Soil seed banks in Pinus ponderosa forests in Arizona: Clues to site history and restoration potential

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Soil seed banks in *Pinus ponderosa* forests in Arizona: Clues to site history and restoration potential

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Abstract

Question: How does the relationship between the viable soil seed bank species composition and the above-ground vegetation in northern Arizona *Pinus ponderosa* forests differ under varying historical land use disturbances (low, intermediate, high)? Is above-ground vegetation correlated to the viable soil seed bank immediately following soil disturbance from restoration thinning treatments?

Location: Northern Arizona, USA.

Methods: Soil seed bank samples were taken along replicated transects and collected with a 5-cm diameter bulk density hammer. Samples included a 5 -cm diameter O-horizon sample (at varying depths) plus the underlying mineral soil to a depth of 5 cm. The seedling emergent method was used to quantify seed bank species composition and density. The herbaceous and shrub plant community was quantified along the same transects using the point intercept method.

Results: Early-successional or ruderal species were common in the soil seed bank at all three disturbance sites. Non-native species, notably *Verbascum thapsus*, were more numerous (up to 940 seeds/m^2) under high disturbance with overgrazing and logging, and less common or absent under low disturbance. Most viable seeds were found in the O-horizon and the upper 5 cm of mineral soil; there was little correlation between species in the soil seed bank and the above-ground vegetation.

Conclusions: We recommend that restoration plans be geared toward minimizing activities, such as severe soil disturbance, that may promote the spread of non-native invasive species, and that manual seeding be explored as an option to restore plant species diversity and abundance.

Keywords: Arizona; Disturbance; Ecological restoration; Ponderosa pine; Tree thinning; Vegetation dynamics.

Nomenclature: USDA Plants database (plants.usda.gov).

Introduction

Pinus ponderosa forests are a dominant vegetation type on the Colorado Plateau in the southwestern US. Prior to Euro-American settlement, these forests were characterized by clumped, old-growth pines and isolated trees with herbaceous understories dominated by grasses (e.g. Cooper 1960). Low-intensity grass-fueled surface fires recurred every 2-20 years and played a major role in determining the structure, composition, and stability of these ecosystems (Fulé et al. 1997; Swetnam & Baisan 2003). However, due to a variety of interacting factors these forests have become dense with small-diameter trees (Moore et al. 1999, 2004). Efforts are under way to reverse this trend toward a more open grass savannah-like structure through restoration tree thinning and prescribed burning (Covington et al. 1997). An important component in predicting the natural revegetation potential following restoration treatments in *P. ponderosa* herbaceous understories is determining the composition and abundance of the soil seed bank. Many seed bank studies in Europe suggest a correlation between land use disturbance history and seed bank composition, indicating an increased abundance of early successional (ruderal) and non-native species in high disturbance sites (Bekker et al. 1997; Bossuyt & Hermy 2000; Bossuyt et al. 2002; Honnay et al. 2002; Matus et al. 2003). Currently, most *P. ponderosa* forests are distinguished by plant communities comprised mainly of native species, harsh growing conditions, and long periods without major disturbance (Laughlin et al. 2004).

There is a wealth of knowledge regarding the role and dynamics of seed banks in numerous ecosystems (Warr et al. 1994). However, no studies have investigated the relationship between historical land use disturbance and soil seed bank composition and abundance in *P. pondersosa* forests, which Bekker and others (1997) indicate is important due to the general assumption that the soil seed bank positively increases plant community diversity. In addition, relatively few seed bank studies have been conducted in this forest type. At a *P. ponderosa* study site near Flagstaff, AZ, Vose & White (1987) found ca. 8 viable-seeds/m^2 in burned plots and 22/m^2 in control plots. A seed bank study conducted in *P. ponderosa* stands in the Black Hills of South Dakota recorded 78 seeds/m^2 prior to fire and 186 seeds/m^2 consisting of ten species (eight forbs, one graminoid, one shrub) following fire (Wienk et al. 2004). In both studies, the relatively low seed numbers indicate that the soil seed bank may not be a significant contributor for natural revegetation following disturbance.

In contrast, buried seeds may be a significant source of colonization in *P. ponderosa* forests of east-central Washington. Pratt et al. (1984) estimated ca. 13 500 viable-seeds/m^2 occurred in the top 10 cm of the mineral soil and associated litter in spring and autumn samples. Seeds of 57 species were found; woody species accounting for only ca. 1% of the seed bank. Two non-native species comprised 50% of the buried viable seeds. The authors suggest that the large number of species in this case may be due to the intermediate successional stage with both climax and early successional species present.

