

FOREST-FLOOR TREATMENTS IN ARIZONA PONDEROSA PINE RESTORATION ECOSYSTEMS: NO SHORT-TERM EFFECTS ON PLANT COMMUNITIES

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ABSTRACT.—Leaf litter accumulation during fire exclusion and increases in tree density in postsettlement southwestern *Pinus ponderosa* forests may limit the establishment of understory vegetation. We performed an experiment in *P. ponderosa* forests of northern Arizona to ascertain plant community responses to forest-floor scarification and Oi removal on thirty-six 100-m² plots overlaid on an existing ecological restoration experiment that involved tree thinning and prescribed burning. Contrasting with findings from many other forest types, forest-floor treatments had no effect on community diversity or composition during the 2-year experiment. Sørensen similarities were as high as 97% between posttreatment years within treatments; and successional vectors also provided little indication that treatments may appreciably affect longer-term successional trajectories. Lack of response to these fairly drastic treatments is surprising given these forests' exceptionally heavy Oi horizons and large proportions of conifer litter. Apparently shading, belowground competition for water or nutrients, or other tree-associated factors more strongly limit understory communities than does leaf litter. Based on sparse A-horizon seed banks averaging <300 seeds · m⁻² and limited aboveground vegetation, we hypothesize that seed shortages, particularly for native perennials, also partly precluded a treatment response. Because extensive unvegetated areas at these restoration sites may be colonized by exotics, conservative management strategies could include testing the seeding or outplanting of desirable native species as an option for filling unoccupied microsites. Reporting of "no treatment effect" experiments such as this one is important to avoid biasing meta-analyses, as is future research to clarify combinations of factors limiting understory communities. Increased understanding of these limiting factors may lead to identification of other treatments that promote recovery of native species during ecological restoration in this region.

Key words: leaf litter, O horizon, ground flora, understory vegetation, soil seed bank, seed limitation, species diversity.

Leaf litter directly and indirectly influences understory vegetation in plant communities. Decomposition of litter can immobilize some nutrients while releasing others and can also produce allelopathic chemicals (Klemmedson et al. 1985). Accumulated litter intercepts light, affects soil microclimates, and can trap seeds or form physical barriers to plant emergence (Facelli and Pickett 1991). Litter also can be a filter in some plant communities that regulates fine-scale species richness and distributions by affecting plant germination and establishment (Sydes and Grime 1981). In a New York deciduous forest, for example, Beatty and Sholes (1988) found that removal of thick litter layers from treefall pits caused species composition of pits to converge with that of treefall mounds. All forbs colonizing litter-free pits had previously been restricted to mounds.

In a variety of ecosystems, litter addition often decreased seed germination, seedling

establishment, and species richness (Monk and Gabrielson 1985, Horman and Anderson 2003). Conversely, litter removal resulted in increased abundance of some species, at least in the short term (Goldberg and Werner 1983, Velend et al. 2000). Carson and Peterson (1990), for example, found that litter removal from 1-m² plots in New Jersey old fields increased plant density within 45 days, with *Oxalis stricta* (common yellow oxalis) increasing by 530 plants · m⁻². Plant community responses to litter manipulations may vary with community type, the composition and quantity of litter, species pools and propagule availability, resource levels, and other factors (Xiong and Nilsson 1999).

After fire exclusion and increases in tree density since the late 1800s, many contemporary *Pinus ponderosa* (ponderosa pine) forests of the southwestern United States contain large amounts of litter from *P. ponderosa* needles,

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cones, bark, and wood (Covington and Sackett 1984). O horizons comprising forest floors, which include recognizable litter (Oi horizon) and decomposed duff (Oe+a horizon), were >5 cm thick and weighed >3000 g · m⁻² in dense northern Arizona *P. ponderosa* stands surpassing 1500 trees · ha⁻¹ (Wollum and Schubert 1975, Klemmedson 1976, Fulé and Covington 1994). These depths and weights equal or exceed those of many world forests (Bray and Gorham 1964, Vogt et al. 1986), suggesting that litter may particularly affect or limit plant communities in contemporary *P. ponderosa* forests.

We performed an experiment in *P. ponderosa* forests of northern Arizona to test the hypotheses that removing litter and scarifying the forest floor (1) increases plant species richness and diversity, (2) changes community composition, and (3) differentially affects individual species. By overlaying this experiment on an existing ecological restoration experiment that included tree thinning and prescribed burning, we sought to measure whether forest-floor manipulations could speed native plant establishment, which sometimes has been slow in this region after thinning and burning (Abella 2004).

METHODS

Study Area

We performed this experiment in the 1200-ha Fort Valley Experimental Forest (35°16'N, 111°43'W) in the Coconino National Forest, 15 km northwest of Flagstaff in northern Arizona. Elevation is ca. 2300 m, and soils are primarily basalt-derived and classified as Mollic Eutroboralfs and Typic Argiborolls (USDA Forest Service 1995). Annual precipitation averages 57 cm and half falls as snow (Western Regional Climate Center, Reno, NV). Forests are pure *P. ponderosa* with graminoid-dominated understories. Major graminoids include *Carex geophila* (White Mountain sedge), *Elymus elymoides* (squirreltail), *Festuca arizonica* (Arizona fescue), *Muhlenbergia montana* (mountain muhly), and *Poa fendleriana* (muttongrass). Before Euro-American settlement (presettlement) in ca. 1875, tree densities averaged ca. 60 trees · ha⁻¹. Surface fires, primarily from lightning ignitions, occurred on average at least once every 10 years (Covington et al. 1997).

Understory vegetation declined after settlement (likely from a combination of livestock grazing, fire exclusion, and increased tree density) and persisted only below canopy gaps or as isolated occurrences on litter-choked forest floors below dense tree canopies (Vose and White 1991).

