ecosystem survey soil types. Soils in these types are primarily classified as Typic and Mollic Eutroboralfs (Miller and others 1995). Annual precipitation at the Flagstaff airport, about 10 mi (16 km) east of the study area, averages 21 inches (54 cm). Approximately 50 percent of this precipitation is snow (1950 to 2006 records; Western Regional Climate Center, Reno, NV). July high temperatures average 82°F (28°C), and January low temperatures average 16°F (-9°C).

Field Sampling

Plots spanned a range of overstory characteristics and were located either in openings or in dense patches of young trees (fig. 1). Locations for plots were established by randomly selecting a geographic coordinate within each soil mapping unit, and then selecting vegetation patches closest to that coordinate using field reconnaissance. Density of trees greater than 0.4 inches (1 cm) in diameter at breast height ranged from 0 to 1,392 trees/acre (3,440 trees/ha) among plots. Basal area ranged from 0 to 274 ft^2/acre (63 m^2/ha). We measured the diameter of every tree (> 0.4 inches [1 cm] in diameter) on each plot and classified tree canopy types as primarily open (usually near old trees > age 120 years based on increment boring) or closed (dense tree patches). These general canopy types are readily recognized in the field (fig. 1) and have been used in several previous studies (for example, Vose and White 1987).

In each plot, we established a total of fifteen, 10.8-ft^2 (1-m^2) subplots per plot. Subplots were systematically located at 2, 16, 41, 66, and 80 ft (0.5, 5, 12.5, 20, and 24.5 m) along the southern, central, and northern 82-ft (25-m) plot lines. In these subplots, we measured litter (Oi horizon) thickness to the nearest 0.04 inch (0.1 cm) and visually estimated areal percent cover (at 0.1, 0.25, 1, or 5 percent intervals) of each plant species rooted in the subplots. We estimated tree canopy cover to the nearest 5 percent using a densitometer (Geographic Resource Solutions, Arcata, CA). We also collected a 0- to 2-inch (0- to 5-cm) sample of the mineral soil seed bank in each subplot using a 1.6-inch (4.2-cm) diameter metal corer. Each sample was 4.3 in^3 (70 cm^3), and we composited samples on a plot basis for a plot seed bank sample of 64 in^3 (1,050 cm^3). O horizons can trap seeds (Abella and Covington 2007; Korb and others 2005), but we focused on mineral soil seed banks because O horizons were sparse on some plots. From soil pits at the southwestern and northeastern plot corners, we collected a composite 0- to 6-inch (0- to 15-cm) mineral soil sample for determining soil texture (hydrometer method; Dane and Topp 2002). We measured litter weight by collecting litter samples in 5.4-ft^2 (0.5-m^2) frames at soil pit locations. We then oven dried these samples at 158°F (70°C) for 24 hours.

Plot and seed bank sampling occurred from June through August 2003. Based on published phenologies in the region (Clary and Kruse 1979), seedbank collections occurred before most species disperse seeds in late summer or fall. Thus, collections likely primarily represent the persistent seed bank (Baskin and Baskin 1998), although it is possible that some early flowering species contributed current-year seeds to samples.

Greenhouse Seed Bank Procedures

On the same day each sample was collected, we placed 7 in^3 (120 cm^3) of the composite seed bank sample from each plot in a greenhouse maintained at 75°F

Figure 1. Examples of ponderosa pine canopy types below which we collected soil seed bank samples southwest of Flagstaff, Arizona. Foreground: open patch dominated by large, old trees. Background: dense canopy of small-diameter trees. Open patches contained larger and richer soil seed banks than patches of dense, small trees. *Photo by S.R. Abella, June 11, 2003 (35°08′54″N, 111°43′43″W).*

