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Forest Ecology and Management 218 (2005) 129–145
Forest Ecology and Management
www.elsevier.com/locate/foreco

Pine-oak forest dynamics five years after ecological restoration treatments, Arizona, USA

Peter Z. Fulé [a,b,*], Daniel C. Laughlin [a], W. Wallace Covington [a,b]

[a] *Ecological Restoration Institute, P.O. Box 15018, Flagstaff, AZ 86011, USA*
[b] *School of Forestry, Northern Arizona University, P.O. Box 15018, Flagstaff, AZ 86011, USA*

Received 3 February 2005; received in revised form 27 April 2005; accepted 12 July 2005

Abstract

Five years after ecological restoration treatments in a ponderosa pine-Gambel oak forest, we re-measured permanent plots to assess changes in forest structure and understory vegetation. The treatments were (1) thinning to emulate pre-fire-exclusion conditions + prescribed burning (FULL restoration), (2) minimal thinning around old trees + burning (MIN), (3) burning alone (BURN), and (4) CONTROL. We expected tree growth and understory abundance to be greatest in the least dense (FULL) treatment. Probably due to drought as well as treatment effects, basal area, tree density, and canopy cover declined 3–20% over the 2000–2004 time period. Smaller trees and those with greater crown scorch were most likely to die. Tree growth differed significantly by species and treatment; ponderosa pine grew faster than oak and the FULL treatment had the highest pine basal area increment and quadratic mean diameter. Understory plant cover and richness differed only slightly by treatment, generally varying more with pre-existing conditions and climate. Exotic species were present but exotic cover and richness were less than that reported after comparable treatments or wildfires in the region. Compared to historical reference conditions at the time of the last surface fire, 1887, the FULL was less dense and all treatments were relatively low in basal area, due to 20th century harvesting of most of the large pines. At current growth rates and without additional mortality, the FULL treatment may be similar to historical forest structures in ~20 years. Tree densities in other treatments are expected to remain above historical levels. The dynamics of stands following alternative restoration treatments are of high interest for management because large areas have been proposed for treatment but there is limited data on effects.

Keywords: Ecological restoration; Ponderosa pine; Kaibab National Forest; Thinning; Prescribed burning; Understory response

1. Introduction

Ecological restoration of forests adapted to frequent surface fire regimes has been widely advocated in the southwestern USA to reduce the hazard of severe wildfires and restore natural habitats. There is a range of views, however, on the appropriate goals and techniques for restoration. Covington (2000) underscored the urgency of habitat loss due to uncharacteristically severe disturbances, calling for rapid management intervention. Evaluating the same situation, however, Allen et al. (2002) emphasized that intervention also

* Corresponding author. Tel.: +1 928 523 1463; fax: +1 928 523 1080.
E-mail address: pete.fule@nau.edu (P.Z. Fulé).

0378-1127/$ – see front matter
doi:10.1016/j.foreco.2005.07.005

posed risks and suggested that diverse treatments, incremental approaches, and careful monitoring would provide the most useful information.

While an extensive program of methodical research would be desirable, however, forest management occurs in a social environment where people may overreact to perceived concern about large wildfires (Kauffman, 2004). Therefore, it is appropriate to learn as much as possible from opportunistic studies and from the relatively few and recent controlled experiments studying restoration alternatives.

Despite high interest, there are only a handful of experimental restoration sites in southwestern forests, such as projects in Colorado (Romme et al., 2003) and Arizona (Covington et al., 1997; Waltz et al., 2003; Skov et al., 2005). Additional experiments are underway in association with the nationwide Fire/Fire Surrogates project, but only limited information is available to date (e.g., Metlen et al., 2004). Substantial testing of restoration of surface fire has been done in the Southwest (e.g., Weaver, 1951; Sackett and Haase, 1998), but the earliest project deliberately aimed at restoring structure, function, and composition of a ponderosa pine ecosystem to conditions within the natural range of variability was initiated at the Gus Pearson Natural Area in 1992 (Covington et al., 1997). The study addressed tree physiological responses (Feeney et al., 1998; Stone et al., 1999) and ecosystem level responses (Kaye and Hart, 1998), showing increased photosynthesis and growth of trees in thinned and thinned + burned areas, as well as sharp increases in understory productivity (Moore et al., in press). The 3-ha Pearson area remains the only experimental site with more than immediate or >3 year post-treatment data. Tree condition was assessed at six years post-treatment by Kolb et al. (2001) and Wallin et al. (2004) reported that physiological changes, such as increased photosynthesis, were sustained in old trees for seven years after treatment. Elsewhere, little is known about the persistence of treatment effects or delayed responses to treatments.

In 1997, we collaborated with the Kaibab National Forest and Grand Canyon National Park to compare three restoration treatments. The treatments included (a) extensive thinning to emulate pre-fire-exclusion conditions + prescribed burning (FULL restoration), to (b) minimal thinning around old trees + burning (MIN), (c) burning alone (BURN), and (d) CONTROL. These activities span a broad range of possible restoration approaches, from a high degree of mechanical manipulation of forest structure to no mechanical intervention whatsoever, relying on fire alone to reduce tree density. After treatments were completed in 1999, forest structures had been substantially altered (Fulé et al., 2002a), with the thinned sites significantly lower in tree density and/or basal area.

Here, we report on re-measurement of permanent monitoring plots in 2004, the fifth year after treatment, to assess changes in light of the following expectations: (1) forest structure would reflect higher growth and lower mortality with decreasing tree density, while regeneration would show no trend, (2) abundance of understory vegetation was expected to increase with decreasing tree density, while composition would show no trend, and (3) forest floor and woody debris were expected to increase with time since burning. We were interested both in the dynamics of forest ecosystem change over the five years since treatment and in the degree to which current forest conditions were consistent with pre-fire-exclusion reference conditions.

2. Study area

We conducted the experiment on a 50-ha site next to Grandview fire tower in the Tusayan Ranger District of the Kaibab National Forest, on the border of Grand Canyon National Park (GCNP), latitude 35°57′40″N, longitude 111°57′29″W. The elevation was approximately 2290 m with gentle slopes, averaging 7%. Tree species were ponderosa pine (*Pinus ponderosa* var. *scopulorum* P.&C. Lawson), Gambel oak (*Quercus gambelii* Nutt.), Utah juniper (*Juniperus osteosperma* (Torr.) Little), and Rocky Mountain pinyon (*Pinus edulis* Engelm.). Soils in GCNP adjacent to the site are classified as fine, smectitic, mesic, Vertic Paleustalfs and Haplustalfs, clay soils weathered from calcareous sandstone parent material (B. Lindsay, National Resource Conservation Service, personal communication, 2000). Average precipitation is 36.8 cm, including average annual snowfall of 177.5 cm, at Grand Canyon Village, approximately 2097 m elevation and

20.4 km NW of the study area (GCNP, 1992). Temperatures range from an average daily maximum of 29 °C in July to 8 °C in January. Precipitation varied substantially in the specific measurement years of this study: in the water year (October 1–September 30) 1997, 43.3 cm precipitation (117% of average) was recorded; in 2000, only 22.4 cm (61% of average) was recorded; in 2001, 50.2 cm (136% of average) was recorded; in 2004, 40.6 cm (110% of average) was recorded. Drought also occurred in 2002, when no data were collected: 26.2 cm (71% of average) (Western Regional Climate Center, weather station Grand Canyon #2, www.wrcc.dri.edu).

