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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

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Abstract

Pinus ponderosa Laws. (ponderosa pine) forests have changed considerably during the past century, partly because recurrent fires have been absent for a century or more. A number of studies have explored the influence of timber harvest or burning on understory production in ponderosa pine forests, but study designs incorporating cutting and prescribed burning in an experimental framework are needed to identify mechanisms responsible for the observed changes. In this study, we first characterized the disturbance history and the soil seed bank of a ponderosa pine stand in the northern Black Hills. We then experimentally addressed the effects of prescribed burning and overstory reduction on understory vegetation. Before Anglo settlement of the area, the mean fire interval was 14 years and no fires were recorded after 1879. Cessation of fires, prolific regeneration of ponderosa pine, and subsequent logging in 1903 has led to a very dense, even-aged ponderosa pine stand with very little understory vegetation and very few viable seeds in the soil seed bank. Only 57 individual plants, or 186 seeds/m^2, emerged from 1080 soil samples. Response of understory vegetation during the first growing season after application of treatments was sparse, with no significant treatment effect. There were, however, significant treatment effects during the second growing season. Total understory biomass ranged from 5.8 kg/ha on untreated plots to 1724 kg/ha on clearcut, unburned plots. Herbaceous dicots comprised over 90% of total understory biomass. Both understory species richness and evenness responded to treatments, but understory woody plant density did not respond to either treatment. Paucity of viable seeds in the soil seed bank does not appear to constrain recruitment of understory vegetation in dense ponderosa pine forests of South Dakota.

Keywords: Black Hills; Fire history; Overstory; *Pinus ponderosa* Laws.; Prescribed fire; Soil seed bank; Stand age; Understory

1. Introduction

Western North American forests dominated by *Pinus ponderosa* Laws. (ponderosa pine) and other conifers have changed considerably during the last century (Weaver, 1943; Cooper, 1960; Covington et al., 1994). Structural and functional changes in these forests include increases in dense thickets of small, young trees, increased frequency and severity of insect and disease epidemics, increased severity of wildfires, and decreased number of large, old trees, tree vigor, and herbaceous production (Weaver, 1943; Wright, 1978; Covington and Moore, 1992; Arno,

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1996). These changes are most often attributed to the interactive effects of active fire suppression, logging, livestock grazing, and geographic fragmentation (Cooper, 1960; Covington and Moore, 1994; Swetnam and Baisan, 1996; McPherson, 1997).

Forests of the Black Hills are no exception to this general pattern. Ponderosa pine is the dominant overstory species in the Black Hills of South Dakota and Wyoming, covering nearly 95% of the forested area (Sheppard and Battaglia, 2002). Historically, recurrent fires were frequent in Black Hills forests (Brown and Sieg, 1996), and were started by lightning and American Indians (Sieg and Severson, 1996). Mean fire interval (MFI) was 20–23 years for interior ponderosa pine stands in the southcentral Black Hills (Brown and Sieg, 1996) and 10–12 years for pine savanna sites in the foothills of the Black Hills (Brown and Sieg, 1999). Since Anglo settlement, fire frequency has decreased substantially. None of the trees sampled in the interior stands had fire scars that formed after 1900 (Brown and Sieg, 1996). Similar MFIs were reported for the Devil's Tower region on the northwestern edge of the Black Hills. The MFI was 14 years between 1770 and 1900, and 42 years since 1900 (Fisher et al., 1987).

Black Hills forests have been managed as intensely as any western timber type; nearly every hectare has been cut at least once during the past 125 years (Ball and Schaefer, 2000). Large-scale timber harvesting began with the gold rush of 1876, followed by the establishment of the Black Hills Forest Reserve in 1897 and the first timber sale from the national forest system in 1899. The combination of intensive silvicultural management and suppression of fires since then have contributed to increased density and extent of ponderosa pine stands (Progulske, 1974; Progulske and Shideler, 1983; Grafe and Horsted, 2002). This has led to decreases in understory productivity, extent of interior prairies and meadows, and species diversity (Parrish et al., 1996). In some areas covered with ponderosa pine in high densities, understory vegetation has been replaced by a thick mat of pine needles.

A number of studies have explored the influence of timber harvest on understory production in ponderosa pine forests, but experimental approaches incorporating cutting and prescribed burning in an experimental framework are uncommon. Such experimental studies that incorporate before-after-control-impact (BACI) designs are especially valuable for quantifying mechanisms underlying structural and functional responses of these systems (Underwood, 1994). After description, elucidation of mechanisms via experimentation is a primary goal of the sciences, as described by Harper (1982).

The first portion of this study was designed to document conditions of a ponderosa pine stand before experimental treatments were applied. Fire history, stand age, and past management were examined to document historical disturbances and pre-treatment conditions of the stand. We also examined the soil seed bank to assess the density of viable seeds in areas where fires have been rare in the last century and almost no understory vegetation is present. After documenting the history and structure of the stand, we experimentally tested the potential for prescribed burning and overstory reduction to increase understory production in dense ponderosa pine stands in the northern Black Hills. The descriptive portion of this study provides context for interpreting the results of the experimental portion of the study. It indicates that this research site is representative of other sites in the Black Hills with a history of timber harvest and fire suppression in the last century.

2. Methods

2.1. Study area

This study was conducted in Lawrence County, South Dakota, in the northern Black Hills. The study area is located on the South Dakota Game, Fish and Parks Badger Game Production Area (GPA) west of Spearfish, South Dakota (Fig. 1). Average annual precipitation in Spearfish is 54 cm, of which 39 cm (71%) usually falls between April and September (Driscoll et al., 2000). Precipitation data were incomplete for Spearfish during this study but in Rapid City it was 32% above average in 1998, 18% above average in 1999, and 9% below average in 2000 (US Department of Commerce, 1998/1999/2000). Average winter temperature is −3 °C with a low record of −34 °C. Average summer temperature is 18 °C with an average daily maximum near 27 °C (Meland, 1979). The growing season is approximately 140 days and extends from early May until late September.

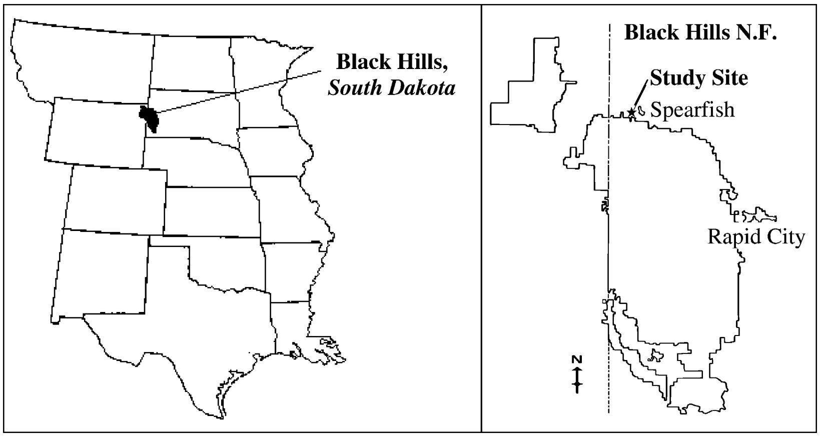

Fig. 1. Location of study site, west of Spearfish, South Dakota.

Soils on the site are of the Vanocker series (loamy-skeletal, mixed, superactive, frigid Hapludalfs), which are formed from limestone and calcareous sandstone parent materials (Ensz, 1990). This soil series is common on the Badger GPA and is relatively common on the Black Hills portions of Lawrence County (Meland, 1979). It is found extensively on the lower limestone plateau and is similar to soils found on the upper limestone plateau (Ensz, personal communication). Elevation of the site ranges from approximately 1220–1280 m.

The northern Black Hills was densely settled following the discovery of gold in 1874 (Progulske, 1974). Timber harvest in the area was unregulated until the establishment of the Black Hills Forest Reserve in 1897 (Ball and Schaefer, 2000). The specific area in which this study was conducted was privately owned from 1903 to 1945 and probably was used primarily for ranching. The state of South Dakota purchased the land in 1945 as a game production area to be managed for deer winter range.

Ponderosa pine is the dominant overstory species. At study initiation, the understory was sparsely vegetated and generally characterized by a layer of pine needles 5–7 cm thick. Understory species included *Apocynum androsaemifolium* L. (spreading dogbane), *Pulsatilla patens* (L.) P. Mill. (American pasqueflower), *Poa pratensis* L. (Kentucky bluegrass), *Carex* spp. L. (sedge species), *Amorpha canescens* Pursh (leadplant), *Juniperus communis* L. (common juniper), *Prunus virginiana* L. (chokecherry) and others encountered less frequently. Nomenclature follows The PLANTS Database (USDA NRCS, 2002).