(24°C). We placed samples in a layer about 0.4 inches (1 cm) thick on top of 18 in^3 (300 cm^3) of sterile potting soil in 43-in^3 (700-cm^3) square pots. We randomly arranged pots on greenhouse benches and watered the samples daily. The greenhouse was maintained with natural lighting, but we also provided samples with four hours of supplemental artificial lighting during fall and winter months (October through February). We identified and counted emerging seedlings (as a measure of seed density) every two weeks for six months. To meet possible chilling requirements for some species, we stored the remainder of samples (57 in^3, 930 cm^3 from each plot) at 23°F (-5°C) for four to six months. We then placed 7 in^3 (120 cm^3) of chilled sample from each plot in each of four separate pots and treated these samples procedurally the same as the unchilled samples. Seed density between chilled and unchilled samples was not appreciably different, so we pooled data from these separate samples into 37-in^3 (600-cm^3) plot samples for calculating 0- to 2-inch (0- to 5-cm) seed densities/ft^2 (0.09 m^2) and species richness/0.13 ft^2 (0.01 m^2). We report richness for this sample area computed from our sample volume because species-accumulation curves are needed for extrapolating richness to larger volumes and areas (Bigwood and Inouye 1988). Plant nomenclature and classification of species as native or exotic followed NRCS (2004).

Statistical Analysis

The seed bank characteristics we analyzed in this study included: (1) total seed densities/ft^2 (0.09 m^2), (2) total species richness/0.13 ft^2 (0.01 m^2), (3) native perennial seed densities/ft^2, and (4) native perennial species richness/0.13 ft^2. We first examined bivariate correlations between these seed bank characteristics and soil and aboveground vegetation variables (table 1). We then used multiple regression and regression trees as exploratory models to estimate seed bank characteristics from these variables with a sample size of 45 plots. Analyses were performed with the software JMP (SAS Institute 2002). For multiple regression, we used a forward stepwise procedure for identifying predictor variables. Regression trees are nonparametric models that partition data into increasingly homogenous subsets and provide dichotomous keys to estimate a dependent variable at different values of predictor variables (Breiman and others 1984). The JMP version allows users to determine the number of splits, so we stopped splitting

Table 1. Correlation matrix (Pearson *r*) between seed bank response (variables 1 through 4) and explanatory variables (5 through 9) included in final multiple regression or regression tree models. Descriptive statistics by tree canopy type are provided for each variable at the bottom of the table.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1 Total seeds/ft^2	1								
2 Total species/0.13 ft^2	0.89	1							
3 Native perennial seeds/ft^2	0.53	0.55	1						
4 Native perennial species/0.13ft^2	0.44	0.57	0.76	1					
5 Plant species/10.8 ft^2	0.54	0.59	0.54	0.59	1				
6 Litter wt. (tons/acre)	-0.47	-0.51	-0.40	-0.39	-0.34	1			
7 Litter thickness (inches)	-0.47	-0.38	-0.39	-0.25	-0.53	0.22	1		
8 Canopy type (open, closed)	-0.53	-0.43	-0.48	-0.49	-0.50	0.11	0.54	1	
9 Canopy cover (percent)	-0.29	-0.19	-0.26	-0.18	-0.42	0.10	0.76	0.67	1
Open canopy, mean±SD	139±98	7.1±4.1	33±32	2.1±1.6	7.2±2.3	2.9±2.3	0.8±0.4	–	27±15
Closed canopy, mean±SD	49±46	3.7±3.0	8±13	0.8±0.8	4.5±2.5	3.3±1.5	1.3±0.4	–	52±14

when adding more predictors resulted in increases of < 0.05 in R^2. We employed JMP's k-fold crossvalidation (k = 5) to compute a cross-validated overall R^2 (1 - [crossvalidated sum of squares error / corrected sum of squares]).

Results

Of 49 total species detected in seed bank samples, 10 percent were exotic and 43 percent were native perennials. Total average seed density was 54 seeds/ft^2 (0- to 2-inch layer; 583 seeds/m^2) on closed tree canopy plots and 149 seeds/ft^2 (1,611/m^2) on open plots. Exotic species contributed 19 percent of these total seed densities on both closed and open plots. Common mullein constituted 78 (closed plots) and 88 (open plots) percent of total average exotic seed density. Native perennials comprised 15 (closed plots) and 22 (open plots) percent of the total average seed density for all species. The most abundant native perennials in seed banks included White Mountain sedge, spreading sandwort (*Arenaria lanuginosa*), mountain muhly, muttongrass, and lobe-leaf groundsel (*Packera multilobata*).