Some studies indicate soil seed banks play a major role in revegetation following disturbance (Milberg 1993; Wilson et al. 1993; Hyatt 1999), while others suggest the seed bank has little to no influence (Bakker et al. 1996; Morgan 1998; Bekker et al. 2000) depending on the plant community, seed densities, seed location in the soil profile, and whether germination requirements were fulfilled. In native ecosystems, many studies have illustrated a low similarity between the composition and density of the seed bank when compared to the above-ground vegetation (Warr et al. 1993), and a higher similarity in managed sites. In contrast, other studies in forest systems have illustrated low correlations between seed banks and above-ground vegetation in both natural (native) and managed habitats (Abs et al. 1999; Bossuyt et al. 2002). Our first hypothesis is that soil seed bank species richness will not be correlated to above-ground vegetation in recently undisturbed *P. ponderosa* communities regardless of historical land use disturbance. Seed bank studies in grasslands generally indicate that the similarity between soil seed bank and above-ground plant community prior to disturbance is low, but increases following disturbance due to the establishment of early successional species (Kirkham & Kent 1997; Akinola et al. 1998; Ohtsuka & Ohsawa 1994; Peco et al. 1998). Our second hypothesis is that above-ground vegetation will be correlated to soil seed bank species composition immediately following restoration thinning in areas categorized as high historical land use disturbance due to early successional species from the seed bank colonizing the newly-exposed mineral soil.
Our objectives were to: (1) assess the relationship between viable soil seed bank species composition in the O-horizon and top 5 cm of mineral soil and the above-ground species composition in relation to historical land use disturbance in three *P. ponderosa* sites in northern Arizona, and (2) investigate the effect of soil disturbance from restoration thinning on the soil seed bank for two growing seasons following the initial disturbance to determine if post disturbance vegetation is correlated with the viable soil seed bank.

Study area

This research was conducted at three sites in northern Arizona that form a historical land use disturbance gradient (Fig. 1). The Mt. Trumbull area within the Grand Canyon/Parashant National Monument north of the Grand Canyon has been the most heavily disturbed by practices such as domestic livestock grazing, some commercial logging and actively suppressed fires and will be referred as the H-site, throughout the manuscript. The next study site will be referred as the, 'intermediate disturbance, or M-site', throughout the manuscript. This site has been further subdivided into two categories: 'intermediate (low)', ML, and 'intermediate (high)', MH, for quantifying the effects of soil disturbance from thinning on soil seed bank dynamics. The Fort Valley Experimental Forest near Flagstaff contains relatively undisturbed expanses – intermediate (low) disturbance, MH-sites, intermixed with areas that have been grazed and commercially logged in adjacent areas on the Coconino National Forest (MH-sites). Both sites have experienced active fire suppression since 1876. The third study site consists of three plateaus on the North Rim of Grand Canyon National Park, which currently serves as our best-known example of a *P. ponderosa* reference site in Arizona (Gildar et al. 2004) and will be referred as the 'low disturbance', L-site throughout the manuscript. Specific detailed information on land use disturbance history, vegetation characteristics, soil type, elevation, and climate for all three study sites can be located at
http:// www.eri.nau.edu/research/ecological_ research_ publications.aspx

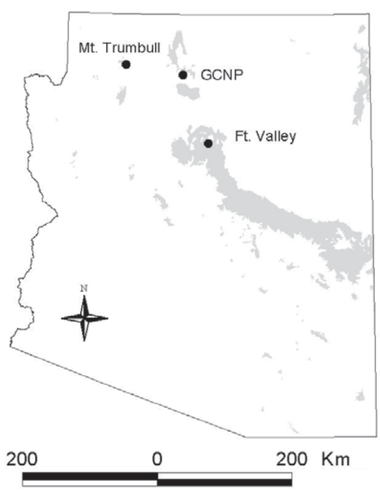

Fig. 1. Study site locations in northern Arizona. Shading indicates areas covered by *Pinus ponderosa* forests. The three study sites form a historical land use disturbance gradient: Mt. Trumbull (high disturbance), Fort Valley (intermediate disturbance), and GCNP (low disturbance).

Material and Methods

Soil seed bank and vegetation sampling

Baseline seed bank studies were initiated at the H-site in 1997 and samples were then collected in 1999 at the MH and ML-sites and in 2001 at the L-site. At all three study sites, soil and vegetation measurements were systematically sampled with minor differences from site to site as methods were refined over time, for a total of 90, 270 and 288 samples collected at the H-, M-, and L-sites, respectively. Soil samples were taken along replicated transects at each site and collected with a 5-cm diameter bulk density hammer (slide hammer). They included a 5-cm diameter O-horizon sample (at varying depths) plus the underlying mineral soil to a depth of 5 cm. Mean O-horizon depth was also measured for each sampling location and was much smaller at the L (1.9 cm) and M-site (2.9 cm) than at the H-site (7.2 cm). While in the field, samples from all sites were kept shaded and dry to prevent damage from heat and mold until they could be transferred to a greenhouse.