2.2. Plot establishment

Eighteen 45 m × 45 m research plots were established in 1998 in a relatively even-aged, high-density (1300–4700 stems/ha) and high basal area (50–80 m^2/ha) ponderosa pine stand representative of ponderosa pine stands in the Black Hills. Plots were placed on western and southwestern aspects, and spanned approximately 1 km along a relatively homogeneous limestone shelf. Distance between plots ranged from 0 to 200 m in an effort to select the most similar sites and avoid anomalous topography. Six 15 m long transects parallel to the slope were established in each plot. Transects were spaced 3 m apart and this design left a 15 m buffer zone in all directions. Sampling for both the descriptive and experimental portions of this study occurred within this plot framework and buffer zones between plots.

2.3. Disturbance history

Twenty-four fire-scarred cross-sections were collected from the study area. These samples were collected in four clusters distributed over an area of approximately 6.3 ha (15 acres). Of these 24 samples, 5 were collected from live trees, 16 from stumps, 2 from snags, and 1 from a downed log. In addition, a master tree-ring chronology was constructed using increment cores from seven living ponderosa pine trees on the study site. The master chronology provided dating control for the remnant (dead) wood samples.

Fire history methods followed those of Brown and Sieg (1996). The goal was to compile an inventory of fire events at this study site (Swetnam and Baisan, 1996). Cross-sections were prepared with progressively finer sandpaper from 60 to 400 grit using a belt sander and hand sander. Standard dendrochronological procedures were followed when cross-dating tree-ring series (Stokes and Smiley, 1968). Tree-ring series were cross-dated using the master chronology as well as existing chronologies and pine ring-width index chronologies from the Black Hills (Drew, 1974; Brown, unpublished data). Dates were assigned to fire scars after all cross-sections were cross-dated and were then compiled into a fire chronology for the site. When possible, position of the fire scar within annual rings was assigned as earlywood, latewood, or dormant season (Baisan and Swetnam, 1990). Dormant-season scars were dated to the earlier year (Brown and Sieg, 1996).

To determine the approximate age of living trees on the study site, cross-sections were collected from 10 randomly selected stumps on each of the 12 research plots that received a cutting treatment. Pith dates were assigned to the cross-sections using the dendrochronological techniques described above. These dates are not exact germination dates, because they were collected 10–20 cm aboveground; rather, they represent age of trees at stump height.

South Dakota Game, Fish and Parks records and historical documents were examined to determine past management activities on the research site.

2.4. Soil seed bank

Soil seed bank was sampled in August 1998 and May 1999 to estimate the number of viable seeds in the soil seed bank before treatments were applied. The May 1999 sample was collected immediately after the prescribed fires, and presumably before any seasonal seed input, to determine if fires provided any environmental cues that may lead to increased seed germination. A seedling emergence method was used to estimate viable seed numbers in the soil (Ferrandis et al., 1996; Kitajima and Tilman, 1996; Ter Heerdt et al., 1996). Sixty soil cores (10 per transect) were collected from each plot to a depth of 3 cm with a 1.9 cm-diameter soil sampler. The litter layer was included with the soil samples because this layer may contain a high number of seeds (Simpson et al., 1989). All cores from a transect were composited into a single subsample and placed in plastic bags for transportation to the lab. Litter and soil samples were stored in darkness for 8–10 weeks at 4–6 °C.

Samples were sieved through a no. 5 soil sieve (4 mm) and then a no. 8 sieve (180 μm) to remove larger material while preventing the loss of seeds. Remaining soil was spread to a depth of 0.5 cm in pots containing sterilized potting soil covered with a 0.5–1.0 cm layer of pure silica sand. Samples were placed in a climate-controlled growth chamber (12 h light, 10–20 °C, 75% RH), watered daily, and checked for new seedlings every 3 days. New seedlings were marked with color-coded toothpicks and removed when they were large enough to identify to guild. Unidentifiable seedlings from the May 1999 sample were transplanted and grown in individual pots until further identification was possible. When no new seedlings emerged for more than 2 weeks, samples were allowed to dry. They were then disturbed by crumbling/mixing the soil and provided water for approximately six more weeks in the growth chamber, while they were again checked for seedlings every 3 days (Ter Heerdt et al., 1996).

2.5. Experimental design

A completely randomized design was used with three replications of two treatments in a factorial arrangement: three levels of overstory removal (clearcut, basal area thinned to about 12 m^2/ha, and uncut) and two levels of burning (burned and unburned). Treatments were randomly assigned to the plots, and plots were experimental units for all analyses.

2.6. Application of treatments

The cutting treatment was applied during the autumn and winter of 1998–1999. Trees were selected for the cutting treatment to leave a basal area of approximately 12 m^2/ha and stems equally spaced across the plots. Trees and slash were removed from plots to simulate whole-tree harvest. This treatment was designed to mimic harvesting treatments currently utilized by the US Forest Service. Skidding the trees off the cut plots disturbed the litter layer, so hand raking was used to redistribute the pine needles before plots were burned.

The objective of the prescribed fires was to reduce the litter layer and create a mineral soil seedbed while minimizing overstory mortality. Plots were burned on 8 May 1999. Conditions were: light winds variable from west to north, temperatures 12–21 °C, and relative humidity 30–60%. A strip-headfire technique was used to burn buffer zones and research plots. The strips varied from 5 to 15 m in width. Flame lengths averaged 0.5–1.25 m.

2.7. Overstory sampling

The overstory was characterized both pre- and post-treatment by measuring tree density, basal area, and overstory canopy cover. Basal area and density were calculated by tallying and measuring diameter at breast height (DBH) of all trees on the center 15 m × 15 m of the 45 m × 45 m plots. Percent overstory canopy cover was measured with a canopy cover tube at 2 m intervals along six permanent 15 m transects in each plot (Hetherington, 1967). Overstory measurements were collected before and after treatments were applied.

Char height and crown scorch were measured in June 1999 on all trees within burned plots. Char height was the maximum height of charring on tree bole, as measured with a telescoping measuring pole. Crown scorch was visually estimated as the percentage of foliage in the live crown that was killed. Mortality of ponderosa pine was calculated as the difference in overstory pine density between 1999 and 2000.

2.8. Understory sampling

Understory vegetation was sampled in August 1998 (pre-treatment), July 1999 (first season post-treatment), and July 2000 (second season post-treatment). Biomass of herbaceous species was estimated by clipping thirty 0.25 m^2 circular quadrats in each plot (5 per transect). The material was sorted by species, placed in paper bags, oven-dried at 60 °C for 48 h, and weighed. Biomass sampling was destructive, so quadrat location along the transect was predetermined so that post-treatment sampling was not repeated in the same location. Density of understory woody plants was measured in twenty-four 1 m^2 quadrats spaced at 2 m intervals along the six 15 m permanent transects. Litter/duff depth was measured with a meter stick at 5 m intervals along the transects (3 per transect).

Species richness and evenness were calculated for all treatments using understory biomass data collected. Richness was the mean number of species per plot. Shannon-Weaver H' and Simpson's c were used as measures of evenness (Shannon and Weaver, 1949; Simpson, 1949).

Shrub biomass was estimated by measuring volume of shrubs in a total of twenty-four 1 m^2 quadrats located at 2 m intervals along the six 15 m permanent transects. Methods used to measure shrub volume follow those used by McPherson and Wright (1987). Height and two diameters (D_1, largest diameter; D_2, diameter perpendicular to D_1) of each shrub were measured. Shrub volume was calculated with the equation: $V = \pi a^2 b/6$, where V is the shrub volume (cm^3), a the minor axis (cm; height or average diameter, whichever is smaller), and b the major axis (cm; height or average diameter, whichever is greater) (Phillips and MacMahon, 1981). Relationship of shrub volume and biomass was determined separately for each species so that biomass could be estimated for shrubs sampled in the plots. Shrubs of each species were located in the buffer zones around the plots, measured for shrub volume, clipped, oven-dried, and weighed. These measurements were used to develop regression equations between biomass and volume for each shrub species ($r^2 > 0.78$).

Soil moisture was measured in August and September of 1998, monthly from May to September of 1999, and monthly from May through July of 2000. A 1.9 cm-diameter soil sampler was used to collect the upper 3 cm of soil from six randomly selected soil cores in each plot in 1998. Sample size was increased to 9 in 1999 and 10 in 2000 because variability in soil moisture was relatively high within each plot. Soil was collected and placed in plastic soil bags, weighed, dried at 100 °C for 48 h, and reweighed. Soil temperature was measured monthly August to September 1998, and again May through July, 2000. Soil thermometers were used at four randomly selected locations in each plot during the peak temperature period of the day (13:00–16:00 h) to capture the maximum soil temperatures.

2.9. Statistical analyses

Mean fire interval and standard deviation were calculated and reported three different ways: (1) all fires from all samples included in analysis, (2) only fires that were recorded by at least four samples included in analysis, and (3) all fires recorded when sample size is >6 trees. MFI was interpreted as the interval between fires that occurred anywhere within the study area. Arithmetic mean and standard deviation were used to describe stand age.