This experiment was overlain on 9 sites of an existing ecological restoration experiment initiated in 1998–1999, which had goals of approximately reestablishing presettlement stand structure, reducing fuels, and increasing understory vegetation (Fulé et al. 2001a). The 9 sites in the restoration experiment included three 14-ha sites for each of 3 restoration prescriptions: control (no thinning, no burning), medium restoration (3-6 thin prescription + prescribed burning), and intensive restoration (2-4 thin prescription + prescribed burning). We did not include a more heavily thinned 1.5-3 prescription in the present forest-floor experiment because this prescription contained less *P. ponderosa* litter, and our goal was to isolate effects of manipulating thicker litter layers that may strongly limit understory communities. Restoration thinning prescriptions represent ratios (e.g., 3-6) at which evidence of presettlement tree locations (stumps, snags, and fallen logs) were replaced by postsettlement trees retained during thinning. The 2-4 prescription (the most intensive thinning prescription we examined) most closely approximated presettlement densities. Pre- and postthinning average *P. ponderosa* densities (number of live trees · ha⁻¹ >1.4 m tall) among restoration prescriptions previously reported by Fulé et al. (2001a) were as follows: 1188 and 1188 (control), 1044 and 243 (3-6 thin), and 1492 and 170 (2-4 thin). All thinning prescriptions were thinned and then burned using strip headfires. Restoration prescriptions served as blocks in the present experiment so that we could more accurately compare responses to forest-floor treatments because forest-floor characteristics and tree densities differed among prescriptions prior to our experiment (Table 1).

Experimental Design and Treatments

We randomly located four 10 × 10-m (0.01-ha) plots at each site for a total of 36 plots ($n = 9$ for each treatment). Plots within a site were separated by 3 m and arranged in a 2 × 2

TABLE 1. Plot characteristics in *Pinus ponderosa* ecological restoration blocks, northern Arizona. Means are presented with the coefficient of variation in parentheses. ER = ecological restoration prescription. Forest-floor treatments: C = control, S = scarification, R = Oi removal, and S + R = scarification + Oi removal.

Prescription Treatment	Stand density ^a (trees · ha ⁻¹)	Oi horizon (g · m ⁻²)	Litterfall (g · m ⁻² yr ⁻¹)	Soil moisture ^b (%)
Control ER				
C	1333 (95)	1302 (63)	129 (20)	6.8 (25)
S	1300 (66)	1349 (55)	118 (50)	—
R	700 (52)	1117 (39)	153 (25)	6.3 (13)
S + R	1233 (68)	1318 (33)	164 (54)	—
Medium ER				
C	333 (96)	893 (41)	95 (7)	7.4 (30)
S	333 (35)	643 (17)	109 (30)	—
R	133 (86)	573 (38)	128 (72)	5.2 (6)
S + R	267 (43)	723 (48)	127 (74)	—
Intensive ER				
C	300 (67)	821 (24)	75 (55)	8.3 (28)
S	400 (25)	687 (79)	74 (41)	—
R	167 (92)	702 (20)	105 (47)	5.3 (36)
S + R	267 (115)	778 (28)	92 (8)	—

^aDensities represent all stems > 1 cm diameter at 1.4 m. Trees and Oi weight were measured after ecological restoration but before forest-floor treatments.

^bPercent of oven-dry weight measured in June 2004 for a 0–10 cm depth; a dash means not measured.

square. One of 4 forest-floor treatments was randomly assigned to each plot at each site in a factorial design consisting of 2 levels of scarification (none, O horizon scarified) and 2 levels of Oi horizon removal (none, Oi removed). Scarification was performed to possibly bring seeds to the soil surface while creating a variegated establishment surface for dispersed seeds (Chambers 2000). Oi horizons were removed to expose mineral soil for a seed bed while eliminating thick litter layers that possibly form a barrier to emergence from soil seed banks (Horman and Anderson 2003). We performed scarification treatments manually by dragging a 45-cm-wide metal rake across plots to break up O horizons and the upper few centimeters of mineral soil. We removed Oi horizons by raking litter off plots using a 75-cm-wide plastic rake, with removals per plot ranging from 290–2200 kg oven-dry weight. Oe+ horizons were thin or absent except in control restoration prescriptions that had not been thinned or burned, and we retained these horizons on plots during Oi removal. During treatment application we observed no apparent damage to existing vegetation during treatments, as treatments were applied by hand and rakes moved over existing vegetation. We conducted treatments in April 2003, and we raked Oi removal plots again in April 2004 to remove litterfall.

Vegetation and Environmental Sampling

We sampled understory vegetation on plots in April 2003 before treatment and in August–October after treatment in 2003 and 2004. We collected pretreatment data as a covariate for repeated measures analysis of variance (ANOVA). Each plot contained six 1 × 1-m subplots that were located at the plot corners and at the midpoints of the bottom and top plot perimeters. Aerial percent cover of plant species rooted in each subplot was categorized as 0.1%, 0.25%, 0.5%, or 0.75% for values below 1% cover, at 1% intervals up to 10% cover, and at 5% intervals above 10% cover. We also recorded species as present or absent on whole plots. We calculated importance values (average of relative frequency and relative cover) for each species on each plot, and we assigned a frequency of 1 to species occurring only on whole plots for these calculations. Nomenclature and native or exotic species classifications followed USDA-NRCS (2004).

We assessed sampling reproducibility by remeasuring a subplot every 3 plots and by checking for consistency of species identification and detection on 2 plots inventoried twice by 2 different observers. Repeated measurements for subplots differed on average from original measurements by 0.17 species · m⁻², and exhibited Sørensen similarities (based on percent cover) of 98%. Repeated and original

measurements for plots differed by 1 species · 100 m⁻², and also varied by 1 species on average among observers who sampled plots during the experiment. Such low measurement error suggests that results from this experiment represent actual occurrences and not sampling artifacts.

On each plot we recorded the diameter at a height of 1.4 m for each tree >1 cm in diameter. We measured litterfall by installing 2 litter traps randomly located around the edge of each plot. Traps consisted of a 0.15-m² plastic bucket 30 cm tall. We collected an Oi horizon sample of 1 m² on each plot before treatment in April 2003, and we oven dried Oi and litterfall samples at 70°C for 24 hours. We gravimetrically measured moisture of the 0–10-cm mineral soil on Oi removal plots and control plots by oven-drying a 415-cm³ sample per plot at 105°C for 24 hours. Soil moisture was measured 9 June 2004 during the driest period of the year in this region when no measurable precipitation had fallen since April (Western Regional Climate Center, Reno, NV).