We also surveyed the herbaceous and shrub plant community along the same transects where soil seed bank samples were collected at each site. Plant species were recorded at systematically located points along each transect and plant species abundance was determined by dividing the number of plant hits by the total number of points for each transect. In addition, tree canopy cover was recorded using a vertical projection densitometer at these same intervals along transects.

At the M-site, additional data were collected to quantify the effects of soil disturbance from restoration thinning on the soil seed bank and above-ground vegetation. Three experimental blocks consisting of two treatment units (ca. 16 ha each) were established in 1998. Units within these blocks were randomly assigned either a control or treatment status (thinning to a low level of replacement trees based upon presettlement tree densities) for a total of six units. Specific details of the thinning treatment prescriptions are outlined in Fulé et al. (2001). There were no significant differences between control and treatment units for vegetation and site characteristics prior to treatment (1998) (Table 1). Thinning significantly reduced tree density and tree canopy cover compared to control units in 2000 (182 trees/ha in the thinned only units compared to 1426 trees/ha in the paired controls) (Table 1).

We also recorded pre-treatment data for the herbaceous understorey composition and abundance, fuel loads, and tree canopy cover in 1998. Post thinning treatment data were collected in 1999 and 2000 (see Fulé et al. 2001 for a description of overstorey sampling methods). These data were not significantly different between the two years; therefore, only post-treatment data from 2000 are presented.

Greenhouse methods

The methodologies for soil seed bank sampling, treatment of samples, and seedling inventory were adapted from Gross (1990), Brown (1992) and Warr et al. (1993). We used the seedling emergence method because of its ability to determine the viable fraction of readily germinable seeds, which is the component of the seed bank most important for restoration management goals. Samples (98.2 cm^3) were immediately placed in the greenhouse after collection and were not cold stratified in this study. They were spread thinly over a layer of ca. 5 cm of sterile soil in plastic flats ca. 11 cm × 11 cm. We then arranged these flats randomly on a greenhouse bench. Control flats holding a mixture of sterilized soil were also randomly placed to account for species germinating due to possible greenhouse contamination. Only one greenhouse contaminate was found in our study, *Rumex* spp., which was not found in the soil seed bank samples, and therefore posed no problem for data analysis. We fertilized flats every two

Table 1. Vegetation and site characteristics for the Fort Valley intermediate (low) ML control and thinned units for pretreatment 1998 data and post-treatment 2000 data. Data are expressed as means (N = 2) ± SEM.

Variable	Pre-treatment 1998 Control stand	Pre-treatment 1998 Treatment stand	Post-treatment 2000 Control stand	Post-treatment 2000 Treatment stand
Tree.ha^{-1}	1415 ± 392	1162 ± 141	1426 ± 330 a	182 ± 34 b
Tree canopy cover (%)	62 ± 6	58 ± 4	61 ± 4 a	34 ± 3 b
Herbaceous cover (%)	10 ± 2	9 ± 1	9 ± 2	11 ± 1
Simpson's diversity index	2.9 ± 0.4	2.9 ± 0.4	2.9 ± 0.6	3.6 ± 0.5
Oi horizon (litter) (kg.ha^{-1})	14211 ± 1508	14134 ± 1980	14363 ± 1508	15625 ± 2598
Oa & Oe horizon (duff)(kg.ha^{-1})	25127 ± 2006	25338 ± 3266	25836 ± 3103	26379 ± 3266

Values indexed by a different letter are significantly different at the $P < 0.05$ level between paired control and treatment units for the same sampling year. Herbaceous cover data were square root transformed prior to analysis.

weeks with a dilute nutrient solution and inventoried seedlings at ca. 14-day intervals. As seedlings germinated and could be identified, we removed them from the flats to prevent competition among seedlings. Samples were watered as needed to maintain moist soil conditions for six months and soil was stirred about every two months to initiate new growth. Although seeds have been shown to germinate in the second year after initiation of seed bank studies, most studies have shown that the majority of seeds germinate within the first two months and there is little to be gained by prolonging seed bank studies for longer than six months (Warr et al. 1993).