Overstory and understory data residuals were visually inspected to ensure that normality, linearity, and homogeneous variance assumptions of analysis of variance (ANOVA) were met before proceeding with analyses (Ramsey and Schafer, 1997). Pre-treatment data were analyzed to assess the homogeneity of research plots. Statistical analyses were completed with JMP IN statistical software (SAS, 1996). Individual ANOVAs were used to determine if pre-treatment differences were present in understory biomass (total and by guild), shrub density, litter depth, and stand characteristics (ponderosa pine density, basal area, canopy cover). Soil moisture and temperature were analyzed with repeated-measures ANOVA. Char height and crown scorch were analyzed with ANOVA, and correlation coefficients were calculated between these two measures and ponderosa pine mortality.

Repeated-measures ANOVA was used to analyze response of soil moisture and soil temperature two growing seasons after application of treatments. Response of litter depth after the first growing season was analyzed with ANOVA. Since there was no response of understory vegetation after the first growing season, ANOVA was used to analyze interactions and main effects of treatments on understory vegetation after the second growing season (2000). Understory vegetation data were transformed with the common log (base 10) transformation for analysis to satisfy the assumptions of ANOVA. When interactions were detected, least significant difference (LSD) was used to determine differences between treatment combinations.

Shannon-Weaver H' and Simpson's c were highly correlated ($r = 0.97$) and only H' is presented. Differences among treatments in richness and evenness were analyzed with ANOVA. In addition, minimum variance analysis (Ward, 1963) was used to display relationships between understory biomass and treatments. Treatment effects on number of viable seeds in the soil seed bank were analyzed with repeated-measures ANOVA.

3. Results

3.1. Disturbance history

Twenty-three of the twenty-four samples were cross-dated and dates were assigned to 161 fire scars (Fig. 2). Frequent fires were recorded on all trees between the mid-1600s and 1879. The fire in 1879 was the last recorded on any living or remnant sample. None of the fire-scarred trees that were alive in the 20th century recorded fires after 1879 and none of the 120 cross-sections from the clearcut and partial-cut plots had any fire scars. Several fire dates were synchronous among most samples, notably 1715, 1743, 1785, 1808, 1834, and 1854. Fires appeared to be less frequent but more synchronous in the 18th and early-19th centuries than during other periods. This period was followed by an increase in fire frequency in the mid- to late-19th century. The majority of fire scars on samples from this site were either late-season or dormant-season scars. The mean fire interval, interpreted as the mean number of years between fires that burned some portion of the study area, was 11–15 years with a range of 1–43 years, depending on which fires were included in the analysis (Table 1).

3.2. Soil seed bank

Number of viable seeds in the soil seed bank did not differ as a function of main or interactive effects of treatments, and did not vary over time ($P > 0.28$; MANOVAR Wilks' Lambda F-test) (Table 2). At least one of the species in the soil seed bank was non-native and it was also present in the understory the second post-treatment growing season.

3.3. Pre-treatment

The pre-treatment stand had high tree density and basal area with little vegetation growing in the understory (Table 3). It was also notably even-aged and relatively young. Over 95% of the pith dates fell

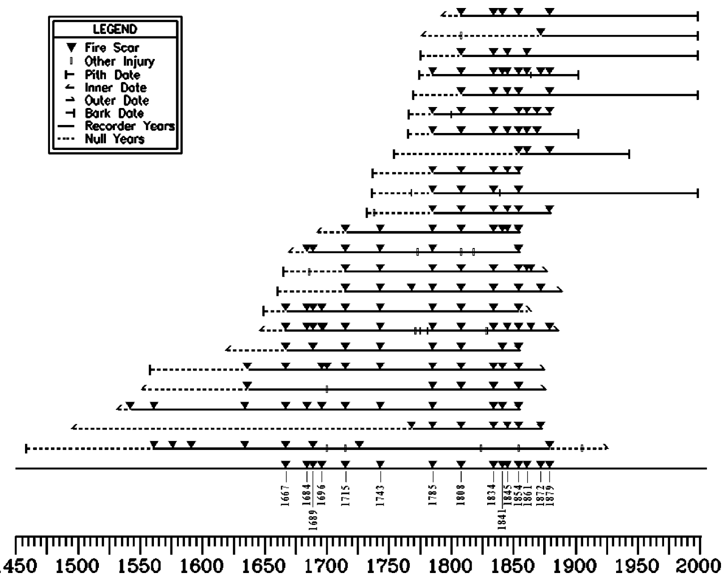

Fig. 2. Fire chronology for a ponderosa pine stand in the northern Black Hills, South Dakota. Time spans of individual trees are represented by horizontal lines, with fire scars noted by triangles at the dates they were recorded. Dates at the bottom of the fire chronology are those years when fire scars were recorded on at least four trees.

between 1883 and 1907 (Fig. 3), and the average age of trees in the stand was 101 years in 1998.

Plots were relatively homogeneous before treatments were applied. Soil moisture ($P \geq 0.35$; MANOVAR Wilks' Lambda F-test), soil temperature ($P \geq 0.56$; MANOVAR Wilks' Lambda F-test), litter depth ($P \geq 0.44$; ANOVA F-test), total biomass ($P \geq 0.09$; ANOVA F-test), herbaceous dicot biomass ($P \geq 0.30$; ANOVA F-test), graminoid biomass ($P \geq 0.37$; ANOVA F-test), and shrub density ($P \geq 0.34$; ANOVA F-test) did not vary between treatments. Plots assigned to the clearcut treatment had greater shrub biomass than those assigned to the partial-cut treatment (54 ± 20 kg/ha versus 2.8 ± 1.6 kg/ha; $P = 0.04$; ANOVA F-test), although all plots were characterized by little shrub biomass. Pre-treatment basal area of ponderosa pine on plots receiving the partial-cut treatment was significantly higher than basal area on plots receiving the clearcut treatment or plots receiving the uncut treatment ($P < 0.05$; ANOVA F-test) (Table 4). Overstory canopy cover and density on plots receiving the partial-cut treatment only differed from plots receiving the clearcut treatment ($P = 0.05$; ANOVA F-test) (Table 4).

3.4. Post-treatment

Significant ponderosa pine mortality resulted from prescribed fires, and was higher on partial-cut plots than on uncut plots ($81 \pm 7\%$ versus $39 \pm 5\%$;

Table 1
Fire history statistics calculated with three different restrictions placed on fires included in the analyses

	Period of analysis[a]	No. of intervals	MFI (±S.D.)	Range of intervals	Years since last fire
All fires	1450–1998	26	13 ± 10	1–43	119
>3 samples scarred	1450–1998	14	15 ± 11	4–42	119
Sample size >6	1667–1998	20	11 ± 8	1–26	119

Number of fire intervals, mean fire intervals, ranges of fire intervals, and number of years since last fire for South Dakota Game, Fish and Parks Badger Game Production Area (GPA) west of Spearfish, South Dakota.

[a] Fire-free period from 1879 to 1998 was not used to calculate fire history statistics.

Table 2
Total number of seedlings in 1080 soil seedbank samples collected in August 1998 and May 1999 in dense ponderosa pine stands in the Black Hills, South Dakota

	1998	1999
Graminoid	3	2
Herbaceous dicot	17	50
Herbaceous monocot	4	4
Shrub	0	1
Total seedlings	24	57
Total seeds/m^2	78	186
Antennaria sp.		1
Campanula rotundifolia L.		4
Conyza canadensis (L.) Cronq.		5
Iris sp.		4
Melilotis officinalis (L.) Pall.[a]		1
Rhus glabra L.		1
Rumex sp.		31
Verbena sp.		4
Unknown dicot		4
Unknown graminoid		2
Total seedlings		57
Total seeds/m^2		186

August 1998 seedlings were not identified taxonomically.
[a] Non-native species.

Table 3
Pre-treatment stand characteristics measured in 1998 on the South Dakota Game, Fish and Parks Badger Game Production Area (GPA) west of Spearfish, South Dakota

Overstory canopy cover (%)	96 ± 0.8
Density (stems/ha)	2700 ± 200
Basal area (m^2/ha)	60 ± 2
Litter depth (cm)	6.5 ± 0.1
Graminoid production (kg/ha)	0.9 ± 0.4
Herbaceous dicot production (kg/ha)	1.2 ± 0.6
Shrub production (kg/ha)	24 ± 8.7
Total production (kg/ha)	26 ± 9.0
Richness	3.9 ± 0.8
H'	0.6 ± 0.1

Means (±S.E.) are presented.

$P = 0.008$; ANOVA F-test). Reduction of basal area was also greater on partial-cut plots than on uncut plots (69 ± 10% versus 17 ± 5%; $P = 0.01$; ANOVA F-test), but overstory canopy cover was not reduced. Crown scorch did not differ between partial-cut and uncut plots (70 ± 10% versus 74 ± 2%; $P = 0.78$; ANOVA F-test), but char height was significantly higher on partial-cut plots than on uncut plots (9.1 ± 0.5 m versus 4.3 ± 0.8 m; $P = 0.006$; ANOVA F-test).