Pretreatment measurements were taken in 1997, followed by thinning and burning in 1999. Post-treatment measurements were completed in 2000, the first year following treatment, and results were reported by Fulé et al. (2002a). Measurements of understory vegetation only were done in 2001 and all variables were measured in 2004, the fifth year following treatment. One CONTROL plot was accidentally burned in 1999; it was removed from all analyses.

3. Methods

3.1. Field

Each treatment was applied on a ~12-ha forested unit. We established twenty 400 m^2 (11.28 m radius) circular fixed-area plots arranged in a 60 m × 60 m grid in each of the four treatment units. Overstory trees taller than breast height (137 cm) were measured on each plot, including species, condition (living or snag/log classes [Thomas et al., 1979]), diameter at breast height (dbh), and a preliminary field classification of pre- or post-fire-exclusion origin, were recorded for all live and dead trees over breast height, as well as for stumps and downed trees that surpassed breast height while alive. We tallied regeneration (trees below breast height) by three height classes (0–40, 40.1–80, and 80–137 cm) on a nested 100 m^2 (5.64 m radius) subplot. We assessed dwarf mistletoe rating (DMR) on a scale of 0–6 on each ponderosa pine tree.

We sampled understory vegetation using belt and point-intercept transects in 1997 (pre-treatment), 2000 (post-treatment), 2001, and 2004. Complete species lists of all vascular plants and trees <1.4 m in height were collected in one 10 m × 50 m belt transect per plot. A 50-m point-intercept transect was established in the center of each belt transect, and species presence was recorded at a point every 30 cm along each transect. Plant species were classified into four groups: annual and biennial forbs, perennial forbs, graminoids, and shrubs. We calculated plant foliar cover (%) by dividing the number of points containing a plant by the 166 points per plot. We recorded tree canopy cover measured by vertical projection (every 30 cm in 1997, changing to every 3 m in 2004) along the line transect.

Collecting vegetation data using quadrats has been shown to be a superior method compared to the point-intercept method in southwestern ponderosa pine forests (Korb et al., 2003; Abella and Covington, 2004). The point-intercept method tends to over-estimate plant cover and underestimate species richness. Therefore, in 2004, we additionally sampled ten 1-m^2 quadrats per plot arranged along the center of the -intercept transect. We measured species presence and foliar cover (%) for each quadrat. Plant cover was averaged and species richness was totaled across the 10 quadrats per plot. We continued using belt and point-intercept transects in 2004 for consistency in detecting relative changes from pretreatment conditions. We measured dead woody biomass and forest floor depth on a 15.2 m planar transect in a random direction from each plot center (Brown, 1974).

3.2. Laboratory

We carried out statistical analyses of forest structure and forest floor variables on the 20 plots per treatment unit with repeated measures ANOVA. The 20 plots in each treatment unit were pseudo-replicates, since only one instance of each experimental treatment was implemented to the ~12 ha units. Inferences are therefore limited to these particular sites. Alpha level was 0.05. We transformed variables (square-root or natural logarithm) where necessary to meet ANOVA assumptions of normality and homoskedasticity. Following a statistically significant ANOVA result, we compared treatment means with a post hoc Tukey's procedure.

Previously, we had compared pre- and post-treatment forest structures (Fulé et al., 2002a). Now, we used post-treatment (2000) data as a covariate (ANCOVA) to account for differences in forest structure among treatments, testing whether among-treatment differences had changed over time. We used the Kruskal–Wallis/Mann–Whitney test for nonparametric data (crown scorch, bole char). Fates of individual large trees (ponderosa pine ≥ 37.5 cm dbh, other species ≥ 20 cm dbh) were followed to track survival, snag creation and retention, and snag loss.

Univariate understory vegetation data from the three post-treatment years were analyzed with a repeated measures MANOVA using pre-treatment data as a covariate. Data from the three post-treatment years are presented as the difference from pre-treatment data to account for pre-existing differences. If significant treatment $\times$ time interactions occurred, we used one-way ANOVA and Fisher's L.S.D. post hoc tests to compare treatment differences within years.

Overstory–understory relationships were examined with linear regression. We modeled plant cover, species richness, and plant diversity in 1997 (pre-treatment) and 2004 (five years post-treatment). We used step-wise regression to determine the best fitting models. We introduced 20 independent variables into the step-wise procedure: tree canopy cover (%), total basal area, basal area of juniper, pinyon pine, ponderosa pine, and oak, total tree density, density of juniper, pinyon pine, ponderosa pine, and oak, litter depth, duff depth, total forest floor depth, fine fuels (1, 10, 100 h), total fine fuels, rotten CWD, and sound CWD. For analyses of 2004 data, we introduced three 'dummy' variables into the set of independent variables to determine if the four treatment levels had a detectable effect on overstory–understory relationships.

Indicator Species Analysis (ISA; Dufrêne and Legendre, 1997) was used to determine most common species within treatment areas. We applied a hierarchical approach to determine indicator species: first, we compared treatments, then we compared years within treatments (FULL in 1997 versus FULL in 2004). Species were considered indicators of the treatment and/or year for which they had their largest indicator value (INDVAL). We restricted our attention to species with $P < 0.05$ (assessed using Monte Carlo randomizations with 999 permutations) and INDVAL > 25.

We used nonmetric multidimensional scaling (NMS) ordinations to illustrate compositional differences between plots. We conducted ordinations using PC-ORD software (version 4.25; McCune and Mefford, 1999). NMS arranges the plots in a configuration that minimizes the inter-plot distances (stress). We used the Bray–Curtis distance measure with random starting configurations, 100 runs with real data, a maximum of 400 iterations per run, and a stability criterion of 0.00001. A Monte Carlo test with 9999 randomizations was used to determine how likely the observed stress value of the final solution would be by chance alone. We omitted species that occurred on <5% of the plots from the ordination and from analyses of species composition but included them in univariate analyses of species richness (McCune and Grace, 2002).

We tested whether the treatments differed from one another in community composition in 1997, in community composition in 2004, and we tested for a time $\times$ treatment interaction. Treatment comparisons in 1997 and in 2004 were made with PERMANOVA software (Anderson, 2005). This software permits the analysis of univariate or multivariate data using any distance measure and linear model. The calculated statistic (pseudo-F) is calculated, like a traditional F-statistic, as the sum of the squared distances among groups divided by the sum of the squared distances within groups (see, for details, Anderson, 2001; McArdle and Anderson, 2001). Data were untransformed and unstandardized. We calculated dissimilarities using the Bray–Curtis distance measure (Faith et al., 1987). P-values were calculated by permuting the observations 9999 times, so no assumptions of the distributional form of the data were required.