Total seed densities in mineral soil seed banks were positively correlated with aboveground plant species richness/10.8 ft^2 (1 m^2; Pearson $r = 0.54$) and plant cover ($r = 0.34$). However, these seed densities were negatively correlated with ponderosa pine tree density ($r = -0.40$), basal area ($r = -0.39$), and litter thickness and weight ($r = -0.47$ for both). Similar to total seed densities, native perennial seed densities exhibited the following correlations with vegetation and forest-floor variables: aboveground plant richness ($r = 0.54$) and cover ($r = 0.45$), ponderosa pine tree density ($r = -0.38$) and basal area ($r = -0.27$), and litter thickness ($r = -0.39$) and weight ($r = -0.40$). Total and native perennial species richness in seed banks had relationships with these vegetation and forest-floor variables similar to those of seed densities. Additionally, neither seed density nor species richness were strongly correlated ($|r| <0.32$) with 0- to 6-inch (0- to 15-cm) percent sand, silt, or clay.

Aboveground species richness, tree canopy type (open or closed), and litter weight explained 49 percent of the variance in seed bank total seed densities and species richness in multiple regression models (table 2). These three predictors explained 41 percent of the variance in native perennial seed densities. Fifty-two percent of the variance in native perennial species richness was explained by these predictors and tree canopy percent cover.

Regression trees explained 47 to 59 percent of the variance in seed density using two or three predictors (fig. 2). Similar to multiple regression, aboveground species richness and tree canopy type were important predictors in these models. Litter thickness, rather than litter weight as in multiple regression, also was an important predictor. The greatest seed densities occurred on plots containing thin litter layers, high aboveground plant richness, and open canopies.

Discussion

The basic insights gained from the regression models include: (1) densities and species richness of seeds in mineral soils increased with decreasing forest-floor litter weight and thickness; (2) both total and native perennial seed densities and species richness in mineral soils were highest in areas with high aboveground plant species richness/10.8 ft^2 (1 m^2); and (3) patches with open canopies, typically near old trees, supported

Table 2. Multiple regression models estimating seed densities and species richness in 0- to 2-inch (0- to 5-cm) soil seed banks in ponderosa pine forests southwest of Flagstaff, Arizona.

Predictor[a]	**Coefficient**	**SE**	***t*-statistic**	**Prob. >*t***	**Cum. R^{2}**[(b)]
	Total seeds/ft^2				
Intercept[c]	100.9756	35.1	2.88	<0.01	—
Plant species/10.8 ft^2	7.0217	4.2	1.68	0.10	0.29
Tree canopy type (0, 1)	32.2178	10.9	2.96	<0.01	0.39
Litter weight (tons/acre)	-15.5909	5.3	-3.19	<0.01	0.49
	Total species/0.13 ft^2				
Intercept	4.7100	1.6	2.91	<0.01	—
Plant species/10.8 ft^2	0.5047	0.2	2.63	0.01	0.35
Litter weight (tons/acre)	-0.7338	0.3	-2.99	<0.01	0.45
Tree canopy type (0, 1)	0.8156	0.5	1.63	0.11	0.49
	Native perennial seeds/ft^2				
Intercept	15.0924	11.4	1.32	0.19	—
Plant species/10.8 ft^2	2.7957	1.4	2.06	0.04	0.29
Tree canopy type (0, 1)	7.5809	3.5	2.15	0.04	0.35
Litter weight (tons/acre)	-3.5714	1.7	-2.07	0.04	0.41
	Native perennial species/0.13 ft^2				
Intercept	-0.2001	0.7	-0.27	0.78	—
Plant species/10.8 ft^2	0.2038	0.1	3.05	<0.01	0.35
Tree canopy type (0, 1)	0.6667	0.2	3.13	<0.01	0.40
Tree canopy cover (percent)	0.0245	0.0	2.31	0.03	0.47
Litter weight (tons/acre)	-0.1662	0.1	-1.96	0.06	0.52

[a] Plant species richness represents aboveground vegetation. Tree canopy type corresponds to open old-tree patches (0) or dense patches of small trees (1).

[b] Cumulative proportion of variance explained for the dependent (y) variable based on stepwise predictor selection.