Statistical analysis

We used repeated measures multivariate analysis of variance (MANOVA) in SPSS version 8 (Anon. 1997) to determine the effects of thinning on viable soil seed bank species composition and abundance. The soil seed bank location (O-horizon or mineral soil), treatment (control or thinned), and time since thinning (one or two years) were categorical variables in the general linear model (GLM). Significance for analysis of variance tests was accepted at $p \leq 0.05$. Tukey's Honestly Significant Difference (HSD) test was used to make multiple comparisons of means following a significant result. The Shapiro Wilks test was used to test data for normality and Levene's test was used to test for homogeneity of the variance (Milliken & Johnson 1984). Soil seed bank and herbaceous plant abundance were square root transformed to improve normality and homoscedasticity assumptions when necessary (Zar 1984). The Jaccard similarity index was used to compare whole-site seed bank species richness and whole-site vegetation species richness.

Results

Seed bank ecology – historical land use disturbance gradient

At the H-site, the seed density for the O-horizon plus the top 5 cm of mineral soil was ca. 1560 seeds/m^2. The soil seed bank contained 19 species: 12 native forbs (including three ruderal species), three non-native forbs, two grasses, one shrub and one unknown monocot. 60% of the seed bank was comprised of viable seeds of the non-native species, *Verbascum thapsus* (940 seeds/m^2), an early successional species of disturbed habitats. See Table 2 for other common species.

There was little correlation between the soil seed bank and the above-ground vegetation at the H-site (Jaccard similarity of 0.19). A total of 24 species was recorded in the above-ground vegetation in the transects where seed bank samples were collected. Of those species, only seven were found in the soil seed bank samples. With the exception of the genus *Poa*, all other species unique to the soil seed bank were annual, biennial or ruderal species (see Table 3). *Verbascum thapsus* was the only non-native species inventoried in the above-ground vegetation. In the above-ground vegetation 14 native forbs were found (only two of them annuals), one non-native forb, four trees, three shrubs, and two grasses.

At the M-site, the seed density for the O-horizon and top 5 cm of mineral soil was 1263 seeds/m^2. There were about three times more seeds in the top 5 cm of mineral soil than in the O-horizon. There were 24 seed bank species: 15 native forbs (of which seven were considered ruderal), two non-native forbs, six native graminoids, and one tree species. The most common species, similar to the site H, was *Verbascum thapsus*. *Elymus elymoides*, an early successional native C_3 grass (although it also acts as a generalist), also had numerous seeds in the soil seed bank. Other common species are listed in Table 2. Species not recorded in the above-ground vegetation on transects, although observed elsewhere in the study area and therefore unique to the soil seed bank, are listed in Table 3.

As at the H-site, there was little correlation (Jaccard similarity of 0.29), between the soil seed bank and the

Table 2. Species with the highest number of viable seeds in the 0-5 mineral soil seed bank samples collected from three *Pinus ponderosa* forests in northern Arizona along a historical land use disturbance gradient.

High disturbance (H-site)		Intermediate disturbance (M-site)		Low disturbance (L-site)	
Species	Seeds/m^2	Species	Seeds/m^2	Species	Seeds/m^2
Verbascum thapsus	940	*Verbascum thapsus*	566	*Carex* spp.	269
Conyza canadensis	192	*Carex* spp.	181	*Poa* spp.	149
Chenopodium botrys	68	*Gnaphalium exilifolium*	73	*Pinus ponderosa*	71
Arabis fendleri	57	*Pseudognaphalium macounii*	69	*Antennaria parviflora*	67
Mimulus rubellus	57	*Elymus elymoides*	51		

Samples from the O-horizon were not included because of differences in O-horizon depth.

above-ground vegetation at the M-site. The 51 species in the above-ground vegetation were more than double the number of species found in soil seed bank samples. Of the 24 species found in the seed bank only 13 were also in the above-ground vegetation. The majority of the species present in the seed bank and absent from the above-ground vegetation were either ruderal or non-native species with no non-native species inventoried in the above-ground vegetation. The above-ground vegetation was comprised of 28 native forbs, six ruderal native forbs, 13 native graminoids, three shrubs, and one tree. Only four of the 28 native forbs were found in both the seed bank and above-ground vegetation and three of the ruderal forbs were found in both: *Erigeron divergens*, *E. flagellaris* and *Pseudognaphalium macounii*. Five of the 13 extant native graminoids were recorded in the seed bank. *Panicum bulbosum* was present in the seed bank and absent from the above-ground vegetation. Native graminoids were the most abundant species in the above-ground vegetation. Of the ten most abundant species in the above-ground vegetation, seven were graminoids, comprising 83.4 % of the total foliar cover.