There were no interactive or main effects of treatments on understory biomass after the first growing season ($P \geq 0.22$; ANOVA F-test). After the second growing season, total understory biomass was affected by an interaction between cutting and burning ($P = 0.05$; ANOVA F-test). Within the unburned

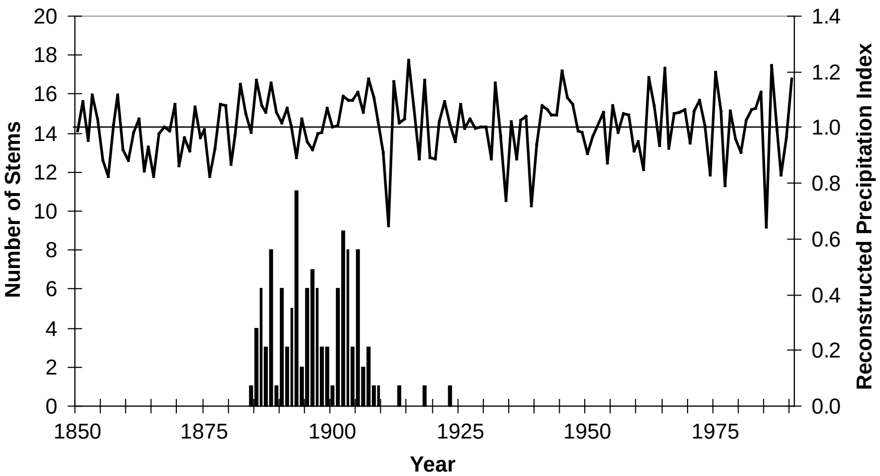

Fig. 3. Pith dates from 120 tree cross-sections collected from cut trees in the overstory removal treatment plots in the northern Black Hills, South Dakota. These pith dates provide age at stump height of the living trees on the research site in 1998. The last fire burned on this site in 1879 and the stand was logged in 1903. Precipitation index, reconstructed using tree-ring data, is presented as a percentage of the 1919–1989 August to July annual mean precipitation from instrumental stations in the Black Hills and northern plains (Sieg et al., 1996).

Table 4
Pre-treatment overstory characteristics by cut treatment, collected in 1998 on the South Dakota Game, Fish and Parks Badger Game Production Area (GPA) west of Spearfish, South Dakota

	No cut	Partial cut	Clearcut
Canopy cover (%)	95 (1.7) ab	99 (1.0) b	94 (0.7) a
Density (stems/ha)	2600 (220) ab	3400 (390) b	2300 (290) a
Basal area (m^2/ha)	58 (1.8) a	67 (3.7) b	55 (2.3) a

Means (S.E.) are presented. Numbers within the same row followed by similar letters did not differ ($P > 0.05$).

treatment, understory cover and production increased with decreasing overstory cover: complete removal of the overstory resulted in the greatest amount of production in the understory (Table 5). Within the burned treatment, both levels of overstory reduction resulted in approximately the same increase in understory production. Burning increased total understory production on uncut and partial-cut plots ($P < 0.05$), but not on clearcut plots ($P > 0.05$) (Table 5). Herbaceous dicots dominated the understory during the second growing season, so results of analysis on herbaceous dicot production were very similar to total production results. The only differences were that burning did not increase herbaceous dicot production on uncut plots and the partial-cut treatment did not elicit increased production on unburned plots (Table 5). Shrub production and woody plant density were unaffected by main or interactive effects of burning and overstory reduction ($P \geq 0.18$; ANOVA F-test).

Eleven taxa comprised over 93% of the total understory production. Three of the 11 most common taxa were non-native species and two of these (*Chenopodium album* (lambsquarters) and *Lactuca serriola* (prickly lettuce)) comprised 50% of the understory biomass in the second post-treatment growing season (Table 6). Prickly lettuce responded to an interaction between burning and overstory reduction ($P = 0.004$; ANOVA F-test), while lambsquarters responded to the main effect of cutting ($P = 0.03$; ANOVA F-test). Complete removal of the overstory with no burn elicited the largest response of prickly lettuce (Table 7). Response of lambsquarters was larger on clearcut plots than on uncut plots (125 ± 70 kg/ha versus 0 ± 0 kg/ha). Spreading dogbane, the third most common taxa, did not respond significantly to either treatment ($P \geq 0.08$; ANOVA F-test).

The interaction between overstory reduction and burning affected richness ($P = 0.04$; ANOVA F-test), but not evenness ($P = 0.49$; ANOVA F-test). In the absence of burning, there was an inverse relationship between overstory remaining and species richness (Table 8), whereas overstory reduction had no effect on species richness in burned plots. Species richness increased in response to burning only in plots with an intact overstory. Overstory reduction had no effect on evenness ($P = 0.49$; ANOVA F-test), while burned plots were more diverse than unburned plots (1.45 ± 0.10 versus 0.94 ± 0.13; $P = 0.01$; ANOVA F-test). Many plants that responded to overstory reduction and burning were non-native species. The number of non-native species in this stand increased from 0 (pre-treatment) to 12 (post-treatment) (Table 9).

Cluster analysis revealed clear differences in understory vegetation biomass in response to burning and overstory reduction. Unburned plots subjected to partial overstory reduction had high similarity to burned, uncut plots (plots 12, 13, 17, 5, 3, 8, 16, 10, and 6), whereas the remaining nine plots were added individually to the groups, with a few exceptions (i.e. plots 9 and 1, and plots 7 and 14) (Fig. 4).

Table 5
Understory biomass (kg/ha) measured in July 2000 in a ponderosa pine stand in the South Dakota Game, Fish and Parks Badger Game Production Area (GPA) west of Spearfish, South Dakota

	Total		Herbaceous dicot		Graminoid		Shrub	
	No burn	Burn	No burn	Burn	No burn	Burn	No burn	Burn
No cut	5.8 (4.9) Aa	35 (23) Ba	0.3 (0.3) Aa	13 (5.5) Aa	0.0 (0.0) Aa	3.3 (2.8) Aa	5.4 (4.5) Aa	19 (15) Aa
Partial cut	57 (23) Ab	508 (129) Bb	31 (24) Aa	497 (127) Bb	1.0 (1.0) Aa	2.7 (2.2) Aa	25 (4.1) Aa	7.9 (3.8) Aa
Clearcut	1724 (462) Ac	989 (343) Ab	1497 (511) Ab	955 (357) Ab	52 (27) Aa	7.7 (7.2) Aa	175 (158) Aa	26 (12) Aa

Means (S.E.) are presented. Numbers in the same row followed by similar uppercase letters did not differ ($P > 0.05$). Numbers in the same column followed by similar lowercase letters did not differ ($P > 0.05$).

Table 6
Biomass (kg/ha) of the 11 taxa that comprised more than 93% of the total understory production in the second growing season (2000) in a ponderosa pine stand in the Black Hills, South Dakota

	Ambrosia artemisiifolia	*Amaranthus retroflexus*	*Apocynum androsaemifolium*	*Chenopodium album*[a]	*Chenopodium simplex*	*Cynoglossum officinale*[a]	*Helianthus annuus*	*Lactuca serriola*[a]	*Carex* sp.	*Amorpha canescens*	*Juniperus communis*	Total production
CCBU	0 (0)	51 (50)	52 (30)	156 (142)	290 (290)	16 (16)	147 (132)	182 (137)	7.6 (7.0)	15 (8.3)	0 (0)	989 (343)
CCNB	0 (0)	0 (0)	239 (220)	93 (58)	0 (0)	104 (68)	0 (0)	997 (495)	32 (19)	30 (19)	129 (129)	1724 (462)
PCBU	82 (72)	0 (0)	85 (28)	88 (33)	78 (39)	0 (0)	0 (0)	150 (73)	2.6 (2.4)	0 (0)	0 (0)	508 (129)
PCNB	0 (0)	0 (0)	22 (22)	0 (0)	0 (0)	0 (0)	0 (0)	3.5 (3.4)	1.1 (1.1)	16 (6.9)	0 (0)	57 (23)
NCBU	0 (0)	0 (0)	4.7 (1.0)	0 (0)	0 (0)	0 (0)	0 (0)	2.1 (2.1)	0 (0)	12 (11)	0 (0)	35 (23)
NCNB	0 (0)	0 (0)	0.5 (0.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4.4 (4.3)	0 (0)	5.8 (4.9)

Means (S.E.) by treatment combination are presented. Treatments are: CC, clearcut; PC, partial cut; NC, uncut; BU, burn; and NB unburned.

[a] Species considered non-native to the US, according to USDA NRCS (2002).

Table 7
Biomass (kg/ha) of *Lactuca serriola* during the second post-treatment (2000) growing season in a ponderosa pine stand in the Black Hills, South Dakota

	Lactuca serriola	
	No burn	Burn
No cut	0 (0) Aa	2.1 (2.1) Aa
Partial cut	3.5 (3.4) Aa	150 (73) Bb
Clearcut	997 (495) Ab	182 (137) Bb

Means (S.E.) are presented. Numbers in the same row followed by similar uppercase letters did not differ ($P > 0.05$). Numbers in the same column followed by similar lowercase letters did not differ ($P > 0.05$).