[c] As an example, the equation for estimating total seeds/ft^2 is the following: y = 100.9756 + 7.0217(aboveground plant species/10.8 ft^2) + 32.2178(canopy type) – 15.5909(litter weight). Metric conversions are as follows: seed bank seeds/ft^2 = seeds/0.09 m^2, seed bank species/0.13 ft^2 = species/0.01 m^2, and aboveground plant species/10.8 ft^2 = species/m^2.

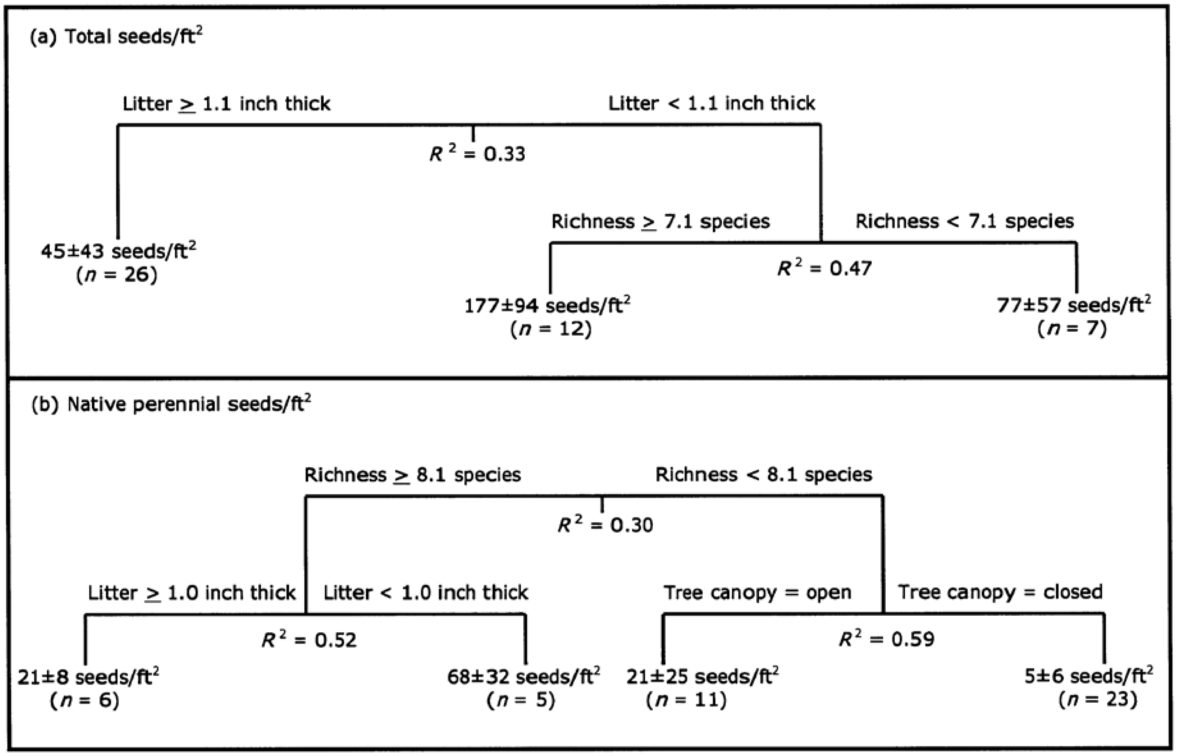

Figure 2. Regression trees estimating 0- to 2-inch (0- to 5-cm) soil seed bank: (a) total seeds/ft^2 (0.09 m^2) and (b) native perennial seeds/ft^2 (0.09 m^2) based on litter thickness (Oi horizon), aboveground plant species richness/10.8 ft^2 (1 m^2), and tree canopy type. The cumulative proportion of variance explained (R^2) is shown at each division. Estimated values at each node are the mean ± 1 standard deviation. Cross-validated R^2 for whole models was 0.41 for (a) and 0.39 for (b).

larger and richer soil seed banks than patches of denser canopies containing many closely spaced small trees (figs. 1, 2).