At the L-site, seed density for the O-horizon and top 5 cm of mineral soil averaged over the three Plateau sites was 272.5 seeds/m^2. Galahad Plateau samples contained the most viable seeds/m^2 (411) and Rainbow and Powell Plateau had fairly similar numbers of seeds (195 and 212 seeds/m^2 respectively). The seed bank was comprised of 28 species and combined genera, including 18 native forbs, two ruderal forbs, five native graminoids, two non-native grasses and one tree species. The most common species are listed in Table 2 and species unique to the soil seed bank are listed in Table 3. Of the 20 native forbs, two species were considered ruderal and six species were annuals. The only non-native species recorded from the seed bank were *Bromus tectorum* and *Phalaris canariensis* (11 seeds/m^2 and 4 seeds/m^2 respectively). The genus *Poa* could not always be accurately identified to species in the greenhouse and therefore this grouping may have contained some non-native *Poa* species.

Table 3. Species unique to soil seed bank samples (not recorded in the above-ground vegetation) collected from three *Pinus ponderosa* forests in northern Arizona subject to high (H), intermediate (M) and low (L) disturbance, respectively.

H-site	M-site	L-site
Chenopodium album	*Arabis spp.*	*Chamaesyce serpyllifolia*
Chenopodium botrys	*Arenaria lanuginose*	*Claytonia lanceolata*
Chenopodium graveolens	*Chenopodium* spp.	*Phalaris canariensis*
Conyza canadensis	*Conyza canadensis*	*Piptatherum micranthum*
Corydalis aurea	*Gnaphalium exilifolium*	*Pseudognaphalium macounii*
Gayophytum diffusum	*Laennecia shiedeana*	*Schizachyrium scoparium*
Lactuca serriola	*Linum aristatum*	*Zigadenus* sp.
Mimulus rubellus	*Nama dichotomum*	
Nama dichotomum	*Panicum bulbosum*	
Phlox gracilis	*Senecio multilobatus*	
Poa pratensis		

The correlation between above- and below-ground species was very low (Jaccard similarity of 0.18), similar to the H-site. In total 20 species were recorded both in the above-ground vegetation and in the soil seed bank; 78 species were unique to the extant vegetation, but only seven species were unique to the seed bank (Table 2). Detailed information on the above-ground herbaceous plant community can be found in Gildar et al. (2004).

Seed bank response to soil disturbance from small-diameter tree thinning

Although average herbaceous plant cover tended to be higher in thinned units than in control units 18 months after treatment, the differences were not significant (Table 4). The herbaceous plant communities in the experimental blocks at the M-site (Fort Valley) were dominated by native graminoids followed by non-leguminous forbs, legumes, and woody shrubs following thinning. *Carex* spp. dominated the herbaceous cover along with C_3 grasses including *Elymus elymoides* and *Poa fendleriana*. *Muhlenbergia montana* was the only abundant C_4 grass in the experimental blocks and it was consistently less common than the abundant C_3 grasses.

Six months after soil disturbance from thinning,

Table 4. Viable soil seed bank species density (seeds/m^2) for functional groups in the O-horizon and top 5 cm of mineral soil from the Fort Valley intermediate (low) ML disturbance control (C) and paired thinned-only (T) units in 1999, six months after thinning, and in 2000, 18 months after thinning. Data expressed as means ± SEM (N = 2; 90 13.85-cm^2 soil cores/replicate). There were no non-native or ruderal grasses or trees/shrubs viable seeds present in the soil seed bank in intermediate (low) ML disturbance units.

Functional group	O-horizon				Mineral soil (0-5 cm)			
	1999C	1999T	2000C	2000T	1999C	1999T	2000C	2000T
Non-native forbs	0 ± 0	5.5 ± 0.3	8.5 ± 1.2	6 ± 0.7	20 ± 5.2	17 ± 2.2	19.5 ± 4.4	23 ± 1.7
Ruderal forbs	42.5 ± 11.5	20 ± 3.8	23 ± 2.9	9 ± 1.5	9 ± 1.7	28.5 ± 6	20 ± 3.6	19.5 ± 5.8
Native forbs	17.5 ± 8.1	29 ± 4.7	9 ± 2.1	9 ± 0.6	29 ± 4.4	23 ± 6.3	6 ± 0.7	20.5 ± 3.4
Native grasses	40 ± 14.2	40.5 ± 13.7	15.5 ± 6.3	53.5 ± 23.6	93.5 ± 34.4	31 ± 10.8	31 ± 14.2	40.5 ± 17.1
Native trees/shrubs	6 ± 2.4	0 ± 0	37 ± 9.8	25.5 ± 11.1	3 ± 0.9	5.5 ± 2.3	14 ± 5.7	17.5 ± 9.5
Average seeds/m^2	106 ± 11	95 ± 12	93 ± 9	103 ± 7.5	154.5 ± 27	105 ± 18	90.5 ± 11	121 ± 20