Soil moisture did not respond to interactions between sampling date, overstory reduction, and burning ($P > 0.15$; MANOVAR Wilks' Lambda *F*-test), but soil temperature responded to an interaction between sampling date and burning ($P = 0.04$; MANOVAR Wilks' Lambda *F*-test). Afternoon soil temperatures were higher on burned plots and those with reduced overstories ($P < 0.0001$; MANOVAR Wilks' Lambda *F*-test). Within all sampling dates, soil temperature was higher in burned plots than in unburned plots ($P < 0.0012$; MANOVAR Wilks' Lambda *F*-test) (Fig. 5). Soil moisture responded to the main effect of overstory removal ($P = 0.0002$; MANOVAR Wilks' Lambda *F*-test), but not burning ($P = 0.07$; MANOVAR Wilks' Lambda *F*-test). Overstory removal generally increased soil moisture (Fig. 6).

Litter depth was not affected by an interaction between overstory reduction and burning ($P = 0.84$; ANOVA *F*-test). Burning significantly reduced the litter layer (3.6 ± 0.3 cm versus 5.0 ± 0.2 cm; $P = 0.005$; ANOVA *F*-test) and there was no effect of cutting treatments on litter depth ($P = 0.96$; ANOVA *F*-test).

Table 8
Species richness (mean number of species per plot) during the second post-treatment (2000) growing season in a ponderosa pine stand in the Black Hills, South Dakota

	No burn	Burn
No cut	2.7 (0.7) Aa	8.3 (3.0) Ba
Partial cut	8.0 (2.0) Ab	10.0 (0) Aa
Clearcut	15.3 (1.5) Ac	11.7 (0.7) Aa

Means (S.E.) are presented. Numbers in the same row followed by similar uppercase letters did not differ ($P > 0.05$). Numbers in the same column followed by similar lowercase letters did not differ ($P > 0.05$).

4. Discussion

4.1. Disturbance history

The historic fire regime of the current study more closely resembles that found in foothills ponderosa pine stands (Brown and Sieg, 1999) than that reported for higher elevation, interior ponderosa pine stands (Brown and Sieg, 1996). Some fire dates from this site coincide with fire dates found at sites in the southern Black Hills (e.g. 1684, 1785, and 1845 in foothills and interior stands, and 1879 in interior stands; Brown and Sieg, 1996, 1999). The fire of 1879 is also the last fire recorded on trees sampled at this site. The cessation of fires generally coincides with Anglo settlement of the area. It has been proposed that large, infrequent, catastrophic fires were a part of the natural disturbance regime in ponderosa pine forests of the Black Hills (Shinneman and Baker, 1997). It is difficult to infer fire severity from these data, however many of the trees sampled in this study lived through several fires, including the 1879 fire (Fig. 2).

Increased fire frequency during the period from the mid- to late-19th century parallels other sites in the Black Hills, and it has been speculated that this was a result of increases in American Indian activities and/or activities of early Anglo settlers (Fisher et al., 1987; Brown and Sieg, 1996, 1999).

In this study, two cut stumps had outer dates (1902 +) that appear to be death dates and may have been cutting dates. Nearly 25% of the samples collected from stumps on cut plots exhibited rapid growth between 1903 and 1908. Such rapid growth may have resulted from removal of large trees, which subsequently released resources for remaining seedlings and saplings. Historical records substantiated this dating. A bill of sale was filed at the Lawrence County, South Dakota Register of Deeds Office, on 23 January 1903 for saw timber on the quarter section where this study was conducted. In this document, timber harvest was to commence no later than 1 June 1903.[1]

[1] Lawrence County, South Dakota Register of Deeds, Book 167, p. 333.

Table 9
Taxa sampled on research plots in a ponderosa pine stand in the Black Hills, South Dakota

Native	Non-native
Graminoids	
Andropogon gerardii Vitman[a]	*Bromus japonicus* Thunb. Ex Murr.[a]
Bouteloua curtipendula (Michx.) Torr.[b]	*Setaria viridis* (L.) Beauv.[a]
Carex spp.[b]	
Dichanthelium oligosanthes (Schult.) Gould[a]	
Elymus trachycaulus (Link) Gould ex Shinners[a]	
Poa pratensis L.[b]	
Schizachyrium scoparium (Michx.) Nash[c]	
Herbaceous dicots	
Ambrosia artemisiifolia L.[a]	*Chenopodium album* L.[a]
Amaranthus retroflexus L.[a]	*Convolvulus arvensis* L.[a,d]
Apocynum androsaemifolium L.[b]	*Cynoglossum officinale* L.[a]
Artemisia ludoviciana Nutt.[c]	*Lactuca serriola* L.[a]
Chenopodium berlandieri Moq.[a]	*Medicago lupulina* L.[a]
Chenopodium pratericola Rybd.[a]	*Melilotus officinalis* (L.) Pall.[a]
Chenopodium simplex (Torr.) Raf.[a]	*Nepeta cataria* L.[a]
Conyza canadensis Cronq.[a]	*Taraxacum officinale* Weber[a]
Glycyrrhiza lepidota Pursh[a]	*Tragopogon dubius* Scop.[a]
Helianthus annuus L.[a]	*Verbascum thapsus* L.[a]
Maianthemum stellatum (L.) Link[c]	
Penstemon albidus Nutt.[a]	
Pulsatilla patens (L.) P. Mill.[b]	
Solidago missouriensis Nutt.[a]	
Solidago sp.[c]	
Verbena bracteata Lag. and Rodr.[a]	
Shrubs and trees	
Amelanchier alnifolia Nutt.[b]	
Amorpha canescens Pursh[b]	
Juniperus communis L.[b]	
Juniperus horizontalis Moench[c]	
Mahonia repens (Lindl.) G. Don[b]	
Pinus ponderosa Laws.[b]	
Prunus virginiana L.[b]	
Quercus macrocarpa Michx.[b]	
Rhus glabra L.[a]	
Ribes sp.[a]	
Rubus idaeus L.[a]	
Symphoricarpos occidentalis Hook[c]	
Toxicodendron rydbergii (Small) Greene[b]	

Nomenclature follows The PLANTS Database (USDA NRCS, 2002).
[a] Observed only the second growing season (2000).
[b] Observed both pre- and post-treatment.
[c] Observed only before treatments were applied (1998).
[d] Regulated non-native plant species in South Dakota (South Dakota Code, 1996. Plant Quarantine and Treatment, Chapter 24–38, Article 12:51; South Dakota Code, 1997. South Dakota Weed and Pest Control, Chapter 22–38, Article 12:62, State of South Dakota).

This stand apparently established after the 1879 fire, probably in response to a series of years in the 1880s receiving above-average precipitation combined with the apparent absence of fires in the area beginning in 1879 (Fig. 3). Ponderosa pine reportedly has episodic germination and often establishes during wet periods (Savage et al., 1996). This cohort of ponderosa pine trees would have been too small to be harvested in

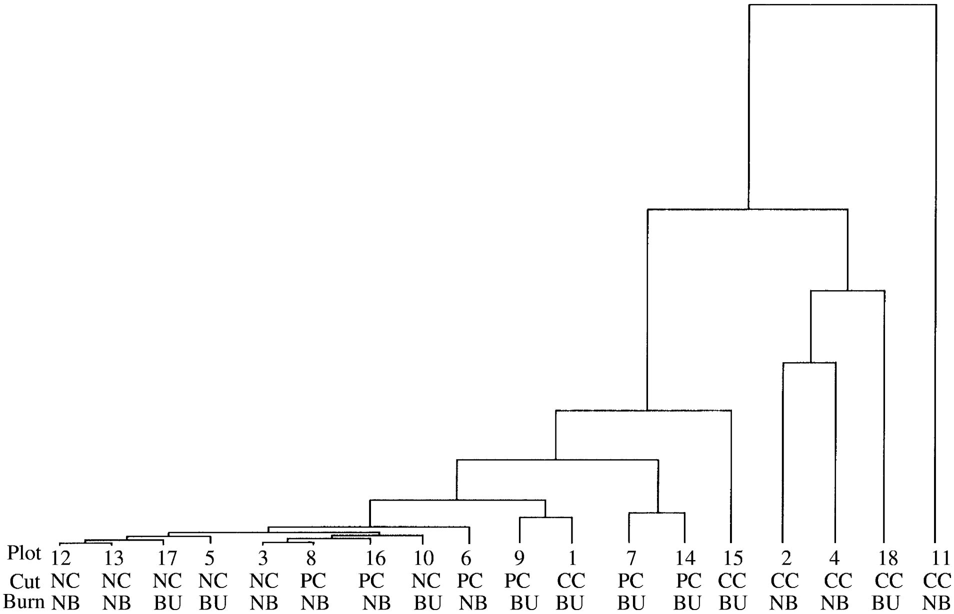

Fig. 4. Cluster analysis of understory biomass the second growing season post-treatment (2000) in a ponderosa pine stand in the Black Hills, South Dakota. Treatments are: CC, clearcut; PC, partial cut; NC, uncut; BU, burned; NB, unburned.

1903. Thus, trees in the current stand apparently established in the 1880s and were not harvested in 1903 because of their smaller size.