Seed Bank Procedures

We collected fifteen 208-cm³ seed bank samples per plot (5 systematically located samples along each of the bottom, middle, and top plot axes) of the 0–5-cm A horizon from control and Oi removal plots. We combined these samples on a plot basis (18 composite samples). We also collected Oe+a samples from control plots in control restoration prescriptions (3 composite samples) and Oi samples from all control plots (9 composite samples). Oi and Oe+a samples were collected as grab samples, each ca. 15 g of field-moist matter (225 g of composite samples on a plot basis), and we sieved Oi samples through a 4-mm sieve. Samples were collected and started in a greenhouse on 25 June 2004. We selected this collection and germination period to estimate which species may emerge in the field during monsoonal rains, which typically begin in July in this region. We placed 120 cm³ of each horizon for each plot in separate 700-cm³ plastic pots filled with 300 cm³ of sterile soil (United Industries Co., St Louis, MO). Then we randomly arranged the pots in a greenhouse maintained at 24°C without artificial lighting, watered the samples daily, and monitored emergence for 6 months.

Statistical Analysis

We analyzed 3 field-plot response variables: species · m⁻², species · 100 m⁻², and Shannon's diversity index—in a repeated measures ANOVA with pretreatment data as a covariate and restoration prescriptions as blocks. The following model was used: 2003 and 2004 y = covariate + blocks + scarification + Oi removal + scarification × Oi removal. To track community compositional changes of individual plots across sampling periods, we computed Sørensen similarities for importance value and presence-absence data. We compared Sørensen similarities among treatments using a 2-factor ANOVA consisting of scarification and Oi removal as factors with restoration prescriptions as blocks. The raw data approximated equal variance (Levene test) and normality (Shapiro-Wilk W test), and we used $\alpha = 0.05$ for measuring statistical significance. We performed analyses in SAS JMP (SAS Institute, Inc. 2002). We also ordinated community data (importance values) with successional vectors using nonmetric multidimensional scaling (autopilot, thorough mode) in PC-ORD (McCune and Mefford 1999). Because the seed bank data contained means that equaled 0, we analyzed them descriptively rather than by using inferential statistics.

RESULTS

Forest-floor treatments did not significantly affect species richness or diversity during the 2-year experiment based on repeated measures ANOVA (Table 2). The covariate (pretreatment data) and blocks (restoration prescription) were significant in all ANOVA models. This indicated only that the covariate was correlated with posttreatment data and that the restoration prescriptions differed before and after treatment, reducing variance in treatment means. Time was significant only for species · m⁻², with slight increases occurring on average across all treatments from 2003 to 2004 (Fig. 1).

High Sørensen similarities (>75%) indicated that little compositional change occurred between posttreatment 2003 and 2004 measurements for individual plots in any treatment (Fig. 2). Lower similarities between pre- and posttreatment 2003 measurements simply reflect season-of-sampling effects (spring versus fall) because similarities did not differ significantly

TABLE 2. Summary of repeated-measures ANOVA for forest-floor treatments in northern Arizona *Pinus ponderosa* forests. S = scarification and R = Oi removal.

Effect	Species · m ⁻²		Species · 100 m ⁻²		Diversity ^a	
	F	P	F	P	F	P
Between subjects						
Blocks	14.78	<0.01	18.84	<0.01	16.70	<0.01
Covariate	29.15	<0.01	19.84	<0.01	26.53	<0.01
S	0.32	0.58	0.10	0.76	0.90	0.35
R	0.03	0.87	0.02	0.89	0.28	0.60
S × R	0.62	0.44	0.06	0.81	1.02	0.32
Within subjects						
Time	5.11	0.03	0.00	1.00	1.29	0.27
Time × block	0.65	0.53	0.51	0.60	1.57	0.23
Time × S	0.01	0.92	0.22	0.65	0.02	0.90
Time × R	1.10	0.30	0.26	0.61	0.77	0.39
Time × S × R	0.54	0.47	0.00	0.98	0.00	0.96

^aShannon's diversity index

among treatments. Successional trajectories from repeated-measures community ordination provided no evidence that plots of similar forest-floor treatments converged in species composition, suggesting only loose groupings of plots within restoration prescriptions (Fig. 3).

Forest-floor treatments had no clear effect on frequencies of individual species, with only restoration prescription and time effects apparent for some species (Table 3). The exotic species *Linaria dalmatica* (Dalmatian toadflax) and *Verbascum thapsus* (common mullein) were more frequent in restoration than in control prescriptions, with seedlings of *V. thapsus* increasing in frequency from 2003 to 2004. Short-lived but primarily native species, including the annuals *Chenopodium graveolens* (fetid goosefoot), *Muhlenbergia ramulosa* (green muhly), and *Nama dichotomum* (wishbone fiddleleaf), were also more frequent in restoration prescriptions and exhibited overall increases through time. The number of annual *Laennecia schiedeana* (pineland marshmallow) and *P. ponderosa* seedlings, however, sharply decreased from 2003 to 2004, but these decreases appeared to be largely independent of forest-floor treatments. In contrast, frequencies of the perennials *Carex geophila*, *Festuca arizonica*, *Geranium caespitosum* (pineywoods geranium), *Muhlenbergia montana*, *Poa fendleriana*, and *Solidago velutina* (three-nerve goldenrod) changed little or not at all during the experiment.

Nine species emerged from seed bank samples collected in 2004, *Elymus elymoides* being most frequent (Fig. 4). *Gnaphalium exilifolium*

(slender cudweed), an annual, was the only species detected in seed bank samples that did not occur in the aboveground vegetation of at least 1 plot. Seed density averaged <300 seeds · m⁻² except for a higher density in Oi horizons of control forest-floor treatments in intensive restoration prescriptions. This high average density of 1250 seeds · m⁻² occurred because 1 plot contained an unusually high seed density (2917 seeds · m⁻²).