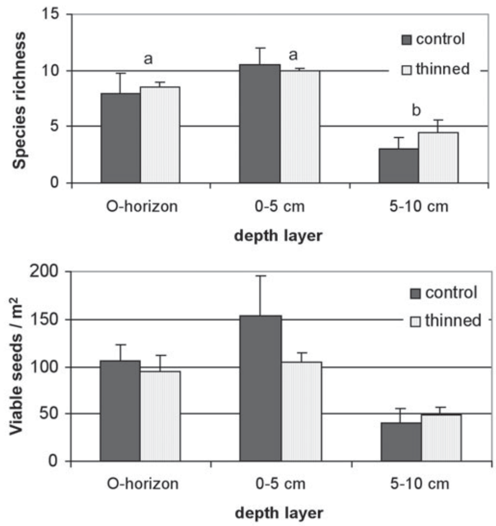

Fig. 2. a. Viable soil seed bank species richness for the Fort Valley intermediate (low) ML control and thinned units; **b.** viable soil seed bank species density (seeds/m^2) for the control and thinned units in 1999, six months after thinning, in the O-horizon, 0-5 top cm of mineral soil, and 5-10 top cm of mineral soil. Data expressed as means ($N = 3$; 90 13.85-cm^2 soil cores/replicate). Values indexed by a different letter are significantly different at the $p < 0.05$ level between different soil layers. There were no significant differences between paired control and treatment units for individual soil layers.

there were significantly fewer species (Fig. 2a) and a lower total number of viable seeds/m^2 (Fig. 2b) in the mineral soil compared to the O-horizon for both the control and thinned units in 1999. There were no significant differences between paired control and thinned units for individual soil layers (O-horizon, 0-5 cm mineral soil, 5-10 cm mineral soil) for either seed bank species richness or the total number of viable seeds/m^2, indicating that soil disturbance from thinning did not affect seed bank species richness or the total number of seeds per m^2 in 1999 ($p > 0.05$). Likewise, when the soil seed bank was divided into functional groups, neither location (O-horizon or top 5 cm of mineral soil), treatment (control or thinned unit), nor time since thinning (six or 18 months post-thinning) showed significant differences ($p > 0.05$). Native graminoids, including sedges, in general had the most abundant viable seeds in both the O-horizon and top 5 cm of soil for the control and thinned units in 1999 and 2000 (Table 5).

Only data from the ML experimental blocks ($n = 2$) were used to assess responses of the seed bank and vegetation changes to soil disturbance from thinning because large differences in the seed banks were noted between the intermediate disturbance ML and MH-units, which most likely corresponded to different historical land use disturbance. While statistical comparisons should not be made between the ML and MH-units, qualitative assessment can provide insight into the relationship between historical land use disturbance and soil seed banks. *Verbascum thapsus* was the dominant non-native species in the seed bank for all of the ML and MH-units (Table 5). The only other non-native species recorded in the seed bank was *Linaria dalmatica*, which is a noxious weed in Arizona (Table 5). Seed bank samples in MH units had about seven times the overall number of total non-native and ruderal seeds per m^2 over the ML-units in 1999 (six months after thinning), and ca. 20 times the overall number of total non-native and ruderal seeds/m^2 compared to ML units in 2000, 18 months after thinning (Table 5).

Jaccard similarity values were low between seed bank and above-ground vegetation in ML control and thinned units for 1999 and 2000 (Fig. 3a). Similarly, low similarity values (ca. 0.20) were found between the seed bank and the above-ground vegetation in the MH control unit for 1999 and 2000 (Fig. 3b). In contrast, Jaccard values were 0.42 and 0.68 between the seed bank and above-ground vegetation in the MH thinned-units for

Table 5. Viable soil seed bank species density (seeds/m^2) for non-native and ruderal species in the O-horizon and top 5 cm of mineral soil from the Fort Valley paired control (C) and thinned-only (T) units in 1999, six months after thinning, and 2000, 18 months after thinning. Data are presented separately for the intermediate (low) ML-sites (180 13.85-cm^2 soil cores from four experimental units) and intermediate (high) MH-units (90 13.85-cm^2 soil cores from two experimental units).