The test for a time $\times$ treatment interaction required that we account for autocorrelation between repeated measurements of permanent plots. We accounted for autocorrelation between repeated measurements by calculating the multivariate dissimilarity (Bray–Curtis distance) between the 1997 and 2004 data for each plot (this is analogous to calculating the difference between two values in a paired t-test). This calculation produced a univariate response variable that we analyzed using a Kruskal–Wallis test and we made pairwise comparisons with a Wilcoxon two-sample test; a significant result indicated that the treatment with greater dissimilarity experienced a greater change in community composition between 1997 and 2004.

3.3. Analysis of covariance

Data obtained from the quadrats in 2004 could only be useful if we could account for pre-existing differences between the treatments in 1997, since no quadrat data was collected in 1997. To test for differences among treatments while accounting for possible pre-existing differences, we used analysis of covariance (ANCOVA). We analyzed plant cover differences in 2004 with a covariate of cover from the point-intercepts in 1997 to represent pre-existing differences. We analyzed species richness differences in 2004 with a covariate of species richness from the belt transects in 1997 to represent pre-existing differences. We analyzed diversity differences in 2004 with a covariate of diversity from the point-intercepts in 1997 to represent pre-existing differences. The covariates were useful in the analyses since they all covaried with the respective response variables using data from 2004 (all R^2 ranged between 0.10 and 0.50, all $P < 0.01$).

4. Results

4.1. Forest structure

As expected, the FULL treatment was significantly lowest in basal area, tree density, and canopy cover in 2004 (respectively, $F = 15.1$, 21.6, 11.9, $P < 0.0001$ for all variables) (Table 1). The MIN treatment was second lowest, though not significantly different from the BURN and CONTROL treatments. Analysis of covariance showed that the first post-treatment forest structure measurement (2000 data) explained all of the significant differences in forest structure (respectively, $F = 646$, 1301, 42, $P < 0.0001$ for all variables), indicating that no statistically significant changes in forest structure had occurred between the first post-treatment year (2000) and the fifth (2004).

Basal area, tree density, and canopy cover declined over the 2000–2004 time period, but the CONTROL unit consistently had the smallest reduction (Table 1). The CONTROL declined 3.2% in basal area, compared to 6.2–8.5% in the treatments, and 7.3% in tree density, compared to 10.6–17.7% in the treatments. Smaller trees were the most likely to die in each treatment between 2000 and 2004, as reflected in the consistent increase in quadratic mean diameter for each species (Table 1). Across all treatments, out of 1764 trees that were alive after treatment in 2000, a total of 213 trees were dead in 2004 (12.1%). Average diameters of recently killed trees were lower than those of surviving trees, significantly lower in MIN and BURN but not in FULL. In the FULL treatment, dead trees averaged 12.0 ± 4.0 cm ($\pm$1S.E.) and living trees averaged 16.8 ± 1.5 cm ($U = 530$, $P = 0.26$). In the MIN treatment, dead trees averaged 7.7 ± 0.7 cm and living trees averaged 12.8 ± 0.5 cm ($U = 11938$, $P < 0.001$). In the BURN treatment, dead trees averaged 8.0 ± 0.7 cm and living trees averaged 11.5 ± 0.3 cm ($U = 38397$, $P < 0.001$).

Trees dying between 2000 and 2004 had significantly higher canopy scorch as measured by percent volume lost. In the FULL treatment, scorch of dead trees averaged $58 \pm 11\%$ ($\pm$1S.E.) and living trees averaged $22 \pm 3\%$ ($U = 509$, $P = 0.001$). In the MIN treatment, dead trees averaged $58 \pm 5\%$ and living trees averaged $33 \pm 1\%$ ($U = 10000$, $P < 0.0001$). In the BURN treatment, dead trees averaged $62 \pm 3\%$ and living trees averaged $32 \pm 1\%$ ($U = 49070$, $P < 0.0001$). Scorch height and maximum bole char height were significantly higher in dead than living trees in the BURN treatment only. Dwarf mistletoe rating did not differ between living and dead trees.

The fates of large trees, defined as ponderosa pine ≥ 37.5 cm dbh and other species ≥ 20 cm dbh, were consistent with the overall declines in tree variables. Since there were relatively few large trees in the experiment, the following data are presented in both absolute numbers and percentages. In the CONTROL unit, 1 of the 32 large pines (3%) and none of the 38 large oaks that were alive in 2000 had died by 2004. One of the five large pine snags (20%) but none of the two large oak snags was lost (i.e., fallen). In the FULL unit, 1 of 11 large pines (9%) that were living in 2000 died by 2004. None of the 23 large oaks died but 2 of the 10 large snags (20%) present in 2000 were lost by 2004. In the MIN unit, there was change neither to the 14 large pines and 1 large pine snag nor to the 2 large oaks and 1 large oak snag. The MIN unit was the only unit to contain large pinyon and

Table 1
Forest structure in 2004, five years after ecological restoration treatments at Grandview, Arizona

Treatment	Basal area (m^2 ha^{-1})			Tree density (trees ha^{-1})			QMD (cm)		Canopy cover (%)		
	Mean	S.E.M.	Change since 2000	Mean	S.E.M.	Change since 2000	Mean	Change since 2000	Mean (%)	S.E.M. (%)	Change since 2000 (%)
CONTROL											
JUOS	0.0001	0.00007	0	2.6	1.8	0	0.7	0			
PIED	0.003	0.003	0	2.6	2.6	100%	7.9	46%			
PIPO	16.3	2.6	−3.6%	380.3	76.3	−6.5%	23.3	1.3%			
QUGA	5.6	1.5	−2.0%	314.5	91.8	-8.8%	15.1	4.1%			
Total	21.9 a	2.6	−3.2%	700.0 a	118.2	−7.3%			49.1 a	4.3	−6.1
FULL											
JUOS	0	N/A	N/A	0	N/A	N/A					
PIED	0	N/A	N/A	0	N/A	N/A					
PIPO	3.7	1.1	−13.0%	35.0	8.0	−17.6%	36.7	3.4%			
QUGA	2.0	0.6	1.4%	102.5	30.5	-7.8%	15.8	7.5%			
Total	5.6 b	1.2	−8.5%	137.5 b	31.8	−10.6%			22.4 b	2.8	−10.0
MIN											
JUOS	2.4	1.3	0.3%	70.0	24.8	−9.6%	20.9	6.1%			
PIED	0.1	0.1	−7.2%	6.3	4.0	−16.7%	14.2	0			
PIPO	9.8	1.5	−6.1%	460.0	90.1	−17.3%	16.5	7.1%			
QUGA	0.3	0.1	−39.4%	27.5	12.2	−37.1%	11.8	2.5%			
Total	12.6 a	1.4	−6.2%	563.8 a	95.2	−17.7%			35.9 a	3.1	−4.5
BURN											
JUOS	0.3	0.2	−44.0%	7.5	3.7	−53.8%	22.6	14.1%			
PIED	0.0003	0.0003	N/A	1.3	1.3	N/A	1.7	N/A			
PIPO	15.7	2.1	−6.3%	1047.5	168.6	−10.2%	13.8	1.5%			
QUGA	4.2	1.3	−4.9%	181.3	56.5	−12.7%	17.2	4.9%			
Total	20.2 a	2.5	−6.9%	1237.5 c	170.0	−11.0%			43.1 a	4.3	−19.7

QMD: quadratic mean diameter; S.E.M.: standard error of the mean. Change was calculated as a percentage relative to measurements taken in 2000, one year after treatment. N/A: not applicable. Different letters (a–c) following totals within columns indicate significant differences ($P < 0.05$).

juniper trees. There was no change to the one large living pinyon. Twenty of 21 large junipers, which were living in 2000, were still living in 2004 (5% mortality) and all 3 of the large juniper snags present in 2000 persisted in 2004. Finally, in the BURN unit, 2 of 15 large pines that were living in 2000 died by 2004 (13%) and 3 large pine snags persisted in 2004. Two of 32 large oaks died (6%) and the 1 large oak snag present in 2000 remained unchanged in 2004.