DISCUSSION

Absence of Treatment Effects

Scarification and Oi removal forest-floor treatments had no measurable effect on species richness or plant community composition during the 2-year experiment, and successional trajectories provided little evidence for potential long-term effects (Fig. 3). Sampling included complete species inventories of replicated plots and was reproducible across years, ruling out inadequate sampling as a reason for the observed absence of treatment effects. Our results contrast with many other published studies of a variety of forest types where some type of community response to litter manipulations occurred in <3 years (Beatty and Sholes 1988, Carson and Peterson 1990, Vellend et al. 2000). Furthermore, Xiong and Nilsson's (1999) meta-analysis found that effects of litter manipulations on plant establishment were greater in field than in greenhouse experiments, in 2- versus 1-year experiments, in coniferous compared to deciduous

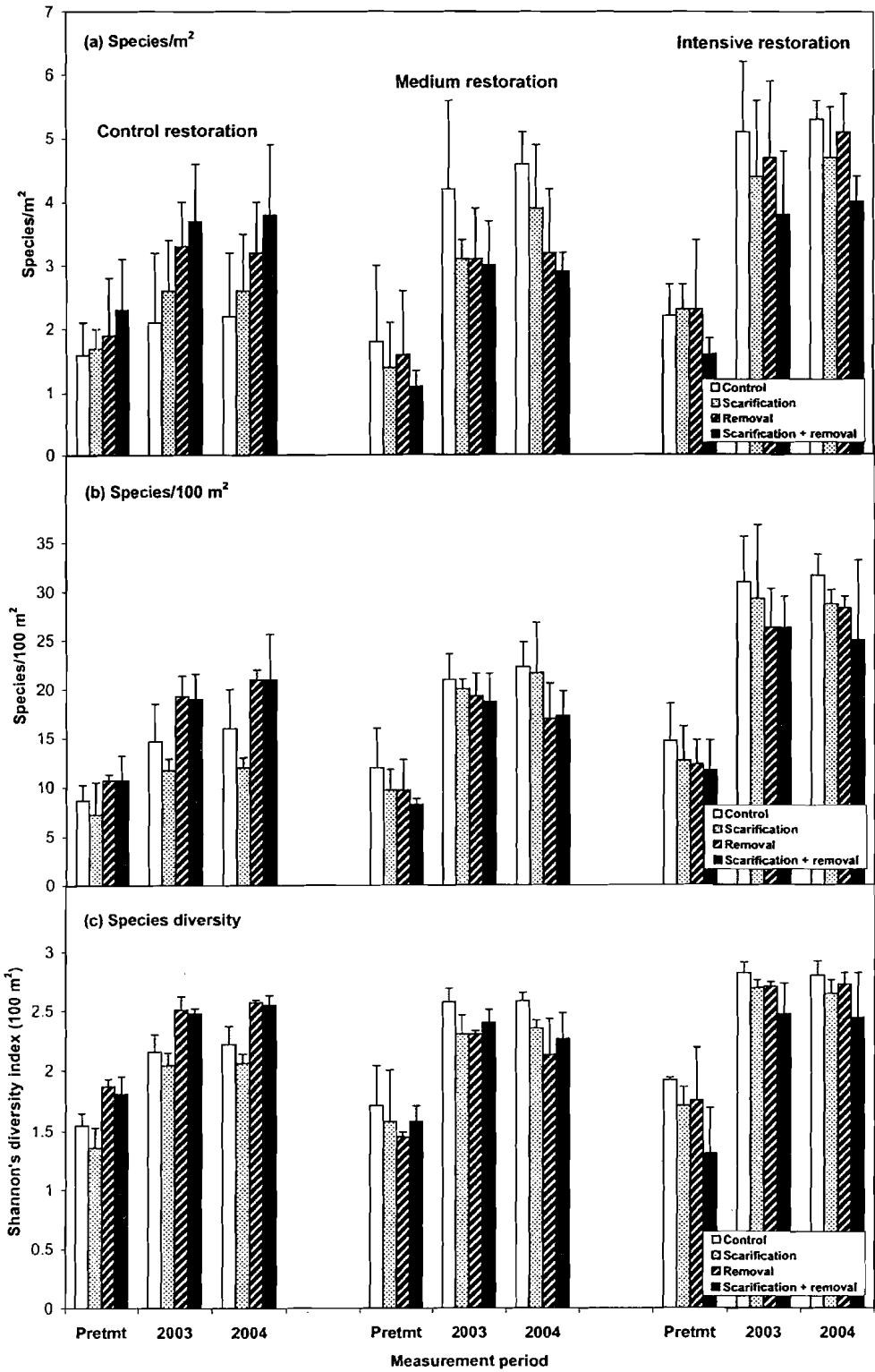


Fig. 1. Mean plant species richness and diversity among ecological restoration prescriptions and forest-floor treatments in northern Arizona *Pinus ponderosa* forests. Error bars represent 1 standard deviation.