Several factors could cause mineral soil seed banks to be smaller in areas with thick and heavy litter. Seeds may become trapped in litter so that fewer reach mineral soil (Korb and others 2005) or retain viability. Litter abundance increases in areas of high pine density, which may decrease seed banks by decreasing aboveground vegetation that provides seed inputs. This conjecture is consistent with the strong positive relationship we observed between seed bank density and aboveground plant richness. Aboveground richness itself was negatively correlated with pine density ($r = -0.66$) and basal area ($r = -0.52$). Our finding of larger and richer seed banks in openings usually near large, old trees concurs with Vose and White's (1987) data on seed rain by understory vegetation. These authors found that grass + forb seed rain averaged more than 10 times greater below openings than below dense tree canopies in ponderosa pine forests near Flagstaff, Arizona (fig. 3). These data suggest that many seeds in our seed bank samples probably originated from relatively recent inputs by aboveground vegetation. However, some seeds, such as those of common mullein that are long-lived in seed banks, were possibly deposited in our samples long ago (Warr and others 1993).

Regression models explained 41 to 59 percent of the variance in seed bank densities using three or fewer predictor variables (table 2, fig. 2). Imperfect measurement of predictors, plot-scale disturbance history, or other unmeasured factors could have resulted in unexplained variance. Our method of locating plots was not intended to assess the effects of disturbance history on seed banks. Increasing our understanding of relationships between disturbance history and contemporary seed banks would probably improve our ability to estimate seed bank size and composition (Korb and others 2005).

Management Implications

Our study and previous research (Vose and White 1987) suggests that positive feedbacks exist between soil seed banks and aboveground vegetation. Seed banks, overall and specifically for native perennials, are richer and larger in patches where aboveground understory vegetation is most abundant. Unfortunately, this indicates that seed banks are less useful for increasing

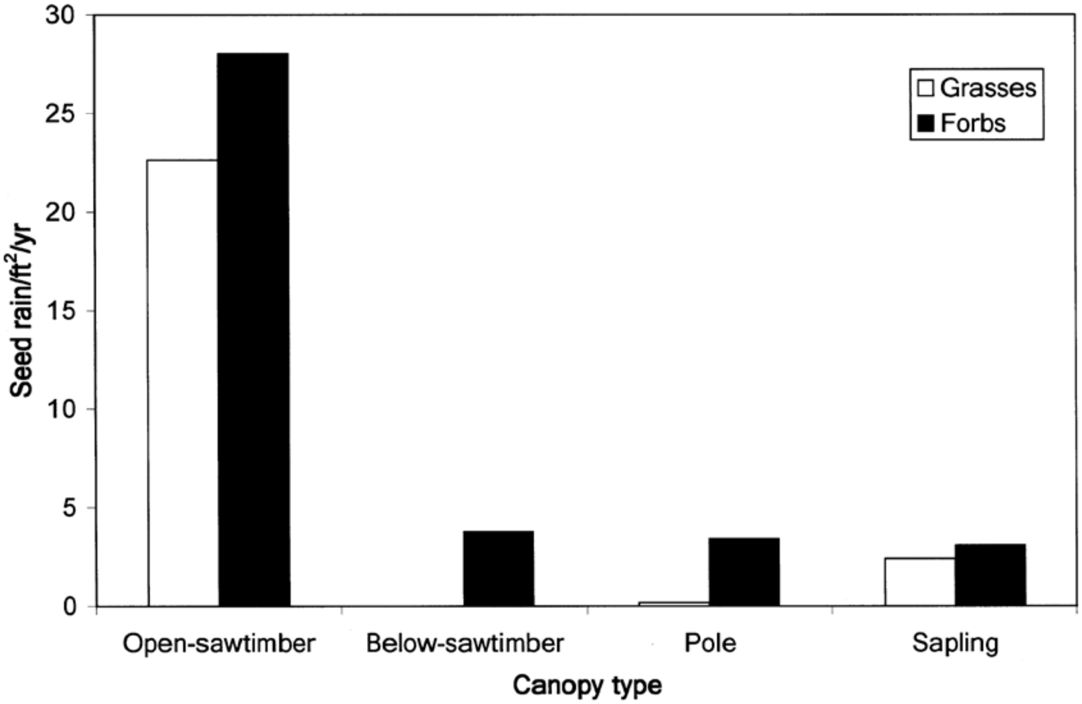

Figure 3. Seed rain by grasses and forbs among canopy types from fall 1982 to fall 1983 after a prescribed burn in ponderosa pine forests in the Fort Valley Experimental Forest, northern Arizona. Seed rain was greatest in openings that contained abundant understory vegetation. Data from Vose and White (1987).

native understory vegetation in dense pine stands where existing understory vegetation is most depauperate. Our findings suggest that seed banks of some native perennials can be enhanced by increasing the vigor and richness of understory vegetation containing these species. Management techniques for accomplishing this could include tree thinning, reducing grazing pressure especially during periods of seed production, prescribed burning timed to maintain seed production, or actively planting or seeding understory species.