Species	O-horizon								Mineral soil (0-5 cm)							
	1999C		1999T		2000C		2000T		1999C		1999T		2000C		2000T	
Disturbance history	ML	MH	ML	MH	ML	MH	ML	MH	ML	MH	ML	MH	ML	MH	ML	MH
Non-natives																
Linaria dalmatica	-	-	-	-	-	-	-	96	-	-	-	-	-	-	-	-
Verbascum thapsus	-	11	11	23	11	13	-	334	34	521	34	272	39	249	40	221
Ruderals																
Chenopodium graveolens	-	-	-	-	-	-	-	125	-	-	-	-	-	11	-	108
Gnaphalium exifolium	-	-	6	-	11	-	-	-	-	56	-	-	-	108	11	11
Laennecia schiedeana	11	17	28	-	11	48	-	23	-	17	45	23	11	28	22	17
Pseudognaph. macounii	57	-	6	17	57	-	-	62	6	-	-	45	-	-	-	23
Total	68	28	51	50	90	61	0	640	40	594	79	340	50	396	73	380

1999 and 2000, respectively (Fig. 3b). Ruderal and non-native species were more abundant in the above-ground vegetation in the MH thinned units than L-units for both 1999 and 2000. These species were also present in more abundant numbers in the seed bank in the MH-thinned units (see Table 5 for a list of species).

Discussion

We found little correlation between the seed bank and above-ground vegetation at the H, ML, and L-sites, which supports our hypothesis that soil seed bank species richness would not be correlated to above-ground vegetation in recently undisturbed *P. ponderosa* communities regardless of historical land use disturbance. Soil seed bank composition of sites with high and intermediate historical land use disturbance is generally comprised of annuals, ruderals, and many non-natives. These species often utilize mechanisms geared toward wide dispersal of seeds and seeds that accumulate and persist in the soil for long periods despite changes in the above-ground vegetation (Ingersoll & Wilson 1993). Perennial species have a reduced tendency to form a persistent seed bank in comparison (Rees 1994; Morgan 1998; Thompson et al. 1998). Milberg & Hansson (1994) have postulated that native perennials offset the need for a large seed bank from which to recruit after disturbance by instead demonstrating vegetative persistence, which can be considered the ecological equivalent to regeneration through a persistent seed bank (Parker et al. 1989). In contrast, some non-native seeds can remain viable for 50-100+ years in the soil and can be present in large quantities (Baskin & Baskin 1985). In our study, the MH sites had approximately seven times the number of ruderal and non-native seed densities than the ML sites**.** This high density of ruderal and non-native seed densities at the MH and H-sites is consistent with a study by Tsuyuzaki & Kanda (1996), which illustrated that despite 20 years since disturbance, ruderal and non-native species were still abundant in the seed bank.

Tree thinning can significantly affect soil processes due to soil profile disturbance and compaction (Jurgensen et al. 1997), but the amount of disturbance varies with the type of equipment used, number of trees removed, soil moisture content at the time of thinning, and soil characteristics (e.g., amount of soil surface organic matter) (Howard et al. 1981; Rab 1996). Our results indicate that soil disturbance from thinning did not affect the distribution of seed composition or density within the soil profile. Since the majority of viable seeds tend to be concentrated near the surface, with the O-horizon generally containing the greatest seed densities (Strickler & Edgerton 1976; Granström 1982), this finding may equate

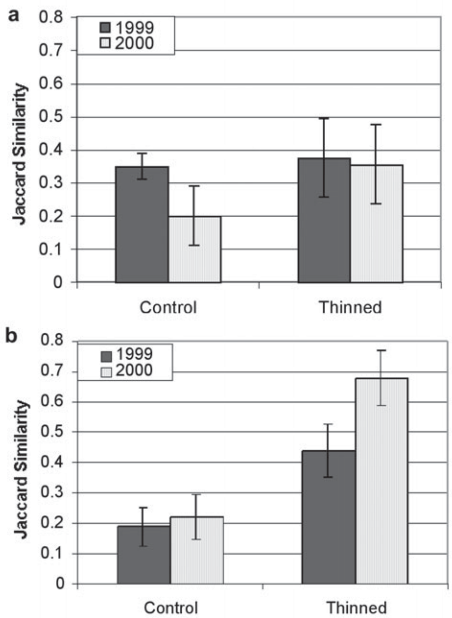

Fig. 3. a. Mean Jaccard similarity for comparison between whole-site seed bank species composition and whole-site vegetation species composition from the Fort Valley intermediate (low) L thinned and paired control units in 1999, six months after thinning, and 2000, 18 months after thinning; **b.** Jaccard similarity for comparison between whole-site seed bank species composition and whole-site vegetation species composition from the Fort Valley intermediate (high) MH thinned and paired control units in 1999, six months after thinning, and 2000, 18 months after thinning.

to an increased regeneration of the herbaceous community following thinning because the majority of viable seeds in the soil seed bank could germinate once triggered by increased light, nutrients or moisture. The high correlation between the soil seed bank and above-ground vegetation in the MH thinned-unit in 1999 and 2000, but not in the paired MH control unit that had a similar seed bank composition and density for these same years, supports our hypothesis and other research that areas with annual, ruderal, and non-native seed banks will have a higher correlation between the seed bank and above-ground vegetation following disturbance than prior to disturbance, once seeds have germinated (Tsuyuzaki & Kanda 1996; Smith et al. 2000; Zabinski et al. 2000). Many of these species require sufficient light levels for germination, and changes in the light environment through reduced tree canopy cover can allow them to become established if their seeds are present in the seed bank (Cook 1980) since the majority of viable seeds are located near the surface (Moore & Wein 1977; Pérez et al. 1998; Kramer & Johnson 1987).