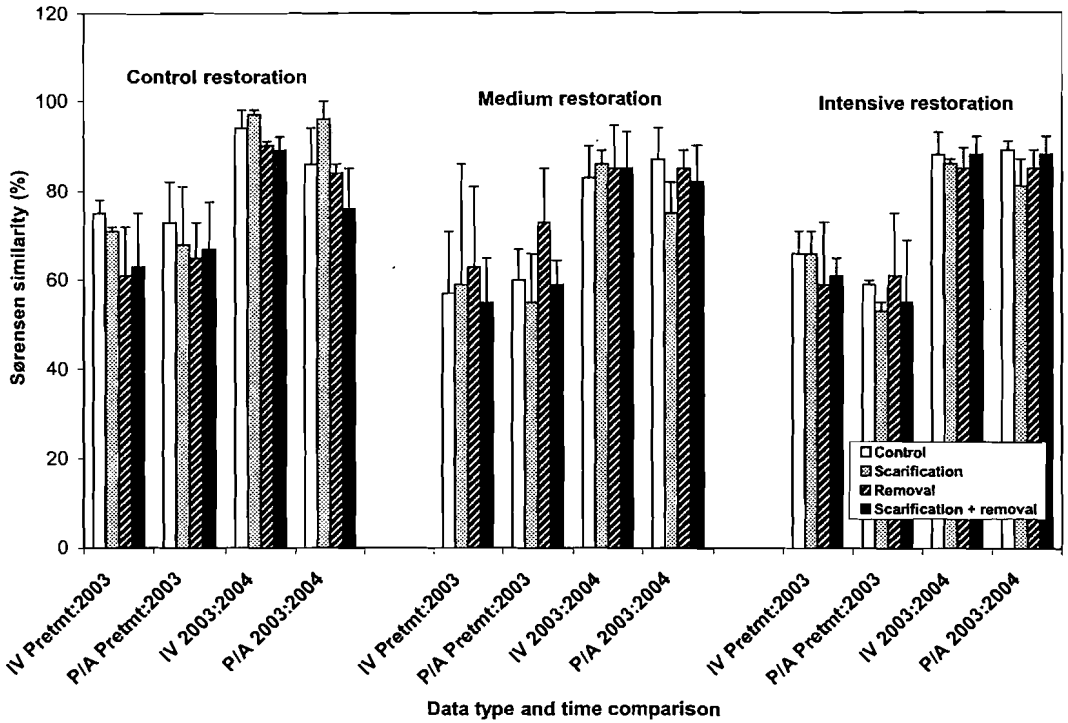


Fig. 2. Mean multivariate similarities through time based on species importance values (IV) and presence/absence (P/A) among ecological restoration prescriptions and forest-floor treatments in northern Arizona *Pinus ponderosa* forests. Error bars represent 1 standard deviation.

forests, and in communities with large amounts of litter—all conditions which characterized our experiment. Treatments were also fairly drastic, removing up to 2200 kg of litter on a plot. Our plot sizes of 100 m² also were much larger than the ≤1-m² plots used in many litter experiments, although treatment effects did not occur in our experiment at 1-m² scales either.

Limitations to Treatment Response

A number of factors may have limited understory responses to treatments in this experiment, including climate, *P. ponderosa*-associated variables other than litter, grazing, competition with existing vegetation, nutrients, and seed limitations (DiTommaso and Aarssen 1989). A period of below-average annual precipitation has occurred in the study area since 1999 after restoration treatments were implemented, and the year before initiation of our experiment (2002) was particularly dry (Fig. 5). However, growing-season and total precipitation

were near or slightly above normal during both posttreatment years in 2003–2004.

High densities of *P. ponderosa* in postsettlement forests are well known to reduce understory vegetation, presumably from shading, allelopathic litter production, and competition for water or nutrients (Moir 1966, Lodhi and Killingbeck 1982, Naumburg and DeWald 1999). For example, plant cover and diversity increased during trenching experiments that severed *P. ponderosa* roots in Oregon (Riegel et al. 1992) and in northern Arizona (Fulé et al. 2001b). Although tree densities were reduced in restoration prescriptions in our experiment (Table 1), there was no trend for effects of forest-floor treatments to be greater on lower density plots. Tree densities in restoration prescriptions still exceeded presettlement densities by ca. 100–300 trees · ha⁻¹, however, and may still have been too high for forest-floor treatments to elicit a response (McLaughlin 1978, Moore and Deiter 1992, Abella and Covington 2004). In these restoration prescriptions, we previously found in 2002 that species

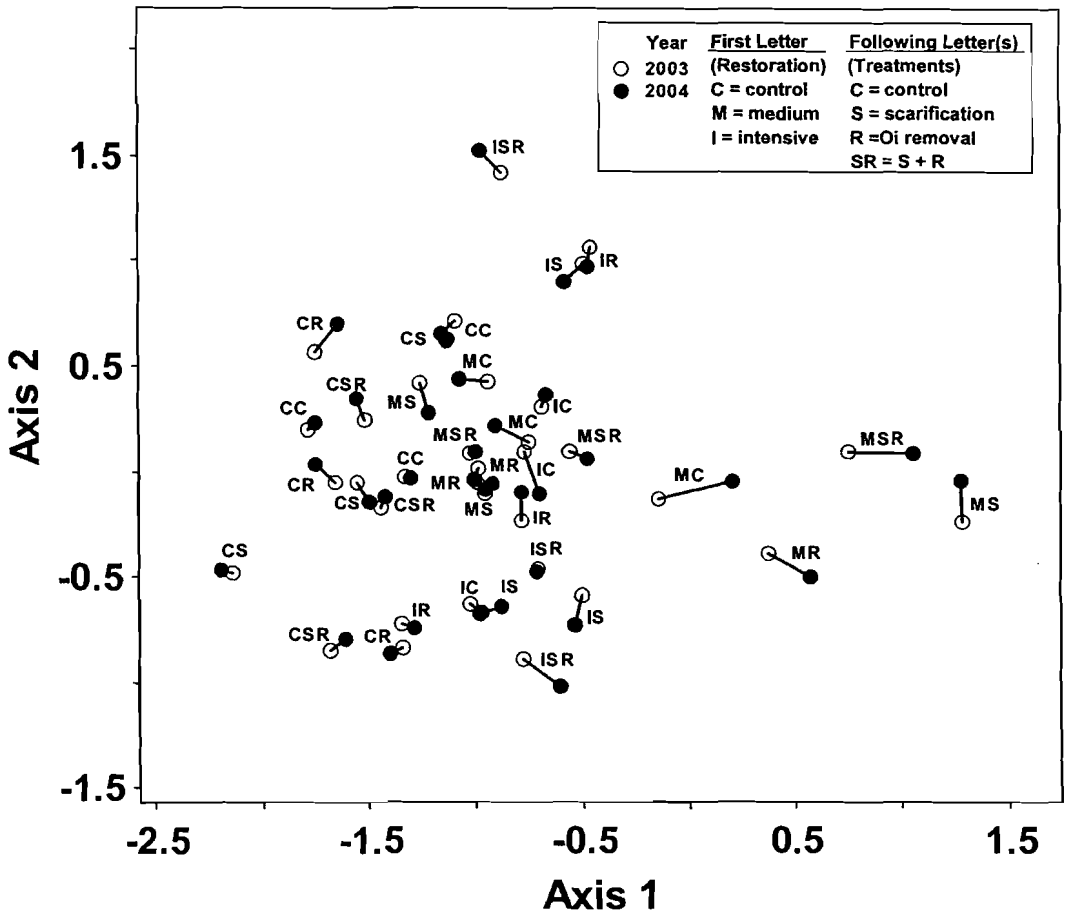


Fig. 3. Nonmetric multidimensional scaling successional vectors of understory composition among ecological restoration prescriptions and forest-floor treatments in northern Arizona *Pinus ponderosa* forests.