Tree diameter growth differed significantly among treatments and ponderosa pines consistently grew more than Gambel oaks, but the differences between treatments did not follow the expected pattern of higher growth with lower density. Compared to pre-treatment (1997) values, the MIN unit had the largest average diameter increment, 1.27 cm, for all trees still living in 2004 (Table 2). Ponderosa pine diameter increments were not different in the CONTROL, FULL, and MIN treatments, but the BURN was significantly lower ($F = 9.3$, $P < 0.0001$; Table 2). Oak diameter increments were significantly different among treatments in an overall anova ($F = 3.5$, $P = 0.016$) but none of the means were separated by a Tukey's test. There were too few junipers and pinyons for testing.

Unlike diameter growth, ponderosa pine basal area increments differed significantly in each treatment ($F = 46.9$, $P < 0.0001$), covering a broad range from 76.6 cm^2 in the FULL down to 21.6 cm^2 in the BURN treatment, generally conforming to our hypothesis. Basal area increment (BAI) was correlated with diameter increment (range of $R = 0.7$–0.9) but BAI provides a better expression of tree growth because it includes circumference effects. The BURN treatment had a significantly lower basal area increment than the other treatments ($F = 11.0$, $P < 0.0001$). Oak basal

Table 2
Diameter growth and basal area increment from 1997 (pre-treatment) to 2004 (five years after treatment) at Grandview, Arizona

Treatment	Average all species	JUOS	PIED	PIPO	QUGA
Diameter growth (cm)					
CONTROL					
Mean	1.02 a	0.80*	1.60*	1.43 a	0.53 a
S.E.M.	0.04	0.40	1.60	0.06	0.04
FULL					
Mean	0.81 a	N/A	N/A	1.40 a	0.61 a
S.E.M.	0.10			0.28	0.09
MIN					
Mean	1.27 b	0.96	0.56*	1.36 a,b	0.72 a
S.E.M.	0.06	0.19	0.13	0.06	0.12
BURN					
Mean	1.00 a	0.50*	0*	1.10 b	0.40 a
S.E.M.	0.03	0.15		0.03	0.04
Basal area increment (cm^2)					
CONTROL					
Mean	27.7 a	1.6*	1.61*	41.4 a	11.9
S.E.M.	1.5	1.1	1.61	2.4	1.1
FULL					
Mean	31.1 a	N/A	N/A	76.6 b	15.6
S.E.M.	6.4			21.0	3.5
MIN					
Mean	26.8 a	21.1	12.5*	28.8 c	11.7
S.E.M.	1.5	6.3	5.6	1.5	3.3
BURN					
Mean	19.8 b	7.5*	0*	21.6 d	10.1
S.E.M.	0.8	2.6		0.9	1.2

S.E.M.: standard error of the mean; N/A: not applicable. Different letters (a–d) following totals within columns indicate significant differences ($P < .05$).

* Fewer than 10 trees in this category.

area increments did not differ among treatments ($F = 1.4$, $P = 0.24$).

Dwarf mistletoe rating (DMR) declined or remained unchanged between 2000 and 2004, from 1.4 to 0.9 in CONTROL (36%), 0.3–0.1 in FULL (67%), unchanged at 0.1 in MIN and 0.01 in BURN.

As expected, tree regeneration (trees shorter than breast height, 1.37 m) varied widely among treatments (Table 3) but there were no significant differences in the two shortest height classes (Kruskal–Wallis test, $P = 0.22$ for regeneration 0–40 cm in height and $P = 0.72$ for regeneration 40.1–80 cm in height). Gambel oak sprouts comprised 97–100% of regeneration in the shortest height class. There was a significant difference among treatments only in the tallest height class (Kruskal–Wallis test, $P = 0.03$), with FULL and BURN having approximately eight times higher densities (average of 65 trees ha^{-1} versus average of 8 trees ha^{-1} in MIN and CONTROL).

4.2. Understory vegetation

Changes since treatment were more pronounced in understory vegetation than in tree structure (Fig. 1), although all of the changes covaried significantly with pre-existing characteristics (Table 4). Plant cover (%) in 2004 on the quadrats covaried with cover in 1997 on point-intercept transects, but plant cover was highest in FULL in 2004 and not significantly different from MIN. Richness in 2004 on the quadrats covaried with richness in 1997 on belt transects, but species richness was highest in FULL and CONTROL and lowest in BURN in 2004. Diversity in 2004 on the quadrats covaried with diversity in 1997 on the point-intercept transects, but diversity (Simpson's Index, D') did not differ among treatments (Table 4).

The understory plant community responded strongly to inter-annual climatic differences (Fig. 1), but there were significant treatment effects and treatment × time interactions for plant cover and annual species richness (Fig. 1a,b, and e). Change in cover from 1997 was significantly greater in the three treatments than the control in all three years of re-measurement, but we did not find the expected differences among treatments (Fig. 1a). Though the majority of the increases in total cover were due to native plants, there was a significant treatment × time interaction for exotic plant cover (Fig. 1b). There were no clear differences of exotic plant cover among treatments, but the FULL treatment yielded greater change in all three years of re-measurement. Change in species richness was lowest in the BURN treatment across all years but the other treatments did not differ from the control (Fig. 1c). Change in exotic species richness did not differ among treatments (Fig. 1d). Greater change in annual species richness occurred in the FULL and MIN treatments (Fig. 1e). Change in plant diversity (Simpson's Index) was highest in the FULL treatment in 2000 but was not different than the control and there were no differences in any other year.