The current ponderosa pine stand at the research site probably looks considerably different than it did 125 years ago. What was presumably a more open ponderosa pine stand is now a very dense stand of relatively small diameter trees with little understory vegetation. The average diameter at breast height of trees in this stand was just over 15 cm in 1998. By comparison, the average DBH was approximately 26 cm in an open ponderosa pine stand in the central Black Hills (Wrage, 1994). The understory currently consists of a thick layer of pine needles.

Understory production in this stand before treatments were applied was similar to that reported in other dense ponderosa pine forests. In the Black Hills, total understory production was reported between 25 and 113 kg/ha under dense stands (37–46 m^2/ha basal area) of ponderosa pine (Pase and Hurd, 1957; Uresk and Severson, 1998), which resembles dense ponderosa pine forests outside the Black Hills. Herbaceous understory production ranged from 6 to 30 kg/ha in dense stands (46–70 m^2/ha basal area) of ponderosa pine throughout the western US (Jameson, 1967; Ffolliott et al., 1977). In contrast, relatively open ponderosa pine stands (<23 m^2/ha basal area) in the central Black Hills are characterized by understory production between 203 and 1750 kg/ha (Wrage, 1994; Uresk and Severson, 1998).

A likely series of events that led to the current stand conditions encapsulates environmental, climatic, and anthropogenic factors. Frequent fires burned through this stand for at least 300 years before Anglo settlement of the area. Cessation of the natural fire regime coincided with Anglo settlement. Following a fire in 1879, favorable climatic conditions resulted in germination of one or more cohorts of ponderosa pine in the 1880s. The area was intensely logged in 1903 and 1904 to support a burgeoning human population. At this time the cohort(s) of ponderosa pine that germinated in the 1880s were too small to harvest, so they were left to regenerate the stand. In the absence of fires or timber harvest, the stand remained densely populated and even-aged. During the ensuing century, the overstory canopy closed and a layer of pine needles replaced vegetation.

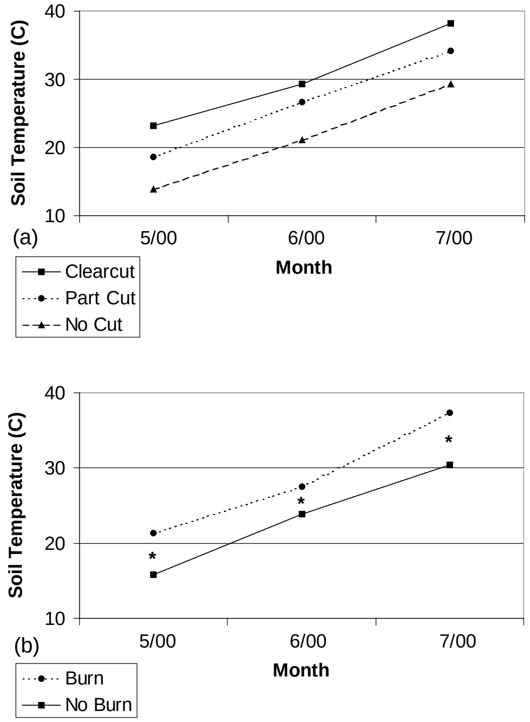

Fig. 5. (a) Afternoon soil temperatures (°C) in the second growing season post-treatment (2000) in a ponderosa pine stand in the Black Hills, South Dakota. (b) Afternoon soil temperatures (°C) in the second growing season post-treatment (2000) in a ponderosa pine stand in the Black Hills, South Dakota. Asterisk (∗) denotes differences in soil temperature within a month ($P < 0.05$).

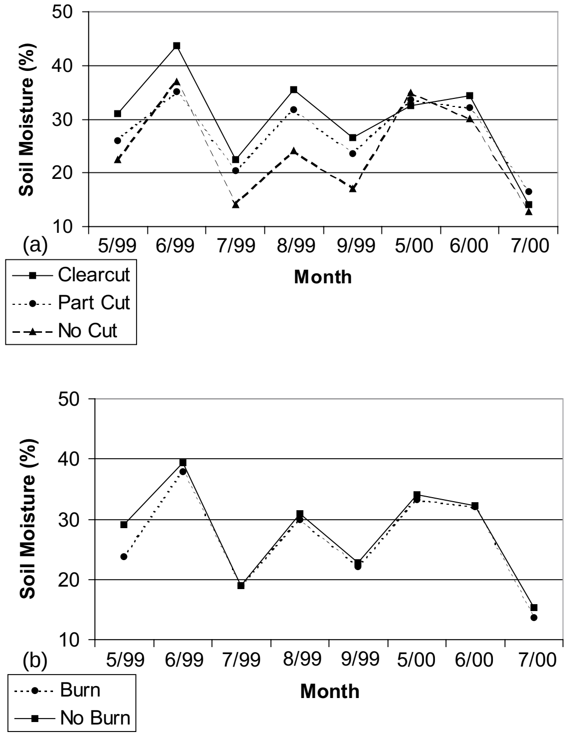

Fig. 6. Post-treatment soil moisture (%) in a ponderosa pine stand in the Black Hills, South Dakota.

4.2. Soil seed bank

We found very few viable seeds in the soil seed bank beneath the ponderosa pine stand in this study. A wide range of viable seed densities has been reported from other seed bank studies in ponderosa pine forests. Two studies conducted in northern Arizona reported seed densities of 8–3152 seeds/m^2 (Vose and White, 1987; Springer, 1999), and a study conducted in Washington reported viable seed densities from 13,052 to 14,463 seeds/m^2 (Pratt et al., 1984). The latter study was conducted in a stand with a diverse and abundant understory located in a transition zone between meadow steppe and ponderosa pine forest, which probably contributed to high densities of viable seeds.

4.3. Understory response

Overstory reduction and prescribed burning show promise for promoting understory production in ponderosa pine stands in the Black Hills. Understory vegetation did not respond the first growing season after treatments were applied, but responded vigorously the second growing season. Production ranged from 6 kg/ha on untreated plots to 1724 kg/ha on clearcut/unburned plots, and there was no difference in vegetation biomass between clearcut/burned and clearcut/unburned plots.

These results are similar to previous studies of overstory removal in Black Hills ponderosa pine stands. Concurrence of experimental results with prior descriptions lends considerable support to the observed patterns (Romesburg, 1981). Vegetation production was 1214 kg/ha on a west-facing slope 3 years after clearcutting pine in the northern Black Hills (Thompson and Gartner, 1971) and 1931 kg/ha on clearcut plots 10 years after overstory removal (Uresk et al., 2000). Understory biomass was 1179 kg/ha 13 years after thinning the stand to a basal area of approximately 14 m^2/ha in the latter study. Similar patterns of understory production were observed in Black Hills ponderosa pine stands with varying overstory canopy cover and basal area (Pase and Hurd, 1957; Pase, 1958; Wrage, 1994).

No studies of the effects of prescribed burning combined with overstory reduction have been conducted in the Black Hills, and few comparable studies have been conducted elsewhere. Understory herbaceous production increased to a greater extent after thinning a pole-sized stand than after a combination of thinning and prescribed burning in northern Arizona (Covington et al., 1997). Other northern Arizona studies have documented increased herbaceous biomass production in response to thinning and burning, but also recognize the importance of confounding factors such as pre-treatment plant communities, varying stand type (size and spacing of remaining trees), timing of treatment and time since treatment, plus subsequent precipitation (e.g. Korb, 2001; Korb and Springer, 2003). In the current study, partial or complete overstory reduction, in combination with burning, produced a similar response in understory biomass. It is possible that the level of overstory reduction was confounded by mortality of ponderosa pine from the prescribed burn, as fire-induced mortality was higher in partial-cut plots than in uncut plots.

The prevalence of non-native species in the understory following treatments is consistent with studies in ponderosa pine forests in other regions following cutting and burning treatments as well as wildfires (Crawford et al., 2001; Lehmkuhl, 2002; Sieg et al., 2003). The majority of the non-native species observed in our study are not considered ‘‘invaders’’, or species vigorous, persistent, prolific, and widespread enough to cause serious economic and environmental impacts (Vitousek et al., 1996; Novak and Mack, 2001), and few are legally designated as ‘‘noxious’’ in western states. Evidence from other areas suggests that lambsquaters and prickly lettuce, the most common non-native plants in the first two growing seasons in our study, may increase with increasing fire severity (Beaulieu, 1975; Turner et al., 1997), but are not frequently designated as noxious species in the US and southern Canada (Skinner et al., 2000). *Verbascum thapsus* (common mullein), designated as a noxious species in one western state (Sieg et al., 2003), is often transient following disturbances such as burning (Ffolliott et al., 1977).

The 1-year lag in response of understory vegetation in the current study reflects patterns observed in ponderosa pine forests of northern Arizona following wildfire (Pearson et al., 1972; Campbell et al., 1977). A similar pattern was observed during an experimental overstory removal study in oak woodlands of southeastern Arizona (McPherson and Weltzin, 1998). McPherson and Weltzin hypothesized that the lag resulted from time required to colonize the understory or a lag in increased nutrient availability. Either of these hypotheses could explain the delayed response in this study. The paucity of viable seeds in the soil seed bank observed in this study could be seen as support for the hypothesis of time required to colonize the understory. It is unlikely that this lag response is due to inadequate soil moisture, as annual precipitation in the region (Rapid City) was above average in the first growing season and below average in the second growing season post-treatment.