composition and richness $\cdot m^{-2}$ differed only in a heavily thinned 1.5-3 prescription (not included in the present study) from control, 3-6, and 2-4 restoration thinning prescriptions (Abella and Covington 2004) where we applied forest-floor treatments in the present study. Tree densities might need to be below a certain threshold for understories to respond. If this were the case, it seems that reductions in shading or decreased belowground competition accompanying these lower tree densities might be more prominent than leaf litter effects in governing understory communities.

Grazing by livestock and other ungulates also affects community composition in northern Arizona *P. ponderosa* forests (Clary 1975). Although livestock grazing has been excluded from the study area since at least 1998, Huff-

man and Moore (2003) found that heavy grazing by *Cervus elaphus* (Rocky Mountain elk) reduced *Ceanothus fendleri* (buckbrush) in the study area. Grazing thus may have affected composition during our experiment. Because plant cover averaged $<10\%$ on plots in this experiment, it does not seem plausible that all niches and microsites were filled and that competition from existing vegetation precluded a treatment response. Nutrient availability could have been limiting, but prescribed burning before our experiment may have released nutrients, at least in the short term (Covington and Sackett 1984, Kaye and Hart 1998).

Seed bank data indicated that A-horizon seed banks were sparse or essentially absent, and aside from 1 plot, few seeds were trapped in O horizons (Fig. 3). Thus, few seeds were

TABLE 3. Mean 2004 1-m² percent frequency and percent change (in parentheses) from 2003 to 2004 for the 25 most frequent species among ecological restoration prescriptions and forest-floor treatments in northern Arizona *Pinus ponderosa* forests (*n* = 3 for each category). In column headings the first letter identifies the ecological restoration prescription (C = control, M = medium, and I = intensive) and the following letter(s) identifies the forest-floor treatment (C = control, S = scarification, R = Oi removal, and SR = scarification + Oi removal).

Species	CC	CS	CR	CSR	MC	MS	MR	MSR	IC	IS	IR	ISR
<i>Carex geophila</i>	44 (0)	33 (0)	39 (0)	44 (0)	72 (+16)	44 (0)	39 (-11)	56 (0)	55 (0)	50 (0)	50 (+6)	44 (-12)
<i>Ceanothus fendleri</i>	0 (0)	0 (0)	0 (-6)	11 (0)	6 (0)	0 (0)	0 (0)	0 (0)	6 (-5)	17 (0)	0 (0)	0 (-6)
<i>Chenopodium graveolens</i>	0 (0)	6 (0)	0 (0)	0 (0)	33 (+22)	39 (+17)	33 (+16)	33 (+16)	11 (+11)	17 (+11)	22 (+22)	17 (+11)
<i>Cirsium wheeleri</i>	0 (0)	0 (0)	11 (+5)	6 (0)	22 (+5)	17 (+6)	11 (+5)	0 (0)	29 (+17)	28 (+6)	33 (+5)	22 (-6)
<i>Elymus elymoides</i>	61 (0)	61 (0)	56 (-5)	67 (0)	72 (+16)	66 (+16)	78 (0)	56 (0)	89 (+11)	94 (+22)	78 (+11)	72 (0)
<i>Eriogonum divergens</i>	0 (0)	0 (0)	11 (+11)	11 (+11)	6 (+6)	0 (0)	0 (0)	6 (+6)	0 (-6)	6 (0)	11 (+5)	6 (+6)
<i>Festuca arizonica</i>	0 (0)	6 (0)	6 (0)	17 (0)	0 (0)	11 (0)	11 (0)	6 (+6)	17 (0)	17 (0)	11 (0)	11 (0)
<i>Geranium caespitosum</i>	0 (0)	0 (0)	6 (0)	17 (0)	0 (0)	6 (0)	6 (-5)	0 (0)	17 (0)	0 (0)	17 (0)	0 (0)
<i>Hieracium fendleri</i>	6 (0)	0 (0)	0 (-6)	0 (-6)	6 (+6)	0 (0)	6 (+6)	0 (0)	11 (0)	17 (+6)	6 (-5)	11 (0)
<i>Laemnecta seluedeana</i>	0 (0)	0 (0)	6 (-5)	6 (-11)	17 (-22)	0 (-11)	22 (-17)	28 (-5)	6 (-33)	17 (-33)	17 (-16)	17 (-5)
<i>Linaria dabnatica</i>	0 (0)	0 (0)	0 (0)	0 (0)	5 (+6)	11 (0)	0 (-6)	11 (0)	0 (0)	0 (0)	11 (+5)	0 (0)
<i>Lotus urighii</i>	0 (-6)	0 (0)	6 (+6)	6 (0)	17 (0)	0 (-6)	0 (0)	11 (0)	11 (+5)	11 (+5)	28 (0)	11 (0)
<i>Muhlenbergia montana</i>	22 (0)	33 (0)	11 (0)	17 (0)	11 (0)	22 (0)	6 (0)	0 (0)	28 (0)	6 (0)	17 (0)	0 (0)
<i>Muhlenbergia ramulosa</i>	6 (+6)	11 (0)	0 (0)	11 (+11)	11 (0)	17 (+17)	0 (0)	11 (+11)	28 (+11)	17 (0)	22 (+11)	22 (+5)
<i>Nama dichotomum</i>	0 (0)	0 (0)	0 (0)	0 (0)	6 (+6)	0 (0)	6 (-5)	0 (0)	17 (+17)	0 (0)	11 (+11)	22 (+11)
<i>Packeria multilobata</i>	0 (0)	0 (0)	6 (+6)	0 (0)	11 (0)	11 (+5)	17 (0)	17 (+6)	22 (0)	17 (0)	22 (+11)	0 (0)
<i>Pinus ponderosa</i>	6 (0)	6 (0)	0 (0)	0 (0)	11 (-28)	11 (-33)	6 (-33)	22 (+5)	6 (-11)	11 (-17)	0 (-28)	6 (-5)
<i>Pod fendleriana</i>	11 (0)	11 (0)	33 (0)	17 (0)	0 (0)	11 (0)	17 (0)	6 (0)	17 (-5)	6 (0)	0 (0)	11 (+5)
<i>Potentilla crinita</i>	6 (0)	0 (0)	17 (0)	22 (-6)	0 (0)	0 (0)	6 (0)	0 (0)	0 (0)	0 (0)	6 (0)	0 (0)
<i>Potentilla suberosa</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	6 (0)	11 (-6)	0 (-6)	0 (0)	0 (0)	0 (-6)
<i>Pseudocymopterus montanus</i>	6 (0)	0 (0)	6 (-5)	0 (0)	6 (0)	6 (0)	6 (0)	0 (0)	22 (+5)	0 (-6)	11 (0)	6 (0)
<i>Pseudognaphalium macranthii</i>	0 (0)	11 (+5)	0 (0)	0 (0)	0 (-6)	0 (0)	0 (-6)	0 (-6)	6 (0)	6 (-5)	0 (0)	11 (0)
<i>Solidago velutina</i>	22 (0)	6 (0)	39 (0)	17 (0)	17 (0)	6 (0)	17 (0)	0 (0)	6 (0)	0 (0)	22 (0)	11 (0)
<i>Verbascum thapsus</i>	0 (0)	0 (0)	0 (-6)	6 (0)	11 (0)	17 (+6)	22 (+11)	28 (+28)	56 (+17)	56 (+28)	39 (+17)	33 (0)
<i>Vicia americana</i>	6 (+6)	11 (0)	6 (0)	22 (-6)	6 (0)	6 (0)	17 (+6)	11 (0)	6 (0)	17 (0)	33 (0)	6 (0)