We detected 138 vascular plant species on the plots in 1997 and 2004 but our analysis of species

Table 3
Regeneration density five years after ecological restoration treatments at Grandview, Arizona

Treatment	Total (trees ha^{-1})	JUOS (trees ha^{-1})	PIED (trees ha^{-1})	PIPO (trees ha^{-1})	QUGA (trees ha^{-1})
Regeneration 0–40 cm in height					
CONTROL					
Mean	1205.3	5.3	0	36.8	1163.2
S.E.M.	217.0	5.3		21.9	214.2
FULL					
Mean	4965.0	0	0	10.0	4955.0
S.E.M.	1547.2			6.9	1546.4
MIN					
Mean	2540.0	10.0	15.0	15.0	2500.0
S.E.M.	728.6	10.0	10.9	10.9	731.5
BURN					
Mean	1885.0	10.0	0	20.0	1855.0
S.E.M.	357.9	6.9		11.7	358.8
Regeneration 40.1–80 cm in height					
CONTROL					
Mean	52.6	5.3	0	15.8	31.6
S.E.M.	17.7	5.3		8.6	17.2
FULL					
Mean	930.0	0	0	5.0	925.0
S.E.M.	582.3			5.0	577.6
MIN					
Mean	70.0	10.0	0	10.0	50.0
S.E.M.	21.9	10.0		10.0	17.0
BURN					
Mean	125.0	0	0	75.0	50.0
S.E.M.	44.1			41.0	25.6
Regeneration 80.1–137 cm in height					
CONTROL					
Mean	10.5	0	0	5.3	5.3
S.E.M.	7.2			5.3	5.3
FULL					
Mean	70.0	0	0	0	70.0
S.E.M.	39.1				39.1
MIN					
Mean	5.0	5.0	0	0	0
S.E.M.	5.0	5.0			
BURN					
Mean	60.0	0	0	45.0	15.0
S.E.M.	19.7			18.5	10.9

S.E.M.: standard error of the mean.

composition focused on the 83 species that occurred on >5% of the plots. Species composition differed among treatments in 1997, prior to treatment ($F = 9.8$, $P < 0.0001$), and after treatment in 2004 ($F = 7.5$, $P < 0.0001$). However, there was a significant year × treatment interaction ($U = 16.2$, $P = 0.001$); the composition in the FULL and MIN treatments changed the most in comparison to the other treatments (Fig. 1). Pairwise comparisons showed that the rate of change in the FULL treatment was greater than

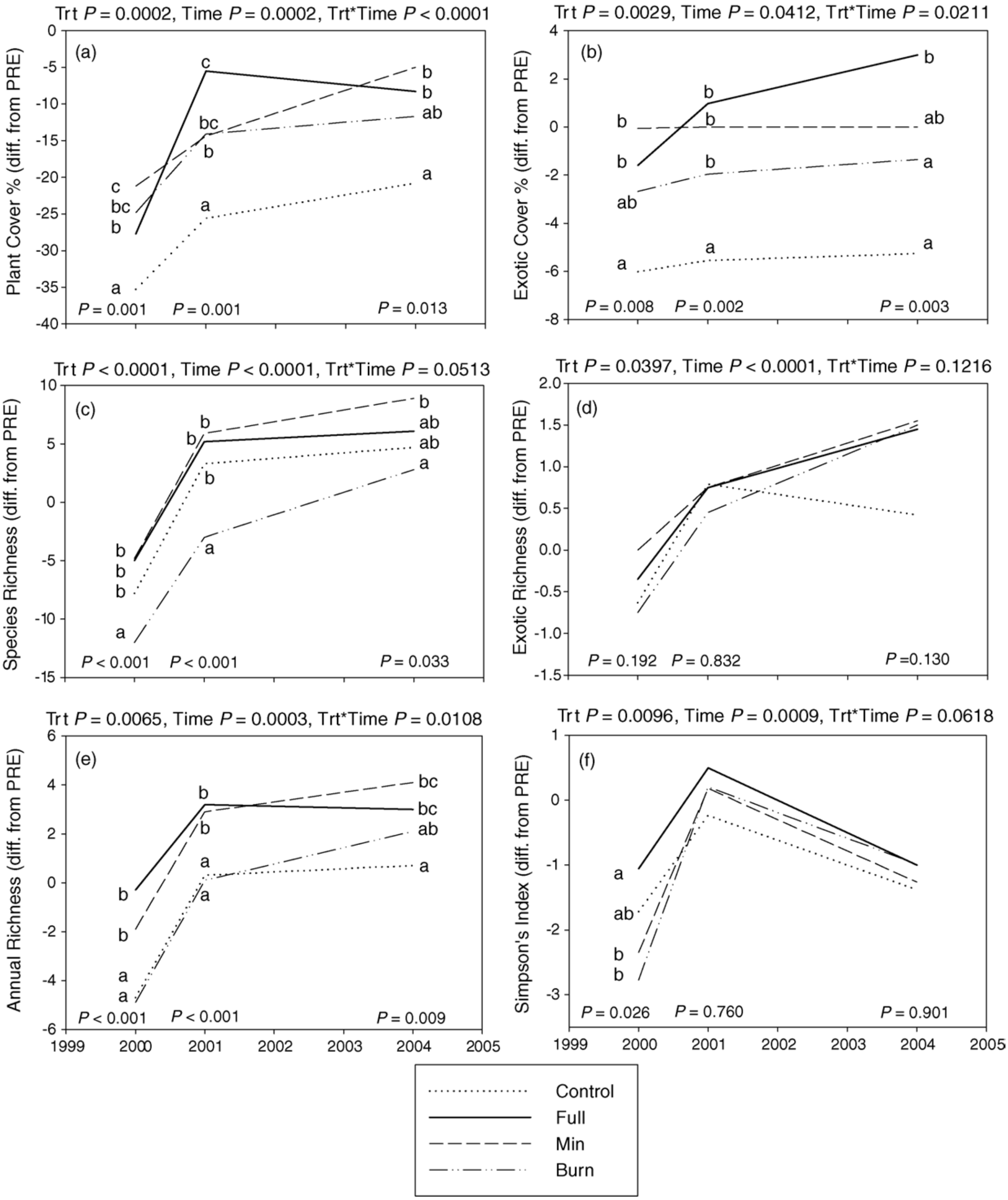

Fig. 1. Understory plant community characteristics plotted as their difference from pre-treatment (1997) data through time for all three treatments and control. If significant treatment × time interactions occurred, one-way ANOVA *P*-values are listed under the treatments within years, and differing lowercase letters denote significant differences tested with Fisher's L.S.D. post hoc comparisons. Variables are (a) plant cover, (b) exotic cover, (c) richness, (d) exotic richness, (e) annual richness and (f) Simpson's Index.

Table 4
Understory vegetation community characteristics (mean ± S.E.M.) derived from 2004 quadrat data analyzed with ANCOVA using pre-treatment data from 1997 as covariates

Treatment	Cover (%)	Species richness (per 10 m^2)	Simpson's Index
CONTROL	9 ± 1 a	26.1 ± 1.2 a,c	7.6 ± 0.6
FULL	12 ± 1 b,c	26.2 ± 0.8 a	5.9 ± 0.5
MIN	10 ± 1 b,c	22.0 ± 0.8 b,c	5.7 ± 0.4
BURN	8 ± 1 a,c	20.5 ± 1.0 b	6.4 ± 0.3
1997 Covariate *P*-value	< 0.0001	0.0311	0.001
ANCOVA *F*-value	0	8.7	1.6
ANCOVA *P*-value	0.001	<0.0001	0.19

Lower-case letters (a–c) within columns indicate significant differences among treatments.

the CONTROL and BURN (both $P < 0.01$), but was not different than MIN ($P = 0.19$); the rate of change in MIN was not different than BURN ($P = 0.09$) but was greater than the CONTROL ($P = 0.02$).