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References

Abella, Scott R.; Covington, W. Wallace. 2007. Forest-floor treatments in Arizona ponderosa pine restoration ecosystems: no short-term effects on plant communities. Western North American Naturalist. 67:120-132.

Abella, Scott R.; Springer, Judith D.; Covington, W. Wallace. 2007. Seed banks of an Arizona *Pinus ponderosa* landscape: responses to environmental gradients and fire cues. Canadian Journal of Forest Research. 37:552-567.

Bakker, J.P.; Poschlod, P.; Strykstra, R.J.; Bekker, R.M.; Thompson, K. 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerland. 45:461-490.

Baskin, Carol C.; Baskin, Jerry M. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. San Diego, CA: Academic Press. 666 p.

Bigwood, Douglas W.; Inouye, David W. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. Ecology. 69:497-507.

Breiman, Leo; Friedman, Jerome H.; Olshen, Richard A.; Stone, Charles J. 1984. Classification and regression trees. Belmont, CA: Wadsworth Inc. 358 p.

Clary, Warren P.; Kruse, William H. 1979. Phenology and rate of height growth of some forbs in the southwestern ponderosa pine type. Res. Note RM-376. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 8 p.

Dane, Jacob H.; Topp, G. Clarke, eds. 2002. Methods of soil analysis. Part 4. Physical methods. Soil Science Society of American Book Series No. 5. Madison, WI: Soil Science Society of America, Inc. 1692 p.

Glass, Steve. 1989. The role of soil seed banks in restoration and management. Restoration and Management Notes. 7:24-29.

Koniak, Susan; Everett, Richard L. 1982. Seed reserves in soils of successional stages of pinyon woodland. American Midland Naturalist. 108:295-303.

Korb, Julie E.; Springer, Judith D.; Powers, Stephanie R.; Moore, Margaret M. 2005. Soil seed banks in *Pinus ponderosa* forests in Arizona: clues to site history and restoration potential. Applied Vegetation Science. 8:103-112.

Miller, Greg; Ambos, Norm; Boness, Pat; Reyher, Deanna; Robertson, George; Scalzone, Ken; Steinke, Rory; Subirge, Tom. 1995. Terrestrial ecosystems survey of the Coconino National Forest. U.S. Department of Agriculture, Forest Service, Southwestern Region. 405 p.

NRCS [U.S. Department of Agriculture, Natural Resources Conservation Service]. 2004. The PLANTS database. Baton Rouge, LA: National Plant Data Center. http://plants.usda.gov/

Roberts, H.A. 1981. Seed banks in soils. Advances in Applied Biology. 6:1-55.

SAS Institute. 2002. JMP version 5 user's guide. Cary, NC: SAS Institute, Inc. 263 p.

Springer, Judy; Hastings, Rob. 2004. Soil seed banks in coniferous, fire-adapted, and southwestern U.S. ecosystems: an annotated bibliography. Flagstaff, AZ: Ecological Restoration Institute. 67 p.

Thompson, K. 1987. Seeds and seed banks. New Phytologist. 106 (Suppl.):23-34.

van der Valk, A.G.; Pederson, Roger L. 1989. Seed banks and the management and restoration of natural vegetation. In: Leck, Mary Allessio; Parker, V. Thomas; Simpson, Robert L., eds. Ecology of soil seed banks. NY, NY: Academic Press: 329-346.

Vose, James M.; White, Alan S. 1987. Processes of understory seedling recruitment 1 year after prescribed fire in an Arizona ponderosa pine community. Canadian Journal of Botany. 65:2280-2290.

Warr, Susan J.; Thompson, Ken; Kent, Martin. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. Progress in Physical Geography. 17:329-347.

Wienk, Cody L.; Sieg, Carolyn Hull; McPherson, Guy R. 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. Forest Ecology and Management. 192:375-393.

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