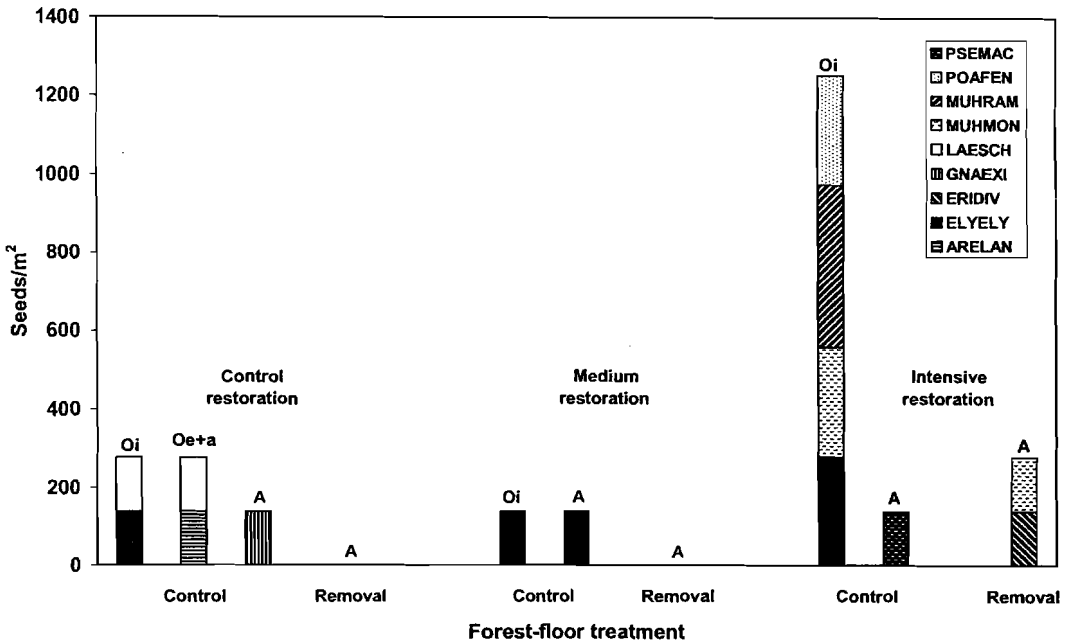


Fig. 4. Seed bank composition by species and soil horizon among control and Oi removal forest-floor treatments and ecological restoration prescriptions in northern Arizona *Pinus ponderosa* forests. Values of seeds \cdot m⁻² are standardized to represent a 0–5-cm depth (0.05 m³), with the Oi horizon representing material passing a 4-mm sieve. ARELAN = *Arenaria lanuginosa*, ELYELY = *Elymus elymoides*, ERIDIV = *Erigeron divergens*, GNAEXI = *Gnaphalium exilifolium*, LAESCH = *Laennecia schiedeana*, MUHMON = *Muhlenbergia montana*, MUHRAM = *Muhlenbergia ramulosa*, POAFEN = *Poa fendleriana*, and PSEMAC = *Pseudognaphalium macounii*.

likely removed by forest-floor treatments. Sparse seed banks, particularly of perennial forbs, also were previously reported in the study area (Vose and White 1987, Korb et al. 2004) and typify many northern Arizona *P. ponderosa* forests (Abella 2005). In their seed budget study, Vose and White (1987) also found that seed rain was fairly impoverished, ranging from 14–547 seeds \cdot m⁻²yr⁻¹ and concentrated around existing plants. Propagule limitations have been reported in about 50% of seed-augmentation experiments, and have been particularly severe in communities, such as in our experiment, that exhibit sparse seed banks, paltry aboveground vegetation producing few seeds, and much bare ground (Turnbull et al. 2000). Seeding and outplanting have shown success in the limited areas where they have been studied in Arizona *P. ponderosa* forests (Steed and DeWald 2003, Springer and Laughlin 2004), and testing for propagule limitation in these forests is an important research need.