Indicator Species Analysis identified species that increased in particular treatments since pre-treatment (Table 5) and explains which species are driving the differences illustrated in the ordination (Fig. 2). Indicator species of treatment units were not included in Table 5 since they indicate pre-existing treatment unit differences rather than real changes over time due to treatment. Three of the five indicators of FULL in 2004 and five of the eight indicators of MIN in 2004 were annual or biennial species (Table 5).

Understory characteristics were significantly related to forest structure and fuel loads prior to treatment. Plant cover was positively related to oak basal area, and negatively related to pine density and tree canopy cover ($R^2_a = 0.49$, $P < 0.0001$). Species richness was positively related to oak basal area, and negatively related to pine density and rotten CWD ($R^2_a = 0.32$, $P < 0.0001$). Plant diversity was negatively related to pine density and tree canopy cover ($R^2_a = 0.40$, $P < 0.0001$). However, in 2004, these relationships weakened or became absent entirely.

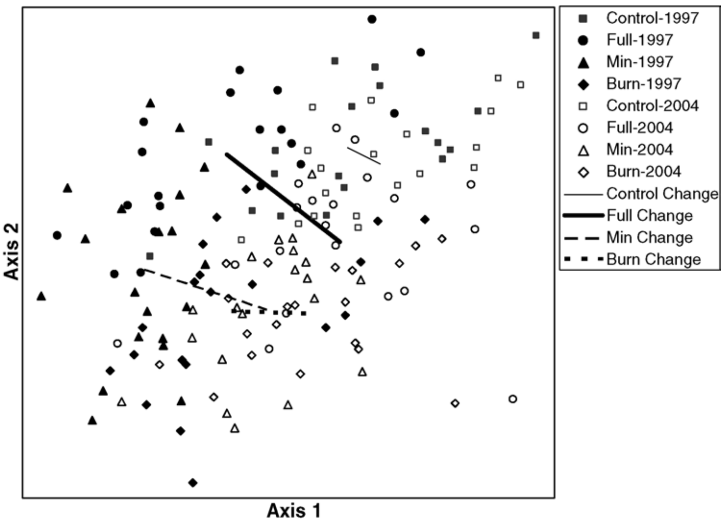

Fig. 2. Nonmetric multidimensional scaling (NMS) ordination of species composition on experimental plots in the Kaibab National Forest. The greatest compositional change occurred on the FULL and MIN restoration plots, as shown by the lines connecting the centroids (average position within each treatment-year) of treatments among years. This plot was configured using presence of 83 species on 79 plots in 1997 and 79 plots in 2004. The final solution had two-dimensions; stress = 21.6; $P = 0.0099$.

Table 5
Indicator Species Analysis of experimental plots in the Kaibab National Forest

Indicator species	Life form[a]	INDVAL[b]
CONTROL in 1997		
Gayophytum diffusum	A	71.1
CONTROL in 2004		
Androsace septentrionalis	P	45.0
Arenaria lanuginosa ssp. *saximontana*	P	57.8
Plantago argyrea	A	55.6
Silene scouleri	P	35.6
Sporobolus cryptandrus	G	25.0
FULL in 1997		
Blepharoneuron tricholepis	G	45.5
Epilobium brachycarpum	A	36.8
FULL in 2004		
Astragalus castaeniformis	P	76.9
Chamesyce serpyllifolia	A	40.0
Erigeron divergens	AB	69.0
Lupinus kingii	A	66.2
Trifolium gymnocarpon ssp. *gymnocarpon*	P	80.3
MIN in 1997		
Calochortus nuttalii	P	30.0
MIN in 2004		
Astragalus humistratus	P	50.0
Bromus tectorum	G	46.5
Chenopodium graveolens	A	45.5
Chenopodium leptophyllum	A	53.6
Chenopodium spp.	A	56.2
Guttereizia sarothrae	S	41.7
Phlox gracilis	A	62.5
Verbascum thapsus	AB	40.0
BURN in 1997		
Lomatium foeniculaceum spp. *macdougalii*	P	51.6
BURN in 2004		
No indicator species	–	–

All species were significant ($P < 0.05$).
[a] Life forms codes: A, annual forb; AB, annual/biennial forb; P, perennial forb; G, grass; S, shrub.
[b] INDVAL: indicator value, see Dufrene and Legendre (1997) for details.

Plant cover and species richness remained negatively related to pine density, but the relationships were much weaker ($R^2_a = 0.12$, 0.15, respectively, both $P < 0.01$). Diversity was not correlated with any variable in 2004. The introduction of 'dummy' variables to represent treatments did not improve the models.

4.3. Forest floor and woody debris

Duff depths were significantly lower in the FULL and MIN treatments in 2004 ($F = 8.2$, $P < 0.0001$) (Table 6). The post-treatment (2000) duff depth was a significant covariate ($F = 10.9$, $P = 0.0014$) but did not change the pattern of differences by treatment in 2004. Although total woody debris varied over a wide range, from 5.4 Mg ha^{-1} in BURN to 15.9 Mg ha^{-1} in CONTROL, the differences were not statistically significant ($F = 2.7$, $P = 0.052$).

5. Discussion

5.1. Forest dynamics

Five years after thinning and burning treatments in ponderosa pine–Gambel oak forest, changes in forest structure were relatively minor. The predominant changes were in tree growth, generally following the expected pattern of higher growth in less dense forests, mortality of small and fire-damaged trees, and understory vegetation responses that were highly correlated with pretreatment patterns (Fig. 3). Since the experiment was unreplicated, inferences about significant differences in response variables among treatments are limited to the study sites. However, the pretreatment similarity of the units, the before–after control–impact (BACI) design, and the fact that the treatment impacts were not subtle, support relatively strong causal inferences about variables that were directly affected by tree cutting and burning such as tree structure and forest floor variables. Weaker inferences about causation would be more appropriate for understory vegetation variables, which were linked more closely to pre-existing conditions. These inferential distinctions were carried through the analysis, where tree and forest floor variables were compared directly across treatments while understory vegetation variables included pretreatment conditions as covariates.

We found that basal area increment in ponderosa pines was associated with the degree of thinning, although radial increment was similar across all but the MIN treatment. Skov et al. (2005) showed that radial ponderosa growth rate, expressed as a proportion of pretreatment growth rate, varied with degree of

Table 6
Forest floor and woody debris in 2004, five years after ecological restoration treatments at Grandview, Arizona

Treatment	Litter (cm)	Duff (cm)	Forest floor (cm)	1H (Mg ha^{-1})	10H (Mg ha^{-1})	100H (Mg ha^{-1})	1000H sound (Mg ha^{-1})	1000H rotten (Mg ha^{-1})	Total woody debris (Mg ha^{-1})
CONTROL									
Mean	1.4	1.5 a	2.9	0.09	0.7	1.5	13.1	0.4	15.9
S.E.M.	0.2	0.2	0.3	0.04	0.3	0.5	6.0	0.4	6.2
FULL									
Mean	1.2	0.4 b	1.6	0.2	0.8	3.9	7.9	0	12.8
S.E.M.	0.2	0.1	0.2	0.05	0.2	1.5	2.6		3.9
MIN									
Mean	0.5	0.7 b	1.2	0.2	1.0	2.3	3.4	0	6.9
S.E.M.	0.09	0.1	0.2	0.05	0.2	0.7	1.7		1.8
BURN									
Mean	1.0	1.5 a	2.5	0.2	1.1	0.7	3.3	0	5.4
S.E.M.	0.2	0.2	0.3	0.09	0.3	0.4	2.2		2.4