There was no apparent correlation between understory vegetation and viable seeds in the soil seed bank, and species that comprised a majority of the biomass the second growing season, including some non-native species, tended to be species considered ‘‘weedy’’ with small, easily dispersed seeds. This lends support to the hypothesis that the species that initially responded to the treatments of burning and overstory reduction were not present in the soil seed bank, but colonized the site from external sources. All species that colonized the site are common in the local area. This is consistent with findings of a soil seed bank study in a ponderosa pine forest in northern Arizona (Vose and White, 1987).

Abiotic conditions necessary for colonization of understory vegetation probably existed the first growing season after treatments were imposed. Reduction or removal of the overstory increased light availability and soil moisture, and an increase in soil temperature on treated plots was still evident in the second growing season. Burning had a similar, but less substantial, effect on soil moisture and a greater affect on soil temperature. Assuming that all the abiotic conditions for vegetation growth existed, lack of a soil seed bank could explain the lack of response by understory vegetation in the first growing season after application of treatments. The paucity of viable seeds in the soil seed bank may have resulted from the absence of disturbances in this stand for nearly a century. The number of viable seeds in the soil seed bank of forests with very long fire intervals probably declines as a result of seed death and decreases in seed input (Peterson and Carson, 1996).

The inverse relationship between species richness and overstory cover documented on unburned plots in this study parallels findings from other ponderosa pine stands in the Black Hills (Uresk and Severson, 1989; Wrage, 1994). However, burned plots were equally rich regardless of the extent of overstory reduction and species were distributed more evenly on burned plots than on unburned plots. Three shrub taxa (*Rhus glabra* L. (smooth sumac), *Ribes* sp. L. (currant species), and *Rubus idaeus* L. (red raspberry)) colonized disturbed plots during the second growing season. Chokecherry, *Amelanchier alnifolia* Nutt. (Saskatoon serviceberry), and *Mahonia repens* Lindl. (Oregon grape) were also present during the second post-treatment growing season, but as seedlings, they comprised a small fraction of the total production. However, they do have the potential to contribute substantial biomass in the future. There were more new species of herbaceous dicot than any other guild in the second growing season.

At the community level, the cluster analysis revealed differences in vegetation response to treatments. Understory species composition was little altered by burning beneath an uncut overstory, which matched understory response beneath unburned stands that were partially cut. In contrast, composition of the herbaceous understory was relatively heterogeneous in response to other combinations of overstory removal and application of fire; this heterogeneity was reflected in the results of cluster analysis, which displayed little similarity among plots that were partially cut and burned or clearcut.

Not surprisingly, prescribed burning decreased the depth of the litter layer. Burning reduced the litter layer by about 30% in a patchy pattern, such that mineral soil was exposed in some areas. The prescribed burns were surface fires, so the overstory canopy was not consumed. However, there was considerable mortality of ponderosa pine that resulted from prescribed fires. Fire season may have contributed to the high mortality, as higher ponderosa pine mortality has been reported following spring and summer prescribed burns than after autumn prescribed burns (Swezy and Agee, 1991; Harrington, 1993). Fine-root mortality also has been suggested as a possible factor in ponderosa pine mortality following prescribed burning (Swezy and Agee, 1991).

Unintended fire-induced mortality of ponderosa pine on the partial-cut plots possibly confounded the results of vegetation response on these plots. The similarities between clearcut/burned plots and partial-cut/burned plots potentially will become more pronounced as the remaining needles are lost from the canopy, the branches weather and break off, and eventually the snags fall down.

Response of understory vegetation to overstory reduction and prescribed burning is encouraging. Total understory production increased significantly two growing seasons after cutting and burning treatments, despite the apparent lack of viable seeds in the soil seed bank before treatments were applied. Complete overstory removal produced the greatest response in total understory biomass, and response was unaffected by prescribed burning. If promoting understory production is a management goal, small patch cuts may be an appropriate treatment. Combinations of overstory reduction and prescribed burning may be desirable if increasing understory species diversity is the goal because overstory reduction increased understory species richness while prescribed burning increased understory species evenness. If clearcutting, even in small patches, is not a management option, then partial overstory reduction combined with prescribed burning appears to be a better option than no treatment to increase understory production. The burn prescription probably should be modified to reduce overstory ponderosa pine mortality in thinned stands. Specifically, we recommend burning in the fall and perhaps using a backing fire ignition technique or a strip-headfire technique with strips ≤ 5 m to control fire intensity.

Our rigorous experimental approach quantitatively identified effects of overstory reduction and fire on understory production, and interpreted the resulting data within the context of previous descriptive research and our own description of the soil seed bank and site history. The experimental approach is noteworthy because it is necessary to determine causality and, paradoxically, it is relatively rare in ecological research (Gurevitch and Collins, 1994; McPherson and Weltzin, 2000). Before-after-control-impact designs, such as the one employed in this research (Underwood, 1994), are surprisingly uncommon in the research on restoration. However, these designs offer the best opportunity to enhance statistical power and elucidate mechanisms responsible for treatment effects. Statistically significant effects of experimental treatments were evident despite the relatively small sample size ($n = 3$), which engenders considerable confidence in these results. Nonetheless, caution is warranted when extrapolating these results beyond the geographic scope of the present study because of its limited temporal and spatial scope and because experimental plots were not randomly selected from the entire population of Black Hills ponderosa pine stands. Similar experimental designs that incorporate BACI designs and control for confounding variables, such as variations in pre-treatment forest structure, understory, soils, elevation, and slope, as well as timing of treatments and time since treatment, are needed in other regions to evaluate the general applicability of these results.

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References

Arno, S.F., 1996. The concept: restoring ecological structure and process in ponderosa pine forests. In: Hardy, C.C., Arno, S.F. (Eds.), The Use of Fire in Forest Restoration. USDA For. Serv. Gen. Tech. Rep. INT-GTR-341. Intermountain Research Station, Ogden, UT, pp. 37–38.

Baisan, C.H., Swetnam, T.W., 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. Can. J. For. Res. 20, 1559–1569.

Ball, J.J., Schaefer, P.R., 2000. Case no. 1: one hundred years of forest management. J. For. 98, 4–10.

Beaulieu, J.T., 1975. Effects of fire on understory plant populations in a northern Arizona ponderosa pine forest. M.S. Thesis. Northern Arizona University, Flagstaff.

Brown, P.M., Sieg, C.H., 1996. Fire history in interior ponderosa pine communities of the Black Hills, South Dakota, USA. Int. J. Wildland Fire 6, 97–105.

Brown, P.M., Sieg, C.H., 1999. Historical variability in fire at the ponderosa pine—northern Great Plains prairie ecotone, southeastern Black Hills, South Dakota. Ecoscience 6, 539–547.

Campbell, R.E., Baker Jr., M.B., Ffolliott, P.F., Larson, F.R., Avery, C.C., 1977. Wildfire effects on a ponderosa pine ecosystem: an Arizona case study. USDA For. Serv. Res. Pap. RM-191. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Cooper, C.F., 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecology 42, 493–499.

Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. J. For. 95, 23–29.

Covington, W.W., Everett, R.L., Steele, R., Irwin, L.L., Daer, T.A., Auclair, A.N.D., 1994. Historical and anticipated changes in forest ecosystems of the inland west of the United States. J. Sustain. For. 2, 13–63.

Covington, W.W., Moore, M.M., 1992. Postsettlement changes in natural fire regimes: implications for restoration of old-growth forests. USDA For. Serv. Gen. Tech. Rep. RM-213. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. J. For. 92, 39–47.

Crawford, J.A., Wahren, C.-H.A., Kyle, S., Moir, W.H., 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. J. Veg. Sci. 12, 261–268.

Drew, L.G. (Ed.), 1974. Tree-ring Chronologies of Western America, vol. IV, Colorado, Utah, Nebraska and South Dakota, Chronology Series I. Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ.

Driscoll, D.G., Hamade, G.R., Kenner, S.J., 2000. Summary of precipitation data for the Black Hills area of South Dakota, water years 1931–1998. US Department of Interior Geological Survey Open-file Report 00-329. Denver, CO, 151 pp.

Ensz, E.H., 1990. Soil survey of Custer and Pennington Counties, Black Hills parts, South Dakota. USDA Soil Cons. Serv., USDA For. Serv., South Dakota Agriculture Experiment Station.

Ferrandis, P., Herranz, J.M., Martinez-Sanchez, J.J., 1996. The role of soil seed bank in the early stages of plant recovery after fire in a *Pinus pinaster* forest in SE Spain. Int. J. Wildland Fire 6, 31–35.