Potential Long-term Species Composition

Species composition and diversity at the onset of this experiment differed between control and restoration prescriptions that included thinning and burning. However, aside from transitions in *P. ponderosa* seedlings and in short-lived species like *Laennecia schiedeana*, *Chenopodium graveolens*, and *Verbascum thapsus*, community composition as a whole was fairly stagnant in restoration prescriptions in 2003–2004 during our experiment (Table 3). Apparently there was an initial increase in plant cover after the 1998–1999 restoration treatments, driven primarily by species that do form fairly large, persistent seed banks (Korb et al. 2004), but little change since. Bartha et al. (2003) reported a similar pattern in a 40-yr study of a New Jersey old-field succession, where the number of colonizing species rapidly declined after the first few years of succession. However, increases in colonization rates then occurred after dry years

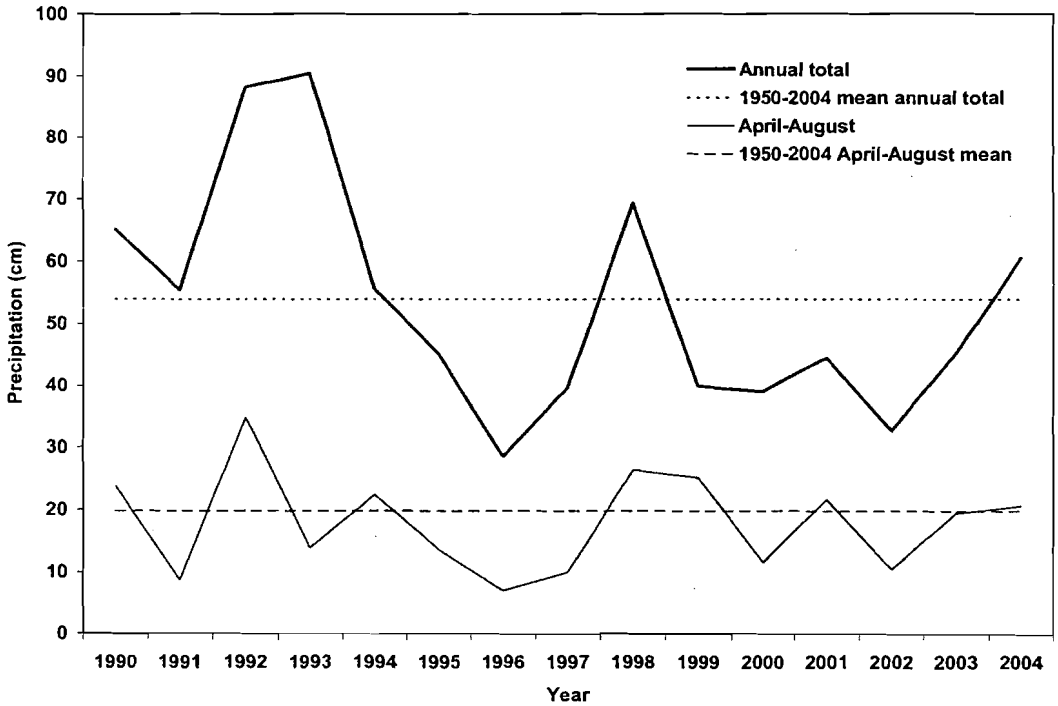


Fig. 5. Recent and long-term precipitation records measured at the Flagstaff Airport, northern Arizona, obtained from the Western Regional Climate Center (Reno, NV).

during “colonization windows” in their study. Such increases have not occurred to date in our experiment except possibly for undesirable species like *V. thapsus*. The biennial *V. thapsus*, usually thought to rapidly decline following initial postdisturbance increases (Gross and Werner 1978), remained frequent in restoration areas and even sharply increased on control forest-floor plots in the intensive restoration prescription 6 years after restoration treatments (Table 3). Although this species was not detected in our seed bank samples, possibly because its germination requirements were not met at the time of sample collection (Baskin and Baskin 1981), *V. thapsus* is known to form large and persistent seed banks (Gross and Werner 1978).

Extensive bare ground, which provides colonization sites for exotic species such as *V. thapsus*, is a concern given increasing unease about exotic species invasions in northern Arizona forests (Sieg et al. 2003). Because these unoccupied microsites could continue to fill with exotics like *V. thapsus*, *Linaria dalmatiana*, or additional undesirable species not presently

found in current species pools, a conservative management strategy is to test seeding or out-planting of native perennials for potential to vegetate unoccupied ground.

Nonsignificant Results

This paper reports a main finding of “no treatment effect” on plant communities from fairly drastic forest-floor manipulations in a reproducibly sampled experiment that likely would have detected trends had they existed. Underreporting of statistically nonsignificant, but properly collected and analyzed data is a form of publication bias that has long been suspected in ecology and increasingly is being quantitatively assessed (Møller and Jennions 2001, Murtaugh 2002). Reporting of nonsignificant results is particularly important to avoid biasing meta-analyses, which are being used increasingly to synthesize research findings in ecology (Osenberg et al. 1999, Gurevitch and Hedges 1999). Results of our experiment contrast sharply with results of most of the published studies included in a recent meta-analysis of leaf-litter manipulation experiments, which

found strong treatment effects in many other ecosystems (Xiong and Nilsson 1999). Our results do not mean that leaf litter has no influence on plant communities in *P. ponderosa* forests, but rather that treatment responses were precluded by other factors which would be important to identify in future research in order to find ways to increase native plant cover. If seed shortages prevented responses, for example, it is unclear whether seeding would be more successful with or without litter. This experiment portrays that economically and ecologically effective treatments supplementary to thinning and burning still need to be identified and tested to determine whether they promote native vegetation more rapidly in *P. ponderosa* restoration ecosystems.

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