S.E.M.: standard error of the mean. Woody debris is classified by moisture timelag class, e.g. 1H: 1-h timelag class (Anderson, 1982).

thinning as well as interannual precipitation and tree age. Younger trees grew significantly faster and responded more strongly to thinning than older trees; Skov et al. (2005) suggested that a residual threshold of $\leq 16.0\ \mathrm{m}^2\ \mathrm{ha}^{-1}$ was needed before older trees would respond. The FULL and MIN treatments at Grandview fell below this threshold but the data set contained too few trees for a comparison between young and old trees. However, the fact that basal area increment was significantly highest in the heavily thinned FULL treatment suggests that the larger tree size was important: since average radial growth per tree was similar in all treatments except BURN, the expression of that growth over the larger trees in FULL led to a higher basal area increment.

Physiological explanations of increased growth following restoration thinning and burning were studied at the Gus Pearson Natural Area near Flagstaff in northern Arizona, about 100 km southeast of the Grandview study site. Under conditions of reduced tree competition and increased soil moisture due to thinning from $\sim$34.5 to $13.0\ \mathrm{m}^2\ \mathrm{ha}^{-1}$, presettlement trees exhibited higher predawn water potential, stomatal conductance, leaf nitrogen concentration, higher resin flow, and tougher foliage than paired trees in the control area (Feeney et al., 1998; Stone et al., 1999). These conditions persisted for seven years (Wallin et al., 2004). Skov et al. (2004) compared physiological responses at nearby sites across a range of thinning intensities, finding that increased predawn water potential was a consistent effect of treatment but stomatal conductance and net photosynthetic rate were significantly affected only under dry conditions; young trees displayed greater positive responses to thinning and burning treatments than older trees. We expect that similar changes in physiological and morphological characteristics would have been associated with the increased ponderosa pine growth in the FULL treatment at Grandview, with the implication that these trees would be more drought-, bark beetle-, and folivore-resistant than similar trees in the more dense treatment units.

Though ponderosa pines exhibited relatively high growth rates in our study, stand level growth differences were diminished by the smaller variation in Gambel oak growth. Oaks in the FULL treatment had the highest basal area increment, but the difference was not significant. Onkonburi (1999) also found relatively little change in Gambel oak growth following thinning or burning treatments.

Tree mortality leading to the declines in basal area, density, and canopy cover across all treatments between 2000 and 2004 was probably a consequence of drought in addition to delayed treatment effects. The below-average precipitation in 2000 and 2002 was especially severe across the Southwest (Cook et al., 2004). If the decline in these variables in the CONTROL were considered as a baseline of change without treatment, then the additional mortality

Fig. 3. Understory growth was the most evident change from 2000 (one year after treatment, top photo) to 2004 (five years after treatment, bottom photo), in the MIN thinning unit.

associated with the treatments would have averaged ≤6% in basal area and ≤10% in density.

Delayed tree mortality is common after fire, both from heat injury and post-fire bark beetle attacks (McHugh and Kolb, 2003; Wallin et al., 2003). Since Sackett et al. (1996) traced substantial mortality of large ponderosa pine trees to cambial girdling, we had removed fuels from the base of all large trees, except in the BURN. There were few large trees, so only very limited evidence suggested that cambial girdling had some effect by the fifth year after fire: in the FULL and MIN combined, only one large tree died out of 50 large pines and oaks, while large-tree mortality in the BURN was only slightly higher, with four large trees dying out of 47 large pines and oaks. The CONTROL lost one out of 70 trees. The findings that delayed mortality was significantly concentrated in smaller trees and those with higher crown scorch were consistent with data from other fires in northern Arizona (McHugh and Kolb, 2003), suggesting that direct heat damage was probably an important factor predisposing trees to death. McHugh and Kolb (2003) reported that consistent ponderosa pine mortality began around 70% crown scorch and increased sharply after 80%; we found that 32% of pines with scorch ≥70% and 37% of pines with scorch ≥80% that were considered alive in 2000 died by 2004.

Understory vegetation dynamics were more complex than tree changes because of the interacting factors of significant pre-existing differences, climate effects, and treatment effects. FULL and MIN were highest in cover and FULL was highest in richness in 2004, consistent with findings at other restoration sites (Korb and Springer, 2003), but the mean absolute differences among treatments were small (3% range in cover, two species range in richness). Pre-treatment understory conditions were significant covariates with 2004 conditions, supporting Vose and White (1991) observation that post-fire responses were linked to the pre-fire plant community. Vegetation dynamics followed similar patterns across treatments in 2000, 2001, and 2004 (Fig. 1), influenced in large part by climate. Nearly all measures declined substantially in the drought year of 2000, relative to pretreatment (1997) measurements, then recovered sharply in 2001 and maintained relatively similar patterns in 2004. Community composition differed among treatments in both 1997 and 2004, but the scale of overall change (vectors in Fig. 2) was much greater in the units with more intensive treatment, FULL and MIN, than in BURN and CONTROL.

Ruderal annual and biennial forb species that characterize recently disturbed habitats were more common in the treated areas. Annual species richness differences from pretreatment were highest in the treatments and did not change in CONTROL (Fig. 1e). The majority (62%) of indicator species of FULL and MIN in 2004 were annual or biennial forbs (Table 5). An increase in native annuals after fires has also been reported on the North Rim of GCNP (Laughlin et al., 2004; Huisinga et al., in press). Large increases in exotic species richness and abundance have been reported in northern Arizona following thinning and burning treatments (Griffis et al., 2001) and wildfires (Crawford et al., 2001), although responses to low-and high-intensity fires on the North Rim of GCNP were almost exclusively by native plants (Laughlin et al., 2004; Huisinga et al., in press). Korb et al. (in press) compared soil seedbanks at Grand Canyon (minimal human-caused disturbance) with other sites that had extensive harvesting and grazing histories, finding that native species were poorly represented in seedbanks and disturbed sites had high densities of exotic seeds. Since the Grandview site had been heavily harvested in the early twentieth century (Fulé et al., 2002b), an increase in exotics might have been expected to immediately follow the treatments. Exotic richness differences from pre-treatment in the three burned treatments were higher but not significantly different than CONTROL in 2004, but exotic plant cover differences from pretreatment averaged +3% in FULL, which was significantly different than BURN and CONTROL but not MIN. This suggests that exotic species cover, not exotic richness, is increasing in FULL at a greater rate than the other treatments. The ISA identified two exotics in MIN, *Bromus tectorum* and *Verbascum thapsus*, but no exotics in FULL. Continued monitoring is warranted, however, given other studies that have detected large increases in exotics following thinning and burning.