Ffolliott, P.F., Clary, W.P., Larson, F.R., 1977. Effects of a prescribed fire in an Arizona ponderosa pine forest. USDA For. Serv. Res. Note RM-336. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Fisher, R.F., Jenkins, M.J., Fisher, W.F., 1987. Fire and the prairie-forest mosaic of Devil's Tower National Monument. Am. Midl. Nat. 117, 250–257.

Grafe, E., Horsted, P., 2002. Exploring with Custer—the 1874 Black Hills Expedition. Golden Valley Press, Custer, SD.

Gurevitch, J., Collins, S.L., 1994. Experimental manipulation of natural plant communities. Trends Ecol. Evol. 9, 94–98.

Harper, J.L., 1982. After description. In: Newman, E.I. (Ed.), The Plant Community as a Working Mechanism. Blackwell, Oxford, UK, pp. 11–25.

Harrington, M.G., 1993. Predicting *Pinus ponderosa* mortality from dormant season and growing season fire injury. Int. J. Wildland Fire 3, 65–72.

Hetherington, J.C., 1967. A simple device for the measurement of the crown diameter of standing trees. Commonwealth For. Rev. 46, 5.

Jameson, D.A., 1967. The relationship of tree overstory and herbaceous understory vegetation. J. Range Manage. 20, 247–249.

Kitajima, K., Tilman, D., 1996. Seed banks and seedling establishment on an experimental productivity gradient. Oikos 76, 381–391.

Korb, J.E., 2001. Understory plant community dynamics in southwestern ponderosa pine forest restoration. Ph.D. Dissertation. Northern Arizona University, Flagstaff.

Korb, J.E., Springer, J.D., 2003. Understory vegetation. In: Friederici, P. (Ed.), Ecological Restoration of Southwestern Ponderosa Pine Forests. Island Press, Washington, DC, pp. 233–250.

Lehmkuhl, J.F., 2002. The effects of spring burning and grass seeding in forest clearcuts on native plants and conifer seedlings in coastal Washington. Northwest Sci. 76, 60.

McPherson, G.R., 1997. Ecology and Management of North American Savannas. The University of Arizona Press, Tucson, AZ.

McPherson, G.R., Wright, H.A., 1987. Factors affecting reproductive maturity of redberry juniper (*Juniperus pinchotii*). For. Ecol. Manage. 21, 191–196.

McPherson, G.R., Weltzin, J.F., 1998. Herbaceous response to canopy removal in southwestern oak woodlands. J. Range Manage. 51, 674–678.

McPherson, G.R., Weltzin, J.F., 2000. The role and importance of disturbance and climate change in US/Mexico borderlands: a state-of-the-knowledge review. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-50. Rocky Mountain Research Station, Fort Collins, CO.

Meland, A.C., 1979. Soil survey of Lawrence County, South Dakota. USDA Soil Conserv. Serv., USDA For Serv., South Dakota Agriculture Experiment Station.

Novak, S.J., Mack, R.N., 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (cheatgrass). BioScience 51, 114–122.

Parrish, J.B., Herman, D.J., Reyher, D.J., 1996. A century of change in Black Hills forest and riparian ecosystems. USDA For. Serv., South Dakota Agriculture Experiment Station B 722, South Dakota State University, Brookings, SD.

Pase, C.P., 1958. Herbage production and composition under immature ponderosa pine stands in the Black Hills. J. Range Manage. 11, 238–243.

Pase, C.P., Hurd, R.M., 1957. Understory vegetation as related to basal area, crown cover and litter produced by immature ponderosa pine stands in the Black Hills. In: Proceedings of the Society of American Foresters, Syracuse, NY.

Pearson, H.A., Davis, J.R., Schubert, G.H., 1972. Effects of wildfire on timber and forage production in Arizona. J. Range Manage. 25, 250–253.

Peterson, C.J., Carson, W.P., 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. Can. J. For. Res. 26, 45–52.

Phillips, D.L., MacMahon, J.A., 1981. Competition and spacing patterns in desert shrubs. J. Ecol. 69, 97–115.

Pratt, D.W., Black, R.A., Zamora, B.A., 1984. Buried viable seed in a ponderosa pine community. Can. J. Bot. 62, 44–52.

Progulske, D.R., 1974. Yellow ore, yellow hair, yellow pine: a photographic study of a century of forest ecology. Agriculture Experiment Station Bulletin 616. South Dakota State University, Brookings, SD.

Progulske, D.R., Shideler, F.J., 1983. Following custer. Agriculture Experiment Station Bulletin 674. South Dakota State University, Brookings, SD.

Ramsey, F.L., Schafer, D.W., 1997. The Statistical Sleuth: A Course in Methods of Data Analysis. Duxbury Press, Belmont, CA.

Romesburg, H.C., 1981. Wildlife science: gaining reliable knowledge. J. Wildlife Manage. 45, 293–313.

SAS, 1996. JMP Start Statistics. JMP IN version 3.2.6. SAS Institute, Cary, NC.

Savage, M., Brown, P.M., Feddema, J., 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ecoscience 3, 310–318.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, IL.

Sheppard, W.D., Battaglia, M.A., 2002. Ecology, silviculture and management of Black Hills ponderosa pine. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-97. Rocky Mountain Research Station, Fort Collins, CO.

Shinneman, D.J., Baker, W.L., 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. Conserv. Biol. 11, 1276–1288.

Sieg, C.H., Severson, K.E., 1996. Managing habitats for white-tailed deer in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming. USDA For. Serv. Gen. Tech. Rep. RM-GTR-274. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Sieg, C.H., Meko, D., DeGaetano, A.R., Ni, W., 1996. Dendroclimatic potential in the northern Great Plains. In: Dean, J.S., Meko, D.M., Swetnam, T.W. (Eds.), Tree Rings, Environment and Humanity. Radiocarbon. University of Arizona, Tucson, AZ, pp. 295–302.

Sieg, C.H., Phillips, B.G., Moser, L.P., 2003. Exotic invasive plants. In: Friederici, P. (Ed.), Ecological Restoration of Southwestern Ponderosa Pine Forests. Island Press, Washington, DC, pp. 251–267.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.

Simpson, R.L., Leck, M.A., Parker, V.T., 1989. Seed banks: general concepts and methodological issues. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Banks. Academic Press, San Diego, CA, pp. 3–8.

Skinner, K., Smith, L., Rice, P., 2000. Using noxious weed lists to prioritize targets for developing weed management strategies. Weed Sci. 48, 640–644.

Springer, J.D., 1999. Soil seed bank in southwestern ponderosa pine: implications for ecological restoration. Thesis. Northern Arizona University, Flagstaff, AZ.

Stokes, M.A., Smiley, T.L., 1968. An Introduction to Tree-ring Dating. University of Chicago Press, Chicago, IL.

Swetnam, T.W., Baisan, C.H., 1996. Historical fire regime patterns in the southwestern United States since AD 1700. In: Allen, C.D. (Ed.), Proceedings of the Second La Mesa Fire Symposium. USDA For. Serv. Gen. Tech. Rep. RM-GTR-286. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, pp. 11–32.

Swezy, D.M., Agee, J.K., 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Can. J. For. Res. 21, 626–634.

Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M., Bakker, J.P., 1996. An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. Funct. Ecol. 10, 144–151.

Thompson, W.W., Gartner, F.R., 1971. Native forage response to clearing low quality ponderosa pine. J. Range Manage. 24, 272–277.

Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, H.H., 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol. Monogr. 67, 411–433.

Underwood, A.J., 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecol. Appl. 4, 3–15.

Uresk, D.W., Severson, K.E., 1989. Understory–overstory relationships in ponderosa pine forests, Black Hills, South Dakota. J. Range Manage. 42, 203–208.

Uresk, D.W., Severson, K.E., 1998. Response of understory species to changes in ponderosa pine stocking levels in the Black Hills. Great Basin Nat. 58, 312–327.

Uresk, D.W., Edminster, C.B., Severson, K.E., 2000. Wood and understory production under a range of ponderosa pine stocking levels, Black Hills, South Dakota. West. N. Am. Nat. 60, 93–97.

USDA NRCS, 2002. The PLANTS Database, Version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA.

US Department of Commerce, 1998/1999/2000. Annual Climatological Summary. Asheville, NC.

Vitousek, P.M., D'Antonio, C.M., Loop, L.L., Westbrooks, R., 1996. Biological invasions as global environmental change. Am. Sci. 84, 468–478.

Vose, J.M., White, A.S., 1987. Processes of understory seedling recruitment 1 year after prescribed fire in an Arizona ponderosa pine community. Can. J. Bot. 65, 2280–2290.

Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. J. Am. Stat. Assoc. 58, 236–244.

Weaver, H., 1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific Slope. J. For. 41, 7–14.

Wrage, K.J., 1994. The effects of ponderosa pine on soil moisture, precipitation, and understory vegetation in the Black Hills of South Dakota. Thesis. University of South Dakota, Vermilion, SD.

Wright, H.A., 1978. The effect of fire on vegetation in ponderosa pine forests: a state-of-the-art review. College of Agricultural Science Publication T-9-199. Texas Tech University Range and Wildlife Information Series No. 2. Lubbock, TX.