The soil seed bank at the H and HM-sites consisted mainly of ruderal and annual species. Ruderals comprised 50% of the species at the M, 33% at the H, and only 11% of the species at the L-site. *Verbascum thapsus* was by far the most common species in the soil seed bank at both the H- and M-sites and made a significant contribution to the overall number of seeds per square meter. In contrast, *V. thapsus* was not observed in the soil seed bank of the L-site, perhaps contributing to significantly lower numbers of seeds per square meter. *V. thapsus* is a biennial species that may produce over 100 000 seeds per plant with 95% of the seeds falling within 5 m of the parent plant (Gross 1980). Therefore one or a few samples collected in the vicinity of a prolific plant could easily skew the results of a seed bank study because of the sheer number of seeds in the soil. *Verbascum thapsus* seeds can also remain viable in the soil seed bank for over 100 years (Gross & Werner 1978). Gross (1980) demonstrated that *V. thapsus* seedlings grew 4-7 times faster and produced 2000 times more biomass when growing in bare (non-vegetated) sites, such as those often created in *P. ponderosa* forests following restoration treatments. Dormancy in *V. thapsus* seeds is broken by alterations in light or daily temperature changes (Vanderberghe & Van Assche 1986). The requirements to break dormancy were more prevalent in thinned units than in controls, which is most likely the main contributing factor for the dramatic increase of *V. thapsus* plants in the above-ground vegetation following thinning at the MH-unit. *V. thapsus* is not generally considered to be invasive, but due to fast growth rates, large numbers of seedlings and large basal leaf size, there is the potential for seedlings of this species to outcompete native seedlings in the early stages of colonization following restoration activities.

Perhaps of greater concern, particularly at the H-site, is the lack of native perennial grasses when compared to the M and L-sites. In communities where annuals, ruderals, and/or non-native species dominate the seed bank, where the above-ground vegetation is patchy, or where native seed sources are far from the area undergoing restoration, the soil seed bank cannot be relied upon to reintegrate species lost due to historical land use disturbance or changes in climate (Morgan 1998; Halpern et al. 1999).

Management implications

One major goal of *P. ponderosa* restoration is to restore the native herbaceous and shrub plant community within a range of historical natural variability. Therefore, land managers should factor in the soil seed bank when designing restoration plans and ensure that opportunities for non-native recruitment from the soil seed bank and replenishment of a non-native seed bank are minimized (Smith et al. 2000; Honnay et al. 2002). Priority for restoration should be in areas with low historical land use disturbance where native species are more abundant than ruderals and non-natives in the soil seed bank. This recommendation is similar to re-vegetation recommendations for restoration in other habitats such as European grasslands (Bekker et al. 1997), fen meadows in The Netherlands (Matus et al. 2003), and European temperate forests (Bossuyt & Hermy 2001). In addition, under some circumstances of severe disturbance (e.g., slash pile burning and road building), restoration may be dependent on the reintroduction of propagules by direct seeding or planting (Korb et al. 2004; Springer & Laughlin 2004) rather than the exploitation of the seed bank as found in other studies (Bakker et al. 1996; Morgan 1998; Arkle et al. 2002).

Our study indicates that soil seed bank species vary greatly across southwestern *P. ponderosa* forests based at least in part on historical land use disturbance. A lack of native perennial species in the soil seed bank combined with a paucity of native perennials in the above-ground vegetation will almost certainly lead to long periods of time for native re-establishment following restoration activities, particularly during periods of lower than average precipitation. Likewise, non-native species in the seed bank will lead to the presence of these species in the above-ground vegetation following disturbance, and therefore monitoring and control for non-native species of concern, such as noxious weeds, should be a priority. The success of increasing current low levels of species diversity and abundance will depend upon the availability and colonization rates of extant plants and viable seeds in the soil seed bank as well as on the seed rain. Manual seeding is not commonly utilized in southwestern forest restoration due primarily to high cost, limited native seed supplies and genetic considerations, but it warrants further investigation.

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