5.2. Comparison to reference conditions

These treatments were specifically aimed at ecological restoration (Allen et al., 2002), taking the historical ecosystem structure, composition, and function prior to fire-xclusion, harvesting, and other changes associated with Euro-American settlement in the late 19th century as the point of reference. Reference conditions are understood with varying degrees of certainty, ranging from relatively precise information about tree structure and fire regime to very limited information about herbaceous species, wildlife dynamics, or human effects on the environment (SNEP, 1996; Swetnam et al., 1999). Here, we assess the characteristics of the Grandview experiment, five years after initial treatment, in terms of our incomplete knowledge about reference conditions and draw inferences about the implications for the future development of these sites.

Forest structural variables, such as basal area and density, have been widely applied for reference data because they are important descriptors of forest condition and because the data are accessible. Pre-fire-exclusion forest structural conditions can be reconstructed due to the persistence of long-lived trees and decay-resistant dead wood (Covington and Moore, 1994), drawn from early historical surveys (Moore et al., 2004), measured in relict sites (Youngblood et al., 2004), or inferred from similar stands that remain in nearly natural conditions (Stephens et al., 2003).

At the Grandview site, historical forest conditions were reconstructed with dendroecological modeling by Fulé et al. (2002b) in 1887, the year of the last surface fire of the frequent-fire regime. Reconstructed basal area values ranged from ~11 to 20 $m^2\ ha^{-1}$ and tree densities from ~90 to 175 trees ha^{-1}. While many contemporary southwestern forests are considered excessively dense, the Grandview units fall toward the lower end of modern densities because of past tree harvesting, estimated to have averaged 12.6 $m^2\ ha^{-1}$ of ponderosa pine basal area removed (Fulé et al., 2002b). Additionally, in the case of the FULL treatment, heavy dwarf mistletoe infestation (DMR = 5 or 6) in many young ponderosa pine trees led to their being considered unsuitable for retention because their lifespan would be short (Hawksworth and Geils, 1990). Only the CONTROL, at 21.9 $m^2\ ha^{-1}$, slightly exceeded the range of reconstructed basal area; the FULL treatment, at 5.6 $m^2\ ha^{-1}$, remained well below the lower range. In terms of density, all treatments except FULL (137.5 trees ha^{-1}) remained higher than the historical range. However, the average size of ponderosa pine trees in 2004 was much smaller than in 1887: quadratic mean diameters in 2004 ranged from 13.8 to 36.7 cm, highest in FULL, as compared to 47–53 cm in 1887. In sum, five years after treatments, only the FULL treatment is close to the range of historical variability for density and quadratic mean diameter, with the MIN and BURN treatments continuing to support large numbers of small trees.

The FULL treatment poses concerns with respect to restoration when compared to the reference conditions for that unit (data for 1887 from Fulé et al., 2002a): basal area in 2004 was 5.6 $m^2\ ha^{-1}$, compared to 13.0 $m^2\ ha^{-1}$ in 1887 (57% less), ponderosa pine density was 35.0 pines ha^{-1}, compared to 60.0 pines ha^{-1} in 1887 (42% less), and quadratic mean diameter of ponderosa pine was 36.7 cm in 2004, compared to 41.3 cm in 1887 (11% less). Although mortality in the FULL unit between 2000 and 2004 was comparable in proportion to the declines in the other treatments, the effect may be more important because the unit is already in such an open condition relative to historical conditions. Finally, regeneration of ponderosa pine was very limited in FULL, averaging only 15 pines ha^{-1} with none in the tallest height class. Counterbalancing these trends is the finding of increased growth in FULL. If the current basal area growth rate were sustained, 0.4 m^2 ha^{-1} would be added per year, taking approximately 20 more years to regain the 1887 level. Low regeneration may not be an obstacle to sustaining the forest as long as at least a few young trees become established per decade. Mast et al. (1999) suggested that establishment of a range of 0.4–3.6 trees ha^{-1} decade^{-1} was adequate to maintain a long-lived ponderosa pine forest and Bailey and Covington (2002) found that these levels were met across several restoration sites in northern Arizona.

Understory vegetation is difficult to assess with respect to reference conditions, since these are less well understood for herbaceous plants than for trees. Three factors were consistent with ecological restoration goals: by 2004, total plant cover was highest in the treatments with the lowest basal area (FULL and MIN), total species richness was highest in the FULL treatment, and there was no significant increase in exotic species richness (though there were modest increases in exotic plant cover). At relict ponderosa pine forests on the North Rim of GCNP, exotic species were rare and total plant cover on point-intercept transects was slightly higher than that recorded in FULL and MIN treatments in 2004 (Laughlin et al., in press); however, understory reference conditions are highly variable (Gildar et al., 2004) so strict reference targets are harder to define for the understory plant community. According to strong relationships between herbaceous production and forest structure (Moore and Deiter, 1992), we expected to detect stronger differences in plant cover among treatment units since they differ in forest density and basal area. The long-term drought during the study duration may be hindering a full recovery of herbaceous vegetation in treated units, so continued monitoring will be necessary to determine long-term changes among treatments.

Repeated use of surface fire in the treatment areas is planned. In the historical fire regime, mean fire frequency averaged 6.9 year for all fires, 9.5 year for fires scarring 25% or more of fire-scarred samples in a study of the landscape surrounding the study site; fires ceased after 1887 (Fulé et al., 2003). Future fires are likely to continue to affect forest floor variables but have only minimal effects on tree growth (Peterson et al., 1994) or mortality because established trees are highly resistant to fire (Sackett and Haase, 1998), especially after the fuels that accumulated over an extended period of fire exclusion have been consumed.

The Society for Ecological Restoration (SER) developed nine ‘‘attributes of restored ecosystems’’ that range from the local site (maintaining a ‘‘characteristic assemblage’’ of species, minimizing non-natives, ‘‘sustaining reproducing populations’’) to the surrounding environment (‘‘integrated into a larger ecological matrix’’, resilient to ‘‘normal periodic stress events’’) and finally to long-term sustainability ‘‘to the same degree as its reference ecosystem’’ (SER, 2002). Assessing the Grandview treatments according to the SER criteria, all treatments are currently dominated by native species and appear to sustain reproducing populations. None of these small sites are integrated into a fully natural matrix, being surrounded by forests in varying conditions, fragmented by roads and powerlines, and subject to recreational and wildlife use. Based on resistance to crown fire, discussed by Fulé et al. (2002a), and growth differences that are likely associated with resistance to herbivores (Wallin et al., 2004), we expect that the FULL treatment is most capable of withstanding stress factors such as fire, insects, and drought. The FULL treatment is also most likely to foster a vigorous understory vegetation response because of the open canopy structure. However, continued monitoring will be important to determine whether growth and regeneration over time will bring the FULL unit closer to an open pine-oak forest dominated by large trees, or whether continued mortality may preclude a return to conditions similar to historical patterns.

Acknowledgments

Thanks to the Tusayan Ranger District, Kaibab National Forest, especially R. Stahn and D. Mills, and the staff and students of the Ecological Restoration Institute, especially J. Crouse and S. Curran. T. Kolb provided helpful comments. Funding for re-measurement and analysis in 2004 was provided by the USDA Forest Service, #03-DG-11031600-088.

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